

PHYSIOLOGICAL AND BIOCHEMICAL CRITERIA FOR BREEDING FOR DROUGHT TOLERANCE IN COCONUT

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Abstract: The ability of coconut genotypes to withstand drought conditions depends upon various physiological and biochemical factors which impart drought tolerance. Among these, the pattern of soil moisture depletion by the roots and transpirational loss of water through the leaf surface were found to be important. The accumulation of wax on the leaf surface and the stability of the activity of certain enzymes were found to have a bearing on stress tolerance. On the basis of the above criteria, coconut genotypes were ranked according to the degree of tolerance. The hybrids, WCT x WCT, LO x GB, LO x COD and WCT x COD; the tall, WCT (selections) and Andaman Giant proved to be drought tolerant having a relatively high depletion of soil moisture by the roots, low transpirational loss from the leaf surface and the high content of cuticular wax, all desirable traits in the conservation of water by the tissues. The dwarfs, COD, MYD, GB and MOD; the tall cultivar, Laccadive Micro; and the hybrid, COD x WCT were characterized by an imbalance of water relations. Their low soil moisture depletion and higher rate of transpiration resulted in their susceptibility to drought; these genotypes also had low wax deposition. Further evidence was obtained through the determination of enzyme activities of glutamate oxalacetic transaminase (GOT) and acid phosphatase (APH), which showed distinct differences between the tolerant and susceptible genotypes. Thus, the much needed link between cellular processes and external manifestation of stress symptoms in coconut was established. The implications of these findings in the breeding programme for drought tolerance in coconut are discussed.

INTRODUCTION

The impact of drought on coconut yield is well documented in literature (Rao, 1986; Rajagopal *et al.*, 1986a; Liyanage, 1987). Unlike the annuals, the adverse effect of drought, caused either by low rainfall or delayed onset of monsoon or both at any given time, persists for the subsequent two or three years and this is explained on the basis of the relationship between the degree and intensity of dry spell and the ontogeny of coconut inflorescence (Rajagopal and Shivashankar, unpublished). The critical soil moisture level at which the coconut palm suffers from stress and the impact of weather variables on the development of stress in coconut have been reported (Rajagopal *et al.*, 1989a; Kasturibai *et al.*, 1988). Voleti *et al.*, (1989) have demonstrated the differential response of coconut genotypes to soil drought based on a study of different soil types.

The biochemical basis for drought tolerance in coconut has been reported (Shivashankar, 1988; Shivashankar *et al.*, 1989). Based on the parametric relationship with drought tolerance, 23 coconut genotypes have been ranked as tolerant and susceptible (Rajagopal *et al.*, 1989). In order to screen more genotypes for drought tolerance, a rapid method was developed using the measurement of leaf water potential on excised leaves as a function of the time of dehydration in the laboratory (Rajagopal *et al.*, 1988). In the present paper, some of the key distinguishing features such as the pattern of soil moisture depletion, transpirational loss of leaf water and the activities of two important enzymes between the tolerant and susceptible genotypes are described.

MATERIALS AND METHODS

Six coconut genotypes each of tolerant and susceptible groups (Fig 1)

were selected from the randomized block design comprising three replications of four palms each. The growth conditions, soil type and other details have been reported elsewhere (Rajagopal *et al.*, 1988). Transpiration rate was determined on the excised leaflets with the steady state parameter as described earlier (Rajagopal *et al.*, 1986b). Soil moisture content was determined gravimetrically during November (prestress) and March (stress) months at three depths from the soil surface (0-25, 25-50, 50-75 and 75-100 cm). From this, the soil water deficit (SWD) was calculated following the method of Dastane (1972). Epicuticular wax (ECW) was determined as per the method described by Ebercon *et al.* (1977). Acid phosphatase (APH) and glutamate oxalacetate transaminase (GOT) were assayed following Linhardt and Walter (1963) and Bergmeyer (1963) respectively only in four genotypes viz., WCT, COD, WCT x COD and COD x WCT.

RESULTS AND DISCUSSION

The soil water deficit expressed as the difference between the stress and prestress, showed marked variations among the tolerant and susceptible genotypes. In general, the tolerant genotypes recorded significantly higher SWD than the susceptible types. The SWD increased with increasing soil depth in the case of WCT x WCT, WCT and Andaman Giant (tolerant) and MOD and Gangabondam (susceptible) (Fig 1). The SWD exceeded 7.0 mm at 50-100 cm depth in only two of the tolerant genotypes (LO x COD and WCT) but none among the susceptible ones. Surface layer (0.25 cm) had relatively higher SWD in LO x COD and WCT x COD (tolerant) and COD x WCT (susceptible). Table 1 gives the details pertaining to the genotypes, soil depths, prestress and stress stages. The rate of transpiration was less than $3.0 \mu\text{g s}^{-1} \text{cm}^{-2}$, the

highest being in GB (Fig 1). Genotype, prestress vs stress and prestress, stress and genotype interaction were found to be significant within the tolerant and susceptible groups (Tolerant: 467.68**, 5.68** and 2.81**; Susceptible: 116.71**, 15.31** and 5.11** respectively). The interaction between tolerant and susceptible groups was found to be significant (20.13**).

The ECW ranged from 99.25 to $132.62 \mu\text{g cm}^{-2}$ (mean 110.95) among the tolerant while it ranged from 77.33 to $110.48 \mu\text{g cm}^{-2}$ (mean 90.15) among the susceptibles. LO x GB had the highest content ($132.62 \mu\text{g cm}^{-2}$) while the lowest was exhibited by MOD ($77.33 \mu\text{g cm}^{-2}$). Fig 2 illustrates the relationship between ECW and transpiration rate.

The activity of APH did not differ much between a tolerant (WCT) and a susceptible (COD x WCT) genotype under pre-stress conditions (195 and 210 $\text{nmole h}^{-1} \text{g}^{-1}$ fresh weight respectively) whereas with the onset of stress, the activities increased by 78.6 per cent (over prestress) in COD x WCT as against only 43 per cent in WCT (Fig 3). Moisture stress enhanced the activity of GOT two to three fold among the four genotypes; the difference in the increase between the tolerant and susceptible was less than that observed in the case of APH.

Coconut palm experiences severe stress during summer months (January to May) as a result of high evaporative demand in the atmosphere (Light: 1250 to $1700 \mu\text{E m}^{-2} \text{s}^{-1}$; Temp: 30 to 36°C ; RH: 32 to 45 per cent; Pan evaporation: 4.5 to 6.0 mm per day) which reflects on the depletion of soil moisture with time. Thus, both soil and atmosphere droughts co-exist in coconut plantations. From the data on the SWD and plant response, the critical soil moisture level at which coconut expresses stress

Table 1. Anova table for soil water deficit

Source	DF	SS	MSS	F
Tolerant vs susceptible	1	2492.70	2492.70	47.20**
Within tolerant	35	31068.56	887.67	16.81**
Stress levels (S)	1	1132.37	1132.37	21.44**
Depth (D)	2	19750.32	9875.16	186.99**
Genotypes	5	9305.89	1861.17	35.24**
S x D	2	254.34	127.17	2.41
S x Geno	5	69.46	13.89	<1
D x Geno	10	489.01	48.90	<1
S x D x Geno	10	67.14	6.71	<1
Within susceptible	35	39096.37	1117.04	21.15**
Stress levels (S)	1	715.27	715.27	13.54**
Depth (D)	2	17783.77	8891.88	168.38**
Genotypes	5	19048.35	3809.67	72.14**
S x D	2	87.54	43.77	<1
S x Geno	5	31.61	6.32	<1
D x Geno	10	1337.63	133.76	2.53*
S x D x Geno	10	92.17	9.21	<1
Error	72	3802.25	52.81	
Total	143	73967.18		

symptoms could be established (Rajagopal *et al.*, 1989a). Based on the relationship between SWD and stomatal resistance, it becomes clear that coconut palm is subject to severe stress when the SWD exceeds 115 mm. This value can be taken as the critical level for starting irrigation and planning of water application schedules. Similarly, the investigations on the effect of weather variables on stress development in coconut showed that when palms were exposed to an environmental situation wherein the irradiation was around 265 W m^{-2} , temperature 33°C and VPD 26 mbars, the stomatal closure sets in (Kasuribai *et al.*, 1988). Thus, the significance of both soil moisture level and agrometeorological parameters on stress development in coconut have been understood. The genotypic responses of coconut to the prevailing stress condi-

tions in terms of stomatal regulation and water potential have been reported (Rajagopal *et al.*, 1988). When coconut genotypes were screened for drought tolerance both with the rapid method under artificial stress created dehydration (Rajagopal *et al.*, 1989b) and under field conditions (Rajagopal *et al.*, 1988) it was found that some of the tall like FMS, Andaman Giant, Fiji, Java Giant, Philippines Ordinary and hybrids like WCT x WCT, LO x GB, LO x COD and WCT x COD were relatively more tolerant to drought than the dwarfs namely MGD, MOD, MYD, GB and COD, tall like Andaman Ordinary, Laccadive Micro and the hybrid COD x WCT.

It was of interest to study the differences in the pattern of soil moisture depletion by the roots and the

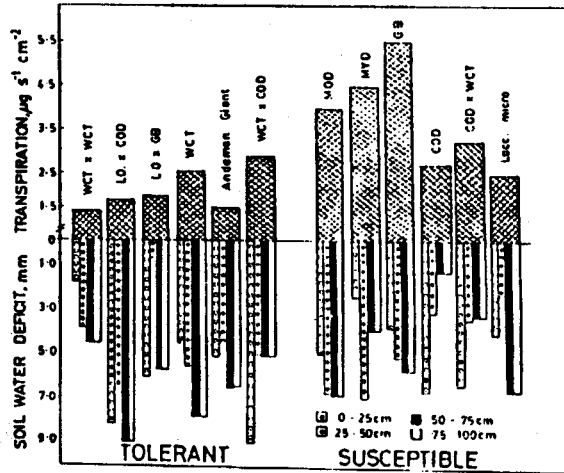


Fig 1. The soil water deficit and transpiration rate in the drought tolerant and susceptible genotypes of coconut, measured during the stress period. Values are mean of six palms

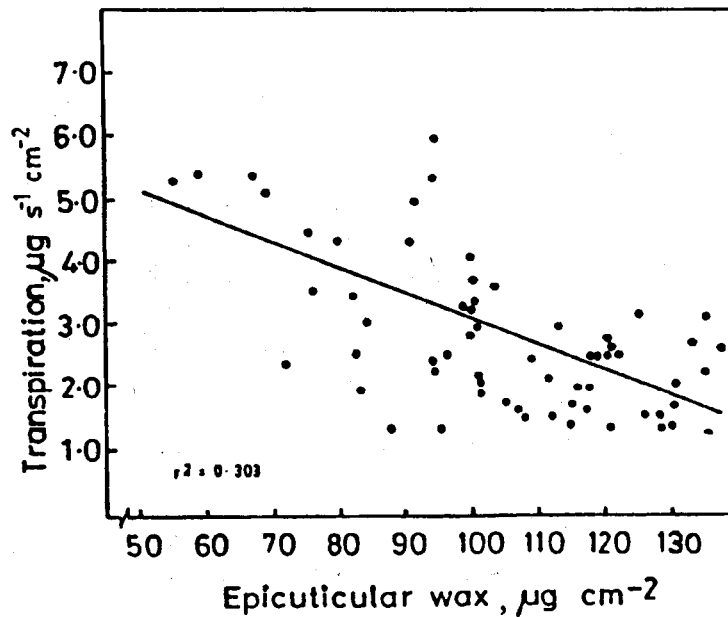


Fig 2. The relationship between epicuticular wax content and transpiration rate during stress period in coconut genotypes

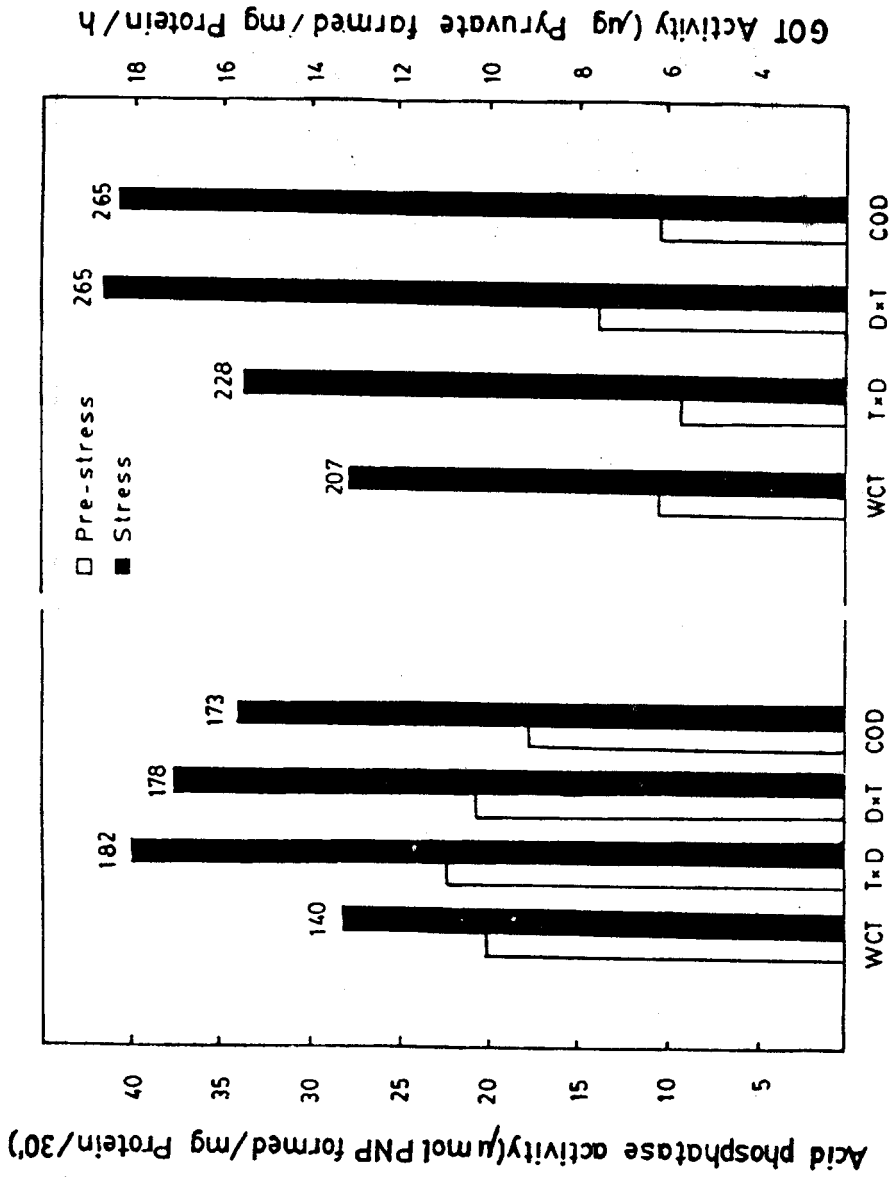


Fig 3. Activity of acid phosphatase and glutamate oxalacetic acid transaminase in four genotypes of coconut during the pre-stress and stress period. Values are mean of three palms each. Figures on the top of closed bars indicate percentage increase in enzyme activity in stressed leaves over pre-stressed leaves

transpirational loss of water through leaves between the drought tolerant and susceptible groups. The data presented in this paper clearly revealed that the tolerant genotypes, in general, extracted more soil moisture from the entire soil profile as compared to the susceptible types, despite minor variations within the groups (Fig 1). However, by reducing the transpiration rate through effective control of stomata, the tolerant genotypes could conserve water in the tissues for physiological and metabolic processes, whereas the susceptible genotypes tended to lose more water and hence became sensitive to drought conditions. For instance, although the SWD from the 0-100 cm profile was nearly the same between a tolerant genotype, WCT (26.15 mm) and a susceptible type MOD (25.7 mm) the latter transpired more water ($5.5 \mu\text{g s}^{-1} \text{cm}^{-2}$) than the former ($2.8 \mu\text{g s}^{-1} \text{cm}^{-2}$). Similarly, WCT x WCT and COD x WCT had similar SWD values (15.2 and 16.8 mm respectively) but the former proved to be more tolerant by virtue of its ability to conserve water in the tissues having a low transpiration rate ($1.8 \mu\text{g s}^{-1} \text{cm}^{-2}$) whereas a high transpiration rate of $4.0 \mu\text{g s}^{-1} \text{cm}^{-2}$ in the latter made it susceptible to drought.

The factors described above clearly reflect on both the root development in terms of total mass and activity and the leaf characteristics like stomatal regulation. In this context, the role of ECW in checking the loss of water in different plant species deserves mention (Hall and Jones, 1961; Baker, 1974). The fact that the most tolerant genotypes like LO x GB and LO x COD have significantly higher ECW content ($> 120 \mu\text{g cm}^{-2}$) than the susceptible ones like MYD and MOD ($< 80 \mu\text{g cm}^{-2}$) clearly indicates the significance of cuticular wax in imparting tolerance to drought. Such genotypic variations in ECW was shown in sorghum (Ebercon *et al.*,

1977), oat (Bengston *et al.*, 1978, and cocoa (Balasimha *et al.*, 1985). As an important component in reducing the transpirational loss of water, deposition of wax on the leaf surface was correlated with the drought resistance in the above crops. Clarke and Levitt (1956) reported an increase in ECW in the stressed leaves of soyabean accompanied by a reduction in transpiration rate. In the present study, there is a clear indication of a negative relationship between ECW and transpiration in that MOD (susceptible) having an ECW of $77.3 \mu\text{g cm}^{-2}$ had high transpiration rate of $4.5 \mu\text{g s}^{-1} \text{cm}^{-2}$ while high value of ECW, $132.6 \mu\text{g cm}^{-2}$ in LO x GB (tolerant) was associated with a low transpiration rate of $1.96 \mu\text{g s}^{-1} \text{cm}^{-2}$. The linear regression equation fitted for transpiration versus ECW was found to be significant (Fig 2) ($r^2 = 0.303$).

From the foregoing it is evident that the internal water balance is well regulated in tolerant genotypes by the development of an efficient root system and favourable leaf characteristics, whereas in the susceptible genotypes even though soil moisture extraction in some cases like MOD, GB and LM is as much as that in the tolerant genotypes the relatively high rate of water loss played crucial role in rendering them sensitive to water stress.

As a consequence of changes in leaf water potential in the tissues during stress, the metabolic status in terms of enzyme activities also showed variations among genotypes (Shivashankar, 1988; Shivashankar *et al.*, 1989).

Among the enzymes studied, the activities of APH and GOT were found to be highly sensitive to stress. The activities of these two enzymes were higher in the dehydrated leaves of susceptible genotypes like LO, GB and COD x WCT than in those of tolerant

ones namely, LO x GB, LO x COD and WCT (Rajagopal *et al.*, 1988). Under field conditions also there existed differences in the enzyme activities between the two groups of palms cultivated under irrigated and rainfed conditions (Shivashankar *et al.*, 1989). Relatively high activity was recorded in COD x WCT as compared to WCT. Considering the metabolic role of these enzymes and their localization in the cell, it is evident that WCT shows better ability to tolerate stress than COD x WCT. From earlier studies on crop plants (Silva, 1974) it has been hypothesized that the increase in activity is due to increased solubilization of APH enzyme following membrane damage. Tolerant varieties possessing more stable membranes show increased activity. The data on tolerant and susceptible genotypes of coconut corroborate the above hypothesis. Thus, the measurement of enzyme activities during stress development could serve to monitor degree of tolerance of coconut genotypes to stress.

Thus, the close relationship between the soil water components and the physiological and biochemical responses of the coconut palm reflecting on the cellular processes could be established in coconut genotypes differing in their tolerance to drought.

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