CHANGES IN EPICUTICULAR WAX, LIPIDS AND MEMBRANE STABILITY OF COCONUT GENOTYPES DURING STRESS DEVELOPMENT

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VENUGOPALAKRISHNA KURUP V.

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To

My Parents

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CERTIFICATE FROM THE GUIDE

This is to certify that the dissertation entitled 'Changes in epicuticular wax, lipids and membrane stability of coconut genotypes during stress development' submitted in partial fulfilment for the award of the degree of 'Master of Philosophy' in Bioscience (Plantation Crops) of Mangalore University is a record of *bona fide* research work carried out by Mr. V. Venugopalakrishna kurup under my guidance and supervision. No part of the dissertation has been submitted for any other degree or diploma.

V. Rajagopal

(Dr. V. Rajagopal)
Plant Physiologist,
Division of Plant Physiology,
C.P.C.R.I., Kasaragod,
Kerala-670 124.

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INTRODUCTION

1. INTRODUCTION

The availability of water is one of the basic inputs for crop production. Plants use enormous amounts of water during their life time. In order to obtain maximum production, required amounts of water must be ensured to plants either by natural means viz. rainfall or artificial means i.e., irrigation. There is an increasing demand for agricultural production due to increase in world population. This demand can be met only if adequate water resources are available for agricultural purposes. In India out of the total cropped area of 172.63 m ha about 76% is under rainfed condition and about 24% under irrigated condition (Anonymous, 1986).

However periodic water deficit occurs in nature due to inadequate rainfall coupled with erratic distribution. This results in droughts of different intensities. During dry weather, high evaporative demand prevails resulting not only in atmospheric drought but also in the soil drought. The duration and intensity of water deficit is location specific and can vary from year to year because of disturbed rainfall. In the post-independent India there was a severe drought in 1963, 1979 and 1983 and 1987. It affected the growth and development of crops thereby led to heavy yield losses.

In general the annual rainfall ranges from 2500 mm to 3700 mm in Kerala. Northern Kerala is characterized by higher rainfall than the southern Kerala, but the distribution is erratic in the former. At Kasaragod, out of the total rainfall of 3500 mm (average of 20 years), 85% is received during the South West monsoon, (June to September) 7.5% during the North East monsoon (October to November) and 7.5% as non seasonal rainfall. Thus the rainless period ranges from 5 to 8 months either due to early cessation of S.W. monsoon or failure of N.E. monsoon and non seasonal rains. Thus Kerala represents a peculiar situation of drought occurrence inspite of heavy rainfall.

Soil texture varies from region to region and it is estimated that laterite soil constitutes nearly 60% while alluvial and coastal sandy and sandy soils 15% each, with 10% of reclaimed soils. Although coastal sandy or sandy loam soils constitute only 15% of the total soil types, it is estimated that approximately 70% of cropped area is under coconut in these soils. These soils are characterized by poor water retention capacities which further accentuates the drought effects on plant metabolism and ultimately yield.

Crop plants withstand moisture stress through various adaptation, ranging from morphological and anatomical characters and to changes in physiological and biochemical processes (Hsiao, 1973). This is achieved through different ways like reduction in leaf area, development of waxy layer on the leaf surface, stomatal closure and restricted transpiration.

The physiological and morphological adaptations of cereals and pulses to drought conditions are well understood (Turner, 1982; Seetharama et al., 1982), whereas with regard to plantation crops only limited amount of work has been reported. Thus there is a need to understand the impact of moisture stress in plantation crop like coconut.

Coconut palm (Cocos nucifera L.) grows well in warm weather with abundant sunshine and mean temperature of 27°C ± 6°C with a rainfall between 1300 mm and 2300 mm per year (Murray, 1977). In India coconut is cultivated in about 1.21 m ha, out of which Kerala occupies the first position with 0.69 m ha (57%) (Anonymous, 1987), in various types of soils ranging from coastal sandy loam,

REVIEW OF LITERATURE

2. REVIEW OF LITERATURE

2.1. Coconut palm

The coconut palm is a tropical rainfed crop and grows well in warm weather with temperature ranging from 25°C to 30°C with a rainfall between 1300 mm and 2300 mm per annum (Murray, 1977). The principal coconut growing areas are found on a wide variety of soils ranging from littoral sandy to the heaviest clays and sandyloam soils (Menon and Pandali, 1960; Thampan, 1981; Shanmughanathan, 1987). Most of the soils where coconut is grown do not have adequate water holding capacities (Haridasan, 1978). As coconut grows mostly on sandyloam soils, the crop experiences moisture stress. (Rajagopal *et al.*, 1989 a, Kasturibai *et al.*, 1988). The positive influence of summer irrigation on nut production is well established (Padmanabhan, 1973; Venkitesan, 1973; Nelliat and Padmaja, 1978).

2.2. Soil drought

Plants are normally affected by both soil drought and atmospheric drought; although it is difficult to delineate between the two. The relationship between the changes in soil water potential and plant responses is well established (Slatyer, 1967; Turner, 1974; Blum, 1974). Changes in the soil water potential affects leaf water potential and related physiological and bio-chemical processes (Turner, 1979; Levitt, 1980). The soil water characteristics of red sandy loam soil indicated that the field capacity varied from volumetric moisture content from the upper to the lower soil depths (Joshi, 1986). Haridasan (1978) reported that laterite soils are deep with low hydraulic conductivity (11.9 - 30.8 cm/hr) and have higher cation exchange capacity than red-sandy loam soils (Mu 3a) which are rich in coarse sand, low cation exchange capacity and higher hydraulic conductivity (40-114 cm/hr). In coconut the total biomass responses to SWD implies that palms are highly sensitive to water deficit conditions in terms of photosynthetic activity, CO_2 assimilation, dry matter production and partitioning (Rajagopal *et al*., 1989 a).

2.3. Atmospheric drought

The influence of agrometeorological parameters such as light, temperature and relative humidity on stomatal regulation in many crops is well documented in literature (Raschke 1975). The agrometeorological variables play a major role in water balance of coconut palm through the stomatal regulation (Milburn and Zimmermann, 1977; Rajagopal et al., 1986). The relationship between the weather variables (light intensity, ambient temperature and vapour pressure deficit) and stomatal resistance was reported in coconut palm (Kasturibai et al., 1988). The role of relative humidity on the stomatal closure in oil palm has been reported (Rees, 1961).

2.4. Plant stress parameters

Crop plants withstand drought through various morphological and physiological adaptations. Most of the work on various physiological and morphological adaptations is centered around annuals, biennials and to some extent horticultural tree species. For example a survey of literature indicated the leaf water potential status in sorghum, rice and wheat (Blum, 1974; O'Toole and Moya, 1978; Winter et al., 1988), Stomatal conductance in wheat and sorghum (Jones, 1977; Blum, 1974), epicuticular wax formation in rice and oat (O' Toole et al., 1979; Bengston et al., 1978) membrane stability in wheat and soybean (Blum and Ebercon 1981; Martinan et al., 1979), Stress induced accumulation of proline (Stewart et al., 1966; Barnett and Naylor, 1966; Singh et al., 1972; Sinha and Rajagopal, 1975 and abscissic acid (ABA) (Wright, 1969; Most, 1971; Zeawart, 1971; Kriedemann et al., 1972; Milborrow and Robinson, 1973; Hsiao, 1973; Goldbach and Goldbach, 1977; Quarrie and Jones, 1979; Rajagopal and Anderson, 1980) have been reported in many plant species. Based on these, crops like sorghum, rice etc. have been screened to identify drought tolerant varieties. In case of plantation crops like coconut (Rajagopal et al., 1989 b), cacao (Balasimha et al., 1988) Tea (Renard et al., 1979), Coffee (Renard and Kermoga, 1984; Venkataramanan and Ramaiah, 1986), and rubber (Gururaja Rao et al., 1986), leaf water relations are determined to identify drought tolerant characters.

2.4.1. Water potential

Leaf water potential (Ψ) is often used as an index of moisture stress in plants. During water stress period, plants show changes in water potential components namely, osmotic potential and consequently turgor potential.

In sorghum and maize, ψ was higher in irrigated conditions than in the unirrigated conditions and the difference between the two treatments became greater as the season progressed (Fereres *et al.*, 1978). During water stress condition sorghum showed ψ of - 18.9 bar but maize only - 14.8 bar while in rewatered condition ψ increased to - 5.8 bar in sorghum and - 7.5 bars in maize (Sanhez-Diaz and Kramer, 1973).

Blum (1974 a) reported that a drought susceptible sorghum genotype 'Shallu' had relatively low leaf water potential under increasing soil moisture stress. During drought period rice plants had pre-dawn leaf water potentials ranging from - 3 to - 9 bars and midday values ranged from - 16 to - 30 bars, but in recovery it is - 3 to - 9 bars (O' Toole and Moya, 1978). Leaf water potentials of soybean under irrigated condition was higher than that under stress condition. In some irrigated soybeans the average seasonal pre-dawn and midday leaf water potential were - 4.2 to - 11.6 bars but for non-irrigated conditions it was -5.2 and - 12.9 bars (Carlson *et al.*, 1979; Reicosky andDeaton, 1979; Jung and Scott, 1980). The water potential components of wheat showed differences in irrigated and non-irrigated conditions (Jones, 1977;

Sojka, 1979). Schonfeld *et al.* (1988) observed that of winter wheat during drought period was - 22.00 bars to - 27.5 bars but in well watered condition it was - 12.5 bars. The determination of water potential components of winter wheat was also used as screening technique for breeding for drought resistance. (Winter *et al.*, 1988). The leaf water potential of well watered jojoba plants was - 20 bars at night time, while under stress condition it was below - 50 bars (Adamas, 1978). In case of alfalfa (*Medicago sativa*) well watered plants showed - 1.0 to - 4.0 bars at sunrise and declined to - 8 to - 12.0 bars at midday. Under severe plant water stress, water potentials were below - 20 and - 45 bars at sunrise and midday respectively (Carter and Sheaffer, 1983). Xiloyannis (1980) found that leaf water potentials of peach leaves under irrigated condition was between - 5 and - 8 bars before sunrise while under non-irrigated condition it ranged between - 6 and - 15 bars. In case of florunner peanuts ψ during water stress condition was betwee - 30 bars to - 40 bars while in control plants the ψ was - 12 bars (Pallas *et al.*, 1979). The drought pre conditioned plants of some guinea grass had significantly lower leaf water potential than the daily watered plants (Klar *et al.*, 1978). In some pecan seedlings predawn leaf water potential declined with increasing soil water deficits. At increased soil water deficit condition the leaf water potential was - 3 to - 11 bars but after rewatering the ψ was increased more than 20 bars (Rieger, M and Daniell, J.W. 1988). Ackerson, (1977) found that leaf water potential of cotton in unirrigated condition was lower than that under irrigated condition. Some cultivars of groundnut showed leaf water potential of - 14 to - 16 bars at normal conditions, but under water stress condition it showed about - 26 to - 32 bars (Joshi et al., 1988). In potato leaves 3 cultivars like Kennbec, Bentje and Saturna showed ψ of - 9.7, -10.2 and - 11 bars during water stress condition but under normal condition it was - 6.6, - 7.2 and - 7.0 bars respectively (VOS and Groenwold, 1988).

Seasonal changes in leaf water potential was also noticed in some horticultural plants and plantation crops. In apple trees, between May and September the leaf water potential required for closure of stomata decreased by about - 25 bars (Lasko, 1979). Fanjul and Rosher (1984) found that leaves of potted apple showed about - 5 bars but the field grown plants showed about - 11 bars. Some varieties of orange trees showed water potential between

- 10 and - 66 bars during water stress condition. Some sun leaves of orange trees had lower water potential than the shade leaves (Ferres et al., 1979; Syversten and Abrigo, 1980).

In case of sugarcane water stressed plants had ψ of about - 14.5 bars but the unstressed plants showed about - 12.7 bars (Inman - Bamber and Junger, 1986). In cacao, drought susceptible accessions showed about - 1.1 MPa and the drought tolerant had ψ of about 0.8 MPa (Balasimha et al., 1988). Rajagopal et al. (1988b) reported that the drought tolerant genotypes of coconut showed the ψ of - 1.33 MPa to - 1.17 MPa while drought susceptible genotypes had ψ below 1.52 MPa.

Leaf water potential components during water stress condition was also related to leaf age and leaf position. The flag leaves of wheat had a lower water or solute potential and lower or equal turgor pressure than seventh and fifth leaves (Jones, 1977; Aggarwal and Sinha, 1984). Giulivo (1979) reported that the leaf water potential of vitis was higher in basal leaves. Growing shoot tips of apple was found to have a much higher osmotic potential - 10 to -20 bars than mature leaves (Lasko, 1984). The young leaves of tea clones showed higher water potential than the older leaves (Sandanam *et al.*, 1981). In coconut the spindle leaf (unopened) had higher ψ than the middle or lower whorl leaves (Rajagopal *et al.*, 1987).

2.4.2. Epicuticular wax

Leaf cuticle plays a major role in limiting water loss from leaves. Epicuticular wax (ECW) is an important factor for reducing cuticular transpiration during water stress periods (Skoss, 1955; Hall and Jones, 1961). The development of ECW over the leaf surface depends upon the environmental factors like high radiant energy and low humidity (Baker, 1974).

Quantitative development

The development of ECW during water stress period varies in different crops. The accumulation of ECW in soybean is high in water stress condition (Clark and Levitt, 1956). Daley, (1964) found higher ECW content in Poacolensi species in the summer season, than in the wet season. In Brassica oleracea maximum deposits of ECW are formed during high temperature and low humidity conditions (Baker, 1974). Ebercon et al. (1977) reported that ECW in sorghum ranges from 0.144 $\mu g/cm^2$ to 0.199 $\mu g/cm^2$ during water stress conditions. Giese (1975) reported that barley plants grown at high temperature and in light showed higher ECW (46 $\mu g/cm^2/24$ hr) than those grown in dark (6 $\mu g/cm^2/24$ hr). The content of ECW in oat seedlings increased in all varieties with stress treatment, the variety stormogul II showing 60% increase than the control (Bengston et al., 1978). Under rainfed conditions the amount of ECW in olive CVS was about 220 to 262 $\mu g/cm^2$ while in irrigated condition it showed only 168 to 188 $\mu g/cm^2$ (Baker and Procopion, 1980). In cabbage seedlings the wax content was approximately ten times more in green house grown plants (36.3 $\mu g/cm^2$) than in vitro (3.2 $\mu g/cm^2$) (Sutter and Langhans 1982). The rainfall removes about 15 to 36% of the ECW of Isocoma sp. (Mayeux and Jordan, 1987). Rao and Reddy (1980) found that in some woody semi-arid shrubs the wax content was higher during summer season than that during monsoon, season. In cotton, leaves subjected to stress produced more ECW than leaves prior to stress (Weete et al., 1978). In tobacco, leaves grown under long photoperiods had more ECW (4.2 mg/leaf), in comparison with short photoperiods (2.8 mg/leaf) (Wilkinson and Kasperbauer, 1980). During drought period the lemon showed 31 $\mu g/cm^2$ ECW while in between July and October the ECW content decreased by about 58% (Baker, 1975). Mohamed et al. (1986) observed that some of the clones of the tea plant have higher ECW in the dry season. In case of cacao Balasimha et al. (1985) reported that some drought tolerant accessions showed 339.6 $\mu g/mm^2$ ECW content but drought susceptible genotypes showed less than 32.4 $\mu g/mm^2$. In coconut, drought tolerant genotypes showed higher ECW (> 120 $\mu g/cm^2$) than the drought susceptible genotypes during the drought period (< 80 $\mu g/cm^2$) (Rajagopal et al., 1989 b).

The levels of salinity also affect the quantitative development of ECW. In peanut genotype (Arachis hypogaea L) total wax content showed an increase of 8.54, 17.36, 16.82 and 22.18% over the control in the salinized plants at 10, 15, 20 and 25 days respectively (Gururaja Rao et al., 1981).

Qualitative development

The major components of ECW are esters of higher fatty acid and fatty alcohols. The composition of wax also changes during water stress condition (Parker, 1968). Bengston *et al*. (1978) reported higher fattyacids, primary alcohol and alkanes in some oat varieties during water stress condition whereas some varieties showed low level of alkane. Cabbage plants grown under green house conditions showed higher percentage of polar compounds (fatty acids, primary alcohols, aldehydes and esters) but the cultured plants had less percentage of alkanes and secondary alcohols (Sutter, 1984). Tobacco plants grown under short photoperiods resulted in a reduction of alkane and fattyacid contents, but under long photoperiods alkanes and fattyacid contents were highest (Wilkinson and Kesperbauer, 1980). During summer season some weeds of semi-arid shrubs showed alcohols, mixture of hydrocarbons, fattyacids and aldehydes in increasing order, while in monsoon season a new class of wax components such as β-diketones, secondary alcohols and aldehydes were detected (Rao and Reddy, 1980). A decrease in soil water potential increased the proportion of alkanes and wax esters in apple (Darnell and Ferree, 1983).

Under salinity condition the composition of ECW also changes. In peanut genotypes (*Arachis hypogaea*-L) under normal conditions, fatty acids, primary and secondary alcohols, β-diketones were present while in saline condition, in addition to above fractions, hydroxy β-diketones, primary and secondary alcohols and aldehydes were present (Gururaja Rao *et al.*, 1981).

The quantity and quality of ECW is also related to leaf age and development. The old leaves of Ficus showed more amount of ECW than the young leaves (Bass, 1982). Bukovac *et al.* (1979) reported that the development of ECW in Redhaven peach leaves increased with leaf development.

Role of ECW in cuticular Transpiration

The quantitative and qualitative amount of ECW is related to cuticular transpiration. Parker (1968) reported that the deposition of ECW on the cuticle retarded the cuticular transpiration. The sorghum genotypes with a reflective waxy bloom on the leaf surface had higher water use efficiency than the bloomless genotypes (Chatterton *et al.*, 1975). Hull *et al.* (1978) observed that large wax plates in drought tolerant *Eragnostis* plants but absent on drought susceptible plants. O'Toole *et al.* (1979) demonstrated the effectiveness of ECW in increasing cuticular resistance in two rice cultivars. Removal of waxes decreased cuticular resistance by 50 to 60%. The transpiration rate of the apple clearly depend on the resistance to water vapour movement of the appåe cuticle (Horrocks, 1964). During stress treatment the drought resistant variety of the oat showed reduced cuticular transpiration and increase in the amount of ECW (Bengston et al., 1978). Clones of tea (Mohamed et al., 1986) cacao accessions (Balasimha et al., 1985) and coconut genotypes (Rajagopal et al., 1989 b) which had higher ECW during drought, also showed lower transpiration rates during the same period.

The quality of ECW was also related to cuticular transpiration. In Isocoma leaves, cuticular transpiration was associated with waxes that contained high concentrations of fatty acids and alcohols, while low rates of cuticular transpiration were associated with high aldehyde content (Wilkinson and Mayeux, 1987). Ramadas et al. (1979) reported that the alcohols and aldehydes act as suppressors of cuticular transpiration, while fatty acid promote the transpiration. Rao and Reddy (1980) observed that increased level of cuticular transpiration is associated with the absence of aldehydes, secondary alcohols and β-diketones with higher level of fatty acids.

2.4.3. Membrane stability

The capacity of plants to minimize membrane damage is an important feature of tolerance to water stress. The degree of membrane stability to stress is evaluated by electrolyte leakage (Sullivan, 1979). The excessive dehydration is characterised by major increase in permeability (Gaziani and Livine, 1971).

The drought affected crop plants showed cellular membrane integrity and increased electrolyte leakage. Gupta (1977) reported that dessication resistance is more related to solute leakage, because the plasmalemma of sensitive spp. shows greater permeability on re-wetting. In cowpea the rehydrating leaf tissue show increased leakage in proportion to the content of prior dessication (Leopold et al., 1981). Some drought tolerant genotypes of wheat adjusted cell membrane stability to water stress condition (Blum and Eberoon, 1981).

Schwab and Heber (1984) found that drought tolerant plants like Ceraterostigma spp. and Certerach officinaram showed more specific membrance structures, which would increase membrane stability than drought sensitive plants like Spinacia Oleracea. In the cultivated and wild species of tomato, the membrane was found to be more injured under stress in the winter than in the summer. Discs of wild species were more leaky than those of cultivated species during the summer (Tall and Shannon, 1983). The drought susceptible potato plants to water stress affects cellular membrane integrity and causes increased leaching of ions from the cells of leaves (Bensal and Nagarajan, 1983). Martin et al. (1987) found that under low water potential condition electrolyte leakage of the leaves of some woody angiosperm were increased. In sugarcane the CO 419 variety showed 238.8% cellular membrane injury during water stress condition as compared to normal conditions (Venkataramana et al., 1987). Dehydration pretreatment followed by restoration of tissue turgidity caused a decrease in leakage of electrolytes. The leakage of potassium and other electrolytes increased membrane permeability in drought induced winter rye hypecotyls (Sheherba Kova and Kacperska , 1980, '83).

The rate of electrolyte leakage and membrane stability is related to leaf age and leaf development. Martineau,(1979) observed that membrane stability is greatest in newly developed leaves in Soybean plants. In cowpea plants the older leaves showed more solute leakage after exposure to dessication than younger leaves. (Leopold, 1981). The greater leakage of older leaves caused by dessication has also been reported for wheat (Blum and Ebercon, 1981).

Heat and moisture stress affects the amount of phenolic compounds. In low energies of near ultraviolet radiation (3000-4000 nm) simultaneously with visible radiation, the total phenolic compounds were increased in tobacco (Anderson and Kasperbauer, 1973). Duke and Williams (1983) reported no interaction between water stress and three phenolic acids, (p-coumaric, caffeic and ferulic acid) on lettuce (Lactuca Sativa L) seed germination. Senescent tobacco leaves had higher amount of phenol compounds (Kato and Shimizu, 1987).

MATERIALS AND METHODS

3. MATERIALS AND METHODS

3.1. Location

The research studies were carried out at the Central Plantation Crops Research Institute Kasaragod (12° 30'N, 70° 00'E, 11m MSL). In this area the total rainfall averages 360 cm, of which 85% is received during the South West monsoon (June to September), 7.5% during the North East monsoon (October - November) and 7.5% non-seasonal rainfall. Total sunshine hours ranges from 6 to 9 per day during dry months. Typically maximum temperatures vary between 29°C to 34°C with a minimum temperature of 20°C. Solar radiation ranges from 165 wm^{-2} to 330 wm^{-2} with a vapour pressure deficit 1.1 to 3.0×10^{-3} MPa. The mean monthly pan evaporation ranges from 2.3 to 3.6 mm day $^{-1}$ during the rainy months and from 4.1 to 5.2 mm day $^{-1}$ during dry months. In most years, December to April is the rainless period with February - March being the peak dry season.

3.2. Growing conditions

Three genotypes of coconut palms (Cocos nucifera L.) viz., West Coast Tall (WCT), WCT x Chowghat Orange Dwarf (COD) and COD x WCT were planted in 1965 in the Institute Farm under rainfed condition and three levels of fertilizer treatments. These experimental palms were maintained by the Agronomy Division. The treatment consisted of a zero level control (m_o), fertiliser levels of 500 gm N + 500 P_2O_5 + 1000 g K_2O (m_1) and 1000 g N + 1000 g P_2O_5 + 2000 g K_2O/palm/year. It was laid out in a randomised block design with three replications at a spacing of 7.5 x 7.5 m. This monocrop experiment existed on a red/sandy loam soil. The present study was carried out on palms under m_2 fertiliser level only.

3.3. Experimental stages

The experiments were conducted in three different seasons viz., post monsoon of 1987 (October-December), Summer of 1988 (January-May) and monsoon of 1988 (June - August 1988) which represented the pre-stress, stress and post-stress stages respectively. The latter terminologies are used in the text to indicate the stages.

3.4. Determination of soil moisture content

Soil samples were collected from the basins of two palms per genotype at a distance of 1m from the bole region at three depths viz., 0-25, 25-50 and 50-100 cm. Samples were taken during pre-stress, stress and post-stress period. Soil moisture content was determined gravimetrically.

The soil samples were taken in small boxes and the fresh weight of the soil is determined immediately, followed by drying in an electrical oven at 110°C till constant dry weights are obtained. Based on the fresh weight and dry weight differences, soil moisture percentage is calculated.

3.5. Recording of weather variables

Agroclimatological parameters like light, temperature and relative humidity were measured at the vicinity of experimental palms with the steady state porometer (Li-Cor 1600, USA), as described earlier (Kasturibai *et al*., 1988). Data on rainfall and pan-evaporation were collected from the climatological station established in the Institute.

3.6. Determination of Plant stress parameters

Plant stress parameters viz. leaf water potential, epicuticular wax content and membrane stability through electrolyte leakage, potassium and phenol contents were determined at monthly intervals between October 1987 to August 1988, with two consecutive days each month. The data on the first three months i.e. October to December represented 'prestress' stage, while that between January and May the 'stress stage' and that between June and August the 'post-stress' stage. All the measurements were taken between 10.00 h and 12.00 noon, being the optimum period for monitoring the above parameters (Rajagopal *et al*., 1989 b).

3.6.1. Leaf water potential (ψ)

Leaf water potential (ψ) was determined on the leaflets from the 1st and 6th leaf position of 3 palms from each genotype. It was measured by using a scholander pressure chamber (Plant water console, model 3000, Soil Moisture Co;USA) according to the method of Milburn and Zimmerman (1977) and Rajagopal et al., (1987).

According to these methods the leaflets collected are cleaned to roll from the sides of the fronds and introduced into the pressure bomb. This was done without breaking the midrib, keeping the adaxial (upper) surface outermost. Before final enclosure the base of the lamina was trimmed with a sharp knife to free the base of cylindrical midrib. After scraping gently, the leaflet prepared for measuring is sealed in a pressure bomb by forcing it through a rubber stopper fitting into the bomb lid. To create the incipient sap exudation, nitrogen gas was used. The consequent pressure read on scale corresponds to the xylem sap negative pressure.

Two to three leaflets were used in each case.

3.6.2. Epicuticular wax (ECW)

3.6.2.1. Quantitative analysis of ECW

The epicuticular wax (ECW) was extracted from the 1st and 6th leaves (from the top to downwards) of 3 palms per genotype as per the method described by Ebercon *et al*., (1977) and adopted earlier for coconut (Rajagopal *et al*., 1989 b). Segments of 3 x 1 cm were cut from the leaflets and 20 such segments were plunged into 15 ml chloroform and vigorously shaken for 15 to 20 seconds and decanted. This method extracts the wax from both the surface of leaflets. The extract was evaporated under vacuum. 5 ml of potassium dichromate ($K_2Cr_2O_7$) reagent was added to the dry sample. The samples were placed in boiling water for 30 min. After cooling, the volume was made up to 17 ml with distilled water and the colour developed was read at 590 nm on a Perkin-Elmer spectrophotometer. Internal wax is used as standard and the values are expressed in $\mu g/cm^2$.

3.6.2.2. Qualitative analysis of ECW

Qualitative analysis of ECW was carried out by Thin

Layer Chromatography (TLC). For TLC separation, leaflets from 1st and 6th leaf position of 3 palms were taken and cut into small pieces and 10 g of leaf tissue was taken for extraction. The leaf cuttings were stirred with 20 ml chloroform for 20-30 seconds and decanted. The extract was concentrated to 1 ml under vacuum and these aliquots were used for chromatographic separation.

TLC plates were made (Plates 20 cm x 20 cm) of Silica Gel G (1mm thickness) on which 100 microgram samples were loaded. The following solvent systems were used:- Solvent System I - Benzene : acetic acid (100:10), Solvent System-II-Petroleum ether : Toluene : Diethylether : Hexane : methnol (140:30:30:30:10).

Plates were run to 10 cm in solvent system I, taken out and dried at room temperature and again run in solvent system II in the same direction. The spots were detected by placing the plate in a chromatographic chamber saturated with iodine vapour (Barrett, 1962). The brown spots were marked and compared with Duram wheat leaf wax. The Rf values were recorded and photographs were taken wherever possible.

3.6.3. Membrane stability

The rate of injury to cell membranes is estimated through the measurement of the electrolyte leakage ffom the cells. For this the leaf discs of 0.7 cm diameter were taken from the leaflets of 1st, 6th, 14th and 20th leaf position of 3 palms per genotype. The leaf discis were kept in 10 ml distilled water and thei initial conductivity (IC) was determined after 10 minutes with Mullard's conductivity bridge. After the initial measurements discs were returned to the original solution. These tubes were then kep in boiling water bath for about 3 min, and the final conductivity (F C) was measured. The Electrolyte leakage was expressed as the percentage over the initial conductivity.

$$\frac{FC - IC}{IC} \times 100$$

Potassium leakage

The procedure followed is essentially similar to that of electrical conductivity measurements. The potassium leakage is measured on a corning 400 flame photometer before and after boiling the solution. Standard solution was prepared with Analar Potassium Chloride (KCl) and the values of K^+ leachate is expressed as ppm.

Phenols

Ten leaf discs of 0.7 cm diameter were taken from the leaflets of 1st, 6th, 14th and 20th leaf position of 3 palms per each genotype. The leaf discs were kept in 10 ml distilled water for 10 minutes and aliquots were taken for total phenol estimation. As in the case of electrical conductivity and K^+ leakage the samples were kept at boiling water bath for 3 minutes. To above aliquots 0.5 ml diluted Folin and ciocalteu's reagent (1:2 dilution) and 1.0 ml Sodium Carbonate Solution (20%) were added. After the addition of reagents the samples were shaken for one minute and the volume was made upto 25 ml with distilled water. The O.D. values thus obtained were converted into mg of phenol/g fresh weight by comparing with the standard curve using catechol (Bray and Thorpe, 1954).

EXPERIMENTAL RESULTS

4. EXPERIMENTAL RESULTS

4.1. Agroclimatic conditions (Table-1)

During pre-stress (Oct-Dec.) the temperature and relative humidity (maximum and minimum) ranged from 32.9°C to 22°C and 86 to 61% respectively. The light intensity ranged from 900 to 1135 E $m^{-2}s^{-1}$. The total rainfall during this period was 100.5 mm with a pan evaporation rate of 3.73 mm/day.

During stress the maximum and minimum temperatures recorded were 33.1°C and 22.6°C respectively. Pan evaporation rate was 5.5 mm/day, while the daily mean relative humidity varied between 83% and 58%. Light intensity was in the range of 1400 to 1650 E $m^{-2}s^{-1}$. The total rainfall received in the three months (Feb, March, April) was 24.87 mm only.

There was a decrease in maximum temperature (29.6°C) and pan evaporation (3.13 mm/day) between the stress and post-stress period. The relative humidity ranged from 93 to 82%. Due to heavy clouds and incessant rainfall the light intensity could not be measured during this season. A total rainfall of 553.4 mm was received during this period.

Table 1 Agroclimatic conditions

Parameters	Pre-stress	Stress	Post stress
Temperature °C			
Max.	32.9	33.1	29.63
Min.	22	22.6	22.8
Relative humidity %			
Max.	86.33	82.6	93
Min.	60.66	57.67	82
Light $\mu E\ m^{-2}s^{-1}$	900-1135	1400-1650	-
Evaporation rate mm/day	3.73	5.5	3.13
Rainfall mm	100.53	24.87	553.4

4.2. <u>Soil moisture content</u> (Table 2; Figure 1)

The soil moisture content varied among the genotypes between the three stages viz. pre-stress, stress and post-stress. Under pre-stress conditions the soil moisture content was relatively ✗ high in the subsoil surface (0-25 cm) in WCT (7.43%) as compared to either COD x WCT (6.29%) or WCT x COD (6.02%) while the two hybrids had higher moisture content (9.31%, 8.64%) at the lower depth (50-100 cm) than WCT; There was little difference among the three in the middle zone. The soil moisture content declined during the stress period at all the depths to different degrees in the three genotypes. When the total soil profile was considered it was found that the moisture decline between the pre-stress and stress was found to be more in WCT (34.7%) than in the hybrids (27.4% in COD x WCT and 28.4% in WCT x COD). The soil moisture content recovered at all the depths as a result of monsoon i.e. post-stress period.

The statistical analysis revealed that during stress, the decrease in soil moisture content is significant (823.71**), whereas with increase in depth during all the three stages, there is a significant increase in soil moisture (52.84**). The interaction between stage and depth is also found to be significant (3.20*).

Table 2. Soil moisture content

SUMMARY OF ANOVA:(Transformed values)

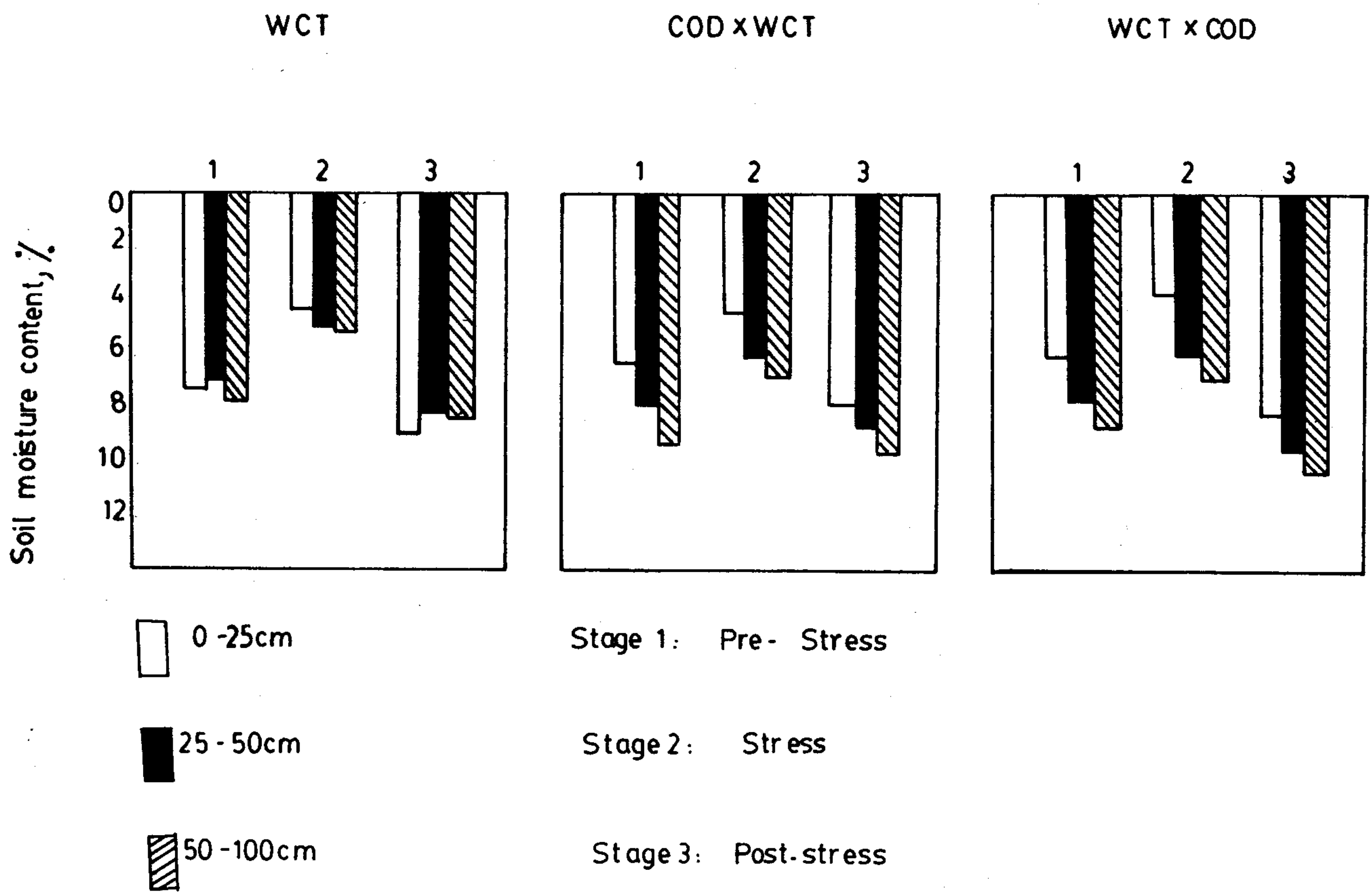
SOURCE	D.F	M.S.S
Replication	1	2.676758
Genotype(G)	2	1.102539
Stage(S)	2	76.943848**
Depth(D)	2	18.174316**
GS	4	0.726074
GD	4	3.539551**
SD	4	1.100342*
GSD	8	0.116699
Error	26	0.343938

* Significant at 5% ** Significant at 1%

TABLE OF MEANS

		pre stress	stress	post stress	mean	0-25	Depth 25-50	50-100
Genotype	WCT	15.78	12.67	17.05	15.17	15.06	15.11	15.33
	CODxWCT	16.16	13.69	17.06	15.64	14.20	15.77	16.93
	WCTxCOD	15.74	13.22	17.64	15.53	13.88	15.84	16.87
	Mean	15.90	13.19	17.25		14.38	15.57	16.38
Depth	0-25	14.84	11.67	16.64				
	25-50	15.84	13.57	17.32				
	50-100	17.01	14.33	17.80				

S.E/plot	0.59	Gen.Mean	15.45	C.V(%)	3.80
C.D. for S	0.40	C.D. for D	0.40	C.D. for GD	0.70
C.D. for SD	0.70				



Figure, 1; Soil moisture profile at three stages in coconut genotypes

4.3. <u>Leaf Water Potential</u> (ψ) (Table 3; Figure *2)

Depending upon the leaf position the leaf water potential (ψ) varied among the genotypes of coconut palms. In general the 6th leaf had lower ψ than the 1st leaf.

<u>First leaf</u>

WCT had higher ψ than either COD x WCT or WCT x COD (‾0.89, ‾0.92 and ‾0.95 MPa respectively), during pre-stress period. The ψ decreased with stress, WCT maintained slightly higher ψ (-1.05 MPa) than either COD x WCT or WCT x COD (-1.09 and -1.08 MPa). WCT and COD x WCT palms have recovered (‾0.73, ‾0.78 MPa). comparatively better than WCT x COD (‾0.98 MPa) during post-stress period.

<u>Sixth leaf</u>

The leaf water potential of WCT during pre-stress condition was higher (‾1.05 MPa) than either COD x WCT or WCT x COD (‾1.30 and ‾1.39 MPa). With the onset of stress the decrease was more pronounced in WCT and also in WCT x COD. The values of ψ ranged from -1.39 to -1.61 MPa during stress among the genotypes. During the post-stress WCT x COD tended to recover better (-1.03 MPa) than COD x WCT and WCT (-1.08 and -1.23 MPa respectively).

Comparison between the leaf positions

The percentage decrease in ψ was higher in 6th leaf (37.8%) than the 1st leaf position for WCT, where as the percentage decrease in ψ ranged from 16 to 13.2 percentage for WCT x COD for 6th and first leaf position. The first leaf of COD x WCT appeared to undergo more stress than the 6th leaf (18.9% and 6.6% respectively). During the post-stress stage the percentage recovery over the stress was higher for WCT, COD x WCT in the first leaf position (30.96 and 28.7 %), while WCT x COD and COD x WCT had shown higher percentage recovery in 6th leaf (36% and 22.7% respectively).

Statistical analysis

The ψ was found to be significant for genotype, stage and position respectively (15.39**, 123.43* and 444.76*). The interaction between genotype to stage and genotype, stage and position were also statistically significant with 5.11** at 1% level but stage to leaf position is significant with 5.05* at 5% level. The interaction between genotype to position was not significant.

Table 3. Leaf water potential

SUMMARY OF ANOVA:

SOURCE	D.F	M.S.S
Replication	2	0.770264
Genotype(G)	2	5.435791**
Stage(S)	2	43.588135**
Position(P)	1	157.056641**
GS	4	1.803223**
GP	2	0.047119
SP	2	1.782227*
GSP	4	6.546753**
Error	34	0.353128

* Significant at 5% ** Significant at 1%

TABLE OF MEANS

		pre stress	stress	post stress	mean	Position 1	Position 6
Genotype	WCT	9.73	12.48	9.80	10.67	8.91	12.43
	CODxWCT	11.12	12.42	9.27	10.93	9.28	12.59
	WCTxCOD	11.71	13.44	10.03	11.73	10.03	13.42
	Mean	10.85	12.78	9.70		9.40	12.82
Position	1	9.22	10.73	8.26			
	6	12.48	14.83	11.13			

S.E/plot	0.59	Gen.Mean	11.11	C.V(%)	5.35
C.D. for G	0.40	C.D. for S	0.40	C.D. for P	0.33
C.D. for GS	0.70	C.D. for SP	0.57	C.D. for GSP	0.99

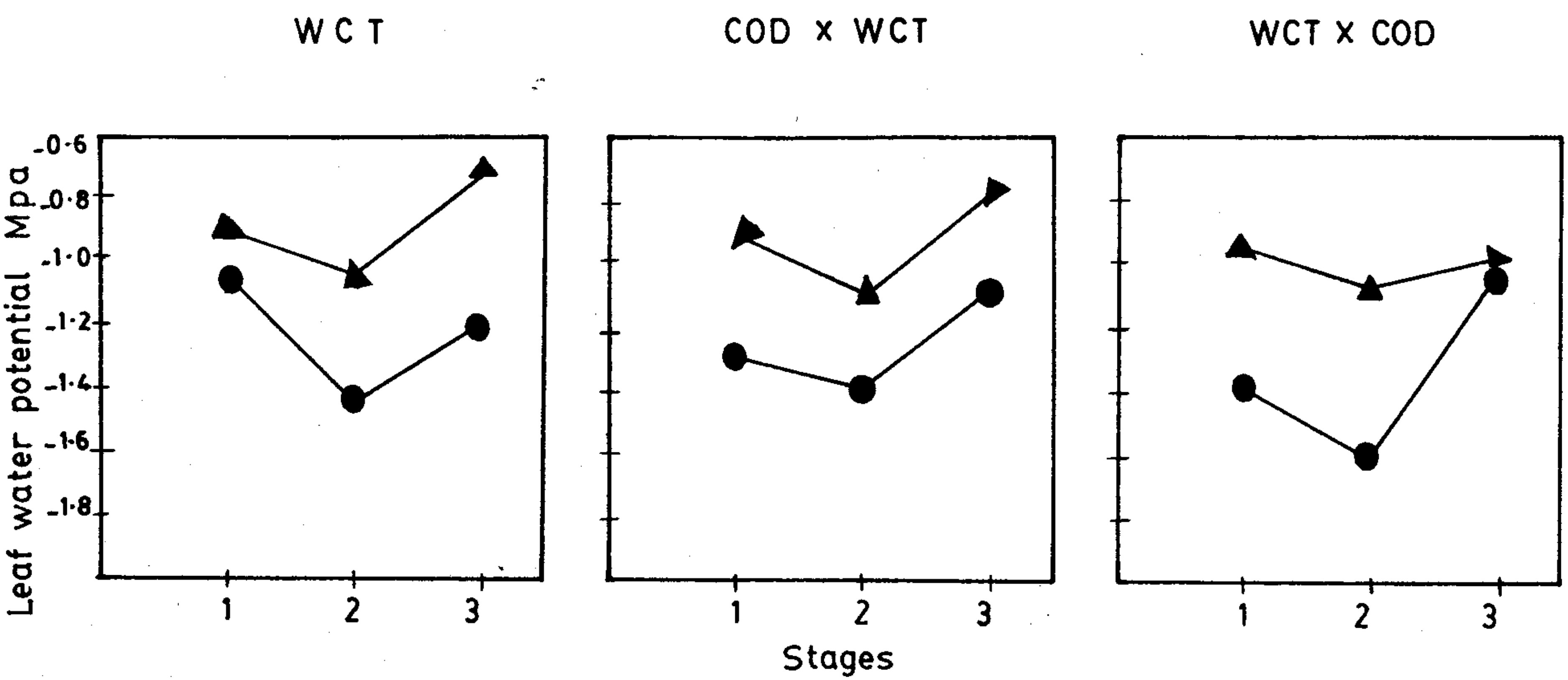


Figure: 2 Leaf water potential in coconut genotypes during stress development

▲—▲ - 1st Leaf ●—● - 6th Leaf

1-Prestress 2- Stress 3-Post stress

4.4. Epicuticular Wax Content (ECW) (Table 4; Figure 3; Plates 1, 2 and 3)

Quantitative analysis

Epicuticular wax content was determined in the first and 6th leaf positions of the three genotypes at all the three stages. Irrespective of the genotypes the ECW content of 6th leaf showed a peak during stress period, while at the other two stages the content was far less. For instance, during pre-stress period the ECW content was 80.8, 75.4 and 77.4 $\mu g\ cm^{-2}$ respectively in WCT, COD x WCT and WCT x COD. With the onset of moisture stress the content of ECW increased to 98.4 95.6 and 101.4 $\mu g\ cm^{-2}$ in WCT, COD x WCT and WCT x COD, accounting for 21.7%, 26.8% and 31% respectively as compared to pre-stress. During recovery stage (post-stress) the wax content declined to 79.1 $\mu g\ cm^{-2}$ in WCT, 75.23 $\mu g\ cm^{-2}$ in COD x WCT and 74.5 $\mu g\ cm^{-2}$ in WCT x COD.

The first leaf had significantly higher ECW in all the genotypes in the pre-stress stage and decreased at later two stages. For example the ECW content declined from 102.9, 105.0 and 101.2 $\mu g\ cm^{-2}$ during pre-stress to 77.6, 69.0, 86.3 $\mu g\ cm^{-2}$ in WCT, COD x WCT and WCT x COD respectively during post stress; the overall decrease being more in COD x WCT.

Statistical analysis

The ECW content was found to be significant for stage and leaf position respectively (122.72** and 59.64**). The interaction between the genotype and stage was statistically significant with 2.80* at 5% level, but genotype, stage and position was statistically significant with 54.78** at 1% level. The interaction between genotype to position was found to be not significant.

Qualitative analysis

Depending on the leaf positions the qualitative development of ECW varied among the genotypes. Under stress period all the three genotypes had more bands than the other two periods. The ECW band pattern is compared with the wheat (Duram) leaf wax as a standard. The Rf values for Duram wheat leaf wax are as follows: 0.94, 0.86, 0.61, 0.49, 0.31 and 0.12.

Table 4. Epicuticular wax content

SUMMARY OF ANOVA:

SOURCE	D.F	M.S.S
Replication	2	32.218750
Genotype(G)	2	43.031250
Stage(S)	2	2071.562500**
P	1	1006.812500**
GS	4	47.296875*
GP	2	33.031250
SP	2	924.703125**
GSP	4	78.929688**
Error	34	16.880514

* Significant at 5% ** Significant at 1%

TABLE OF MEANS

		pre stress	stress	post stress	mean	Position 1	Position 6
Genotype	WCT	91.81	96.49	78.36	88.89	91.67	86.11
	CODxWCT	90.21	98.19	72.14	86.85	91.63	82.07
	WCTxCOD	89.33	99.83	80.42	89.86	95.25	84.47
	Mean	90.45	98.17	76.98		92.85	84.22
Position	1	103.03	97.86	77.66			
	6	77.88	98.48	76.29			

S.E/plot	4.11	Gen.Mean	88.53	C.V(%)	4.64
C.D. for S	2.79	C.D. for P	2.27	C.D. for GS	4.83
C.D. for SP	3.94	C.D. for GSP	6.82		

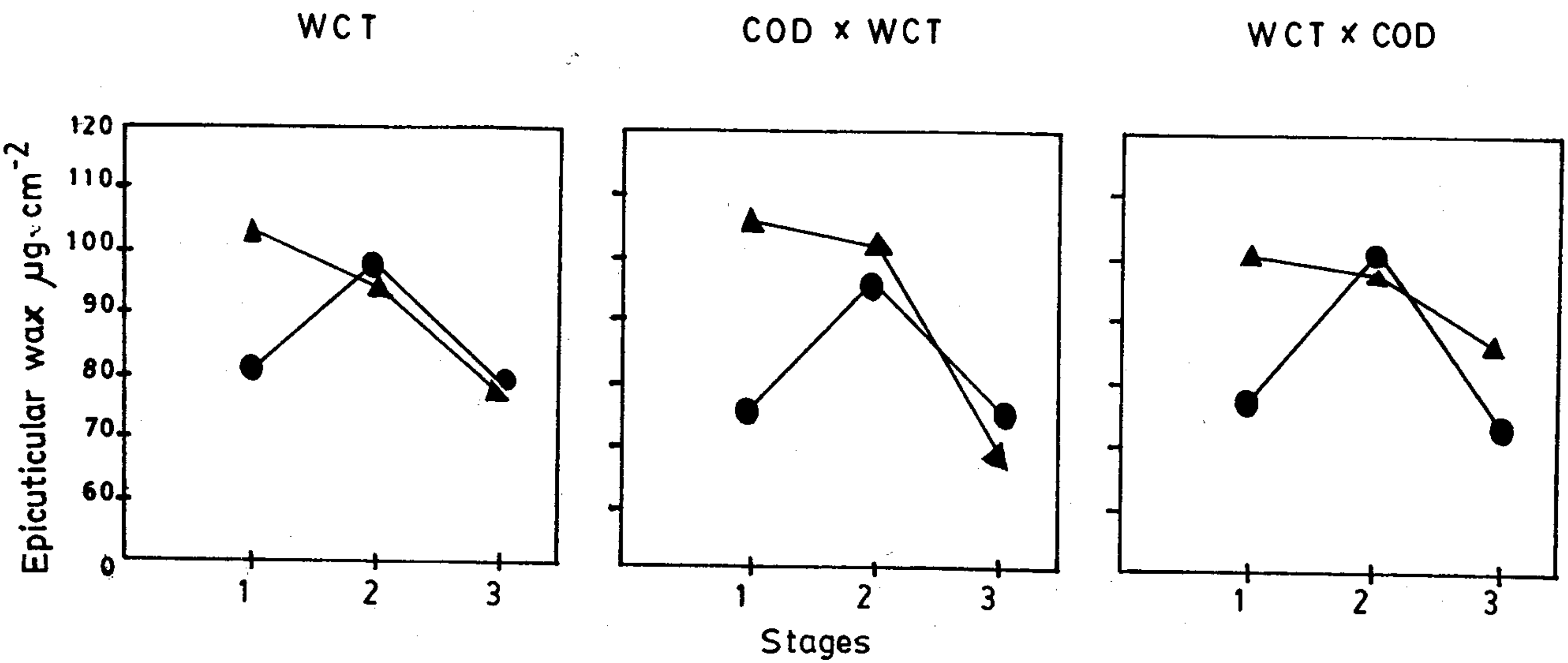


Figure: 3 Epicuticular wax content in coconut genotypes during stress development

▲—▲ 1st Leaf ; ●—● 6th Leaf

1- Prestress 2- Stress 3- Post- stress

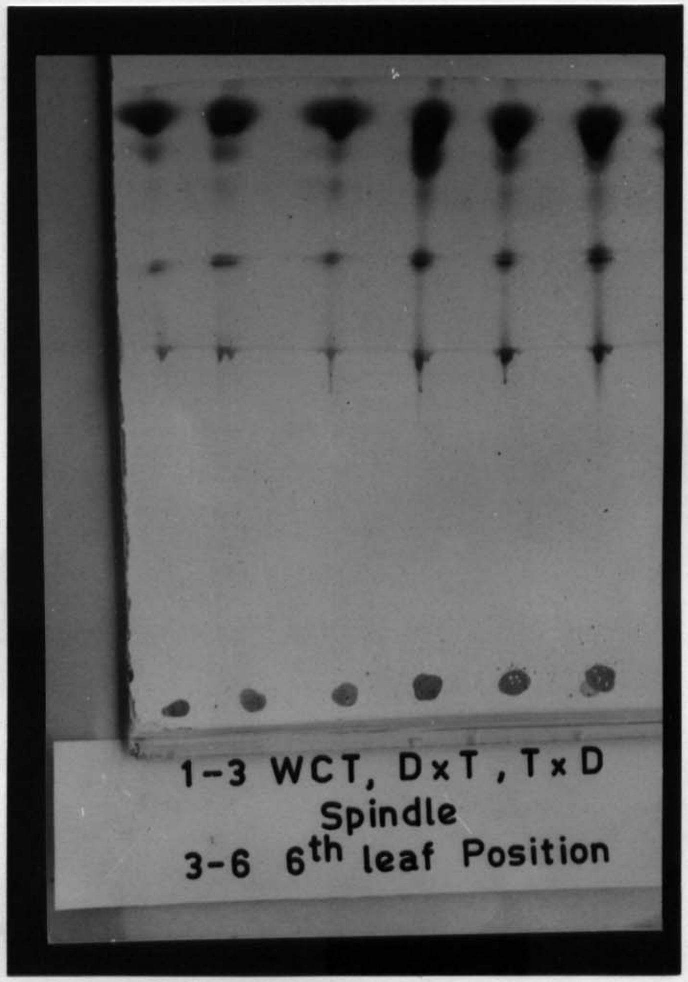


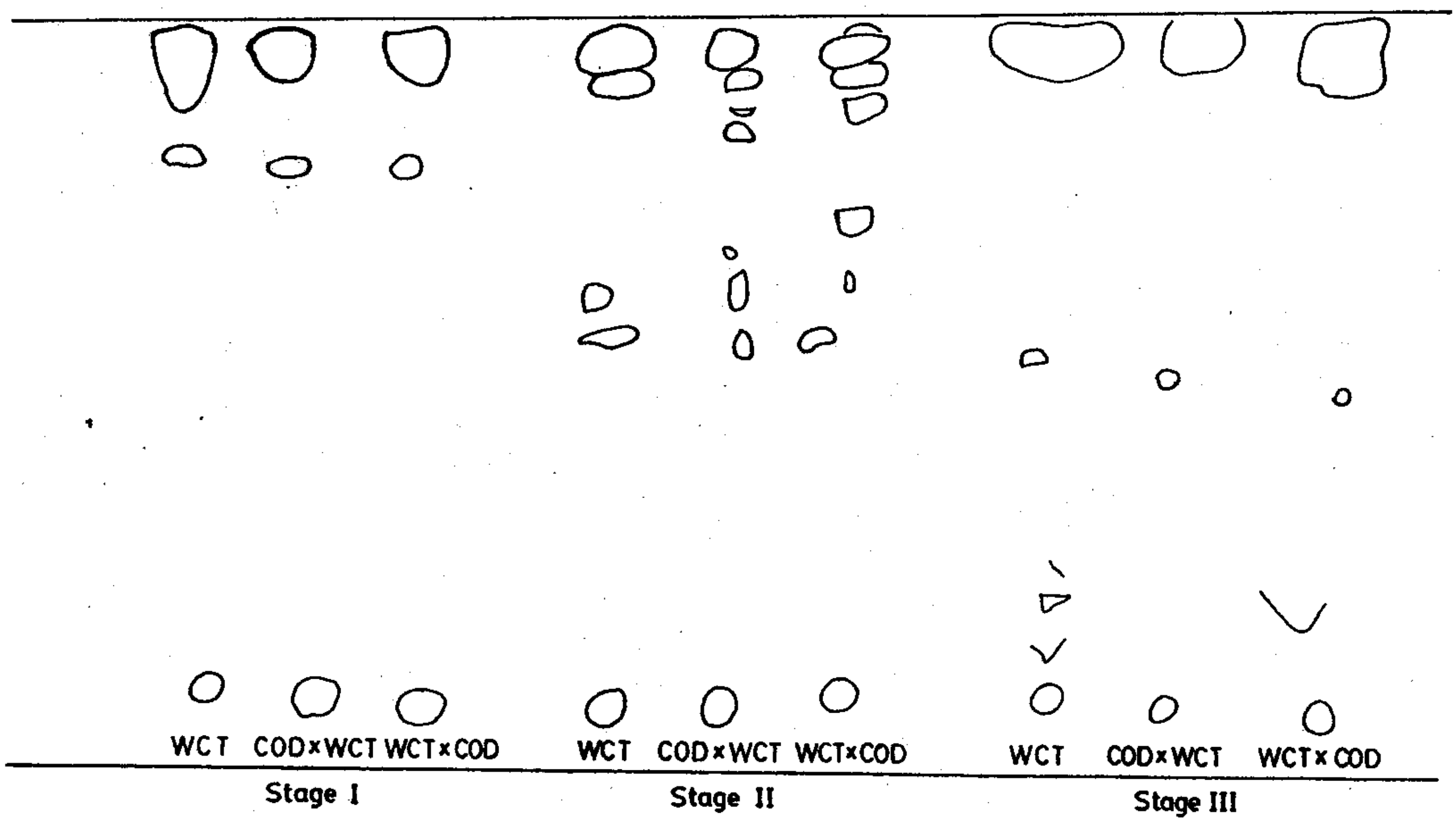
Plate-3 Photograph of TLC plate of epicuticular wax components in the two leaf positions of the three genotypes at stage II (Stress period)

First leaf

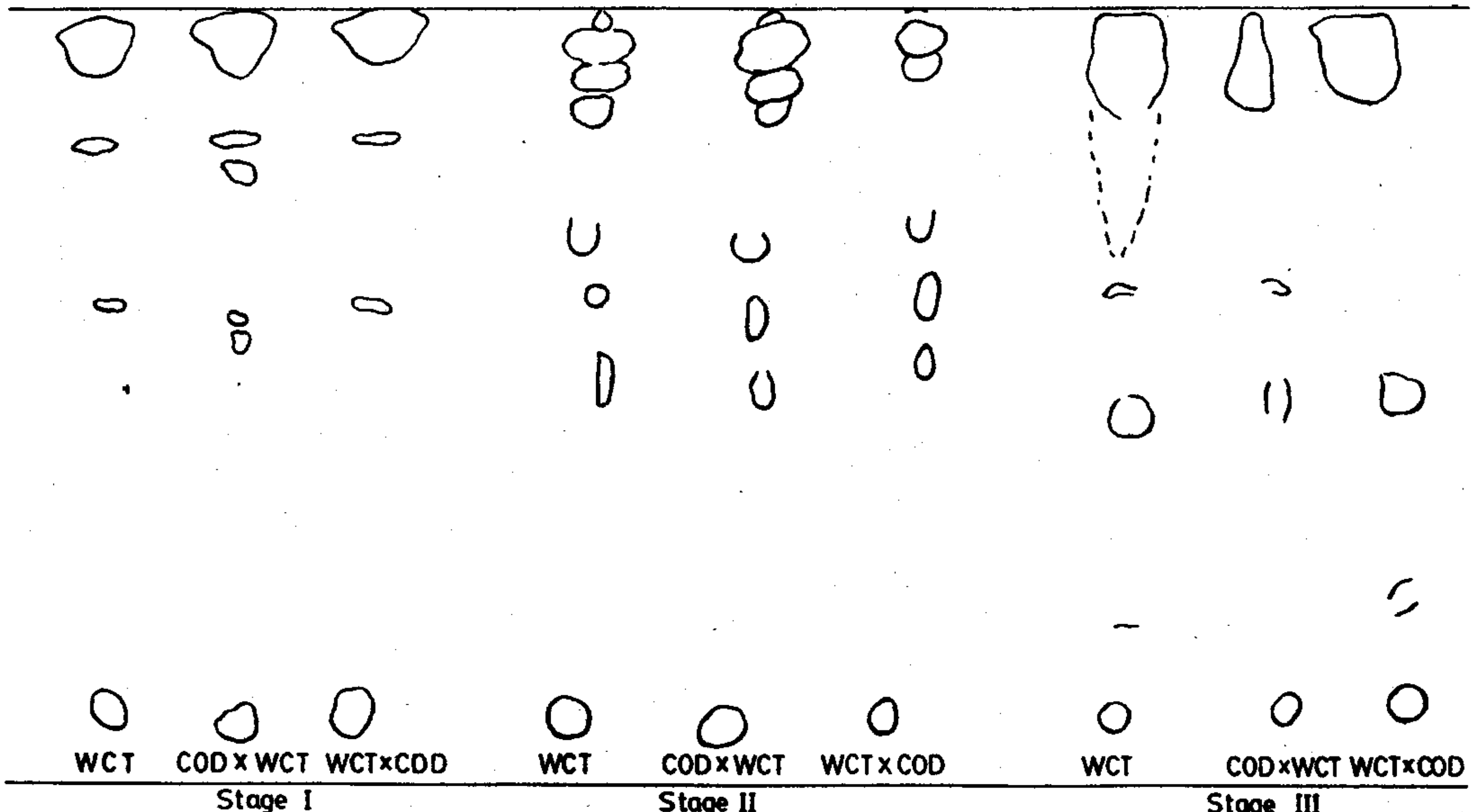
The ECW components during pre-stress period in all the three genotypes showed one band with Rf value of 0.94 as that of wheat. All the three genotypes showed another band with Rf value 0.72 which is not seen in wheat wax. During stress period all the three genotypes had ECW components with two bands having Rf value of 0.94 and 0.86, which are present in wheat wax also. An additional band having Rf value of 0.61 is found in COD x WCT and WCT x COD (as in wheat), while it is absent in WCT. All the three coconut genotypes had shown bands with Rf values of 0.72, 0.55 and 0.52 which are not seen in wheat standard. During post-stress period all the three genotypes had two bands with Rf values 0.94 and 0.31, comparable to wheat wax. An additional band with Rf value 0.12 is found in WCT as in wheat leaf wax, while it is absent in WCT x COD and COD x WCT. All the three genotypes showed one additional band with Rf value 0.52, which is absent in wheat.

Sixth leaf

In the 6th leaf position the ECW components during pre-stress period showed one band with Rf value 0.94 in all



Thinlayer chromatography of ECW from the 1st Leaf of three coconut genotypes (Plate - 1)



Thin layer chromatography of E C W from the 6th Leaf of three coconut genotypes

(Plate - 2)

the three genotypes (which is present in wheat leaf wax), while COD x WCT had one additional band having Rf value of 0.49 which is absent in WCT and WCT x COD. WCT, COD x WCT and WCT x COD had two additional bands with Rf value 0.76 and 0.52 and COD x WCT had one more band with Rf value 0.73 which are not present in wheat leaf wax.

Under stress condition all the three genotypes had three bands with Rf value 0.94, 0.86 and 0.49 which are present in wheat leaf wax. All the genotypes showed three additional bands with Rf value 0.76, 0.73 and 0.52 but WCT and COD x WCT had one more band with Rf value of 0.83 which is not identifiable in wheat leaf wax. During post-stress all the genotypes showed two bands having Rf value 0.94 and 0.49 which are present in wheat leaf wax. All the genotypes had a band with a Rf value 0.52. WCT had one extra unidentified band having Rf value of 0.76 which was absent in the hybrids.

4.5. <u>Membrane stability</u> (Tables 5, 6, 7 and 8)

The degree of membrane stability to heat stress is evaluated by electrolyte leakage (which is expressed as percentage on initial value.

Electrolyte leakage showed differences among the genotypes and with the leaf positions. WCT had electrolyte leakage ranging from 197.9% to 260% among the leaf positions. In the case of WCT x COD also almost a similar range existed. However, in COD x WCT the electrolyte leakage was relatively high in all the leaf positions, the 6th leaf showing the maximum (414.5%). When electrolyte leakage in different leaf positions was compared, it was found that the first leaf of WCT x COD had relatively low electrolyte leakage as compared to that of WCT and COD x WCT, which were almost on par. While the electrolyte leakage of the 6th leaf position showed little difference between WCT and WCT x COD, the hybrid COD x WCT recorded the maximum. A similar trend occurred in the case of 20th leaf. The 14th leaf had almost same electrolyte leakage in the hybrids, while it was less in WCT.

The statistical analysis revealed that electrolyte leakage is not significant between the leaf position as well as among the genotypes.

Potassium leakage (K^+)

Due to heat stress K^+ leakage has increased.

Potassium leakage showed differences among the genotypes and with the leaf positions. It is expressed as percentage on initial value. Considering all the leaf positions WCT x COD showed less leakage than that in COD x WCT and WCT. In the case of 1st leaf K^+ leakage of WCT and COD x WCT was almost similar but WCT x COD showed less leakage. COD x WCT and higher K^+ leakage (319.8%) than WCT (272.2%) and WCT x COD (225.3%) in the 6th leaf. In 14th and 20th leaf positions WCT and COD x WCT showed almost similar K^+ leakage but WCT x COD showed very less leakage.

The statistical analysis revealed that there is a significantly higher (91.08*) leakage in WCT and COD x WCT than WCT x COD, but there is no significant difference between the leaf positions.

Phenols

Due to heat stress the concentration of phenol content increased. It is expressed as percentage increase over the initial value. The concentration of phenols showed differences among the leaf positions and genotypes WCT had the phenol concentration ranging from 211% to

319% among the leaf positions. In the case of COD x WCT also almost a similar range existed. However WCT x COD had relatively less concentration of phenols in all leaf positions. When the concentration of phenol was compared among the leaf positions the first leaf of WCT and COD x WCT showed almost similar value, but WCT x COD showed relatively less value. In the case of 6th leaf WCT showed higher concentration (235%) than the COD x WCT (193.1%) and WCT x COD (140.2%). WCT and COD x WCT showed almost similar concentration of phenols in 14th and 20th leaf but WCT x COD showed less percentage.

The statistical analysis revealed that the concentration of phenol is significantly higher (0.33*) in WCT and COD x WCT than WCT x COD, but there is no significant difference among leaf positions.

Table 5 Electrolyte leakage/micromohs/cm

Leaf position	WCT			CODxWCT			WCTxCOD		
	Initial value	Final value	% increase	Initial value	Final value	% increase	Initial value	Final value	% increase
1	40.8	141.12	245.9	37.44	134.4	258.9	42.24	126.24	198.9
6	42.24	141.12	234.1	29.76	153.12	414.5	42.24	132.36	213.3
14	45.12	134.4	197.9	34.08	121.44	256.34	34.08	117.12	243.6
20	36	129.6	260	30.72	126.72	312	29.9	107.52	259.6

45

Table 6 Potassium leakage

Leaf position	W C T			C O D x W C T			W C T x C O D		
	Initial value	Final value	% increase	Initial value	Final value	% increase	Initial value	Final value	% increase
1	8.33	32.5	290.15	7.5	31	313.33	8.67	27	211.42
6	8.33	31	272.15	6.83	28.67	319.77	9.17	29.83	225.3
14	7.33	25	241.06	6.0	23.5	291.67	7.5	21.17	182.27
20	5.33	24.66	362.66	5.33	23.83	347.09	4.17	16.67	299.77

Table 7 Phenol Content

Leaf Position	W C T			C O D x W C T			W C T x C O D		
	Initial value	Final value	% increase	Initial value	Final value	% increase	Initial value	Final value	% increase
1	0.263	1.102	319.01	0.275	1.121	307.64	0.364	1.149	215.66
6	0.414	1.389	235.5	0.48	1.407	193.13	0.575	1.381	140.17
14	0.578	1.799	211.25	0.58	1.914	230	0.546	1.547	183.33
20	0.6	2.111	251.83	0.583	1.954	235.16	0.632	1.576	149.37

Table 8 Analysis of Covariance of Electrolyte leakage, Potassiaum leakage and Phenol

Source of variation	Df	M.S.S.		
		Electro-lyte lea-kage	Potassium leakage	Phenol
Varieties V	2	869.44	91.08*	0.33*
Position P	3	557.36	41.62	0.04
V x P	6	230.31	1.72	0.03
Error	21	286.34	21.47	0.08

DISCUSSION

5. Discussion

During the experimental period extending from October 1987 to August 1988, there existed three distinct phases as highlighted by agroclimatic conditions. The first phase between October and December was characterised by mean ambient temperature of 32.9°C with RH between 86-61% and radiation of 900-1135 $Em^{-2}s^{-1}$ (Table 1). As there was a total rainfall of 100.5 mm during this period there was no soil stress, although a mild atmospheric stress, was indicated, as also exemplified by the pan evaporation rate of 3.73 mm/day. With increasing temperature and light intensity and concomitant decrease in relative humidity, the next phase between January and May represented high evaporative demand leading to atmospheric drought, accentuated by soil drought as indicated by pan evaporation rate of 5.5 mm/day. This was followed by a drastic change in weather variables typical of south west monsoon with low temperature, low light intensity and high relative humidity with a total rainfall of 553.4 mm. This constituted the third phase. Thus based on the weather variables and soil factors, the above three phases could be distingushed as pre-stress, stress and post-stress. The response of three popularly cultivated coconut genotypes namely WCT, COD x WCT and WCT x COD to the prevailing moisture stress under field conditions was assessed using the sensitive physiological parameters like leaf water potential, epicuticular wax content and membrane leakage. Hsiao (1973) and Raschke (1975) reviewed the influence of weather parameters on stomatal regulation in many crops. Recently Kasturibai *et al.* (1988) found the relationship between the light, temperature and vapour pressure deficit on the stomatal resistance in coconut. According to them the stomatal closure sets when coconut palm is exposed to irradiance of 265 Wm^{-2} temperature of 33°C and vapour pressure deficit of 26 m bar. These correspond to the situation that existed during stress period in the present study.

As the first step towards understanding the genotypic variations, the soil moisture depletion pattern was determined in the three genotypes. The genotypes differed in the soil moisture extraction not only between different stages but also different root depths (Figure-1).

It was found from the data WCT by and large has better extraction than the hybrids. This is in agreement with the earlier observations, wherein the drought tolerant genotype like WCT was shown to have higher water uptake than the drought susceptible genotype like COD x WCT (Rajagopal et al, 1988 b). These three genotypes also differed in their soil water uptake depending on the soil types ie, sandyloam or laterite, where they were cultivated (Voleti et al., 1989). The soil water characteristics of red sandy loam soil was described by Haridasan (1978) and Joshy (1986).

The differential extraction of soil moisture from the root zones of the three genotypes reflect on their rooting pattern and soil moisture extractability. From figure 1 it is evident that during stress period WCT had better extraction of soil moisture from the deeper layers than the hybrids. It is interesting to note that the hybrids particularly CODx WCT tends to extract more water from the sub-soil layers. This perhaps might be the reason for its being sensitive to water deficit under field conditions. However the above situations occured under sandy loam soil, whereas the same hybrid under laterite soil exhibited a different type of soil water extraction reflecting obviously on better rooting behaviour. During post-stress period the soil moisture content showed little variation among the genotypes.

The impact of both the climatic factors and the soil moisture pattern on the plant stress parameters in three genotypes were examined. The relationship between the chanes in soil water potential and plant response is well established in different crops (Slatyer 1967, Turner 1974, Blum 1974 a). In the present study leaf water potential changes were determined in different leaf positions of three genotypes at different stages. Varied among the genotypes depending upon the leaf position, in that the first leaf had higher ψ than the 6th leaf irrespective of the stages. WCT had higher ψ in both first and 6th leaf than the hybrids under non-stress conditions. Even when subjected to moisture stress WCT maintained higher ψ than the hybrids. When the performance of different leaf positions was compared, it was found from the slope of the curve (Fig-2) that the percentage decrease in ψ was high in the 6th leaf of WCT and WCT x COD, while in COD x WCT, this occured in the first leaf. Earlier studies also indicated that the ψ was lower in COD x WCT than either WCT or WCT x COD under field conditions (Rajagopal *et al.* 1989 b). The relationship between leaf age and position to changes in ψ was shown in different crops (Jones 1977, Aggarwal and Sinha, 1984, Giuliyo, 1979; Lasko, 1984). The rapid screening test using the changes during period of dehydration of spindle leaf also indicated that COD x WCT undergoes greater degree of stress than the other two genotypes. (Rajagopal *et al.*, 1988 a). Thus the leaf water potential changes indicate the degree of tolerance to moisture stress in coconut, as it has been used in many other plant species (Slavik 1974, Turber 1974, Blum 1974, Balasimha 1988). In many crops the ψ was lower in rainfed conditions than in irrigated ones (Fereres *et al.* 1978, Carlson *et al.* 1979, Jones 1977). Rajagopal *et al.* (1987) also observed higher ψ in spindle leaves than in the middle or outer leaves of coconut palms, irrespective of the healthy or root (wilt) disease.

With the onset of monsoon ie, the third phase the three genotypes exhibited differential capacity for revival from the stress, as indicated by the ψ . When expressed as percentage recovery over stress period, the first leaf of

WCT and COD x WCT recovered bettwer than WCT x COD, while in the case of 6th leaf WCT x COD recovered better than the other two. It is found that the leaf which has undergone greater degree of stress tended to recover better. Seasonal and daily fluctuations in ψ has been reported in coconut genotypes (unpublished).

As in the case of ψ , ECW also showed differences in the leaf positions among the three genotypes in different stages. During non-stress conditions the 1st leaf had higher ECW than the 6th leaf irrespective of the genotypes and it either maintained same level or decreased during the subsequent stages. A steep increase in ECW was noticed in all the three genotypes, to different degrees from the pre-stress to the stress period (Fig.3). This was followed by drastic decline in ECW during the the post-stress period. In general WCT and WCT x COD had higher ECW than COD x WCT, which is in agreement with the earlier observations (Rajagopal et al., 1989 b). The formation of epicuticular wax layer on the leaf surface is an adaptive mechanism to withstand water deficits in many plants (Hall and Jones, 1961; Baker, 1974). The ECW was shewn to exihibit genotypic variation in sorghum (Ebercon et al., 1977), Oat (Bengston et al., 1978) Cacao (Balasimha et al., 1985) and coconut (Rajagopal et al., 1989 b). As an important component in reducing transpirational loss of water, deposition of wax on the leaf surface correlated with drought resistance in the above crops. An increase in ECW on leaves of drought affected soybeans accompanied by a reduction in transpiration was reported by Clark and Levitt, (1956). A clear negative relationship between ECW content and transpiration rate was shown recently in coconut genotypes including COD x WCT in which lower ECW correlated with relatively high transpiration rate (Rajagopal et al., 1988 b).

The factors such as low relative humidity, high radiation and high temperature have been shown to enchance wax accumulation in different plant species (Wilkinson and Kasperbauner, 1980). This is supported in the present study where the wax accumulation was associated with the prevailing weather variables with high temperature and radiation during the stress period. That the wax content is reduced during the rainy period is indicated in the present study during post-stress period, which is in support of the earlier reports in Brassica and Isocoma leaves (Baker,1974; Mayeux and Jordan, 1987; Wilkinson *et al*. 1987). Variation in ECW of different leaf positions has also been reported in different plant species (Tulloch, 1973; Mayeux and Jordan, 1987, Baker and Greyson, 1988), including coconut (unpublished).

There was also a qualitative difference in the components of ECW among the genotypes during the three periods (Plates e, 2). In general the number of components of ECW was more in both the leaf positions of all the three genotypes during the stress period than either of the two stages. The ECW content of coconut genotypes was compared with ... wheat duram wax. The major components namely hydrocarbons (Rf 0.94) and esters (0.86) were detected in all the three genotypes with varying intensities during different stages. The alcohols (Rf 0.49) could be identified in all the three genotypes only during the stress period, while acids (Rf 0.31) only during the post-stress period. The esters were separated into two bands in case of WCT, COD x WCT while in WCT x COD only one band of ester were observed during stress period. Similarly during post-stress period acids were observed in WCT and WCT x COD, while it was absent in COD x WCT. Although some qualitative differences in ECW existed among the genotypes, it is premature to attribute any significant role related to drought tolerance. The relationship between the quality of ECW and cuticular transpiration was reported in large number of species (Ramadas *et al.*, 1979). In oat, primary alcohols increased during drought (Bengston *et al.*, 1978) while in other species aldehyde components and fattyacid increased during summer season (Rao and Reddy, 1980). A new class of wax components such as β-dikeones, secondary alcohols and aldehydes were detected in monsoon season of some semi-arid shrubs (Rao and Reddy, 1980). Gururaja Rao *et al.* (1981) reported qualitative changes in the wax composition of groundnut varieties under salinity stress.

The stability of membrane was affected to different degrees in the three genotypes. The samples for the study was collected only during the stress period. The degree of membrane stability was expressed in terms of electrolyte leakage, potassium content and phenol content. In general COD x WCT had higher electrolyte leakage, potassium content and phenol content with differences between the first and 6th leaf position than either WCT or WCT x COD. This means that the damage caused to the membranes is higher in COD x WCT than the other two genotypes. Sullivan (1979), Gaziani and Livine. (1971), Gupta (1977), Leopold (1981) and Blum and Ebercon (1981) reported the degree of membrane stability to stress in different species based on the electrolyte leakage. An increase in membrane stability in drought tolerant plants like Cerateroestigma as against lesser stability in drought sensitive spinacia oleracea was reported by Schwab and Heber, (1984). Bansal and Nagarajan, (1983) also reported the decrease in cellular membrane in drought susceptible potatoe. That the membrane stability differs depending on the leaf age is evident from the present study, which is in agreement with earlier reports on different crops (Martineau, 1979; Leopold, 1981; Blum and Ebercon, 1981).

From the foregoing account it is evident that the extensively cultivated WCT palms are less affected by moisture stress than the hybrids, particularly COD x WCT. This drought tolerant nature of WCT was also confirmed through the stomatal regulation (Rajagopal et al; 1989 b). In their extensive studies the authors have screened 23 coconut genotypes for drought tolerance and identified about 10 genotypes including WCT and WCT x COD with desirable traits to withstand drought. In the case of COD x WCT there was high rate of transpiration (i.e. low stomatal resistance) under stress condition, thus leading to imbalance in the water economy. Biochemical studies involving the stability of activities of certain important enzymes like nitrate reductase, acid phosphatase also revealed the drought susceptible nature of COD x WCT (un published). Thus the present investigations contributed to an understanding of the impact of moisture stress in the commonly growing coconut genotypes.

SUMMARY AND CONCLUSIONS

6. SUMMARY AND CONCLUSIONS

The effect of moisture stress on three widely cultivated genotypes namely WCT, WCT x COD and COD x WCT was studied. The experiment mainly consisted of seasonal variations in the agrometeorological parameters and soil moisture content. Based on these variations, three distinct stages namely pre-stress (October to December), stress (January to May) and post-stress (June to August) could be identified to study the response of coconut palms. Sensitive physiological parameters of moisture stress like leaf water potential, epicuticular wax content and membrane stability were determined at three stages in the three genotypes. The degree of stress was quantified in terms of weather variables like light, temperature and relative humidity and soil factors like moisture content and pan evaporation.

While there was no significant differences among the genotypes in the physiological parameters like leaf water potential, ECW or membrane stability either at pre-or post-stress periods, there existed considerable difference among the genotypes during the stress period. There was high evaporative demand during January and May exemplified by weather variables and soil moisture content. The genotypes responded differently to this soil and atmospheric drought conditions. In general, the hybrid COD x WCT was sensitive to moisture stress, as indicated by low leaf water potential, low content of ECW and high electrolyte leakage (i.e., low membrane stability), as compared to WCT and WCT x COD.

From the data collected in the present investigation the main conclusion that could be drawn was that the tall genotype WCT and the hybrid with tall as female parent i.e. WCT x COD are relatively more tolerant to moisture stress than the hybrid COD x WCT.

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