CHAPTER 13

COCOA

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ABSTRACT

Among plantation crops, in cocoa (Theobroma cacao L.), the physiology is studied extensively. The vegetative and reproductive growth of cocoa is influenced by a complexity of environmental factors, particularly rainfall, temperature and wind. The plants are shade tolerant and are generally grown under shade of taller trees. The removal of shade does enhance the yields in initial years of productivity, but will result in deleterious effects in subsequent years. Cocoa is a very sensitive plantation crop to drought. Water stress affects the most important physiological determinants of yield - canopy architecture, photosynthetic production, and partitioning of assimilates between source and sink - are influenced by water stress. Regulation of stomatal closure, high leaf elasticity, maintenance of leaf turgor, higher cuticular wax content and better metabolic activity under stress are among the drought tolerant attributes of some cocoa accessions. The average annual yields in farmers' fields are far below the potential yields. An integration of better agronomic practices to suit environmental factors, physiological determinants and genetical potential is required, to improve further the yields of cocoa.

INTRODUCTION

Cocoa (Theobroma cacao L.; family Sterculiaceae) is indigenous to South America. The plant was cultivated more than 3000 years ago by the Mayas, Toltecs and Aztecs. Cocoa thus has one of the oldest histories among crops cultivated by man. It was only during seventeenth and eighteenth centuries that the cocoa tree was introduced to many other sub-tropical countries. It was introduced to Southern India during the present century

mainly as an intercrop of coconut and arecanut gardens. The physiology of cocoa tree has been studied in greater detail than many other plantation crops. This has facilitated a better understanding of the basic physiological processes which determine growth and productivity of the crop.

AGROMETEOROLOGY

The cocoa tree needs a high and well distributed rainfall, possibly with a short dry spell to stimulate flowering. The climatic conditions suited for cocoa cultivation were found to be under palms in Southern India (Lass and Wood, 1971; Bhat and Bavappa, 1972). The climatic conditions are different in these regions; with well distributed rainfall in Southern Kerala compared with long dry spells during summer months in Northern Kerala and coastal Karnataka. The drought intensity is more pronounced in northern regions of Kerala and coastal Karnataka extending up to 5-6 months subjecting plants to severe stress especially when they are grown as intercrop in rainfed coconut gardens. However, the situation is slightly better in arecanut gardens which are irrigated. But nonavailability of water towards end of summer exposes the plants to stress. Two dissimilar crop patterns are observed under rainfed and irrigated conditions (Alvim, 1976; Subramonian, unpublished).

The climatic conditions in West African countries are similar to those prevailing in Southern India with two main rainy periods viz. March to July and September to December (Asomaning, 1976). In marked contrast to this, the rainfall in Brazil is very well distributed throughout the year. This difference in climate accounts for a bimodal crop pattern in Brazil in contrast to that of single main crop in Africa (Alvim, 1976). The sustained water supply obviously helps in continuous flowering and fruiting throughout the year. Rainfall is also well distributed in other Latin American countries, Malaysia and Sri Lanka. High correlations between rainfall and yield have been reported (Gordon, 1976). Other climatic factors such as temperature, light intensity and day length normally are not limiting factors for cocoa yields except in Brazil which experiences nearly four months of low temperature during winter (Alvim, 1976).

Wind is an important yield determining factor, the duration and intensity

of which vary in different cocoa producing areas. Wind has adverse effects on cocoa, by causing premature leaf fall. In Brazil, some parts of Ghana and Nigeria, cocoa yields are reduced by wind (Alvim, 1977). The synergistic effects of wind and solar radiation cause severe mechanical injury at the pulvinus region (Alvim et al., 1978; Leite et al., 1980). The results suggest that shade trees would provide protection against exposure to solar radiation and serve as well as wind-breaks.

Detailed discussion on soils suitable for cocoa cultivation is beyond the scope of this article, but excellent reviews are available on the subject (Alvim, 1977; Hardy, 1971; Smyth, 1975). For unrestricted growth, soil should be deep, with good moisture retention capacity, well drained and aerated.

SEEDLING GROWTH

The early vigorous growth of seedlings is very important for better establishment and higher yield potential at maturity. There is definite advantage to seedling growth due to seed weight but this disappears with age (Ascenso and Bartley, 1966; Ravindran, 1981). Although quantitative relationships between seedling vigour and yield of trees have not been fully established, it is known that less vigorous seedlings are late bearers and tend to be unproductive (Glendinning, 1960).

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 (Hutcheon, 1978). The seedling vigour or root/shoot ratios were not correlated with drought resistance (Hutcheon, 1984). Management practices to prevent seedling deaths after field planting are available. For example, antitranspirants can reduce the transplant shock during such field planting of seedlings from nursery. Folicote increased stomatal resistance considerably, without directly affecting physiological processes (Hutcheon, 1984). Another antitranspirant 'mobileaf' also reduced transpiration rates in 6-month old seeddlings which suits the time of transplanting (Lima Filho and Alvim, 1978). The application of cycocel and abscisic acid also imparted tolerance under drought in seedlings as shown by growth and metabolic amelioration (Balasimha, 1983a; Balasimha and Subramonian,

1984). The maintenance of better growth, leaf turgidity and metabolic activities was reported in cocoa seedlings under drought when treated with potassium or proline (Balasimha et al., 1984a). These management practices not only help to tide over drought conditions initially but will result in better seedling establishment and yield at maturity.

VEGETATIVE GROWTH

Root growth and function

Cocoa trees possess a strong taproot system extending up to 1.0 - 1.5 m depending on soil conditions. The laterals are mainly horizontal and concentrated to upper 30 cm of soil. When plants are raised from cuttings, 2-3 main roots develop and the root distribution is restricted to the soil surface layer. Major portion of nutrient uptake is accounted for by the fine roots of cocoa as the roots of 1-3 mm diameter are often suberized.

The growth of cocoa tree is characterized by 'flush cycles'. A rhythmic root growth in cocoa was first reported by Vogel (1975). The phase of high root activity (Fig. 1) was associated with low leaf growth and vice

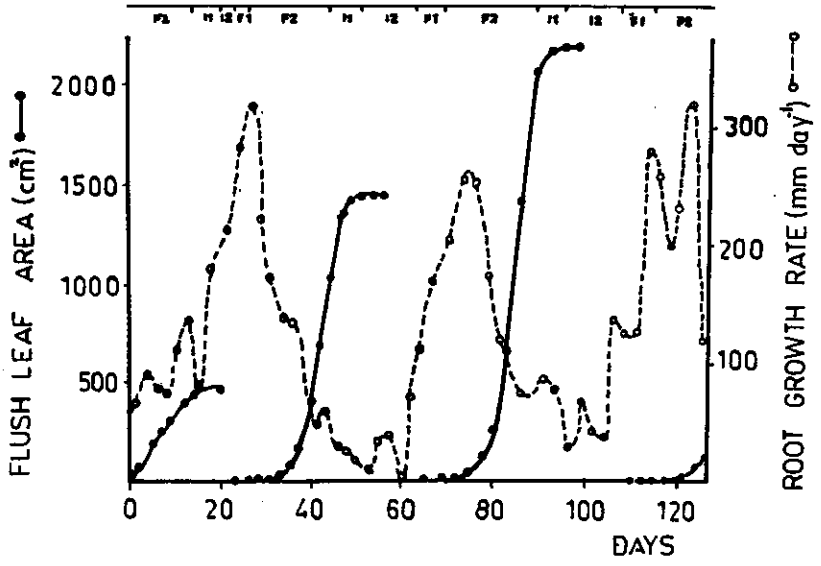

Fig. 1. The root growth during the development of flushes in cocoa plant (Kummerow et al., 1982).

TABLE 1

Mean crop growth rates (dry weight) and canopy development (Balasimha, unpublished).

Months	Dry matter (g month^{-1})			Total dry matter (g plant^{-1})	Canopy area (m^2 plant^{-1})	Girth at collar (cm)
	Stem	Leaf	Root			
1	0.1	0.3	0.1	0.6	0.04	1.3
2	0.7	1.3	0.3	2.8	0.19	2.0
5	0.4	0.4	0.4	6.5	0.18	-
13	1.8	2.1	1.1	46.6	0.37	5.2
18	8.1	1.4	1.8	103.4	0.71	7.9
21	25.7	29.9	2.2	276.8	1.17	10.3
27	29.3	16.6	8.4	602.3	2.05	13.2
33	54.9	43.7	10.6	1257.7	4.74	16.4
40	366.8	129.3	92.4	5378.0	9.28	29.0
50	426.2	206.9	14.0	11850.3	16.78	34.7

versa (Hardwick et al., 1982; Kummerow et al., 1982). The developing shoots function as stronger carbohydrate sinks during rapid leaf expansion periods (Hardwick et al., 1982). It is still not clear whether this is a major phenomenon or growth inhibitors are also involved, as ABA level is shown to be high during this phase (Orchard et al., 1980). Soil moisture, carbohydrate availability and changes in ABA levels seem to interact in the regulation of root and shoot growth. This biphasic episodic growth follows the theory of Borchert (1973) that flushing is a consequence of interaction between shoot and root growth, where the absolute rate of one exceeds the other.

Canopy development and dry matter accumulation

Studies on canopy development and growth rates in cocoa seedlings indicated some genetic differences (Alvim, 1977; Hutcheon, 1984). Alvim and Grangier (1966) reported a higher leaf growth rate and relative growth rate (RGR) in more productive cultivars than unproductive ones, but no difference was noted in net assimilation rate (NAR). The canopy and growth

behaviour of cocoa up to 4 years of age are summarized in Table 1. The increase in mean growth rate (on dry weight basis) was slow during the first year, but faster from second year onwards. Increase in canopy area was also similar. This is expected because the seedling development is dependent on cotyledon reserves for about two months (Hutcheon, 1984). Also there is shock due to transplantation usually done at 3-6 months age, and seedlings take some time for establishment. The trunk diameter increases gradually in accordance with dry matter acumulation. Yields of cocoa varieties were correlated with rate of increase in trunk diameter during prebearing phase (Glendinning, 1966).

Partioning of dry matter is affected by environmental variables, especially rainfall. Variations in bearing of trees from year to year can be explained from the moisture availability of successive years (Glendinning, 1966; Hutcheon, 1978). Seasonal changes in the stem diameter are useful indicators of internal stress (Hutcheon, 1977).

The relationship between canopy structure, leaf area index (LAI) and light interception is illustrated in Fig. 2. Estimates of leaf area index ranged between 3.7 to 5.7 in Brazil (Alvim, 1967) and 1.5 and 6 in Ghana (Hutcheon, 1976a). Though no quantitative information is available on relationships between canopy, LAI and yield, a good canopy in the range of 4 to 6 LAI is expected to give high yield (Alvim, 1977). Canopy architecture showed varietal differences and cultivars adopted for higher radiation levels did not perform well under dense shade conditions (Hadfield, 1981).

Flushing rhythm and leaf growth

Cocoa, like some tropical trees, shows a rhythmic growth of leaf called 'flushing' and a flowering periodicity. The phenomena can be described as seasonal as they are repeated at about the same time of the year, varying according to the region. In Brazil, the main flush occurs in September-October followed by two or three minor flushes (Alvim et al., 1974a). Flushing has two characteristic peaks with major peak in January-February and minor one in April-June in Ghana (Hutcheon, 1977; Owusu et al., 1978). In India, two major peaks occur during January-February and September-November (Balasimha et al., 1984b).

The flushing behaviour is controlled by internal factors as well as

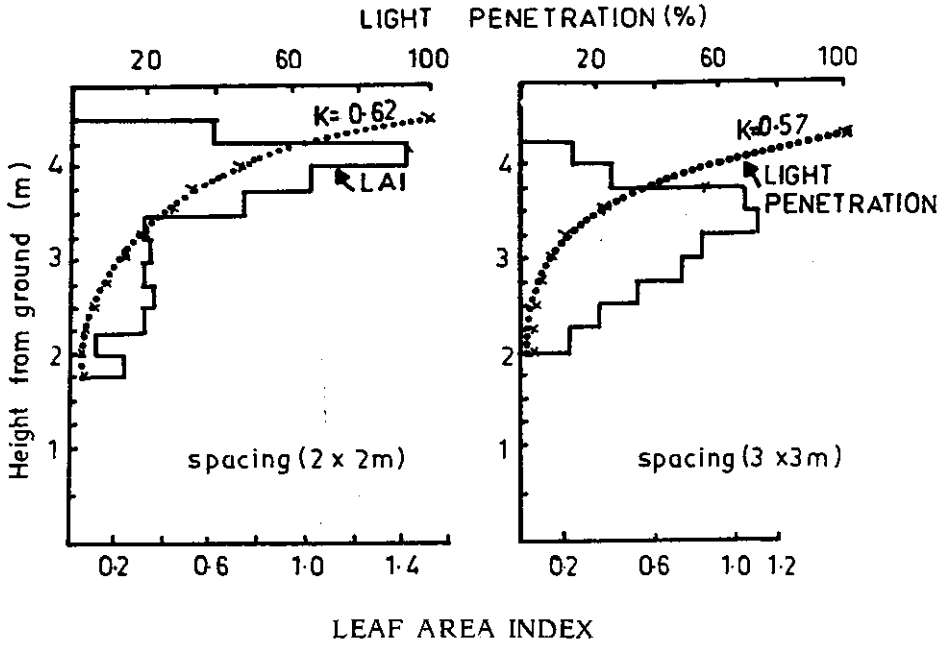

Fig. 2. Leaf area and light penetration through the canopy of 8-year old cocoa trees (Alvim, 1977).

external environmental conditions. Studies have indicated that flushing is correlated with soil moisture and atmospheric relative humidity (Alvim, 1967; Lemee, 1955; Machado and Alvim, 1981) and that flushing, leaf fall, stem diameter changes were interrelated (Alvim, 1967, 1975; Boyer, 1974). Flushing is inhibited by water stress (Hutcheon, 1977) and is stimulated after rewatering. The role of temperature in control of flushing appears to be limited (Greenwood and Posnette, 1950; Humphries, 1944; Sale, 1968). Removal of shade results in a more intensive flushing and this may be because of better photosynthesis and sugar availability (Alvim et al., 1974a; Owusu et al., 1978). This aspect will be discussed in greater detail in the next section.

The most significant endogenous factor that controls flush growth is the level of growth hormones, notably abscisic acid (ABA). Alvim et al. (1974b) reported that ABA levels declined with initiation of flushing. In

the young expanding leaves of cocoa, the level of ABA was very low but increased gradually with maturity resulting in bud dormancy (Abo-Hamed et al., 1981; Orchard et al., 1980). Moisture stress, which is one of the important environmental factors controlling the plant growth, results in accumulation of ABA and can thus cause bud dormancy (Alvim et al., 1974b; Sale, 1970). In marked contrast to ABA levels, cytokinin and auxin levels were high during leaf expansion and declined as leaves matured (Abo-Hamed et al., 1984; Orchard et al., 1981). The leaf expansion is completed by about 20 days (Fig. 3). The leaf elongation rates varied among accessions of cocoa under irrigated and stress conditions, but was not related per se to drought tolerance (Balasimha, 1984). The young expanding leaf has high demand for carbohydrates. The expansion of leaf is not accompanied by either increased chlorophyll (Baker and Hardwick, 1973) or photosynthetic activity (Bird and Hardwick,

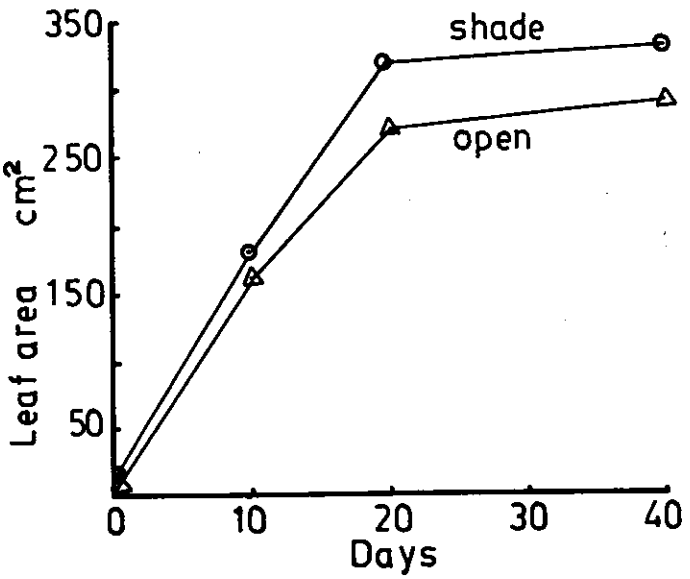

Fig. 3. The leaf area development in cocoa under open and shade conditions (Balasimha, unpublished).

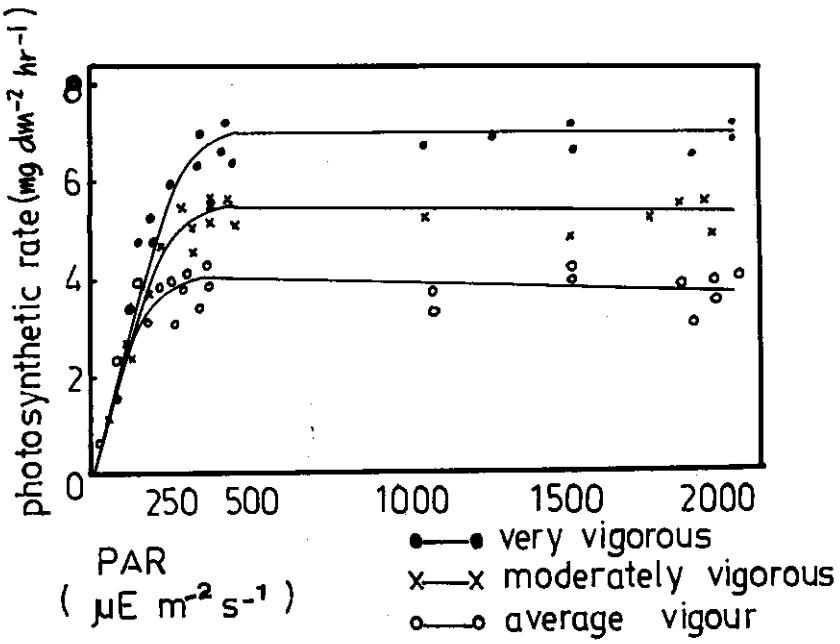

Fig. 4. The light response curve of cocoa leaves (Hutcheon, 1976c).

1982) resulting in a carbohydrate stress to the plant. The young leaves, having not attained their complete photosynthetic ability, are mostly dependent on translocation of assimilates from mature leaves (Baker and Hardwick, 1975; Sleigh et al., 1981). This may partly explain the intermittent leaf growth.

PHOTOSYNTHESIS

Photosynthetic efficiency is a primary determinant of cocoa productivity. The primary photosynthesis can be estimated by the techniques of growth analysis, or by determining the photosynthetic rates of seedlings or individual leaves and ascertaining the canopy structure.

Cocoa has a relatively low NAR (Alvim and Grangier, 1966; Goodall, 1950; Murray, 1953) which ranges from 5 to 20 mg dm^{-2} day^{-1}. However NAR is reported to increase with light intensity upto certain level (Lemee, 1953). Measurements of photosynthetic rates have been conducted by

Baker and Hardwick (1973, 1976), Baker et al. (1975), Hutcheon (1976b) and Okali and Owusu (1975). The following conclusions can be drawn: a high photosynthetic rate is associated with thick leaves or high specific leaf weight (SLW) which is characteristic of vigorous trees. This was also shown by a positive relationship between high yield and high SLW (Balasimha et al., 1985a). The light response curve (Fig. 4) varies with the type of tree growth reaching a saturation point at PAR of about 400 $\mu E\ m^{-2}\ s^{-1}$ (Hutcheon, 1976c).

Cocoa has an unusual development of photosynthetic apparatus. The photosynthetic units viz., chlorophylls, carotenoids, and enzymes do not develop until after the termination of leaf expansion (Baker and Hardwick, 1973, 1976; Baker et al., 1975). With the development of chloroplast lamellae and chlorophyll synthesis, the level of ribulose bisphosphate carboxylase activity and the photosynthetic rate increase. As a result of such pattern in photosynthetic machinery, the soluble sugar concentrations rises only after leaf expansion is complete (Baker and Hardwick, 1975).

A simulation model was used to investigate the potential photosynthetic productivity of cocoa (Ng, 1982). Shade LAI had considerable effect on photosynthesis, the rates declining by 25% and 50% with shade canopy LAI of 0.5 and 1.0 respectively. The productivity of vigorous trees was 7-16% greater than that of a moderately vigorous tree.

Cocoa is relatively tolerant to shade. This is shown by studies on light compensation points and by responses in NAR (Alvim, 1967, 1977) and photosynthetic rates (Guers, 1985) to varying light regimes. Cocoa adapts to shade by modifications in leaf thickness and higher chlorophyll contents (Table 2). The plants grown under light limiting conditions always recorded higher chlorophyll contents on weight/area basis demonstrating more energy investment in the production of light-harvesting system. The nitrate reductase (NR) activity, however, was not affected in shade and open conditions showing that light is not limiting for this key enzyme of nitrate assimilation. However, the response to fertilizers varied with light intensity (Ahenkorah et al., 1974; Cunningham and Arnold, 1962). More light was required to saturate photosynthesis as the leaf nutrient

TABLE 2

Variations in some leaf characteristics with season or shade/open conditions (Balasimha, unpublished).

	Specific leaf weight mg cm^{-2}	Chlorophyll content mg g (fresh wt)$^{-1}$	NR activity nmoles g(fresh wt)$^{-1}$ h^{-1}
SEASON (months)			
January	7.15	1.14	431
April	7.08	1.49	273
June	5.81	1.23	241
September	5.32	1.24	258
December	5.36	1.67	212
C.D.	0.73	0.25	88
GROWTH CONDITION			
Shade	5.49	1.58	290
Open	6.34	1.13	276
C.D.	0.64	0.16	NS*

*Not significant.

status increased (Hutcheon, 1976b). The initial increase in yield with removal of shade is always followed by a subsequent marked decline. Hence for optimal growth, photosynthesis and yield of cocoa trees, shade is advantageous which helps in preventing unfavourable ecological factors like low soil fertility, wind damage, evapotranspiration and water stress.

REPRODUCTIVE GROWTH

Flowering

Cocoa flowering is cauliflorous, giving the impression that the flowers originate directly from bark of the plant. The structure, biology and factors affecting flowering have been reviewed by Alvim (1984). The flowering cycle follows a seasonal pattern. In India, flowering occurs from November to April with a peak in January-February. The peak flowering in Brazil also is similar to this pattern (Alvim, 1967) while in

Ghana two peaks are recorded in January-February and April-June (Owusu et al., 1978). In Costa Rica, flowering peaks varied at different locations studied, which coincided with the beginning of rainy season (Young, 1984). Apart from rainfall, solar radiation is another major factor in influencing flowering. Removal of shade results in an increase in flower production and pod yield (Hurd and Cunningham, 1961). A clear relationship between sugar levels and solar radiation could be established (Owusu et al., 1978) indicating that light is limiting factor in shaded cocoa plants for photosynthesis. Depletions in sugar content coincided with peak reproductive growth (Owusu et al., 1978; Balasimha et al., 1984b). The stem girdling experiments have also confirmed the relationship between photosynthate supply and flowering (Alvim, 1984).

Water stress generally inhibits flowering (Alvim, 1964; Hutcheon, 1977; Sale, 1970). Rains after a long dry period resulted in profuse flowering called 'crazy' flowering (Alvim, 1967; Hutcheon, 1977). In Brazil, decrease in flowering also resulted from low temperatures during winter months (Alvim, 1967). There was also an internal competition for flowering especially when growing fruits were present (Hutcheon et al., 1972). From the data so far available, it appears that 'hydroperiodicity' of the environment and internal competition between fruits and flowers for assimilate supply are two basic factors which control flowering.

Fruit development

The fruits or pods of cocoa take about 5 months on an average for full development, the pod growth following a sigmoid curve. Generally the early sets of the season survive well compared to late ones (Hutcheon, 1977; Uthaiah and Sulladmath, 1985). The rate of dry matter accumulation is slow initially but attains a peak at about 100 days with around 3 g day^{-1} pod^{-1}. The fall in survival rate in fruits which are set late may be because of internal competition for assimilates. Temperature also influenced fruit growth, the fruits grow faster in warmer months (Alvim, 1967). The pod load on the tree is related to the flowering intensity earlier in the seaosn. The flowering is generally suppressed when there is high pod load on the tree (Balasimha et al., 1984b). Water stress not only reduced crop yields, but also significantly reduced the pod value

(Subramonian and Balasimha, 1981). Fruits, which developed under a condition of inadequate water availability, had lower pod-value factors.

Cocoa yields vary with different geographical locations, cultural practices and planting material. The mean annual yields vary from 300 to 500kg dry bean ha^{-1} in farmers plots to as high as 2000 kg ha^{-1} in experimental farms (Alvim, 1977). The record annual yield of 3700 kg ha^{-1} reported by Ahenkorah et al. (1974) may be considered as nearing the maximum potential yield of presently known cultivars. Spacing is equally important and it has been shown that annual yields can be as high as 2000 kg ha^{-1} when planted at 2.7 x 2.7 m spacing under arecanuts which is almost double of 5.4 x 5.4 m spacing, used for open planting. However, individual tree yields are better with wider spacing (Bhat, 1985).

Cherelle wilt

The young pods of cocoa senesce prematurely, the phenomenon commonly known as 'cherelle wilt', resulting in considerable yield losses. Cherelle wilt is caused by blotic factors like fungi and insects (Chandramohanan and Kaveriappa, 1983; Thorold, 1975) as well as physiological factors (Nichols, 1964). Several hypotheses are advanced to explain the physiological cherelle wilt. It was first suggested that this may be caused by low auxin levels (Nichols, 1965). A recent report suggests that abscisic acid like substance may be promoting cherelle wilt of cocoa pods (Uthaiah and Sulladmath, 1986). However, the external application of various growth regulators has not been completely useful (Murray, 1952; Naundorf and Gardner, 1950; Naundorf and Villamil, 1950). One of the reasons for this may be the poor penetration of these chemicals into tissues by the methods used in these studies.

Role of growth regulators were studied by employing an ethylene induced cherelle wilt as a screening technique (Resnik et al., 1980). Only naphthalene acetic acid (among the auxins tested), counteracted ethrel -induced wilt up to 10 day-old fruits. Gibberellic acid exerted the most effective control (Orchard and Resnik, 1982). Similar reduction in intensity of cherelle wilt has been reported in India (Uthaiah and Sulladmath, 1981). The discrepancies between earlier and later reports on the effects

of growth regulators might be due to contrasting environmental evaporative conditions, penetration capacity and translocation within the fruit.

Another important factor is the competition of young cherelles with older fruits and vegetative flushes (Alvim, 1954; Asomaning et al., 1971; Humphries, 1943). The increased carbohydrate demand by growing pods may result in depleted levels (Alvim, 1954) and it is at these low sugar profiles that cherelle wilt reaches maximum levels (Balasimha et al., 1984b; Humphries, 1947; Owusu et al., 1978). Thus, the fruit bearing capacity of the tree and ultimately the productivity is influenced by environmental conditions especially water stress, ratios between pod load: cherelle wilt, competition between vegetative growth to fruit development and endogenous growth regulators/carbohydrate levels.

WATER RELATIONS AND STOMATAL REGULATION

Among plantation crops, cocoa is regarded as one of the most sensitive ones to water stress. Water stress affects several physiological processes leading to a reduction in crop yield. Water potential of leaf is a major quantitative characteristic used to assess water stress. Cocoa plants show changes in water relations when soil moisture drops to 60-70% of available range (Alvim, 1960; Lemee, 1955). The onset of drought decreased water potential and relative water content (Balasimha, 1982, 1983b; Hutcheon, 1977). The relative water content (RWC) of leaves of rainfed cocoa plants were lower than those of irrigated plants. This tends to decrease with progress of summer months. The decrease in RWC even in irrigated plants may be because of progressive increase in daily mean temperature and lower relative humidity leading to higher transpiration rates. During drought, NR activity and chlorophyll content decreased while proline accumulated in the leaves. Diurnal variation exists in water potential; however a plateau in water potential is reached once the stomata close beyond -1.5 MPa (Hutcheon, 1975, 1976c). This is the stage when the 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, 1982, 1983b).

Drought decreased RWC (to 80%) and water potential, increased

stomatal resistance and the level of ABA (Abo-Hamed et al., 1985). The leaf elongation rates were severely inhibited under drought and as the intensity of drought increased other metabolic processes and RWC were affected (Balasimha, 1984). Water potential may vary due to leaf age and position (Alvim et al., 1974a). The 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 than those in the shade.

Drought tolerance

Since cocoa plants experience long periods of drought in Southern India, efforts have been made to identify drought tolerant characteristics in cocoa accessions (Balasimha, 1983b; Balasimha et al. 1985b). The leaf morphology, water relation-components, stomatal behaviour and biochemical factors were studied in cocoa germplasm collection (Table 3). The leaf

TABLE 3

Morphological characters of leaves in relation to drought tolerance (Balasimha et al., 1985b). The data are the means of determinations made on multiple accessions, the number of which is indicated in parentheses.

Leaf character	Tolerant	Susceptible
Specific leaf weight ($mg\ cm^{-2}$)	7.72 (5)	6.95 (10)
Leaf thickness (μm)	147.7 (5)	127.6 (10)
Palisade layer (μm)	37.7 (5)	30.9 (10)
Stomatal frequency ($no.\ mm^{-2}$)	100.1 (5)	102.5 (35)
Epicuticular wax ($\mu g\ cm^{-2}$)	339.6 (5)	32.4 (35)
Leaf area (cm^2)	321.2 (5)	339.2 (10)

TABLE 4

Water relations of cocoa accessions in relation to their adaptive ability to stress, i.e. lowered soil moisture (Balasimha et al., unpublished).

Parameter	Drought tolerant		Drought susceptible	
	Control	Stress*	Control	Stress*
Stomatal diffusion resistance ($cm\ sec^{-1}$)	4.80	10.73	4.06	6.03
Transpiration ($\mu g\ cm^{-2}\ sec^{-1}$)	3.37	2.18	5.82	3.82
Water potential (MPa)	-0.56	-0.88	-0.35	-1.08
Osmotic potential (MPa)	-0.78	-0.91	-0.78	-1.09
Pressure potential (MPa)	0.22	0.03	0.43	0.01

*Approximately 65% soil moisture of field capacity.

morphological characteristics showed significant differences among accessions, noteworthy being SLW and epicuticular wax content (Balasimha et al., 1985b). Data so far available, indicate that thick leaf, higher wax content, efficient stomatal closure and high tissue elasticity were responsible for better adaptation of plants to drought conditions (Table 4). Earlier, it was reported that drought resistance was associated with closure of stomat (Nunes, 1967) and lesser transpiration rate (Segbor et al., 1981). However, stomatal frequency or size did not show any correlation with drought tolerance (Balasimha et al., 1985b). It is possible that the ability to tolerate drought results from stomatal regulation, thus reducing transpirational water loss. The tissue elasticity is also higher as shown by lower bulk elastic moduli. Osmotic adjustment does not appear to be a major contributor as changes in osmotic potential were not high (Table 4), compared to many other crops. The solutes, like sugars and proline which are major contributors

for leaf osmotium, do not accumulate substantially in drought tolerant accessions (Balasimha, 1984). The NR activity showed higher stability under drought in tolerant accessions, possibly because adequate energy pools were available since leaf turgidity was maintained (Balasimha, 1983b, 1984).

However, the rate at which water stress develops within the plant, is dependent on external factors like relative humidity, soil conditions and cropping pattern. If the soil is deep with high water holding capacity stress develops gradually and water is still available to the roots for a long period. The capacity for water uptake and transport may also differ because of resistance to water flow. Since hydraulic flow resistance is expected to be relatively low for cocoa (Hutcheon, 1977) it may not be limiting factor. The overhead shade of cocoa decreases the evapotranspiration thereby reducing water consumption by cocoa plants to some extent. Trees without shade exhibit a high transpiration and a low leaf water potential.

CONCLUSIONS

In the past, selections for high yields or tolerance to stress conditions were made mainly by empirical methods. Little attention was given to analytical methods probably because information on whole-plant physiological aspects were either lacking or insufficient. With the information available now on cocoa physiology, it is possible to take an analytical approach. Yield is not limited by the photosynthetic rate alone, as other climatic and genetical factors also play important roles. The approach to increase crop productivity should identify the multiple plant characters which control yield and incorporate them into breeding programmes to evolve an ideotype.

Basic physiological and genetical investigations have shown that yield potential is rather high and not yet been fully exploited. For example, the potential yields of cocoa can be as high as 3700 kg dry bean ha^{-1} $year^{-1}$ (Ahenkorah et al., 1974). The best selections under optimum management conditions however have yielded only about 2000 kg ha^{-1} $year^{-1}$. Suitable crop models can be derived which integrate photosynthetic productivity, bioclimatology, source-sink relationships and harvest-index. This ultimately should lead to an ideotype with not only high productivity but with a stability in yields under unfavourable environmental conditions. In a heterozygous,

long-generation crop like cocoa, systematic breeding for such ideal characters may be a difficult proposition, but not impossible.

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