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Stomatal Conductance and Photosynthesis in Cocoa Trees

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The relationship between stomatal conductance (g_s), net photosynthesis (A) and transpiration rate (E) have been studied in leaves of drought tolerant and susceptible accessions of cocoa (*Theobroma cacao* L.). Photosynthesis was not significantly different between the accession types. The A/g_s ratio increased during dry months accompanied by a decrease in intercellular CO_2(C_i). The depression in A was due to lower g_s. The instantaneous water use efficiency (A/E) was positively correlated with A and it was higher in drought tolerant trees. The A/C_i ratio decreased in dry season and was positively correlated with A/E. Thus, high A/E and A/C_i along with low g_s and E during stress period may be important factors contributing to drought tolerance in cocoa.

Key words : Cocoa, net photosynthesis, transpiration, water use efficiency, drought tolerance

INTRODUCTION

The net CO_2 assimilation can be limited by stomatal closure in response to water deficits (Chaves 1991, Farquhar and Sharkey 1982) or to an increase in water vapour difference between leaf and air (Bunce 1986, Lange *et al.* 1971). Stomatal regulation and/or net photosynthesis (A) in relation to climatic factors have been studied in coffee (Nunes 1988), coconut ((Kasturi *et al.* 1988), tea (Squire and Callander 1981) and cocoa seedlings (Rajaharun and Hardwick 1988, Joly and Hahn 1989). Balasimha and Rajagopal (1988) found that the stomatal conductance (g_s) in cocoa is reduced by high photosynthetically active radiation (PAR), low 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 hamper carbon assimilation (Jones 1979). The photosynthesis of cocoa was influenced by light, temperature and vapour pressure deficit (VPD), but there was no significant differences between tolerant and susceptible accession types (Balasimha *et al.* 1991). This study gives further evaluation of relationships between stomatal responses and gas exchange parameters in cocoa trees.

MATERIALS AND METHODS

The cocoa (*Theobroma cacao* L.) trees used in the present study (planted in 1970) were grown in the field in a mixed garden with arecanut palms. The details of plant material and measurements are described earlier (Balasimha *et al.* 1991). Measurements of PAR, temperature (T_{air}), VPD, A, g_s, transpiration rate (E), were made using a LI-6200 portable photosynthesis system enclosing up to 30 cm^2 leaf area in a 1l leaf chamber. Water use efficiency (A/E) was calculated as the ratio of CO_2 assimilated to water transpired. The intercellular CO_2 concentration (C_i) was computed in the LI-6200 using initial values of A, E, ambient CO_2 concentration (Ca) and leaf resistance.

RESULTS AND DISCUSSION

The differences in A between drought tolerant and susceptible accessions of cocoa were not significant although there were significant seasonal differences (Balasimha *et al.* 1991). Cocoa effectively conserves water by stomatal closure (Balasimha *et al.* 1988); this view was supported by lower levels of g_s during dry season (Balasimha *et al.* 1991). The A/g_s ratio increased with the progress of dry period and decreased after recovering from stress (Table 1). This increase leads to a decrease in C_i suggesting that the mesophyll factors are not affected much. This depression in A

Table 1. Seasonal changes in C_i, A/g_s and A/C_i in Cocoa

Parameter	Accession type	Feb.	Apr.	May	Jun	Oct.
C_i (ppm)	Tolerant	253	256	258	276	280
	Susceptible	259	255	253	271	284
A/g_s	Tolerant	24.78	28.28	30.85	19.44	15.44
(μmol CO_2/mol $m^{-2}s^{-1}$)	Susceptible	24.10	27.55	27.50	19.50	12.54
A/C_i	Tolerant	0.014	0.008	0.008	0.013	0.015
(μmol CO_2/ppm CO_2)	Susceptible	0.009	0.009	0.008	0.010	0.014

was principally due to lowered g_s as they are positively correlated (Table 2). There was also a significant positive correlation between A and E, and E and g_s (Table 2). Consequently, any fluctuations in g_s will be reflected in the values of A and E. Also, because of the linear relationship of A and g_s, the C_i/C_a ratio remained relatively constant (0.80-0.88) despite the seasonal or accession type variations. Stomatal closure is a major adaptive feature of drought tolerance in cocoa (Balasimha *et al.* 1988) and is indeed one of the first lines of defence against water stress in crop plants.

Table 2. Regression models for A, g_s and E in Cocoa

Sl. No.	Accession type	y	x	Regression equation	r(P-0.01)	SE
1.	Tolerant	A	g_s	$y = 0.00103 \times +1.5156$	0.64	0.0199
	Susceptible	A	g_s	$y = 0.00067 \times +1.7860$	0.68	0.0115
2.	Tolerant	E	g_s	$y = 0.00044 \times +1.8379$	0.41	0.0161
	Susceptible	E	g_s	$y = 0.00123 \times +1.0126$	0.67	0.0224
3.	Tolerant	A	E	$y = 0.5609 \times +1.6536$	0.38	0.2114
	Susceptible	A	E	$y = 0.3003 \times +1.9080$	0.57	0.0702

Despite stomatal control limiting photosynthesis, there is an increase in A/E. In drought tolerant cocoa accessions A was linearly related to A/E (Fig. 1). It was especially noticed that during recovery period A/E was higher in tolerant types indicating that stomata resume their original open condition immediately after stress is relieved. These factors contribute to the maintenance of higher leaf water potential in drought tolerant accessions as compared to susceptible type in dry months (Balasimha *et al.* 1991).

The ratio of A/C_i decreased during dry months (Table 1). A regression model of A/E vs A/C_i was derived (Fig. 2). There was a positive linear and significant relationship between these two characters in drought tolerant accessions, while it was not significant in susceptible types. The slopes of regression lines of both A vs A/E and A/E vs A/C_i with respect to drought tolerance were significant. The A/C_i ratio represents the 'carboxylation efficiency' of the plants (Farquhar and

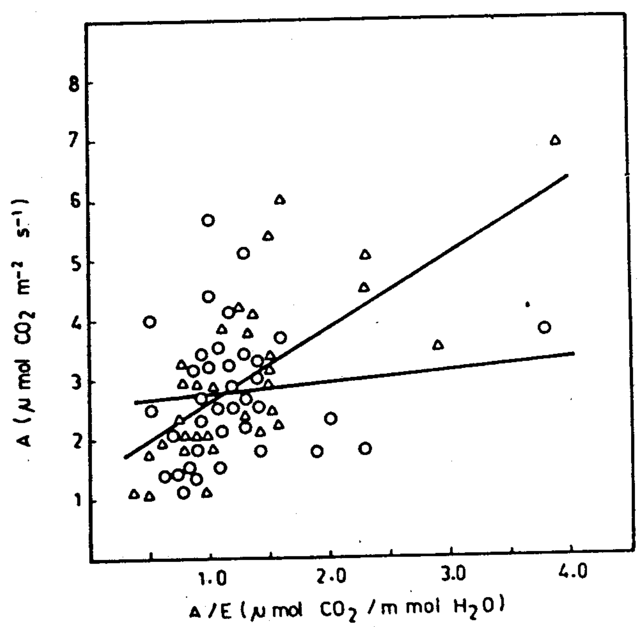

Fig. 1. Relation of A to A/E in leaves of tolerant (Δ; $y = 1.24 \times +1.42$, $r = 0.64$, $P = 0.01$) and susceptible (0; $y = 0.20 \times +2.51$, $r = 0.11$, NS) cocoa accessions.

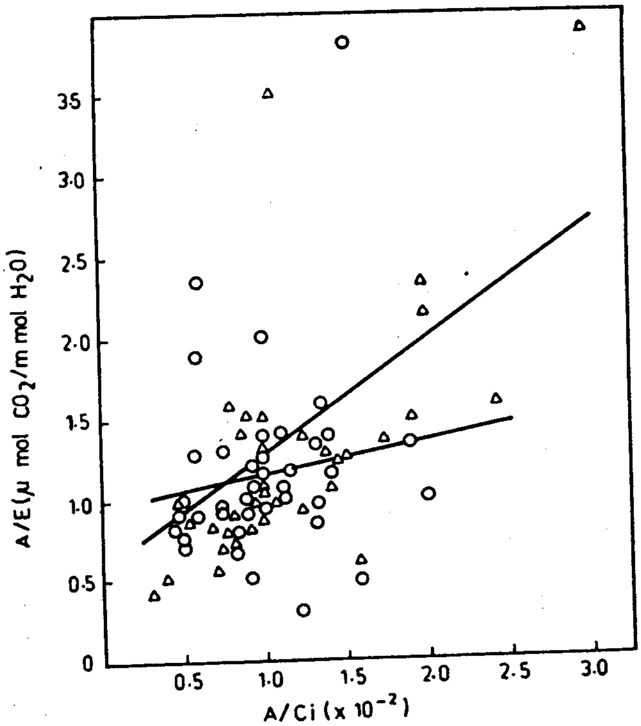

Fig. 2. Relation of A/E to A/C_i in leaves of tolerant (Δ; y = 0.73 × +0.51, r = 0.59, P = 0.01) and susceptible (0; y = 0.20 × +0.98, r = 0.13, NS) cocoa accessions.

Sharkey 1982). In other words, high intrinsic water use efficiency was associated with high carboxylation efficiency in drought tolerant cocoa trees. Thus, the leaf level differences in A, g_s and A/E can contribute to higher productivity and adaptability to periods of water deficits in cocoa.

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