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REVIEW ARTICLE

Water Stress in Banana- A Review

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ABSTRACT

In banana, one of the major constraints for productivity is drought. Water deficit severely affects the plant growth and yield, because it deeply reduces the photosynthetic capacity of the banana plants as the crop sensitivity is reflected by reduced greenness of foliage. Water deficit during the period of finger development inhibits the translocation of assimilates to bunches. The present review made for the better understanding of the effects of water deficit to physiological and biochemical changes in banana.

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INTRODUCTION

Banana is the 'queen of tropical fruits' and is one of the oldest fruits known to mankind from pre-historic times. Today, it is the leading tropical fruit in the world market with a highly organized and developed industry. It is the fourth largest fruit crop in the world after grapes, citrus fruits and apples. India is the largest producer of banana in the world, contributing 19.71 per cent to the global production of banana, with a total production of 19.19 million tones from an area of 0.565 million hectare. In Tamil Nadu, banana production is about 4.64 million tones from an area of 0.94 lakh ha. A declined in production was noticed during 2001-2004 due to severe drought. Bananas are known for its antiquity and are interwoven with Indian heritage and culture. The plants are considered as the symbol of 'prosperoty and fertility'. Owing to its greater socio-economic significance and multifaceted uses, they are referred as 'Kalpatharu' (Plant of Virtues) and Kalpavriksh. Botanically, banana fruits are a wonder berry, which forms the stable food of millions of people across the globe, providing more balanced food than any other fruits or vegetable. As a desert, banana is more filling, easy to digest, fat free, rich source of carbohydrate with a calorific value of 90 Kcal per 100 g fruit. In North Eastern India, banana powder is used as baby food and being a good source of potassium, is good for heart patients. Stem core juice is a well-recognized medicine for dissolving kidney stones. Plantains are rich in vitamin 'A' (beta-carotenes) and they aid in digestion. Ripe fruits are being used in the treatment of asthma.

In banana plantations, 73% of the world crop is grown and consumed in west and central Africa and the cultivars are mostly triploid, crosses between *M.acuminata* and *M.balbisiana.* The Banana is a plant of the tropics and subtropics, requiring hot and humid climate. The cultivated banana is the *Musa* spp., two wild species, namely *Musa acuminata* and *Musa balbisiana* are genetic material source for most of the cultivars. Drought is an insidious hazard of nature. Although it has scores of definitions, it originates from a deficiency of precipitation over an extended period of time, usually a season or more. This deficiency results in a water shortage for some activity, group, or environmental sector. Water deficit occurs when water potentials in the rhizosphere are sufficiently negative to reduce water availability to sub-optimal levels for plant growth and development. On a global basis, it is a major cause limiting productivity of agricultural systems and food production [35]. The banana plants are sensitivity to soil moisture stress is reflected in changes in reduced growth through reduced stomatal conductance and leaf size [99] increased leaf senescence [182]. Bananas (*Musa* spp.) rarely attain their full genetic potential for yield due to limitations imposed by water ultimately limiting the plants photosynthesis. The bananas are thought to be particularly sensitive to changes in the environment. The present study considers investigations into the response of the leaf, root and reproductive system to the environment. Monteith's analysis of the response of plants to intercepted radiation is appropriate for analyzing the productivity of bananas and plantains. Turner and Thomas (1998) reported that, the banana is sensitive to soil water deficits, expanding tissues such as emerging leaves and growing fruit are among the first to be affected. As soil begins to dry, stomata close and leaves remain highly hydrated, probably through root pressure. Productivity is affected because of the early closure of stomata. Bananas use large amounts of water does not have a strong physiological basis. Improvements in water-use efficiency in irrigated plantations could come from a closer match between plant water use and the amount of water applied. The banana is day neutral for floral induction, but photoperiods of less than 12 h are associated with a slowing in the rate of bunch initiation that is independent of temperature expressed as growing degree days. This may contribute to seasonal variations in banana flowering, even in more tropical environments with moderate temperatures.

Turner and Thomas (1998) who showed measurements of leaf water potential using either the exuding xylem or relative leaf water content could not be reliably linked to plant functions such as stomatal movement, net photosynthesis or leaf folding. Water potential measured by the exuding latex method appeared the best for determining leaf water status, but even this shows a small change in plants experiencing soil water deficit [184] supporting the hydrated status of banana leaves although the soil is dry. Drought is the one of the major abiotic stresses limiting plant production.

The world wide water shortage and uneven distribution of rainfall makes the improvement of drought resistance especially important [115]. [184] suggesting leaf folding may reflect leaf water status, albeit somewhat unreliably. However, Lu *et al*. [2002] did not find any link between leaf folding and soil water deficit. [115] measured water use of banana plants using a sap flow system calibrated against gravimetrically determined water loss. Despite our best efforts, there is not a straightforward link between leaf scale gas exchange and leaf water status in bananas. Often, turgor-based changes within leaves such as changes in stomatal aperture or leaf folding or leaf elongation in response to soil water deficit or to high vapour pressure deficit do not correspond with changes in leaf water status measured by classical methods based on either thermodynamics or volumetric water content. Banana plant productivity is greatly affected by environmental stresses such as drought, water and cold. Plants respond and adopt to these stresses to survive under stress condition at the molecular and cellular levels as well as at the physiological and biochemical levels. Physiological responses to soil water deficit are the feature that is most likely to determine the response of the crop to irrigation. The most sensitive indicator of soil water deficit in banana is the rate of emergence of the new leaf [99; 82; 184]. If the soil dries rapidly, the leaf may stop emerging after 2 to 10 d and if it dries slowly, leaves may stop emerging after 23 d. In the experiments of [82] a 21 kPa reduction in soil water potential halved the rate of leaf emergence but at 40 kPa reduction in soil water potential was needed to halve transpiration rate. Thus the rate of emergence of the new leaf is a sensitive indicator of drying soil, more so than the closing of stomata. The plant growth and yield decreased drastically when the interval between watering was increased with the soil moisture falling below 66% of total available soil moisture [153].

Water relations of crop

The general responses of banana to soil moisture status are the plants gradually stop growing, show evidence of desiccation and become yellow and wilted. The first sign of water stress is a yellow cast of pale green colour of the foliage, accompanied by long periods of transient wilting of the leaves during the warmest part of the day. In severe drought, the young bunches may fall to the ground resulting in considerable loss. [76] stated that water stress is a result of an imbalance between three components that determine plant water status, viz., water absorption, translocation and loss.

Banana, as an herbaceous plant, is more sensitive to moisture stress than other fruit crops. [188] reported that the practice of irrigating banana crop every alternate day seem to be too severe. [130] recommended irrigation at 5 to 10 days intervals in dry weather for banana. Irrigating bananas at 10 to 15 days intervals from October to February and 6 to 8 days from March to May was suggested by [72]. Under the conditions of the Jordan Valley (Israel), the range between field capacity and two third of total available water constitute the optimum range of soil moisture for 'Cavendish' bananas, with regard to both physiological activity and yield [164]. [45] concluded that the most suitable soil moisture content for the banana crop was 50 to 60 per cent available soil moisture. According to Simmonds [1966], the water requirement of banana ranged from 50 to 550 mm per month depending on soil and climatic conditions. [107] revealed that when 20 per cent depletion of available soil moisture was maintained throughout the crop growth period of Robusta banana, it consumed 2150 mm water to produce the best result.

Critical stages of crops for water stress

Crops respond differently to moisture tension at different stages of growth. Moisture stress at any stage of the growth of banana reduced the productivity by 30 to 50 per cent considerably. But the effect of stress on growth and yield manifested to varying degrees in different species or genotypes within the species. An evaluation method involving both physiological and biochemical criteria would be more reliable for assessing the water stress tolerance or susceptibility characteristics [107]. As suggested by [36], for banana, the most critical period of drought is from preflowering stage to before ripening. [110], however, found that a moisture deficit is particularly harmful to banana when it occurs at the time of floral differentiation or at the start of flowering.

In banana, water deficit usually affects growth and lowers the yield, the effects usually being manifested several months after drought [16]. [83] while studying the effect of water supply during floral initiation and differentiation of female flower production in 'Robusta' banana found that a continuous and non limiting soil water supply from 120 to 180 days after planting, significantly increased female flower production and thereby the yield of banana as compared to continuous soil water stress. [55] investigated the effects of moisture stress in 'Williams' banana plants with water shortage at different stages of development. Water stress after 7 to 12 leaf stage affected all the plant characters.

Mechanisms of drought tolerance in banana

Drought is a recurrent feature of banana cultivation limiting its growth and productivity. Ironically the timing, intensity, duration and distribution of rain in many part of banana growing areas are uncertain, which cause mild to severe water deficit during different phases of plant growth [164]. It is an interaction between precipitation, evapotranspiration, irradiation, soil physical properties, soil nutrient availability and biological interaction [179].

Drought avoidance

Drought avoidance refers to the strategies adopted by plants to maintain high water potential during period of water deficit. Plants naturally transpire and lose a significant amount of water through stomata. Water deficit causes the guard cells of the stomata to lose their turgor; this closes the stomata and significantly reduces the rate of transpiration. Water deficit leads the plants to synthesize and release elevated levels of abscisic acid (ABA) from the mesophyll cells. This organic acid acts on guard cells to keep stomata closed. Water deficit inhibits growth in the plant because cell turgor is required for cell enlargement. Consequently, the exposed surface is reduced and transpiration decreases. In many species (often monocotyledons), leaves roll up during dry weather. In banana, an adoptive mechanism to water stress is greater allocation of dry matter to the roots which results in a high root to shoot ratio in water stressed plants [86]. Reducing the number of leaves could be a phenomenon by the plants to minimize the transpiration surface. All of these strategies protect plants against water loss, but they also diminish photosynthesis and are therefore harmful to the survival of plants over long periods of time. The pattern of root growth also changes in response to water availability. The more elaborate the root system, the greater the chance that the plant will survive during dry spells [85; 191].

Drought tolerance

Drought tolerance has been considered as a valid screening of banana germplasm for water deficit target to partially compensate for the loss in yield. In banana, some of the cultivar groups with the *balbisiana* (B) genome are considered to be relatively tolerant of seasonal drought [143; 142; 166]. [181] and [178] found that the result of laboratory based leaf gas exchange studies are consistent with the view that the presence of the B genome contributes to drought tolerance. In certain situations, such as extended periods of drought, plants cannot avoid a decrease in water potential. Drought tolerance involves mechanisms that allow plants to maintain their metabolism and limit the harm caused by prolonged drought [51]. These mechanisms can involve different pathways inside the cell, but the end result is expression of stress-response genes. These fall into five categories; osmoprotectants, ion exclusion, ion export, cell membrane modification and antioxidant enzyme systems. Phenotypic traits associated directly with drought tolerance are unclear; however, several investigations noted that osmotic adjustment [116; 98; 195] is associated with drought tolerance. [34] stated that in the early stage of development, leaf evaporation responded in a pattern of 'drought tolerance at high water potential' and later in the season, the response pattern was 'drought tolerance at low water potential'. Osmotic potential is an example of avoidance at the cellular level as a low rate of water loss may allow acclimation to water deficit.

PHYSIOLOGICAL AND BIOCHEMICAL PROCESSES AND SOIL WATER DEFICIT

Photosynthetic pigments

Chlorophyll content of the plant influences photosynthetic rate. Water stress caused a fall in leaf chlorophyll [3]. Increasing intensity of water stress decreased leaf chlorophyll content and tended to increase the chlorophyll a/b ratio [196]. Makhmudov [1983] reported that moisture stress inhibited biosynthesis of the precursor of chlorophyll in wheat leaves which ultimately reduced the chlorophyll content. Thimman [1980] stated that water stress induced leaf senescence leading to decreased photosynthetic activity with the accompanying degradation of proteins and chlorophyll. [47] Found increased level of carotenoid content under drought conditions. The chlorophyll content of the leaf was decreased by water deficit but there was accumulation of large amount of proline in the leaf. [13] stated that total chlorophyll content of the leaf declined under water stress conditions. It may be due to decreased synthesis and increased degradation of chlorophyll in leaves under water stress [57].

Photosynthesis is the basic energy conversion process on earth, which makes possible the utilization of the energy of sunlight for living organisms. Generally, plant photosynthesis are only designed to function well over a rather a narrow range of temperatures. When heated, cytochromes, pigments, and membrane critical to phosphorylations; plant may open stomata and evaporate water which will lower the leaf temperature. In this case, stomatal density may increase or decrease in response to environmental variation in sunlight and water availability. The chlorophyll content of leaf tissue varies with cultivars, age of the crop, growth stages, light and temperature [108]. Correlation between leaf area and yield suggest the importance of chlorophyll and leaf area to determine yield [6]. Plant pigments play important roles in harnessing energy from sunlight. This lesson examines the two major classes of photosynthetic pigments, chlorophylls and carotenoids, their biochemical structures, and their biosynthesis. A photosynthetic potential is directly proportional to the quantity of chlorophyll present in the leaf tissue [42]. In most plants, as a direct response to temperature, the light-saturated rates of photosynthesis are low at extreme low and high temperatures and have an optimum at intermediate temperature. With changes in growth temperature, many plants show considerable phenotypic plasticity in their photosynthetic characteristics. In general, plants grown at higher temperature have a higher optimal temperature of photosynthetic rate [22]. The connection between different parts of the photosynthetic process is considered together with the influence of environmental factor, development and acclimation, and metabolic regulation.

The hydrogen–carbon bonds of the chlorophyll molecule are sufficiently stable to prevent hydrogen exchange in neutral organic solvents in the dark; a tracer experiment is therefore feasible. At least one current school of thought maintains that the participation of hydrogen of the chlorophyll molecule in a chemical reaction is a requisite step in the electron transfer which originates in photoactivated chlorophyll. The spectral quality of light reflected from leaves, manifested in leaf color, has long been relied upon as an indicator of plant stress. However, spectral characteristics of radiation reflected, transmitted, or absorbed by leaves can provide a more thorough understanding of physiological responses to growth conditions and plant adaptations to the environment. In the late nineteenth and early twentieth centuries, technological advances began to allow the examination of changes in leaf spectra that occur with optical properties of stressed leaves in a relatively narrow spectral band near 700 nm and are found crucial for plant stress detection and the estimation of leaf chlorophyll concentration. An increase in total chlorophyll content under moisture stress conditions of groundnut. Ramesh babu *et al.* [1982] stated that an increase an total chlorophyll content under moisture stress contition. Carotenoids are C40 isoprenoids and tetraterpenes that are located in the plastids of both photosynthetic and non-photosynthetic plant tissues. In chloroplast, the carotenoids function act as accessory pigments in light harvesting, but perhaps a more important role is their ability to detoxify various forms of activated oxygen and produced as a result of excitation of the photosynthetic complexes by light. Carotenoids are synthesized from geranyl pyrophosphate from the isoprenoid path way in plastids and thus have common precursor to chlorophyll and tocopherol.

The carotenoids act as competitive inhibitor for the formation of singlet oxygen and this is aided considerably by their proximity to chlorophyll in the light harvesting complex. This method of protection is especially critical as light intensity increases above saturating level [59]. Other form of carotenoid, viz., zeaxanthin has been implicated in the dissipation of thermal energy, but the precise mechanism has not been resolved. Zeaxanthin apparently facilitates the conversion of triplet to singlet chlorophyll in more efficient manner than β-carotene. A de-epoxidase enzyme catalyses the de-epoxidation of violaxanthin to zeaxanthin in the presence of excess light and an epoxidase catalyses the reverse reaction in the darkness or low light. Zeaxanthin therefore accumulates under light intensities that exceed photosynthetic capacity. The de-epoxidase has a low pH optimum [5.1], whereas the epoxidase has a high pH optimum [7.5]. The enzymes for both reactions are in the chloroplast thylakoid lumen and therefore during periods of photosynthesis, the lumen is acidified and zeaxanthin accumulates. The reverse reactions occur in the dark and violaxanthin accumulates.

Chlorophyll Stability Index (CSI)

Chlorophyll Stability Index (CSI) is an indicator of the stress tolerance capacity of plants and is a measure of integrity of membrane [129]. Mohan *et al.* (2000) reported that high CSI value means that the stress did not have much effect on chlorophyll content of plants. A higher CSI helps the plants to withstand stress through better availability of chlorophyll, leading to increased photosynthetic rate, more dry matter production and higher productivity this indicates how well the chlorophyll can perform under stress. CSI has been used as an indicator of stress tolerance in rice as reported by [73] and [192]. Drought tolerant verieties had higher Chlorophyll Stability [158; 10; 132]. The CSI was positively and significantly correlated with root thickness and proline under stress (190). Contradictory results were also reported that the Chlorophyll Stability Index was found to be correlated to drought tolerance in rice by Thangaraj and Sivasubramanian [1990]. Meenakumari *et al.* [2004] reported that chlorophyll content as well as Chlorophyll stability index decreased during drought environments. Konwar [2009] stated that the Chlorophyll stability index decreased with increasing water stress in rice. The genotypes showed higher Chlorophyll stability index under water stress possessed higher glutathione reductase and peroxidase activity.

The decline in the activities of anti-oxidative enzymes inhibited the accumulation of thiobarbituric acid reacting substances and alleviated the reduction of chlorophyll content. It can be concluded that when the leaves were deeply stressed and damaged, through the inhibition of ethylene production, cobalt alleviated the decline in polyamine content and the activities of anti-oxidative enzymes, and hence alleviated the increment in reactive oxygen species levels and membrane damage and showed protective effects on the leaves. The efficiency of leaves to produce assimilates and its persistence depends largely on the photosynthetic pigments of prime importance [9]. The detailed mechanism of the process of pigment change and the product of chlorophyll degeneration are not known [101].

Membrane Stability Index (MSI)

A major impact of plant environmental stress is cellular modification, which results in its perturbed function or total dysfunction. However, the cellular membrane dysfunction due to stress is well expressed in increasing permeability and leakage of ions which can readily be measured by the efflux of electrolytes. Hence, the estimation of membrane dysfunction under stress by measuring cellular electrolytes leakage from stressed leaf tissues into an aqueous medium is finding a growing use as a measure of MSI and as a screen for drought resistance. Most of the abiotic stress factors primarily affect the stability of cell membrane. One of the primary injuries caused by water stress is loss in cell compartmentation due to the disruption of membrane stability. Increased leakage of solutes is an indication of damage caused to membrane. Membrane stability decreased under moisture stress and temperature stress at anthesis stage in wheat [55]. Upadhaya *et al.* (1989) found that the decrease in MSI estimated by taking comparative ion leakage is an indicator of membrane damage as a result of membrane (lipid) peroxidation caused by reactive oxygen species (ROS). Lower membrane injury and hence lesser amount of solute leakage in chickpea cultivars under water stress conditions. The leakage from the water stressed tissue samples is taken as an index of injury or the proportion of dead cells in the tissues [27].

The plasma membrane is generally protected from desiccation induced damage by the presence of membrane compatible solutes, such as sugars and amino acids [60]. Therefore, a link may exist between the capacity for osmotic adjustment and the degree of membrane protection from the effect of dehydration [113]. Maintenance of membrane integrity and functions under a given level of dehydration stress has been used as a measure of drought tolerance by various workers [140]. Selection for osmotic membrane stability, root length and root to shoot length ratio under osmotic stress could be instrumental in predicting the drought tolerance of genotypes [61]. Higher membrane stability under drought contributed significantly to flowering stage drought tolerance in rice. Konwar [2009] found a reduction in MSI in upland rice under moisture stress condition. The reduction in MSI is related to production of ROS which causes damage to membrane lipid and protein. Sairam *et al.* [2008] stated that the genotypes that showed higher MSI under water stress possessed higher activities of glutathione reductase and peroxidase enzyme.

Relative Water Content (RWC)

Relative Water Content (RWC) is the appropriate measure of plant water status in terms of the physiological consequence of cellular water deficit. While water potential as an estimate of plant water status is useful in dealing with water transport in the soil-plant-atmosphere continuum, it does not account for osmotic adjustment (OA). Osmotic Adjustment is a powerful mechanism of conserving cellular hydration under drought stress and RWC expresses the effect of OA in this respect. Hence, RWC is an appropriate estimate of plant water status in terms of cellular hydration under the possible effect of both leaf water potential and OA. [20]. As observed by [96], the photosynthetic rate was strongly influenced by RWC of the leaf in papaya cultivars. When RWC declined to 80 per cent, the reduction in photosynthesis was more than 50 per cent. Slatyer [1955] also reported that a reduction by 5 per cent in RWC led to reduction in photosynthesis by 40-60 per cent in crop plants. In *Theobroma cocoa*, Mohd Razi *et al*. (1992) observed a significant reduction in both photosynthesis and transpiration as a result of drop in leaf water potential below 2.0 MPa.

Drought resistance varieties showed consistently higher leaf water potential in their tissues than susceptible types under soil moisture deficit [132]. Plants under severe drought conditions had a small but significant decrease in RWC of leaves and a higher decrease in gas exchange parameters in legumes [116]. Maintenance of higher water status under drought plays a central role in stabilizing the various plant processes and yield. The solute potential (ψ_s) of the plants decrease under water stress and was accompanied by change in relative water content indicating a higher or lower osmoregulation depending upon the magnitude of the decrease. The decreased RWC under stress may be due to decreased leaf water potential (ψ_w) and decreased availability/absorption and translocation of water from soil to roots and ultimately to leaves. Retention of more water in leaf is known to be important to drought tolerance [127; 65]. Moisture stress is reported to cause decrease in water potential and RWC (185; 118). Reddy and Vora (1986) found significant decrease in RWC under moisture stress; this might be due to decrease in internal water content of protoplasm and loss of chlorophyll a : b ratio which might be the result of premature senescence of leaves.

Epicuticular wax (ECW)

The aerial surfaces of plants are covered with a wax layer that is primarily a waterproof barrier but that also provides protection against environmental stresses. The ubiquitous presence of cuticular wax is testimony to its essential function. The epidermis constitutes the leaf surface. The most characteristic trait of epidermal cells is the fact that they have the cuticle on the outer periclinal wall. The cuticle coats nearly continuously all mature parts of the leaf, and the only breaks or gaps are stomata the pores between guard cells. The cuticular layer, outside the cell wall, consists of lipid substances (such as waxes, cutin and cutan polysaccharides (cellulose and pectins). The cuticular layer is coated with the cuticle proper which lacks polysaccharides and contains more waxes than the underlying layers. On top, there is the epicuticular wax layer, without cutin or cutan. The cuticle proper is covered by a smooth amorphous wax film. Outside the wax film we can find waxes in more ordered form. They form a layer with considerable ultrastructural and chemical diversity. Epicuticular waxes are composed of a mixture of chemical compounds: hydrocarbons, primary alcohols, aldehydes.

The plant cuticle and waxes have many important functions. They reduce the loss of water, reflect or attenuate radiation, form the basis of phyllosphere, protect plant tissues against penetration by fungi, bacteria and insects, as well as from mechanical damage (by wind, rain, soil particles etc.), reduce water retention on the plant surface, and provide a self-cleaning surface.

The plant cuticle plays an important role in protecting plants against water losss. The outermost layer is epicuticular wax, which may be amorphous in form or possess a semi crystalline or crystalline structure [Jenks and Ashworth, 1999]. The cuticle plays a fundamental protective role against water loss, particularly when stomata are closed [92]. Shivasankar *et al.* [1993] reported that the level of ECW was higher in stress condition. When drought progressesed, stomata get closed and water loss occured through the leaf cuticle without CO_2 fixation. Higher deposition of ECW decreased cuticular permeability of water loss and increases the crop albedo [28].

The cuticle, made up of major component called cutin [2] forming a layer of hydrophobic material on plant aerial organs, provides an effective barrier against desiccation and also protects the plants from abiotic and biotic stresses [21]. Particularly the ECW influenced the wettability of the leaf and thus affected the plant water use efficiency, the opportunity for gas exchange and the leaching of the solutes [92]. When plant stomata are closed, gaseous exchanges between the plant and atmosphere occurs across the cuticular barrier [41].

The cutiular waxes are arranged in distinct layers. The intracuticular waxes are embedded in cutin, whereas the wax surface is called extracuticular waxes [93, 94]. These properties depend on the chemical composition and synthesis of wax. Thus, there are genes such as Wax2, win1, Cer1, Cer2, Cer3, Gl2 which are involved in the synthesis of key enzymes of cuticular wax [1; 46; 37]. Alterations in cytoplasmic secretary pathways could alter the deposition of epidermal cell secretary products like cell wall and cuticle constituents. Leaf ECW played a critical role in plant environmental stress resistance and their modification had greater potential in crop improvement [89, 90, 91].

Imino acid plays a number of important functions [79]. Of considerable importance among them is its interaction with membrane proteins which is probably involved in the maintenance of the cell membrane structure [29]. It is known that under stress conditions, the primary objective of injury is the plasmalemma [Levitt, 1980]. A consequence of the altered membrane integrity is the increase of the cell permeability which is accompanied by electrolyte leakage from the cell [28].The physical state of cell membranes is known to be very sensitive monitor of the most diverse environmental changes. This feature was suggested to render cell membranes an ideal location for the primary temperature stress sensor. Membrane stability has also been associated with water and high temperature in various crops plants [155]. Tolerance to drought evaluated as increase in cell membrane stability under water deficit conditions was well differentiated between cultivars [141].

Osmotic Potential (OA)

Banana latex is the fluid cytoplasm that exudes from wounded laticifers. It is a colloidal suspension of diverse organelles, but except for a brief mentions. The structural inclusions in banana latex have not been characterized. Milburn [1993] found that in the water relations of the banana, the latex exudations were found to be the useful guide in determining the water potential of the plant. In banana, the solute potential of exuding latex provided an excellent guide to the water status of the plant during water deficit conditions [99]. According to Fahn [1979] stated that, the lacticiferous plants have shown that the latex contains vacuolysosomal organelles called “lutoids” which are capable of actively transporting ions across the membranes. This phenomenon operates in banana latex also; it would have further implications for the water relations of the plant. [100] reported that banana latex contains large number of lutoids showing osmotic potential activity during stress and well irrigated conditions. Banana latex is rich in ions especially K, Mg, Cl and NO_3. The concentrations of these ions have been shown to fall as exudation progresses. This is due to the influx of water into laticifers as a result of lower turgor release [19]. Turner and Thomas, [1998] found that the latex relates best to other physiological processes that are affected by drought in banana plants. Osmotic adjustment is considered as an important physiological mechanism of drought adaptation in many plants [175]. Osmotic Adjustment requires regulation of intracellular levels of several compounds collectively known as osmolytes [88]. Besides causing the accumulation of specified compounds, water stress is accompanied by shift in the partitioning of photosynthates [79].

Stomatal conductance

Stomata play a major role in water relations and photosynthesis of the plant. this is also true for the water relations of banana, particularly of the Cavendish subgroup (Musa spp., group AAA) [38, 15; 174]. Musa hybrids had intermediate conductance in the afternoon relative to triploids and diploids. But in the morning, conductance was similar in both (lower and upper side) locations. An increased stomatal diffusive resistance was found to be a desirable trait to improve bunch yield of banana in water limited environment [180]. Stomatal diffusive resistance was unaffected by leaf water potential [52]. Ludlow [1986] stated that the main response of increased stomatal resistance by whatever means was to avoid desiccation.

Increase in stomatal diffusive resistance was observed with water deficit [172]. Kumar and Singh [1996] observed a positive correlation between stomatal diffusive resistance and water stress. The banana plant are sensitive to soil moisture stress and is reflected in changes in reduced growth through reduced stomatal conductance and leaf size [99; 181]. [18] stated that water stress decreased stomatal conductance in flag leaves of pearl millet. The stomatal conductance was significantly reduced by the incidence of water stress in okra. The reduction resulted in stomatal conductance in a considerable reduction in photosynthetic rate in banana under water stress [25]. [14] did not find significant relationship between leaf stomatal conductance and photosynthesis under drought in okra [123]. Marler and Mickelbart (1998) pointed out that drought stress reduced net photosynthesis, altered the diurnal pattern of gas exchange and decreased various measurement of photochemical efficiency of papaya plant. The part of the inhibition is attributed to non-stomatal effects at chloroplast level with electron transport and phosphorylation being main targets of inhibition. [95]reported that leaf photosynthetic activity can be used as a helpful way to classify tolerant plants for drought stress. A positive correlation between RWC and gas exchange activities was reported by [56] and the reduction of RWC strongly reduced photosynthesis and stomatal conductance.

Transpiration rate

The rate of transpiration is directly related to the gradient of water vapour concentration in the intercellular spaces of the leaf and the ambient air. Rapid changes in the transpiration rate from a leaf or leafy shoot as a result of excision of the leaf or shoot have been observed in many plants including banana plants [8]. Rufelt (1963) stated that the increased water supply to the leaf is presumably responsible for increased stomatal opening and increased transpiration in banana, which is called "Rufelt's hypothesis". [5] reported that increased stomatal opening as a result of excision of young barley leaves considers this as supporting evidence for Rufelt's hypothesis. High rate of transpiration was recorded even when the stomata were apparently partially closed in banana [164]. A positive correlation between relative water content and gas exchange activities was reported by [56] and the reduction of RWC strongly reduced photosynthesis and transpiration.

Wilting of mesophyll cells and withdrawal of water from the epidermal and subsidiary cells permitted the guard cells to bulge outward causing opening of the stomatal pores. Decreased water supply caused the mesophyll cells to wilt. A strong stomatal opening response was observed under conditions of low transpiration. Under such conditions there would have been very little tension to relieve. Increased stomatal opening also occurred as a result of freezing rather than cutting the vascular supply to the leaf [154]. Shimshi [1963] dealing with the concept of stomata and transpiration stated that stomatal closure was a major cause for decline in transpiration rate during water stress. Under severe water stress condition, water loss was minimized by a steep decline in transpiration [18; 172].

Photosynthesis (Pn)

Drought affects the rate of photosynthesis in water stressed leaves mainly due to stomatal closure [84]. [68] stated that a decrease in photosynthesis under deficit soil moisture may not necessarily be related to stomatal opening rather than non-stomatal control of photosynthesis. Chloroplast metabolism can be inhibited in plants subjected to water deficits [78]. This could substantially contribute to the overall inhibition of photosynthesis in leaves of droughted plants [68]. Spence *et al.* (1986) reported that plant stomata adapted to drought stress maintained stomatal opening at lower plant water potentials than non-adopted plants. In plants, chloroplast obtain high energy by means of photosystem II and I (PS II and PS I), which capture the electrons that become excited when sunlight is observed by chlorophyll molecules. The PS I and PS II are composed of an antenna complex attached to a photochemical reaction centre. This is a precisely ordered complex of proteins and pigments, where the photochemistry of photosynthesis occurs [39]. The two photosystem are normally linked in series and transfer electron from water to $NADP^+$ to form NADPH, with the concominant production of a transmembrane electrochemical proton gradient generating O_2 as a by-product. All electron transport processes occur in the thylakoid membrane to make ATP. In this process, H^+ is first pumped into the thylakoid space and then a backflow of H^+ occurs through an ATP synthase to produce the ATP in the chloroplast stroma [4].

Water stress is one of the most important environmental factors inhibiting photosynthesis [32]. Photosynthetically derived ATP and NADPH are transferred to a large number of biosynthetic reactions, including the reactions of the carbon fixation pathway. Carbon from CO_2 enters the pathway and combines with ribulose 1, 5 biphosphate under the catalytic action of ribulose biphosphate carboxylase (rubisco). Subsequently, ribulose 1, 5 biphosphate is converted to triose phosphates, which are exported to the cell cytosol to provide an organic carbon source for multiple cellular reactions [4]. Many studies have shown that decreases in photosynthesis resulting from water stress can be associated with the perturbation of the biochemical processes of that pathway. Several *in vivo* studies demonstrated that water stress resulted in damage to the oxygen evolving complex of PS II and to the PS I reaction centre [81; 74]. Other studies have shown the inhibition of CO_2 dependent O_2 evolution and net CO_2 assimilation [50]. This may imply that the perturbation of the biochemical processes is not solely responsible for the inhibition of CO_2 assimilation and that stomata may also play a dominant role in the decreased CO_2 assimilation under water stress [50].The reduction in photosynthesis in okra may be associated with the limitation on the source as indicated by substantial reduction in sotomatal conductance in the plants [24]. Blum (1988) stated that water stress limits the stomatal and biochemical reactions known to be responsible for the reduction in photosynthesis. In other vegetable plants, it was found to be the principal factor in the water stress mediated reduction of photosynthesis [24; 26]. Water stress induces limitation on photosynthesis due to increasing leaf senescence [159]. Moisture stress affects many physiological processes including the most sensitive is photosynthesis [18]. Changes in water regime can strongly modify ultrastructural cell characteristic if water stress is severe enough [49]. Water stress can disrupt the ultrastructural features of chloroplasts and mitochondria (9) and alter the nucleus and cell membranes in general. Chloroplast seems to be the organelles that are most sensitive to stress. The main damage to the chloroplast caused by water stress includes structural changes resulting from excessive swelling, distortion of thylakoids and the appearance of lipid droplets [53]. Changes in water supply seem to affect the structural characteristics of chloroplasts differently in various cultivars. Cell membranes are particularly vulnerable to water stress. It has been that plasma membrane stability may be a reliable index of drought and heat resistance in plants.

Poly Phenol Oxidase (PPO)

Poly Phenol Oxidase is widely distributed in the plant. It is a copper-containing enzyme and is responsible for the enzymatic browning reaction occurring in many fruits and vegetables damaged by improper handling, resulting in bruising, comparission or indentations. In the presence of molecular oxygen, PPO catalyzes the *o*-hydroxylation of monophenols to o-diphenols (monophenolase activity) and oxidation of the o-diphenols to o-quinones (diphenolase activity) [44]. The PPOs are very important enzymes in the food industry, due to their involvement in the enzymatic browning impairs the sensory properties and marketability of the product and also lowers the nutritional value [146]. Cano *et al.,* (1997) reported that PPO has been investigated in banana for browning reaction. The synthesis of phenolic compounds is often enhanced in plant tissues under oxidative stresses such as drought and mechanical damage [151] or infection by microorganisms [161]. Similarly, increased amounts of polyphenols were considered as a characteristic feature of secondary metabolism to low temperatures in leaves of crataegus monogyna and wheat [103; 135]. Symptoms such as brown pitting, necrosis, deterioration of mitochondrial activity and cell damage have been associated with increased deposition of phenolic compounds [71]. Accumulation of polyphenols in the plants is controlled by polyphenol oxidase (PPO) also known as phenolase, through the oxidation of O-diphenols to quinines as well as hydroxylation of monophenols (Ose *et al.,* 1999). The PPO is widely considered as a plastid enzyme although it was reported in the cytoplasm of fruit tissues during ripening followed by senescence. Reduced activity of PPO was recorded during low temperature stress in *Ipomoea aquatica* [Ose *et al.,* 1999]. Keshavkant [2000] reported that the considerable reduction in PPO activity during oxidative stress period [136] particularly in leaves can be explained by the location of this enzyme in the leaf tissue, the membrane of which is the primary targets during oxidative stress induced photooxidation.

Active Oxygen Species (AOS)

Plants produce H_2O_2 in metabolic processes and cause damage of cell oxidation function. The enzyme, catalase (CAT) eliminates H_2O_2 and plays a key role in the elimination of active species of O_2^-. Catalse activities were found to be much higher in leaves of lentil, under control and stress conditions [63]. In chickpea, antioxidants like SOD, CAT and POX showed higher levels initially which declined quickly and remained suppressed during drought stress implying a strong impairment of antioxidant generation [133]. The amount of lipid peroxidation has been considered as one of the factors to determine the severity of stress [48]. The free radicals (OH^+, O_2^-) generated during lipid peroxidation readily reacted with protein and lipid membrane causing cell damage [66]. Catalase, peroxidase and super oxide dismutase cause destruction of these free radicals and limit the damage of lipid peroxidation during period of stress. The SOD converts O_2^- radicals into peroxidases which are then degraded by peroxidases and catalases. The activity of SOD and peroxidase were higher in drought resistant cultivars than the susceptible ones in cotton. Sairam *et al.* (1997) reported that the drought tolerance of genotypes was closely associated with antioxidant enzymes system which normally increased under water stress conditions. Tolerant coconut genotypes showed lower peroxidation and increased scavenging enzyme activity. They also reported that there was a direct relationship between drought tolerance of a plant and its capacity to control levels of lipid peroxidation and related enzyme activities.

Super oxide dismutase (SOD) was first isolated by Mann and Kleilin (1938) and thought to be a copper storage protein. Subsequently, the enzyme was identified by a number of names, erythrocuprein, indophenol oxidase and tetrazolium oxidase until its catalytic function was discovered by McCord and Fridovitch [1976]. The SOD is now known to catalyse the dismutation of super oxide to hydrogen peroxide and oxygen.

Therefore, the activity of these enzymes determines the relative proportion of the two constituent of the Haber Weiss reaction that generates hydroxyl radicals. Since SOD is present in all aerobic organisms and most (if not all) sub cellular compartments that generate activated oxygen, it has been assumed that SOD has a central role in the defense mechanism against oxidative stress [23; 31].

In plants, reactive oxygen species (ROS) are produced continuously as byproduct of various metabolic pathways that are localized in different cellular compartment. Under steady state conditions, these molecules are scavenged by various antioxidative defense mechanisms [70]. The equilibrium between the production and the scavenging of ROS may be perturbed by a number of adverse environmental factors. As a result of such disturbance, intracellular levels of ROS may increase rapidly [66]. Precisely how ROS are involved in mediating the plants response to these environmental stress conditions is not known. Generally, ROS have been proposed to affects stress response in two different ways. They react with a large variety of biomolecules such as lipid protein and nucleic acids that are essential to maintain the integrity of cellular structures and thus may cause irreversible damage that can lead to tissue necrosis and ultimately may kill the plant [147; 75]. These observations have been interpreted to suggest that cells have evolved strategies to use ROS as biological stimuli and signals that activate and control various genetic stress response programmes (54).

Oxidative damage in the plant tissue is alleviated by a concerted action of both enzymatic and non-enzymatic antioxidant metabolisms (80). These mechanisms include β-carotein, ascorbic acid, α-tocopherol and enzymes including superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX) and catalase (CAT). There are many reports in the literature that underline the intimate relationship between enhanced antioxidant enzyme activities and increased resistance to environmental stresses [30]. Plant experiences drought stress either when the water supply to roots become difficult or when the transpiration rate becomes very high. These two conditions often coincide under arid and semi-arid climates. Water stress tolerance is seen in almost all plant species but its extent varies from species to species [114]. The scavenging enzymes are concentrated in the chloroplast and the cytosol and protect the photosynthetic apparatus under stress by scavenging excess ROS [170]. The increasing evidences suggest that drought induces oxidative stress in various plants in which ROS such as super oxide radical ($O2^{\bullet\,-}$), hydroxyl radical ($^{\bullet}OH$), hydrogen peroxide (H_2O_2) are produced [128]. The toxic superoxide radical has a half-life of less than one second and is usually rapidly dismutated by SOD to H_2O_2, a product which is relatively stable and can be detoxified by catalse and peroxidases. These metalloenzymes constitute an important primary defense of cells against superoxide free radicals generated under stress conditions and thereby increased SOD activity is known to confer oxidative stress tolerance.

SOD activity increased in all the growth stages. It was reported that SOD enhanced water stress tolerance to plants. In tomato, cytosolic Cu/Zn-SOD was induced strongly by drought, while Cu/Zn-SOD remained largely unaffected [31]. Ascorbate peroxidase activity increased in drought. Asada [1992] reported that the ascorbate peroxidase found in organelles is believed to scavenge H_2O_2 produced from the organelles, whereas the function of cytosolic ascorbate peroxidase is probably to eliminate H_2O_2 that is produced in the cytosol or apoplast which has diffused from organelles. In the chloroplast, H_2O_2 can be detoxified and catalysed by ascorbate peroxidase.

The catalase activity was increased in drought. This result is in accordance with the findings in wheat [162]. The combined action of CAT and SOD converts the toxic $O2^{\bullet\,-}$, H_2O_2 to water and molecular oxygen, averting the cellular damage under unfavorable conditions like water stress [148; 43]. Scavenging of (ROS) Reactive oxygen species scavenging is important in imparting tolerance against oxidative stress and it may be presumed that enhancement of the antioxidative system favours water stress resistance [134].

Catalase is a heme-containing enzyme that catalyses the dismutation of hydrogen peroxide to water and oxygen. The enzyme is found in all aerobic eukaryotes and is important in the removal of hydrogen peroxide generated in peroxisomes by oxidases involved β-oxidation of fatty acids, the glyoxylate cycle (photorespiration) and purine catabolism. Catalase was one of the first enzymes to be isolated in a highly purified state. All forms of the enzyme are tetramers in excess of 220,000 molecular weight. Multiple forms of CAT have been described in many plants. These forms have been cloned from maize [150; 160] and homologous genes have been cloned from several other plants. Maize has three isoforms termed Cat-1, Cat-2 and Cat-3 that are in separate chromosomes and are differentially expressed with independent regulation [160].

Proline

In proline synthesis, pyrroline 5-carboxylate synthesis has two steps catalysed by (P5CS), which is a bifunctional enzyme (Hu *et al.,* 1992) with alpha glutamyl kinase (alpha-GK) and Glu-5-semialdehyde dehydrogenase (GSA) [193]. Under osmotic stress conditions, P5CS plays key role in the biosynthesis of proline and catalyses the major regulated step [104]. Proline, a heterocyclic amino acid, accumulates due to hydrolysis of protein under water stress conditions [106]. High proline accumulation during stress was noted as an adaptive mechanism by which it served as a store of nitrogen and respiratory substrates to facilitate post stress recovery [62]. Several possible functions of proline such as cytoplasmic osmoregulation, prevention of enzyme inactivation and stabilization of bio polymers. Buthanson *et al.* [1979] were of the opinion that proline accumulations were the causes of biotic stress rather that abiotic stress. High leaf proline accumulation under stress in tolerant genotypes of cotton resulted in biomass recovery and less reduction in seed cotton yield [168]. Arora and Saradhi [1989] observed increased level of proline under water stress which was more pronounced in light rather than dark. Upreti *et al.* (1998) observed varietalchanges in proline accumulation under water stress conditions due to variation in tolerance mechanisms.

Proline protects membranes and proteins against dehydration and temperature extremes [137; 157). A decrease in proline oxidation rate can contribute to net proline accumulation during drought stress[104]. The proline dehydrogenase gene (involved in proline oxidation to glutamate) was found to be strongly repressed in response to drought stress in *Arabidopsis*. Therefore, it appears that osmotic stress over-rides proline induction of proline dehydrogenase gene expression [104; 131]. Pestrusa *et al.* [1997] stated that alfalfa plants under oxidative stress rapidly double their proline concentration in the roots.

Level of proline accumulation in banana leaf tissues was associated with the internal water status of the plant. The proline levels started to increase from 45 µg g^{-1} to a one value of 74 µg g^{-1} fresh weights when the RWC of the leaf tissue started to decrease with the onset of water stress from 92 to 72 per cent. It is widely accepted that water deficit enhances accumulation of proline in many plant species and that proline may regulate the osmotic balance of the cell thus relieving the negative effect of stress [86]. Proline concentration in banana leaf tissue was increased with the onset of water stress. The study also showed that stomatal conductance of banana plants was affected with the changes in vapor pressure deficit in both irrigated and water stress plants [86]. To counter the osmotic stress induced by drought, many plants increase their osmotic potential by synthesizing and accumulating compatible osmolytes such as proline and betain. These osmolytes are involved in signaling or regulating plant responses to drought including growth that may be part of the plants adaptation against stress in biosynthesis (Rhodes *et al.,* 1986; 58). Proline accumulation during stress conditions makes the plant to be tolerant to water stress. Proline is a compatible solute that can have a major role in osmotic adjustments and may also have a number of protective roles [189]. These include protecting protein and membrane structure scavenging reactive oxygen species [58] and eliminating the excess reductant or regulating cellular redox status [79]. Proline oxidation rate can contribute to net proline accumulation during drought stress. The proline dehydrogenase gene was found to be strongly repressed in response to drought stress, an indication that water deficit conditions impact plant systems by affecting a shutdown of or otherwise normally functioning biochemical routes.

Drought recovery

The capability of banana germplasm to rehydrate after the stress period is of importance to drought recovery. Recovery of a banana germplasm from drought is related to its ability to retain green leaf area during that period. Plants with good leaf retention can supply more assimilates to the developing fingers during subsequent recovery. These in turn result in production of a large number of fingers and more number of hands per bunches [173]. Leaf wilting coincided with midday leaf water potentials of approximately -2.0 MPa, beyond which, some leaves become yellow and abscised. Upon rewatering, leaves appeared normal (non wilted) and leaf water potential returned to previous levels (-0.6 MPa) in two to three days later. A slow rate of onset of stress may allow for development of adaptive mechanisms such as osmotic adjustment, decreasing leaf area, abscission of leaves, leaf folding, rolling or reorientation of leaves and an increased root growth rate [69].

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