

Water Relations and Physiological Responses to Water Stress in Cacao*

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ABSTRACT

Water Relations and Physiological Responses to Water Stress in Cacao. Balasimha D. (Central Plantation Crops Research Institute Regional Station, Vittal Karnataka, 574243 India). *Plant Physiology & Biochemistry*, 10(Sp. Vol.): 65-71, 1983. Cultivation of cacao, *Theobroma cacao* L. has become quite extensive as an intercrop in coconut and arecanut gardens in Kerala and coastal Karnataka. Cacao plants experience a periodical drought during January to May which affects their growth and yield as these are very sensitive to water stress. Substantial research work has been done on water relations, drought tolerance, and physiological responses to water stress in cacao. Some drought tolerant accessions have been identified and these are being evaluated in the field. This paper reviews some aspects related to water relations and associated physiological changes to water stress in cacao.

Key words : *Relative water content/nitrate reductase/proline/leaf growth/morphological adaptations/drought tolerance/Theobroma cacao L.*

INTRODUCTION

Water deficits in plants affects many important physiological processes ultimately limiting their yield (1). Several plant species, especially in arid to semi-arid regions, face constant drought throughout their life cycles. However, other crop plants grown in temperate and tropical areas, undergo seasonal periods of stress especially during the summer months. The relationship of water stress and various physiological processes have been studied in detail in many annual and biannual crops as compared to perennial plantation crops. This review is an attempt to assess the water relations and tolerance to drought of cacao (*Theobroma cacao* L.) and compare these with those of other perennial crops.

WATER RELATIONS

Water potential of leaf is one of the main quantitative characteristics used to assess water stress. Cacao plants are sensitive to changes in moisture levels (2, 3).

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There is a diurnal variation in water potential changes (3) and when leaf water potential reaches about 15 bars, the stomata tend to close (2). The gradual development of drought results in an increase in water potential and decrease in relative water content (RWC) (3). The RWC of rainfed cacao plants was lower than that of irrigated plants. Under both conditions this showed decrease with progress of summer months (4) (Fig. 1). This might have possibly resulted due to increase in daily mean temperature and solar radiation leading to high transpiration rates.

Seasonal and diurnal variations in leaf water status have been reported in several other tree crops (5-9). Apple trees are relatively tolerant to drought and their leaf turgidity was maintained due to the osmotic adjustment (10). The osmotic adjustment is the ability to accumulate certain solutes like organic ions, cations, amino acids, and sugars to maintain leaf turgor. Such osmotic adjustments have been reported in some cereal crops (11). Very low predawn water potentials in cacao have been reported (12, 13) and this seems to be the lowest on record (3).

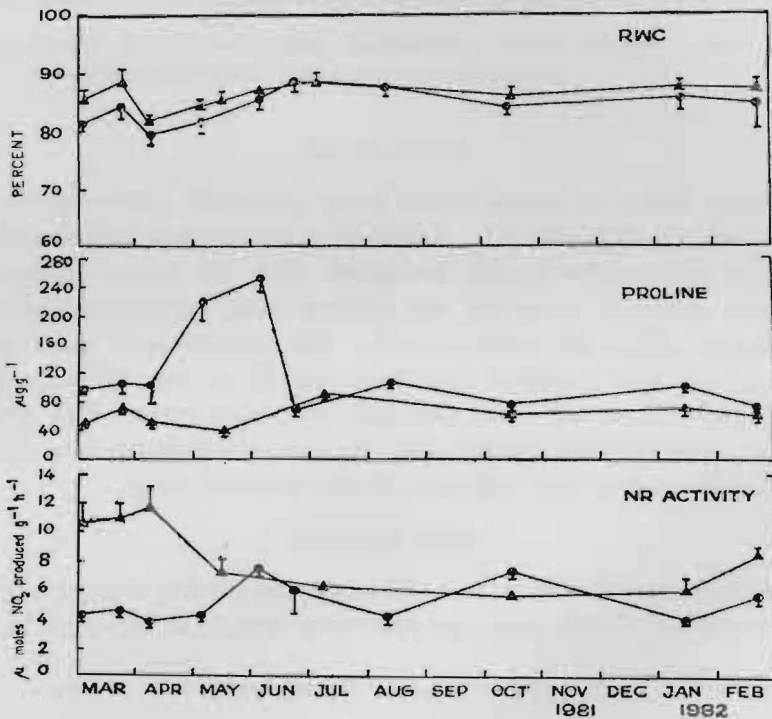


Fig. 1. Seasonal changes in RWC, proline content and NR activity (circles-rainfed; triangles-irrigated). From Balasimha (4)

MORPHOLOGICAL ADAPTATIONS

Many tree crops have well developed physiological and morphological adaptations to 'avoid' or tolerate drought. Several characteristics impart drought tolerance to plants which include increased root/shoot ratio, thick cuticle, epicuticular wax, stomatal density and behaviour, osmotic adjustments, and proline accumulation (14). In cacao the root/shoot ratio does not seem to be important in tolerance mechanisms and the seedling vigour also did not indicate any possible correlation in screening trials (2, 15). Leaf morphology, cuticular transpiration and epicuticular wax were determined in several accessions of cacao. Increased leaf thickness and wax was recorded in drought tolerant accessions (15; Table 1). There was significant positive correlation between specific leaf weight (SLW), leaf thickness and wax content. Epicuticular wax plays an important role in the plant's ability to withstand water deficits (16). Increased wax deposition in drought tolerant cereals has been reported (17). These criteria viz., epicuticular wax and SLW which are relatively easy to determine can thus be employed for screening large number of cacao plants in breeding programmes.

TABLE I

Morphological characters

Leaf characteristics	Tolerant	Susceptible
Specific leaf weight (mg/cm ²)	6.9 - 9.5	5.2 - 6.9
Leaf thickness (m μ)	52.0 - 64.5	46.9 - 54.3
Palisade layer (m μ)	14.3 - 18.3	11.8 - 15.4
Stomatal frequency/mm ²	40.4 - 46.6	36.0 - 122.4
Epicuticular wax (μ g/cm ²)	180.0 - 336.1	12.1 - 92.8

From Balasimha *et al.* (15, 41)

The behaviour of stomata during drought also can be reckoned as one of the important parameters. Nunes (18) reported that drought resistance was associated with closure of stomata and low transpiration at comparatively high moisture levels. However, stomatal frequency or size did not indicate any positive correlation with tolerance (15). In apple trees, growth and stomatal responses are not affected by stress (19) though in several other tree crops the stomata respond with gradual progress of drought (20).

PHYSIOLOGICAL PROCESSES

Several physiological processes are extremely sensitive to water stress in cacao (Table 2). The basic mechanisms of drought tolerance can be understood only after biochemical changes are studied in greater detail. With the onset of drought periods, the apical buds become dormant and on rewatering there is a flush growth which is characteristic of cacao (21) and some other species like oak (22). This is due to the presence of growth inhibitory hormones like abscisic acid (ABA) in the older leaves (21) and it explains the crazy flowering and budburst immediately after the stress is relieved (3). Alvim *et al.* (23) showed that ABA content increased in leaves with progress of imposed drought (Fig. 2). On the contrary gibberellin levels increased during leaf expansion and maturation (24). The accumulation of ABA during stress and dormancy has also been reported in birch (25), Willow (26), *Populus* (27), peach (28), and coffee (29).

TABLE 2
Physiological changes due to stress in cacao seedlings

Parameter	Pre-stress	Stress*	Recovery**
Relative water content (%)	87.9	48.9	87.9
Leaf expansion rate (cm/day)	1.49	0.87	1.03
Proline content ($\mu\text{g g}^{-1}$ fresh wt.)	84.0	908.0	123.0
Nitrate reductase activity ($\mu\text{M NO}_2^-$ produced $\text{g}^{-1} \text{h}^{-1}$)	7.50	5.60	4.90

*Stress was induced by withholding irrigation for 7 days.

**Recovery 4 days after rewatering.

Yellowing and leaf fall are first symptoms of stress in cacao. This is a manifestation of production of several growth inhibiting (ABA) and abscission inducing agents (ethylene). The oldest leaves are shed first and as stress increases, progressively younger leaves fall (3). Involvement of ethylene is also reported in stressed *Populus* cuttings (27).

Certain metabolites accumulate under drought stress in plants. These include free proline, glycylbetaine and reducing sugars. Proline accumulation in leaves of stressed plants is well known in annual plants, but there are only few reports in plantation crops. Proline accumulation in citrus and coffee during drought periods is reported (30, 31, 32). In cacao, proline accumulates under stress by about 10 fold as compared to control (33).

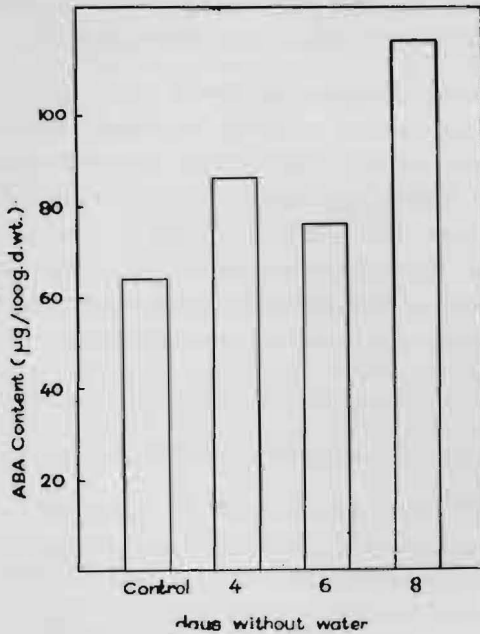


Fig. 2. Changes in ABA content in cacao leaves with progress of drought. From Alvim (23).

The growth of leaves and pods of cacao are extremely sensitive to water stress (3, 34, 35). Though there is an abundance of flower production when water stress is relieved, the pod setting and growth are relatively limited. One of the causes for physiological cherelle wilt could be a limited supply of water. Reduction in fruit set by plant water deficits has also been reported in apple (36).

EFFECTS OF POTASSIUM AND OTHER CHEMICALS

Potassium acts as a cofactor in many enzyme reactions especially those of starch synthesis. Role of starch in opening and closing of stomata is well established and it has been suggested that potassium can be used to enhance tolerance to stress. The adverse effects of drought have been reported to be overcome by K application in various annual crops like wheat, barley, rice, sorghum and cotton (37). The leaf expansion rate, chlorophyll and proline accumulation were higher in K-treated plants of maize under stress (37) thus showing beneficial effects of K. In cacao, application of K and proline to seedlings ameliorated growth and metabolism under drought (38). The maintenance of turgidity (RWC) of leaves by

proline sprays has been reported and whether the endogenously accumulated proline will have similar effects remains to be established (39).

Cycocel or CCC also is known to impart tolerance to drought and frost. The application of cycocel to cacao seedlings improved growth and also in retaining higher nitrate reductase activity possibly due to maintenance of higher RWC of leaves (33). Similarly, external application of ABA also imparted tolerance under drought in cacao seedlings which was counteracted by simultaneous application of Kinetin (40). There was lack of relationship between RWC and ability to accumulate proline. It was assumed that metabolic rates would be higher because leaf turgidity was maintained due to ABA application, and proline might have been utilised more efficiently.

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