Advances in Horticulture Vol. 10 – Plantation and Spice Crops Part 2 (1994). Eds: *K.L. Chadha and P. Rethinam* © 1994 Malhotra Publishing House, New Delhi-110 064, India

Drought Tolerance in Plantation Crops

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1. INTRODUCTION

Soil and plant water deficits limit the yield of crops in many regions of the world. In India, plantation crops are grown in regions receiving high rainfall (3000-4000 mm/annum) during the monsoon period. However, this is followed by long periods of drought which varies in intensity at different regions. In southern Kerala, the rainfall is well distributed with short (2-3 months) dry spell as compared to long droughts (5-6 months) in northern Kerala and coastal Karnataka, the two regions which account for large area under coconut and cocoa cultivation. For the good growth of coconut palm with optimum nut yield, a well distributed rainfall throughout the year, with an annual precipitation between 1300 and 2500 mm, is the most essential requirement. The palm thrives well under the mean annual temperature of 27°C with diurnal variation of about 5°C, abundant sunlight in the range of 250 to 350 wm^{-2} with annual sunshine of 2000 h (at least 120 h per month) and moderate relative humidity (Child, 1964; Murray, 1977). The cocoa tree also needs a high and well distributed rainfall and the severe stress especially when they are grown as intercrop of rainfed coconut gardens affect the yield adversely. The situation is slightly better in arecanut gardens which are irrigated. But non-availability of water towards the end of summer exposes the plants to stress.

The foregoing account reveals that coconut and cocoa are influenced by atmospheric and soil droughts. The impact of drought depends on the soil type as coconut palms are cultivated on the coastal sandy, red sandy loam and laterite soils (Menon and Pandalai, 1958). During the dry season, the water balance of palms is well protected through an effective stomatal movement (Rajagopal *et al.*, 1986). A prolonged dry spell extending from 3 to 6 months affect the palm and such severe drought occurs frequently in different coconut growing areas. For instance, in north Kerala, dry weather prevails with high evaporative demand resulting not only in atmospheric drought but also soil drought during summer months. Depending on the intensity of drought, coconut palms show the symptoms like drooping and drying of leaves, poor spathe development (Figs. 1 and 2), shedding of buttons and poor nut yield (Pomier and de Taffin, 1982; Prasada Rao, 1985, 1986; Ramadasan *et al.*, 1991). While irrigation can increase yields, which is not always possible and as these areas are subjected to periodic water deficits, identification of drought tolerant genotypes of plantation crops becomes essential. To

Fig 1 : Impact of drought on coconut.

Fig 2 : Poor spathe development, sparse retention of buttons/nuts.

achieve this, a basic understanding of the physiological and biochemical mechanisms of drought tolerance in these crops are needed.

2. EFFECT OF WEATHER VARIABLES

A progressive development of stress in coconut was observed between the wet (August) and dry (March) seasons as indicated by the changes in stomatal resistance, an indicator of plant stress (Kasturi Bai *et al.*, 1988). It is clear from Fig. 3 that the leaf diffusive resistance which was low during wet months increased rapidly from January reaching a peak in March, which coincided with high evaporative conditions. This study revealed that coconut under sandy loam in rainfed condition experiences moisture stress when exposed to irradiation around 265 wm^{-2}, temperature of 33°C and vapour pressure deficit of 26 mbar. Thus, atmospheric drought affects the water relations of palms.

An increase in evaporative demand owing to lowered humidity, changes stomatal resistance. Besides, light and temperature also influence stomatal response. There are limited studies on such relationships in plantation crops in India (Balasimha and Rajagopal,

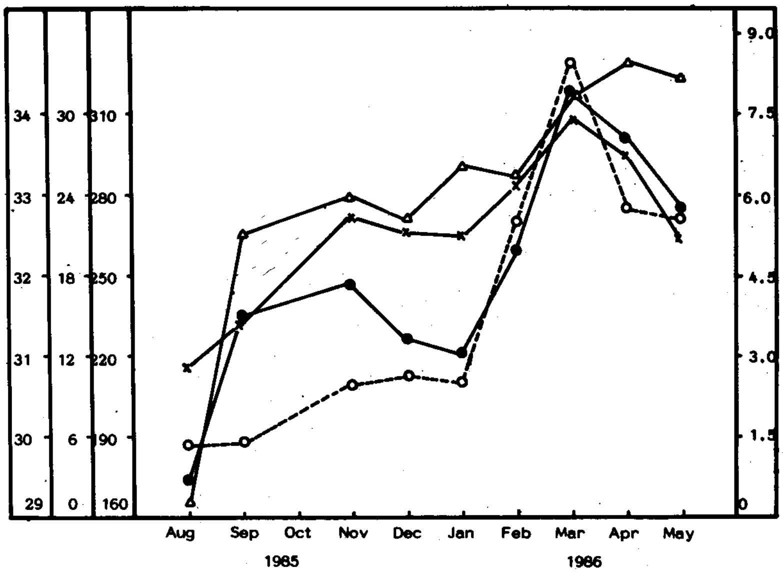

Fig. 3 : Monthly variations in environmental variables and stomatal resistance in coconut palms (cv WCT).

1988; Kasturi Bai *et al.*, 1988). The stomatal diffusion resistance increased with decrease in relative humidity which was magnified by soil moisture stress in field grown cocoa trees (Balasimha and Rajagopal, 1988). Stomata of intact leaves generally open in response to increase in light intensity. In cocoa leaves, however, the effects of humidity and soil moisture stress decreased the effect of light. It indicates that relative humidity has stronger influence than light. The correlation coefficients among various environmental factors and plant responses indicate that ambient temperature did not influence stomatal responses in cocoa, but showed a high significant correlation (r = 0.90**) with leaf temperature. Stomatal regulation by internal (stress) and external factors (humidity) lead to decrease in transpiration rate, which was a major adaptation for water conservation in cocoa plants (Balasimha and Rajagopal, 1988).

3. WATER RELATIONS AND STOMATAL RESPONSES DURING DROUGHT

Among plantation crops, cocoa is regarded as one of the most sensitive ones to water stress. Drought affects several physiological processes leading to a reduction in crop yield. Water potential of leaf is a major quantitative character used to assess water stress. Cocoa plants show changes in water relations when soil moisture drops to 60-70 per cent of available range. The onset of drought decreased water potential and RWC (Balasimha, 1982b, 1983, 1987, 1988). Diurnal variation exists in water potential, however, a plateau in water potential is reached once the stomata close beyond –1.5 MPa (Balasimha *et al.*, 1990). This is the stage when turgor pressure falls and leaves start wilting. The changes in osmotic potential of cocoa during different months were not as marked as water potential (Balasimha, 1988). Leaf water potential was appreciably lower in exposed leaves as compared to shaded ones, presumably due to higher temperature and lower relative humidity in the exposed area.

The relationship between the soil water profile and the stomatal resistance in West Coast Tall palm was stuidied through an experiment with different levels of irrigation based on the cumulative pan evaporation (Rajagopal *et al.*, 1989). A soil water deficit of about 110 mm was found to be the critical level at which coconut suffered most due to moisture stress in sandy loam as indicated by closure of stomata (Fig. 4). The total biomass response to soil water deficit implies that coconut is highly sensitive to water deficit conditions in terms of overall photosynthetic activity, CO_2 assimilation, dry matter production and its partitioning. Exposure of palms to moisture stress for 16 or 24 days led to reduction in the vegetative dry matter by 15 and 18 per cent respectively, while the reproductive dry matter was reduced by 20 and 22 per cent respectively as compared to non-stressed, i.e., irrigated palms.

There is progressive development of stress in the tissues of coconut between December and May. In rainfed plots, the available soil moisture in May was 35 per cent of that in December (Shivashankar *et al.*, 1991). This resulted in a significant reduction in the leaf water potential in rainfed palms (–2.00 MPa) as compared to irrigated palms (–1.25 MPa) in May.

The response of coconut genotypes to soil water deficit varied depending on the soil type. The extraction and utilization of moisture in laterite soil is generally higher

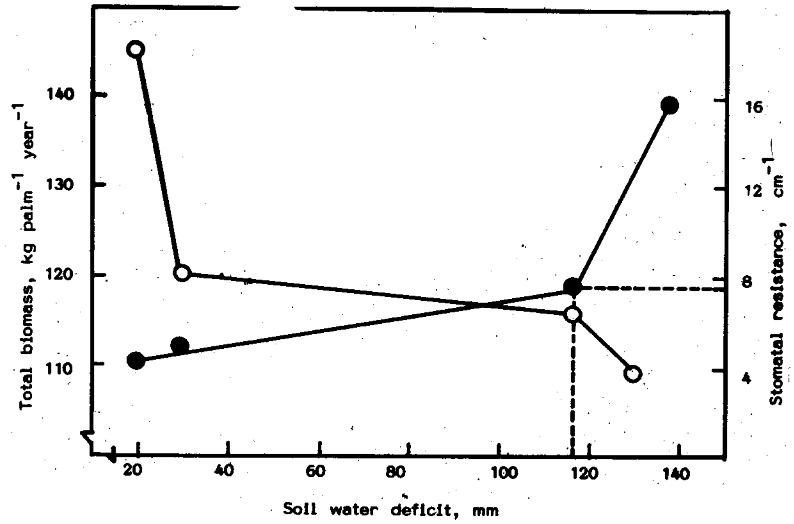

Fig. 4 : Stomatal resistance (•) and total biomass (o) in coconut palms as a function of soil water deficit; Horizontal dotted line indicates 1/2 max value for the stomatal resistance while vertical dotted line denote the corresponding level of soil water deficit (i.e., critical level).

than in red sandy loam soil, so much so the palms suffered more in the latter type, as also indicated by the changes in leaf diffusive resistance and leaf water potential components (Voleti *et al.*, 1993). Both the hybrids WCT x COD and COD x WCT had higher stomatal resistance during stress in laterite soil than in sandy loam soil, which resulted in the maintenance of higher turgidity (Table 1). It is evident that COD x WCT is most sensitive to water stress only in sandy loam soil, which could be attributed to higher depletion of soil water (28.9% between pre-stress to stress period) in sandy loam than in laterite soil (4.6%). When expressed in terms of transpirational loss of water, the hybrid COD x WCT showed 65 per cent decrease between non-stress and stress period in sandy loam soil as against only 35 per cent decrease in laterite soil for the corresponding period.

Table 1 : Leaf water potential components and epicuticular wax content in coconut genotypes under two soil types during pre-stress and stress. Values are means of two leaflets per palm of six palms

Genotype	Leaf water potential –MPa	Leaf osmotic potential –MPa	Leaf turgor potential +MPa	ECW $\mu g\ cm^{-2}$
Sandy loam soil				
WCT	–1.38	–1.70	0.32	109.04
WCT x COD	–1.43	–1.63	0.20	116.72
COD x WCT	–1.46	–1.67	0.21	110.50
Laterite soil				
WCT	–0.90	–1.61	0.71	105.97
WCT x COD	–1.00	–1.64	0.64	108.21
COD x WCT	–0.96	–1.64	0.68	128.16

The regulation of water loss by stomatal movements is an important character for drought tolerance of crop plants (Hsiao, 1973; Jones, 1979). The physiological mechanisms that control stomata is indispensable for the survival of perennial plantation crops. The possible ways that enhance drought tolerance through stomatal behaviour are : (i) conservation of limited water supply, (ii) prevention from damage due to water stress, and (iii) maximization of assimilation with available water.

4. MORPHOLOGICAL ADAPTATIONS

The reduction in cell growth is one of the earliest manifestations of water deficits. This is considered to be more sensitive to water stress than stomatal conductance and CO_2 assimilation, and reduction in leaf area help plants to adopt for periods of drought. A reduction in leaf area might have an advantage in reducing transpiration. However, once the leaf area expansion is complete, an increase in epicuticular waxes of leaves which can reduce cuticular transpiration is beneficial.

In cocoa accessions, there was no significant difference in leaf area under well watered conditions (Balasimha *et al.*, 1985). However, under water stress, the accessions showed variations in leaf expansion rates (Balasimha, 1982a).

The specific leaf weight (SLW) was significantly different among cocoa accessions. Accessions having high SLW (or thick leaf) and higher epicuticular wax were found to be drought tolerant (Balasimha, 1987; Balasimha, *et al.*, 1985). The SLW can be a good indicator of leaf anatomy and positive relation between leaf thickness and palisade layer thickness were obtained. Using some of the morphological attributes, it was possible to screen out 80 per cent of test material in the initial stage for drought tolerance.

The coconut genotypes differed not only in the extractability of soil moisture by roots but also in conserving the water in leaf tissues, i.e., low transpiration rate aided by wax coating on the surface of leaves (Rajagopal *et al.*, 1991). By reducing the transpiration rate through the effective control of stomata, the tolerant genotypes could conserve water in the tissues for various physiological and metabolic processes, whereas the susceptible genotypes tend to lose more water.

5. METHODS OF SCREENING FOR DROUGHT TOLERANCE

Leaf characters and nut yield were used to screen five coconut hybrids and a West African Tall for drought tolerance (Pomier and de Taffin, 1982). The percentage of dry leaves (n) compared to the number of living ones N or n/N x 100 was used as the drought tolerance index, according to which the hybrid PB.121 (Malayan Yellow Dwarf x West African Tall) was found to be most drought tolerant, while the Rennel Tall x West African Tall the most sensitive to drought. The hybrid PB.121 had less reduction in the production of nuts due to moisture stress as compared to other hybrids.

Physiological parameters sensitive to moisture stress like leaf diffusive resistance, leaf water potential and epicuticular wax content were employed to screen for drought tolerance in twenty three genotypes of coconut comprising ten talls, six dwarfs and seven hybrids (Rajagopal *et al.*, 1990). During the moisture stress in March, some of the tall palms and tall hybrids had relatively high stomatal resistance resulting in effective conservation of water in the tissue, i.e., low transpiration rate while the dwarfs and the dwarf hybrid COD x WCT were sensitive to stress with a tendency to lose more water (Fig. 5). About eleven genotypes had maintained high leaf water potential during the stress period (Table 2). Drought tolerant genotypes like LO x COD and LO x GB possessed higher epicuticular wax content with lower transpiration rate than the sensitive genotypes. Based on the parametric relationship with drought tolerance, the rank sum of the genotypes led to the identification of drought tolerant genotypes with the desirable traits. It may be noticed that the released hybrids LO x GB, LO x COD and the promising hybrid WCT x COD proved to be tolerant, while the other popular hybrid COD x WCT is the most susceptible to drought, especially in sandy loam soils. Rajagopal *et al.* (1988) developed a rapid screening method involving the determination of leaf water potential and the activity of acid phosphatase enzyme. Even in this test, the above hybrids (LO x COD and LO x GB) maintained higher leaf water potential and less increase in enzyme activity when subjected to simulated stress conditions, confirming thereby the earlier findings on the degree of drought tolerance.

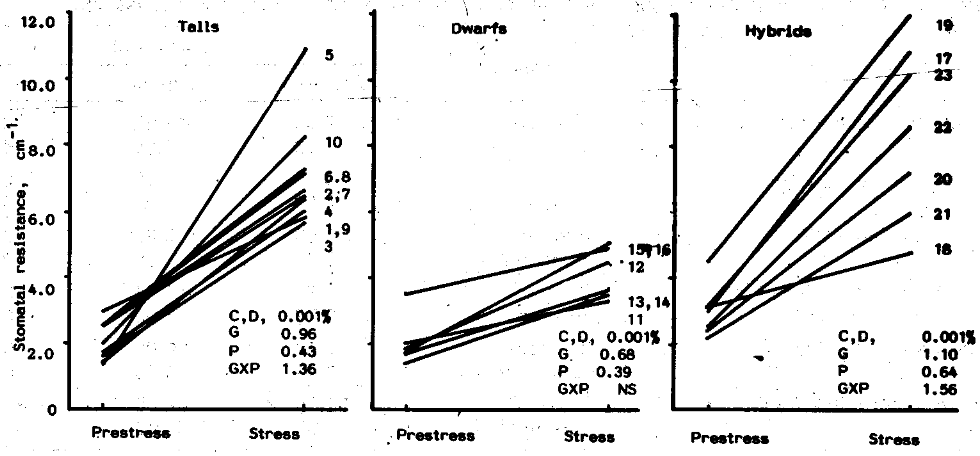

Fig. 5 : Changes in stomatal resistance in coconut genotypes with the progress of stress period.

Table 2 : Effect of moisture stress (March) on the leaf water potential (#) and epicuticular wax content (Ecw) in coconut genotypes

Genotypes	ψ –MPa	ECW–2 µg cm^{-2}	Genotypes	ψ –MPa	ECW–2 µg cm^{-2}
Talls			MYD	–1.48	79.04
WCT	–1.48	109.04	GB	–1.45	90.29
SS Apricot	–1.13	102.13	COD	–1.01	87.58
Andaman ordinary	–1.23	91.92	*Hybrids*		
Laccadive micro	–1.40	96.20	WCT × COD	–1.19	116.72
Andaman giant	–1.12	99.23	COD × WCT	–1.24	110.51
F.M.S.	–1.10	116.72	WCT × WCT	–1.17	117.39
Fiji	–1.23	104.67	COD × COD	–1.36	109.25
Philippines ordinary	–1.32	113.41	WCT × GB	–1.15	109.57
Cochin China	–1.27	110.43	LO × GB	–1.32	132.63
Java giant	–1.41	116.16	LO × COD	–1.26	120.66
Dwarfs			SE/Plot	1.82	15.49
SS Green	–1.32	98.35	Gen. Mean	–1.28	104.49
MGD	–1.36	94.03	C.V. (%)	1.41	14.83
MOD	–1.52	77.03	CD (P = 0.05)	2.08	11.42

The water relation components and stomatal behaviour were determined in 14 accessions of cocoa after a preliminary screening (Balasimha *et al.*, 1988). Differences in plant variables between drought tolerant and susceptible cocoa accessions is presented in Table 3. Based on parametric relationships with drought tolerance, the rank sums of these accessions led to a selection of NC 23, NC 29, NC 31, NC 39 and NC 42. Later studies have identified Amel x Na 33 also to fall in this category. These drought tolerant accessions had effective stomatal regulation resulting in decreased trans-

Table 3 : Differences in plant variables between drought tolerant and susceptible accessions

Variable	Accession type	Treatment		
		Prestres	Stress	Recovery
Stomatal resistance (scm^{-1})	Tolerant	5.04	11.62	3.42
	Susceptible	4.83	7.00	4.08
Transpiration rate ($\mu\ cm^{-2}s^{-1}$)	Tolerant	3.45	1.89	2.55
	Susceptible	4.58	3.30	3.56
Water potential (–MPa)	Tolerant	0.56	0.88	0.57
	Susceptible	0.35	1.08	0.68
Osmotic potantial (–MPa)	Tolerant	0.78	0.91	0.77
	Susceptible	0.78	1.09	0.78
Turgor potential (MPa)	Tolerant	0.22	0.03	0.20
	Susceptible	0.43	0.01	0.10
Relative water content (%)	Tolerant	91.55	82.35	86.52
	Susceptible	89.37	79.43	83.69

pirational water loss. In tea, a significant reduction in transpirational water loss by higher stomatal resistance was reported (Saikia and Dey, 1984).

As a result of reduced transpirational water loss in cocoa under drought, leaf turgidity was maintained resulting in higher leaf water potential. A rapid screening method for drought tolerance in cocoa has been described which eliminates difficulty of screening under field conditions (Balasimha and Daniel, 1988). This method utilizes measurement of water potential in excised leaves. The decrease in water potential was more pronounced in susceptible as compared to tolerant accessions under laboratory stress (Fig. 6).

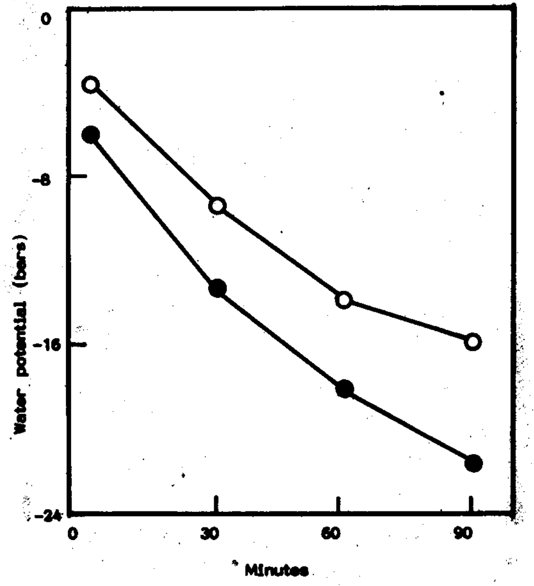

Fig. 6 : Changes in water potential in excised leaves of tolerant (o) and susceptible (•) cocoa trees; the differences significant of 1% level.

6. PHOTOSYNTHESIS

The efficient stomatal closure might hamper carbon assimilation. It was, therefore, necessary to study photosynthesis and yield performance of tolerant accessions *vis-a-vis* susceptible ones. Annual pod yield was higher in tolerant than in susceptible accessions over five years period (Table 4). Since the stomata resume their original open condition immediately after stress is relieved, it is reasonable to assume that stomatal closure has not affected productivity. This is corroborated by the lack of correlation between yield and diffusive resistance due to stress ($r = 0.04$) . It is also of interest to note that there was a positive correlation to yield with diffusive resistance at recovery ($r = 0.52$, $P = 0.05$). Therefore, accessions which display these specific favourable attributes can be used as a source for breeding to bring desirable characters into a single ideotype with a good expectation of increasing drought tolerance. In many woody species and perennial crops, the non-stomatal component of CO_2 fixation declines subsequent to the stomatal inhibition. Thus, the stomatal responses are primary events in affecting the photosynthesis of plantation crops.

Table 4 : Annual pod yield of drought tolerant and susceptible cocoa accessions

Yield (pods tree–1)	Accession type	
	Tolerant ($n = 5$)	Susceptible ($n = 23$)
1982	65.2	46.4
1983	56.8	45.3
1984	81.0	55.1
1985	36.0	26.0
1986	72.6	48.8

The studies on photosynthesis in trees have been done mostly among the temperate species. Among tropical plantation crops, net photosynthesis have been measured in tea (Squire and Callander, 1981), rubber (Satheesan *et al.*, 1989), cocoa (Balasimha *et al.*, 1991), cashew (Balasimha, unpublished), coconut (Kasturi Bai, Rajagopal and Balasimha, unpublished) and arecanut (Chowdappa and Balasimha, unpublished). But photosynthesis in relation to water stress and drought tolerance has been studied in detail only in cocoa accessions. As pointed out earlier, drought tolerance in cocoa is mainly attributable to stomatal regulation which, besides reducing water loss (Balasimha *et al.*, 1988), can also reduce CO_2 assimilation. To obtain a complete picture, it was necessary to study the impact of micro-climatic variables on P_N in cocoa accessions differing in their drought tolerance reaction (Balasimha *et al.*, 1991). Net photosynthesis, transpiratiion rate and stomatal conductance showed significant seasonal variations. During periods of low vapour pressure deficit, P_N was highest. Diurnal patterns of these parameters indicated transient midday water deficits reducing P_N. The drought tolerant accessions maintained higher leaf water potential. There was no significant difference in P_N between tolerant and susceptible accession types. The depression in P_N was principally due to lowered stomatal conductance and this relationship was positively correlated (Fig. 7). Because of such linear relations of P_N to conductance, ratio of CO_2 intercellular/CO_2 ambient remained relatively constant despite seasonal and accession type variations (0.80 to 0.88). This mode of relationship is rarely measured in the field. There was also no significant differences in intercellular CO_2 (230-290 ppm) showing that it did not limit net assimilation rate (Balasimha *et al.*, 1991).

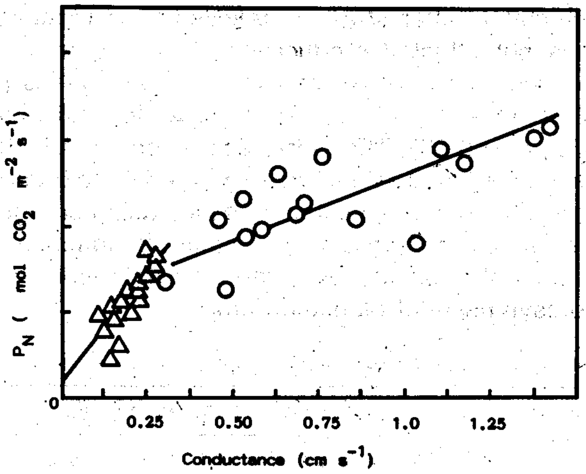

Fig. 7 : Relation of P_M to stomatal conductance in cocoa leaves during October (O, r = 0.54; P = 0.05) and April (Δ; r = 0.92; P = 0.01).

Comparisons of photosynthetic rates and water use efficiency among various plantation crops in dry season is given in Table 5. Among the four species on which data are available, cashew is extremely tolerant to drought conditions. Despite low soil moisture levels, the plants are able to transpire and have high CO_2 assimilation rates with low WUE. Still the water potential is maintained at high level (–0.3 MPa), perhaps because the plants have deep root system with good water extraction capacity. However, arecanut is very sensitive and in cocoa stomatal regulation occurs under drought helping to conserve water to a certain extent. The drought tolerance thus, to a great extent, relates to stomatal diffusive resistance with high WUE or positive carbon balance and the extent to which the photosynthetic recovery occurs in rewatering.

Table 5 : Gas exchance characteristics of plantation crops during dry season

Species	PN (μmol) (CO_2 $m^{-2}s^{-1}$)	Stomatal resistance (s cm^{-1})	Water use efficiency (μmol CO_2 mmol H_2O)
Arecanut	4.06	3.48	1.16
Cocoa	2.23	5.60	1.03
Cashew	8.21	0.80	0.71
Coconut	7.82	2.22	1.62

7. BIOCHEMICAL ASPECTS

7.1 Osmotic Adjustments

The metabolic and biochemical adaptations to drought are not very well understood in plantation crops. There are few reports on the metabolism involving osmotic adjustments. Various organic isolates and ions are known to accumulate in coffee decreasing leaf osmotic potential (Ramaiah and Venkataramanan, 1987). The differential behaviour of coffee cultivars in osmotic adjustments can be used as a screening for drought tolerance (Venkatarmanan *et al.*, 1989). It has also been reported that drought tolerance can be induced by osmotic adjusments through ion sprays (Venkataramanan *et al.*, 1988). Similar osmotic adjustments exist in drought tolerant rubber clones (Satheesan *et al.*, 1982). Soluble sugars and starch contents differed in oil palm cultivars in relation to drought tolerance, starch being more in tolerant ones (Adjahossou and Silva, 1978). Although soluble sugars accumulated with decrease in osmotic potential in cocoa, no relationship with drought tolerance and susceptibility could be established (Balasimha *et al.*, 1988). This has an advantage to cocoa because it does not involve a 'metabolic cost' (Turner and Jones, 1980) to the plant and the major adaptive feature is at the stomatal level.

7.2 Nitrate Reductase and Other Enzymes

The first step of NO_3^- assimilation is through the enzyme nitrate reductase (NR). Two possibilities of water stress effects on nitrate reductase exist: (a) as an effect of low water potential and reducing power, and (b) NO_3^- depletion due to decline in flux in the xylem. This rate limiting enzyme is the only one to be affected considerably in response to water stress in crop plants. The nitrate reductase (NR) activity showed interesting trends in irrigated and rainfed cocoa plants (Balasimha, 1982b). In irrigated plants, NR was high during February to April and low during rainy season, whereas the activity was low in unirrigated plants during dry period. The decrease in NR activity can be a consequence of reduction in respiration and photosynthesis, thus limiting the reducing power required for NR. With recovery from stress, these biosynthetic processes are revived and NR activity also completely recovered. The inhibition of NR activity showed variations among cocoa accessions (Balasimha, 1982a). Under water stress drought tolerant accessions showed higher retention of NR activity. The NR stability under drought was 0.59 and 0.53 in tolerant and susceptible groups (Balasimha *et al.*, 1988). This may be due to higher leaf turgor maintenance as nitrate reduction could occur more efficiently as higher energy pools were available. The changes in NR activity were found to be positively correlated with the changes in RWC in coconut genotypes (Shivashankar, 1990). The author also reported the differences in the thermal stability of NR *in vivo* among the coconut genotypes differing in drought tolerance.

The application of K^+ and proline externally also ameliorated nitrate metabolism in cocoa seedlings under water stress (CPCRI, 1984; Subbaiah and Balasimha, unpublished) (Table 6). Plants treated with K^+ and proline had higher NR activity during drought and recovery. Similar benefit in NR retention was observed in cycocel treated seedlings (Balasimha and Subramonian, 1984).

Table 6 : Effect of K and proline on NR activity and proline content in cocoa seedlings

Treatment	NR activity (nmole NO_2 h^{-1}[illegible])			Proline content (μg g^{-1} fresh wt.)		
	Pre-stress	Stress	Recovery	Prestress	Stress	Recovery
Control	1.10	0.41	0.73	57	333	113
K (10mM)	0.88	0.53	0.56	60	88	113
Proline (0.1mM)	0.99	0.73	0.71	61	128	96

There was a significant difference in the activities of sensitive enzyme like acid phosphatase, L-aspartate-2-oxoglutarate aminotransferase, polyphenol oxidase and superoxide dismutase among the coconut genotypes. The pattern of polyphenol-oxidase isozymes, separated by polyacrylamide gel electrophoresis from the osmotically stressed leaves, showed up two additional fast-moving bands in a drought-susceptible genotype (COD x WCT), while the same was absent in a relatively tolerant one, i.e., WCT (Fig. 8) Shivashankar, 1988). Acid phosphatase enzyme revealed conformational changes in the isozyme II during stress development as indicated by the shift in the optimum temperature and km values (Fig. 9). The stress induced increase in this enzyme could thus be attributed to the changes in its kinetic properties.

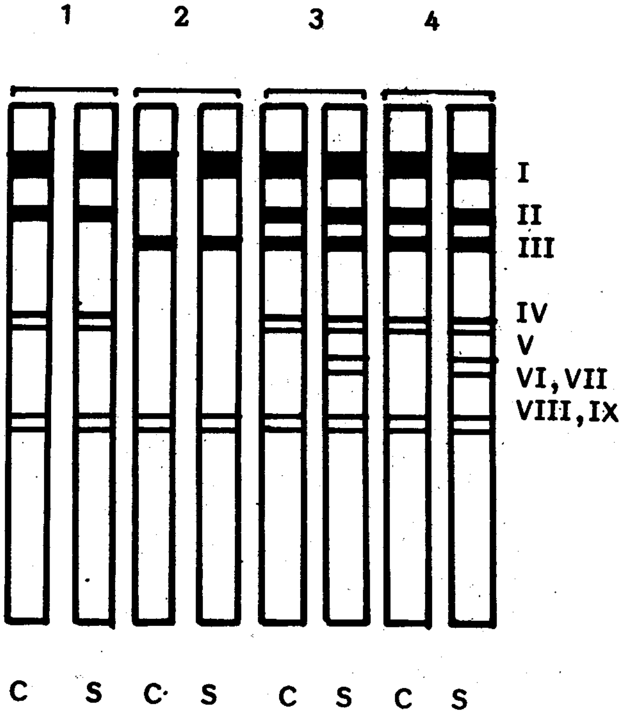

Fig. 8 : Pattern of polyphenol oxidase isozymes in coconut genotypes after induction of stress; C, control; S, stressed; 1-WCT, 2-COD, 3-WCT x COD, 4-COD x WCT (I to IX indicate bands).

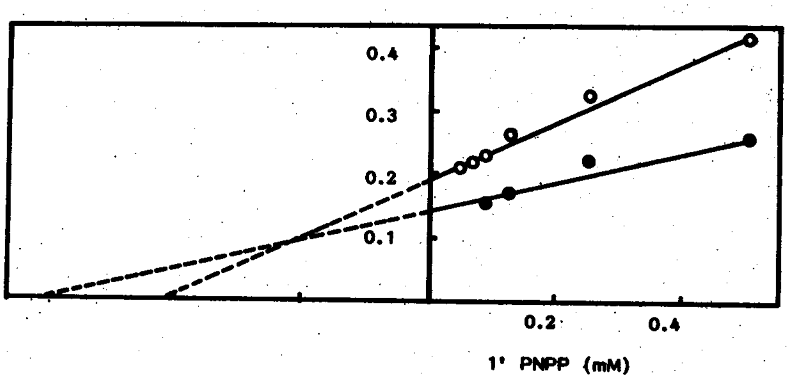

Fig. 9 : Lineweaver-Burk plot for acid phosphatase isozyme II from normal (o) and stressed (•) leaves of coconut.

7.3 Proline Accumulation

The accumulation of proline in mesophytic plants under water stress is well known. Among plantation crops, proline accumulation has been reported in cocoa (Balasimha, 1982 a), coffee (Vasudeva, *et al.*, 1981), tea (Rajasekhar *et al.*, 1988) and coconut (Voleti *et al.*, 1990). In cocoa, the proline accumulation was negatively correlated with relative water content (Fig. 10; Balasimha, 1982a). Thus, in drought tolerant

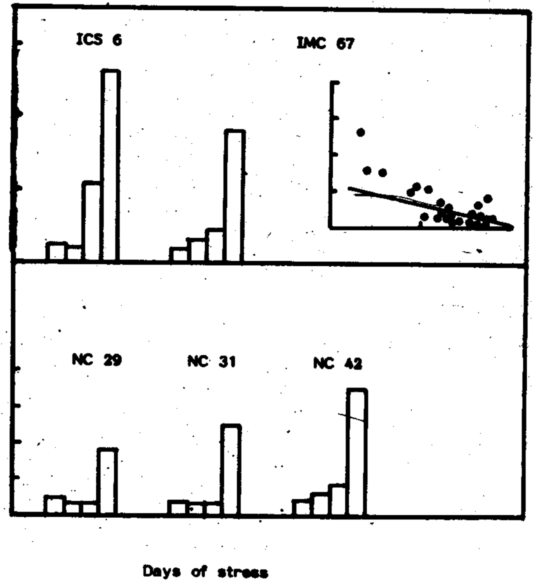

Fig. 10 : Changes in proline content during stress in cocoa; CD ($P = 0.05$) accessions = 0.464 mg g^{-1}, treatments = 0.184 mg g^{-1}. Inset shows regression curve for proline content *vs* relative water content ($r = -0.68$; $P = 0.01$).

accessions when RWC was higher under stress, the proline accumulated to a lesser degree. Similar results were obtained when drought ameliorative sprays of cycocel (Balasimha and Subramonian, 1984), abscisic acid (Balasimha, 1983), K^+ or proline (CPCRI, 1984) were given to cocoa seedlings. Thus, the accumulation of proline was to a lesser extent, whenever the leaf turgidity was maintained. It seems reasonable to assume that, as the metabolic rates are higher because of high leaf turgor, proline might be utilized efficiently. However, in drought tolerant tea clones, water stress led to a significantly higher accumulation of proline (Rajasekhar *et al.*, 1988).

7.4 Leaf Waxes, Lipids and Membrane Stability

The outermost layer of the leaf cuticle, which is easily extracted with organic solvent, forms an epicuticular wax. Numerous functional and adaptational role have been ascribed for the leaf surface lipids. Important among these are their ability to prevent water loss through cuticular transpiration to withstand water deficits. There is a clear indication of negative relationship between wax content and transpiration rate in that the susceptible genotype MOD with ECW of 77.3 $\mu g\ cm^{-2}$ had a transpiration rate of 4.5 $\mu g\ s^{-1}\ cm^{-2}$, while a high ECW content of 132.6 $\mu g\ cm^{-2}$ in the tolerant LO × GB was associated with a low transpiration rate of 1.96 $\mu g\ s^{-1}\ cm^{-2}$. The linear regression equation fitted for transpiration *versus* ECW was found to be significant (Fig. 11). The number of components of ECW, identified through thin layer chromatography, was more during the period of stress than in non-stress conditions and the genotypes showed variation in the intensity of the components. As a result of moisture stress, the membrane stability was disturbed to different degrees among the genotypes, the tolerant ones exhibiting less electrolyte leakage than the susceptible ones (Table 7). Deposition of epicuticular wax to a higher degree in drought tolerant cocoa accessions (Balasimha *et al.*, 1985), tea clones (Rajashekar *et al.*, 1988), rubber (Rao *et al.*, 1988) and coconut

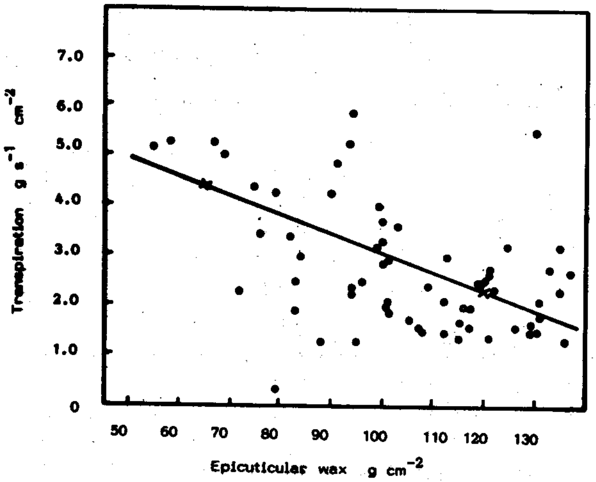

Fig. 11 : Relation between transpiration rate and epicuticular wax in coconut leaves (r^2 = 0.303).

Table 7 : Membrane stability in different leaves of coconut genotypes during moisture stress (Feb-Mar) (Electrolyte leakage %)

Genotype	Leaf position			
	1	6	14	20
WCT	245.9	234.1	197.9	260.0
WCT × COD	198.9	213.3	243.6	259.6
COD × WCT	259.0	414.5	286.3	312.0

(Rajagopal *et al.*, 1990) have been reported. The seasonal and varietal differences in wax content in cocoa has shown that the waxes offer plants to adapt to drought conditions (Table 8) (Bhat, 1988; Bhat *et al.*, 1990). The same trend in wax deposition was also recorded in drought tolerant cocoa accessions (Balasimha, 1982a). Qualitatively, the wax components were separated into hydrocarbons (25-30%), esters (6-11%), ketones (2-9%), alcohols (23-36%) and free fatty acids (15-21%). No qualitative differences were observed between the accession types.

Lipids play an important part in structure and function of cellular membranes. Lipids constituted 0.62 to 1.04 per cent of total leaf fresh weight in cocoa. Water stress decreased total lipid content to an extent of 30 per cent in tolerant and 38 per cent in susceptible accessions (Table 8). While the polar lipids decreased, neutral lipids increased due to stress. The main fatty acids of lipid fractions were myristic, palmitolic, oleic, linolic and linolenic acids. The other fatty acids present in smaller amounts were palmitic and stearic acids. The drought tolerant accessions had lower electrolytic leaching as compared to susceptible ones under water stress which was associated with higher sterol/phospholipid ratio. These changes in wax and lipid fractions increased membrane stability in cocoa leaves (Bhat *et al.*, 1990). A similar trend in electrolyte leakage between the drought tolerant and susceptible coconut genotypes has been observed (Kurup and Rajagopal, unpublished).

Table 8 : Changes in wax. lipids and membrane leaching of cocoa leaves

Parameter	Tolerant		Susceptible	
	Unstressed	Stressed	Unstressed	Stressed
Epicuticular wax (μg cm^{-2})	24.78	38.86	18.01	31.66
Total lipid (mg g^{-1} fresh wt.)	10.46	7.39	9.97	6.27
Neutral lipid (%)	69.4	77.2	66.4	78.0
Glycolipid (%)	20.9	19.1	22.8	17.0
Phospholipid (%)	9.7	3.7	10.7	4.9
Total sterol (%)	3.5	4.4	3.6	4.8
Sterol/phospholipid ratio	0.36	1.19	0.34	0.98
Electrolytic leaching (%)	15.56	20.19	17.96	27.66

8. AMELIORATION OF DROUGHT BY CHEMICAL TREATMENTS

The early vigorous growth of seedlings is very important for better establishment and higher yield potential at maturity. Cocoa progenies which are more vigorous have capacity for high yield but it depends on the effective dry matter partitioning between pod production and vegetative growth in cocoa. The seedling vigour or root/shoot ratios were not correlated with drought resistance. Management practices to prevent seedling deaths after field planting are available. The application fo cycocel and abscisic acid (ABA) imparted drought tolerance in seedlings as shown by growth and metabolic amelioration (Balasimha, 1983; Balasimha and Subramonian, 1984).

The drought ameliorative effects of potassium and proline in 3-month old cocoa seedlings was reported (CPCRI, 1984). Besides improving the survival rate and growth after recovery, both K and proline maintained leaf area expansion (Fig. 12). Leaf growth rate was compared in seedlings of six cocoa accessions differing in their drought tolerance under water stress (Balasimha, 1982 a). The leaf elongation rate was severely inhibited under drought, but recovered faster in tolerant accessions.

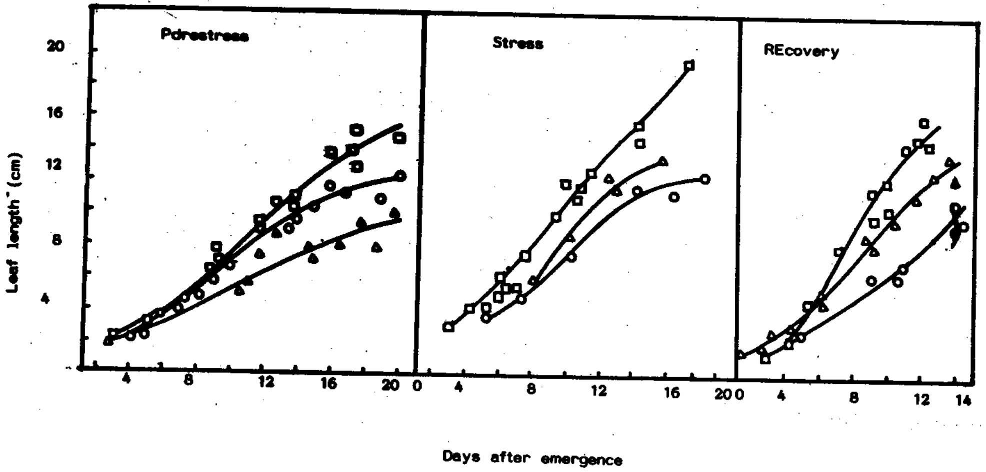

Fig. 12 : Effect of potassium and proline on leaf expansion rate in cocoa seedlings; control (o), potassium () and proline (Δ).

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