Chapter II

Review of Literature On Physiology of Drought Resistence

1. INTRODUCTION :

Water has tremendous role to play in photosynthesis, respiration, absorption, translocation and utilization of mineral nutrients and cell division. Due to this important role water is well known limiting factor in plant growth and development and numerous studies have indicated that it influences almost every aspect of plant. Its shortage as well as its excess affects the growth and development of a plant directly and consequently its yield and quality. It is obvious then that water deficits cause a general reduction in the size of most of the plants.

The cheapest source of natural water supply for crop plants is the rainfall. According to Kanitkar (1960), 77 million acres of land in India can be considered as definitely liable to drought. In dry land agriculture, a greater understanding of crop water deficits and their influence on growth and development; metabolism and yield is essential. Stanhill (1957) , showed that in 66 out of 80 papers dealing with crop response to different soil moisture regimes, water shortage was related to a depression in plant growth and in most cases to a reduction in yield. There has also been a lot of work done on the effect of water stress on plant morphology, physiology and biochemistry (For reviews Crafts, 1968; Parker, 1968; Todd, 1972; Hsiao, 1973).

Drought is a factor in yield reduction even when the damage is not apparent. Drought is also a hazzard to successful crop production throughout the world. It occurs when various combinations of the physical factors of the environment produce an internal water stress in crop plants sufficient to reduce their productivity.

Linsley _et al_. (1959) defined the drought as a sustained period of time without significant rainfall. Katz and Glantz (1977), suggested meteorological and agricultural definitions of drought. A meteorological drought could be defined as, that time period when the amount of precipitation is less than some designated percentage of the long term mean. An agricultural drought is of seasonal vegetation development. Morris (1974), defined it as "an unseasonally rapid rise in agricultural prices". There are many factors that would confound the use of above definitions, particularly in these times when aid intervention is a normal occurance in times of serious drought. A deficiency of water will influence the growth of different plant organs in various ways. Amoung these are :

(1) A decrease in the ratio of shoot to root growth.

(2) A decrease in the proportion of lateral roots to total root length.

(3) A decrease in ratio of leaf to stem.

The progress in drought research has logged because much of the past research on plant response to drought had been based on soil moisture rather than plant water status. Drought has generally been accepted as a deficiency of available soil moisture, which produces water deficits in the plant sufficient to cause a reduction in growth.

2. EFFECT OF WATER STRESS ON PHYSIOLOGY OF A PLANT :

A. Growth and Development :

The relationships between environmental factors and the growth and development of the plants vary from species to species (Sen, 1977). The environmental fluctuations can be promotive as well as disruptive. The observations on growth and developmental responses by plants have established that control of the process is exercised through physical factors in the environment such as temperature, light and soil conditions. The unfavourable environmental factors cause various physiological disorders in the plants which ultimately leads to disturbances in the developmental processes and results in the development of morphological abnormalities. Among the environmental factors which regulate growth, water, light, aeration and temperature are the prominent. The other factors affecting growth are soil and its related things, fertilizers, residues of fungicides, herbicides and insecticides. Water deficits in meristematic regions reduce growth materially (Loomis, 1934; Thut and Loomis, 1944; Wilson, 1948).

Richards and Wadleigh (1952) have presented a thorough review of many investigations which showed that even slight to moderate water stress decreased plant growth. Growth is suspended during moisture stress and resumed upon its elimination. The extent of the damage caused to the plants depends on their physiological age, the degree of water stress and the species concerned (Gates, 1964).

Generally the organ growing most rapidly at the time of stress is the most affected, (Aspinall et al., 1964).

Aspinall et al. (1964) studying the effect of moisture stress on varying stages of plant development, found that all stages were affected, but the most sensitive stage was between the completion of spikelet formation and anthesis. May and Milthorpe (1962) reported that even a short period of water stress at anthesis will markedly reduce the number of flowers that set seed. Water deficit occurs in the plant whenever transpiration exceeds water absorption; this may be due to the excessive water loss, reduced transpiration and absorption or both. According to Shaw and Laing (1968), Water stress does not affect all aspects of plant growth and development equally, some processes are highly susceptible to increasing water stress, while the others are far less affected.

The final yield of crop will be the integrated result of these effects of stress on growth, photosynthesis, respiration and other metabolic processes and reproduction. Water stress may act on the overall uptake process at various stages, eighter by the direct action of low water potential on metabolic processes or by an associated effect of low rates of water flow in the system. Movements of ions in the soil, as well as transport in the plant, may be constrained at low water potentials.

Pitman (1977) found that water availability affects the growth of the plants, due to the interaction between stomatal opening and dry matter production. The rate of accumulation of N, P and K is proportional to the rate of growth, so that, relative contents tend to be constant. The proportionality in uptake and growth can be attributed variously to increasing root size; to feed back processes in the plant, or to the rate of supply of sugars to the root (Pitman and Gram, 1977). Doerffling K. et al. (1985) observed the ABA in leaf epidermis of *Commelina communis* and have shown the results discussed in relation to the hypothesis that ABA regulates stomatal closure in water stressed leaves.

B. Mineral Nutrition :

The most important aspect of plant growth and development is the mineral nutrition. For maximal growth and well adaptation to the environment a balanced mineral status is necessary. This balance is under the control of several factors such as mineral status of the soil, ability of plant to absorb these nutrients selectively and translocate them to the other parts of the plant. Plant leaves probably act both as a source and a sink linking this balance in the plant body. The ability of plants to remobilise nutrients from leaves and transport them to the other organs is also an extremely important property in plant nutrition.

According to Evans (1972); Milthorpe and Moorby (1974), the contribution of minerals to increase in total plant dry matter is much less than that of photosynthesis, ranging among different plant species from 2-20% of the total dry weight. The movement of water in the rhizosphere facilitates the supply of nutrients to the roots, when the movement of soil water ceases because of soil dryness, nutrients uptake occurs only by diffusion close to the root. This sort of supply becomes limiting in a very short time since the nutrients reserves are quickly deplected (Crafts, 1968).

Mederski and Wilson (1960), had reported that regarding the nutrients moving mainly by mass flow, the accumulation of Mg^{2+} was reduced by soil water stress. According to Barber, et al. (1963) the mass flow could account for most of the transport of Ca^{2+}, Mg^{2+} and N while P^{5+} and K^{+} are moved mainly by diffusion which is a very sensitive process to soil water content. Marais and Wiersma (1975), had showed that the plants subjected to water stress had a lower content of P^{5+} and K^{+} than that in control.

The evidence for N is rather contradictory. The increase in the nitrogen content of the tissues with increasing water stress is likely to be associated with effect of nitrate reductase enzyme system (Viets, 1972). In any case the decrease in the microbiological activity of the soil with increasing dryness (Kramer, 1969) cause in the rate of the decomposition of organic matter. This results in a decrease in the rate of both ammonification and nitrification of organic matter, hence in a decrease in the nitrogen availability of soil.

According to Pavlov (1982), the water deficit in the wheat and barley, the uptake of phosphorous and other minerals that move through the soil by means of diffusion is decreased to a degree greater than the uptake of NO_3 that moves by means of mass flow. This movement depends upon transpiration stream. The N/P ratio increases under a water deficit.

Davies and Combrink (1986) observed the effect of Ca, K, B supply on water stress in tobacco (Nicotiana tabacum) and cotton (Gossypium hirsutum). They have studied the influence of Ca, K, ratios and B levels on chlorophyll content of tobacco and cotton leaves grown under glass house conditions. Excised leaf discs were floated on a solution of PEG 6000 to study the breakdown of chlorophyll under stress conditions. The level of B nutrition was found to interact significantly with Ca, K ratios. At the low Ca: high K ratio plants grew well and the application of B retarded chlorophyll breakdown. At the high Ca: low K ratio a K deficiency was observed and the application of B accelerated breakdown of chlorophyll. The chlorophyll content of leaf discs was much lower after the stress but the differences were in the same order.

C. Organic Constituents :

i) Carbohydrates :

Eaton and Ergle (1948), have reported that, total Carbohydrates usually are reduced under moisture stress as a result of inhibited photosynthesis. The water stress also increases severe dehydration, by increased respiration (Woodhams and Kozlowski, 1954). Working with tomato and bean plants Woodhams and Kozlowski, (1954) have reported that, the carbohydrate metabolism is altered as a result of decreasing soil moisture content before the onset of wilting. Water stress reduced carbohydrates more in the leaves than in the stems or roots.

According to Statyer (1969), Carbohydrate metabolism is affected by water stress through direct and indirect effect on photosynthesis and through several intermediate components and processes. Maranville and Paulsen (1970), studied alternation of carbohydrate composition of corn seedlings during water stress.

Lee _et al_. (1974) showed that, drought stress decreases reducing sugars, sucrose and starch concentration in pea. According to Murty and Shrinivasulu (1968), the drought resistant rice variety had higher sugar concentration than that of susceptiable variety even under conditions of drought.

Parker (1970) and Stewart (1971) reported a decrease in starch content due to water stress. Barlow _et al_. (1976), found that in corn seedlings suffering from induced water stress the increase in soluble carbohydrates concentration was inversally related to both rate of leaf elongation and total dry matter accumulation.

Ford _et al_. (1981) showed, the accumulation of reducing sugars and total sugars in stressed leaves and considered that contribution of carbohydrates to the osmotic adjustment is relatively small than the accumulation that an increase in leaf carbohydrates helps in osmotic adjustment during water stress in cotton. Ackeyson Robert C. (1985) studied osmoregulation in cotton (*Gossypium hirsutum*) in response to water stress. He observed that high P increased leaf sucrose and glucose concentration in both control and water stressed plants.

ii) Polyphenols :

They are the products of secondary metabolism in plants. The synthesis of polyphenols and their different compounds is influenced by several environmental and endogenous factors which are bound to change during life cycle of a plant.

Zucher *et al*. (1965) reported that, polyphenol synthesis is found to be regulated by light. Finkle (1967) reported that the mode of action by which the phenolic acids affect the growth of the plants is that they inhibit an enzyme that oxidatively destroys IAA and thus its harmonal effect. Tsai and Todd (1972), who observed 25% decline in the phenolic contents in both resistant and susceptible varieties of wheat due to water stress. According to them if phenolic compounds are involved in cellular injury following water stress it might be due to release of these substances into cytoplasm rather than to increased synthesis. Todd (1972), further claims that such a release might be affecting synthetic activities.

Talha (1975) reported that, there was considerable increase in the alkaloid content of Catharanthus roseus due to moisture deficit. The anatomical structure of leaves of Impatiens balsamica suffering from water stress has a greater number of tannins and raphide sacs (Todd et al., 1974). Jadhav (1984) reported that, increase in the polyphenol contents in the leaves of Panicum milliaceum (L.) during water stress.

iii) Total Nitrogen :

The major plant constituent found in plants is the nitrogen. Because the nitrogen is found in the protoplasm in about 90%. The major part of proteins and many physiological reactions center around protein molecules. Nitrogen is the nutrient which most often is limiting the plant growth. It is generally accumulated to the greatest extent by plants. It is highly essential for synthesis of many other organic compounds such as, simple and conjugated proteins.

Petrie and Wood (1938 a,b) found that formation of proteins from amino acids decreased with increasing moisture stress. Ishizuka and Tanaka (1954) reported, the accumulation of nitrogen in rice plant during growth stages. Ivanov (1965) reported decreased amino acid synthesis with moisture deficit. Zholkevich and Koretskaya (1959) showed that, the protein component of the total nitrogen was maintained falling to 77% of normal only at the end of the drought period. During the early part of the drought period, sugars in the roots increased; later there was loss under severe stress. Kozlowski (1964) had shown that, the nitrogen content of apple, tomato and tabacco are increased in plants under stress.

William and Diatloff (1975), Habish and Mahdi (1976) reported that, the nitrogen fixation is more sensitive to stress than the uptake of mineral nitrogen. Kunio Miura _et al_. (1978) observed nitrogen accumulation in _Eleusine coracana_ at early growth stages. Moisture deficits are reported to bring about increases in nitrate in bean with less effect on solube organic nitrogen. Jadhav (1984) reported the decrease of the nitrogen content in the leaves of _Panicum miliaceum_ (L.) when subjected to water stress.

iv) _Proline_ :

It is a type of cyclic amino acid which plays an important role in the stress resistance. In the last ten years a large amount of data has been accumulated which throws light on the important role played by this amino acid in stress resistance.

The investigators like Vidhyasekaran (1972), Kannaiyan _et al_. (1973 b), Sivaprakasam _et al_. (1974) and Hegade and Karande (1978) are of opinion that, proline also helps the pathogen in colonising the host tissues during diseases development.

Hsiao (1973), shown that, proline accumulates rapidly in excised and intact leaves under water stress. The rate of proline accumulation differs from species to species. Stewart and Lee

(1974) observed that, proline accumulates for osmotic adjustment. It is suggested that the accumulation of proline under water stress conditions is one of the mechanisms in plants. However, the exact role of the proline in the mechanism of drought resistance is not clearly understood. According to Dove (1968), proteolysis is a common feature in cut plants that are allowed to wilt. Thus the content of free amino acids is increased considerably due to water stress, (Barlow et al., 1976).

According to Naylor (1972), there is no uniform hydrolysis of proteins due to water stress because the number and amounts of the amino acids do not reflect hydrolysis of the 'average' ptotein of the cell. There is however, marked accumulation of free proline when plants are exposed to water stress (Barnett and Naylor, 1966; Sing et al., 1973; Rajgopal et al., 1977).

Naylor (1966) reported a 10 to 100 fold increase in proline content due to water stress in Cynadon dactylon. Baskin and Baskin (1974) noticed 115% increase in the total amount of amino acids due to water stress in Astragales tennesseensis. The effect of dehydration on proline accumulation was investigated by Palfi et al. (1974). They observed that not all species accumulate proline under water deficit; which are Zea mays, Phaseolus vulgaris, Spinacia oleracea, Chenopodium album and Beta vulgaris.

Among the 60 plants studied, mejority of herbaceous mesophytes and cultivated plants belonging to families like Solanaceae, Umbelliferae, Compositae, Leguminosae and Graminae accumulate proline under water deficit. Recently Stewart et al. (1977) suggested that proline accumulation results from inactivation by water stress of normal mechanism by inhibiting proline oxidation.

Haung and Cavalieri (1978) have studied proline oxidase and water stress induced proline accumulation in Spinach leaves. According to them Spinach (Spinacia oleracea L.) leaf discs accumulated free proline when exposed to polyethylene glycol solutions of water potential less than -10 bars. At -20 bars, the accumulation was 11 micromoles per gram original fresh weight in a 24-hour period. Tymms and Gaff (1979) have studied proline accumulation during water stress in Resurrection plants. They have shown that free proline increased in nine species and remained unchanged or declined in two other tolerant species.

Ilahi et al. (1982) observed the accumulation of proline and abscisic acid within 4 days of drought in resistant cultivar of maize and considered that proline and ABA are possibly biochemical indicators of resistance against drought. Jadhav (1984) observed that the proline content in Proso millet leaves is high during vegetative and grain filling stage. During drought conditions Proso millet plant accumulates proline which may play a key role in stress recovery.

Daniel P.D. (1985) reported, nocturnal accumulation of acid in leaves of Wall Pennywort following exposure to water stress. He observed physiological responses to water stress (drought) by comparing control and water stressed plants. L.N. Rao et al. (1985) shown sugar and proline accumulation in glossy and non-glossy cultivars of Foxtail millet grown under water stress; he observed that glossy accumulate more sugars and proline than non-glossy cultivars.

Gaikwad (1987) also reported that, there is accumulation of proline in Moth bean when the plants are subjected to water stress.

D) Effect on Generalized Sensitivity of Plant Processes :

According to Hsiao, Acevedo, Fereres, and Henderson, (1976) effect of water stress on generalized sensitivity of plant processes or characters are listed as follows :-

1)	Cell growth	-	decreases
2)	Wall synthesis	-	"
3)	Protein synthesis	-	"
4)	Protochlorophyll synthesis	-	"
5)	Nitrate reductase level	-	"
6)	Stomatal opening	-	"
7)	CO_2 assimilation	-	"
8)	Respiration rate	-	"
9)	ABA synthesis	-	Increases
10)	Proline accumulation	-	"
11)	Sugar level	-	"

Almost every process in plant cells has been found to be affected by water stress. As successively greater water stress is applied, successive metabolic disturbances become apperant. Growth is extremely sensitive to water stress and growth rate may begin to decrease as soon as water content falls below full saturation. The inhibition of growth and associated biosynthesis may induce further deleterious physiological effects through the accumulation of matabolic intermediates that can not be utilised.

Photosynthesis (CO_2 assimilation) is affected at quite moderate levels of water deficit in measophytes and rapidly declined to zero. Overall protein content tends to fall, soluble protein levels may decrease by 40-60% and the levels of some individual enzymes such as nitrate reductase decrease. The activities of some hydrolytic enzymes on the other hand rise. The increased hydrolase activity combined with inhibited synthesis probably accounts for the overall decline in protein content. Over a period of time a combination of such physiological effects could lead to an overall metabolic disturbance sereve enough to cause death.

The turgor pressure however, diminishes very rapidly in the initial stages of water loss. Plant cell will grow only when the protoplast exerts a positive pressure on the cell wall. The loss or decline of turgidity might affect the properties of cellular membranes, the permeability and possibly enzymatic properties. Stomatal opening also depends on turgidity of guard cells, and decline in the rate of photosynthesis is to some extent secondary to stomatal closure, in both mesophytes and xerophytes.

Karamanos A.J. (1978) studied the water stress and leaf growth of field beans (Vicia faba L.) in the fields. He observed the total leaf area of well watered plants was about double that of the non-watered ones. He also observed that leaf death was affected by drought earlier than leaf production and unfolding.

Sung and Krieg (1979) have studied relative sensitivity of photosynthetic assimilation and translocation of ^{14}carbon to water stress. They observed the relationship between photosynthesis and translocation rate changes as affected by water stress intensity and stage of plant development was evaluated in cotton and sorghum, representing a C_3 and C_4 photosynthetic type, respectively. Photosynthetic rates were reduced as midday leaf water potentials declined from -14 to -27 bars in both species. Sorghum maintained higher photosynthesis and translocation rates compared to cotton at comparable leaf water potentials; however the rate of sorghum than in cotton. Photosynthetic rates were reduced with increasing water stress prior to any significant change in translocation rates suggesting that photosynthesis is the more sensitive to the two processes. Severe water stress, corresponding to leaf water potentials of -27 bars, did not completely inhibit eighter photosynthesis or translocation.

3. MECHANISM OF DROUGHT TOLERANCE :

A. Introduction :

Drought is defined as "prolonged dry weather". However, prolonged and dry are the relative terms as drought in world's wet tropics would be a flood in the arid zones. For a period of dry weather to affect a plant community, the rainfall deficit must lead to a soil water deficit and ultimately to a plant water deficit. The degree to which a rainfall deficit is translocated into a soil water deficit depends on the rate of evaporation during the rain free period and on the physical and chemical characteristics of the soil.

B. Classification of Drought Resistance :

The literature on stress physiology consist of numerous variations in terminology. According to Levitt (1980) there are three kinds of stress -

(a) Stress resistance -

The ability of a plant to endure an extremely applied stress.

(b) Stress avoidance -

The ability of a plant to prevent an extremely applied stress from producing an equivalent internal stress in plants.

(c) Stress tolerance -

The ability of a plant to endure an internal stress enduced by the extremely applied stress.

May and Milthorpe (1961), Turner (1979) suggested three primary types of drought resistance which are listed below :-

(a) Drought escape -

Drought escape is the ability of a plant to complete its life cycle before a serious plant water deficit develops.

(b) Drought tolerance at low tissue water potential -

The ability of a plant to endure rainfall deficits at low tissue water potential is known as drought tolerance at low tissue water potential. Plants may withstand periods of low water supply and remain green, potentially photosynthetically active plants, but their productivity during this period will be low (Fischer and Turner, 1978).

(c) Drought tolerance at high tissue water potential -

It is the ability of plant to endure periods of rainfall deficit while maintaining a high tissue water potential. Levitt (1972), Arnon (1975) considered this aspect of plant as drought avoidance.

Thus mechanism of drought resistance during sereve water shortages may have little significance in an agricultural context in which productivity and yield are important. So the valuable research on drought resistance is more bebeficial in the irregular periods of rainfall.