
An attempt has been made here to review briefly the various but salient aspects of drought in terms of metabolism, growth and yield.

**Seed germination:**

For the proper establishment of the seedling an adequate supply of water should be maintained; otherwise the germination may be delayed or arrested with increasing soil moisture stress, Doneen and MacGillivray, (1943); Hunter and Erickson (1952) and Ayers (1952). Williams and Shaykewich (1971) consider soil water matric potential
controls hydraulic conductivity, effective stress, aeration and seed soil liquid contact area collectively as soil moisture stress and their studies indicated a slower rate of germination and with a significant reduction of total germination with increasing soil moisture stress.


Recently various osmotica have been employed by various workers to simulate water deficit. These osmotica are polyethylene glycol of various molecular weights, mannitol and other sugars such as sucrose, fructose, glucose and glycerol etc. However, conflicting results have been reported. Uhvits (1946) employed NaCl and mannitol as osmotica to study their effects on germination of alfalfa.
Germination was reduced and the reduction was more in NaCl than in mannitol. Thimann (1954) is of the opinion that mannitol acts solely as an osmotic agent in preventing water uptake and has little direct effect on cell metabolism. Mannitol has been widely used to increase the osmotic concentration. Ordin et al. (1955, 1956, 1957; Ordin and Bonner, 1957; Cleland, 1958, 1959, 1963, 1967) and Jackson, (1965) found no effect of mannitol on Avena coleoptile section growth in concentrations up to 0.02 M. Bayley and Setterfield (1957) and Baker and Ray (1965) observed inhibition of cell elongation and synthesis of cell wall material by mannitol. Lagerwerf et al. (1961) found carbowax (6,000 mole wt.) toxic, but carbowax (20,000 mole wt.) satisfactory after dialysis. Jackson (1962) undertook an evaluation of polyethylene glycols (PEG) as osmotic agents, he found that there was complete inhibition of growth of root-hairs of redtop grass seedlings. Mannitol was found to be rapidly absorbed and metabolized and served as stimulation like glucose and sucrose for elongation of root hairs of redtop grass seedlings by Jackson (1965). Mannitol was found to be used up in the respiration in 15 out of 26 plant species examined by Trip et al. (1964). They have recommended use of mannitol as an osmoregulator in short term experiments. Manohar and Heydecker (1965) found that mannitol penetrated germinating seed. Its stimulatory effect on the
root growth of *Agrostis* was reported by Jackson (1965). He also recommended use of mannitol as a satisfactory osmotic agent. He, however, cautions not to assume mannitol as nonabsorbable and metabolically inert in higher plants. He found mannitol to have effects upon metabolic processes independently of its role in increasing the osmotic concentration of the external medium and toxic effect to redish was observed by Taylor (1965). In the water stress studies, Manohar and Heydecker (1965); Cheesman et al. (1965) and Janes (1966) found carbowax i.e. PEG satisfactory. Ordin (1958, 1960) in his water deficit experiment in *Avena* coleoptile with non permeabilng mannitol and permeabilng NaCl, He was able to get similar water deficit and water potentials, but difference osmotic potentials and turgor pressures. Cell enlargement was reduced and mannitol caused more reduction with the decrease turgor and increase in osmotic potentials did not inhibit metabolism of noncellulosic, polysaccharide. Reduction in turgor influences cell wall metabolism and cell elongation.

Parmar and Moore (1968) compared the osmotic effects of PEG (6000 mole wt.), mannitol and NaCl on germination of corn and found that all the solutions had a detrimental effect on the germination of corn being greatest with PEG and least with NaCl and they suggested PEG may simulate the soil closely in terms of the effect of water deficit of
germination. According to Barrs (1968) carbowax is probably the safest plasmolytical substance available. Farr and Norris (1971) examined the effects of the above osmotic agents on the elongation of *Avena sativa* coleoptile tissue in the presence and absence of IAA. They observed stimulatory effects of sucrose, fructose and glucose on elongation both in aqueous solution and in IAA. Galactose was inhibitory. They found the ethylene glycol, propylene, glycol, pentaerythritol and sorbitol and mannitol could be used as osmoregulators; polyethylene glycol 1000 and glycerol had stimulated. According to Kaufmann and Eckard (1971) PEG of high molecular weight (6,000), when added to a nutrient medium causes changes in plant water relation similar to those expected in dry soil. PEG of lower molecular weights are not recommended for causing water stress. Arrested germination of Brown sarson under increasing osmotic potential of PEG was reported by Pandya et al. (1972, 1973). Parmar and Moore (1968) and Pandya et al. (1972) reported decreased fresh and dry weights in corn and Brown sarson seedling respectively under various osmotica. They also reported lower moisture content under osmotica. Germination of bean seed was studied at various osmotic pressures 3.5, 7.5, 11.0, 16.0 atm. water stress reduced germination percentage, root growth and early seedling development, Magalhaes and Carella (1972). Prisco
and O'Leary (1970) reported lower moisture content in the embryo axis of germinating *Phaseolus vulgaris* seeds under osmotica. Vora et al. (1976) reported lower fresh weights of maize seedlings by various osmotica such as polyethylene glycol (6,000 mole wt.) mannitol and NaCl.

**Growth and development in relation to drought:**

One of the indices and indicators of the deleterious effects of water deficit is growth of the plants and various reviews have appeared from time to time on the effects of water deficit on plant growth and development (Richards and Wadleigh, 1952; Shaw and Laing, 1965; Gates, 1954, 1968; Slatyer, 1967; Crafts, 1968 and Kozlowoski, 1968, 1972).

The effects of water at different stages of growth have been reviewed by Salter and Goode (1967). Their review includes about 1100 references indicating a tremendous interest in this subject covering agricultural crop and horticultural plants. It was observed that different organs and different phases of the plant are differently affected by water deficiency (Gates, 1964; Chinoy and Nanda, 1950, 1952; Burstrom, 1956; Iljin, 1957; Stocker, 1960; Lerman, 1963).

Chinoy (1962, 1968) observed that in the same plants the younger tissues were more hardy than older ones. Similar observations have also been observed by Levitt, (1956;
Wagermann, 1961; Jarvis and Jarvis, 1963 and Chen et al., 1968). Effects of wilting treatment given at a particular growth stage may be either deleterious or beneficial, for example, in wheat and barley wilting treatment given at an early stage of development resulted in better growth and yield, while at subsequent stages, it was harmful (Chinoy, 1968; Vyas, 1971).

Under water stress, size of the plants, especially, the height is generally reduced. Robins and Domingo (1953) noted a shortening of the internode of the corn particularly in the upper portion of the plant. According to Skazkine (1954) the time course of the drought effects depends closely, both quantitatively and qualitatively on the developmental phases of plants. Some phases are more critical than others. Gates (1955) found that the growth of leaf was more sensitive than that of the stem. According to Williams and Shapter (1955) the changes in the sensitivity of the various growth phases to stress reflected an enhanced sensitivity of the rapidly growing tissues. Kozlowski (1965) observed that the water stress greatly influenced the distribution of the essential factors, whether nutrients or hormones within the apex; even the food substances to the developing floret are diverted under water stress. Low water potential caused decrease in dry matter production, photosynthesis and translocation as
reported by Etherington (1967). Effects of water stress on apical morphogenesis and flower formation in cereals, have been studied by Nicholls and May (1963), Husain and Aspinall (1970). Gates (1968) suggested that the apex is particularly sensitive to water stress during both vegetative and floral development.

Pringle and Chary (1968); Champbell et al. (1969) observed that under continuous water stress growth and yield of plant was retarded. Moisture stress reduced growth and yield of finger millets depending on the time at which the stress was given, Thimmagocado et al. (1976). Drought condition reduced percentage germination as well as the seed weight of Peanut seeds, Pallas et al. (1977). When maize roots were placed in PEG -12 bars, there was an immediate cessation of growth, Acevedo et al. (1971).

Enzymes and water relation:

Relationship between drought resistance and enzymic activity was explained by Stocker (1960). According to him, the shift of equilibrium towards hydrolysis was more pronounced in drought sensitive than drought resistant varieties. All oxidation and reduction processes occur at a faster rate; this was apparently not due to an increase in metabolism but utilization of energy in vital processes.

Effect of water stress on enzyme activities has been
reviewed by Stocker (1960) and Evenari (1962) and more recently by Todd (1972). Hydrolyzing enzymes were increased under wilting which worked on the hydrolytic side in comparison to their synthetic activity (Kramer, 1955, 1956). Stocker (1960) considers two phases in understanding the mechanism of drought resistance, these phases are (i) the reaction phase and (ii) the restitution phase. The reaction phase is a oxidative-hydrolytic and destructive one. The restitution phase as reductive - synthetic - constructive phenomenon. Changes in behaviour of hydrolyzing enzymes on the water stress reported by various workers have been mentioned along with their substrates.

Decrease in peroxidase with increase in dryness in desiccated wheat leaves was reported by Todd and Yoo (1964). Dehydrogenase activity slightly rose and sharply declined when leaves had lost 60% of their original water content. Low catalase activity of plant tissues under water stress was also reported by Dorogannovskaya (1956); Chinoy et al. (1969); Acharya (1974) and Vora et al. (1974). Farkas and Rajathay (1955) and Lukicheva (1968) reported increased catalase activity and decreased peroxidase activity in water stressed tomato and wheat plants. Polimbetova et al. (1964) also reported higher catalase activity under water deficit. Polimbetova et al. (1964) further reported that in drought resistant varieties of wheat on dry plots, oxidation-
reduction processes were not as highly activated as in less drought resistant varieties.

In detached rapidly desiccated wheat leaves, phosphatase activities decreased as reported by Todd and Yoo (1964). Further, the water deficit is differently responded by different enzymes. Thus, for example, with increased water deficit, nitrate reductase activity disappeared at a much faster rate than soluble proteins but peroxidase decreased at a lower rate than proteins as reported by Stutte and Todd (1969) and Mattas and Pauli (1965). Protease activity in tobacco leaves (Kawashita et al. 1967, 1968) and ribonuclease in several species increased with dehydration treatment, Kessler (1961).

Takaoki (1968) observed that the peroxidase activity was not affected by soil moisture levels. The enzyme was more in older leaves than younger or medium aged leaves. He also found that phosphorylase and phosphomonoesterase were more active in plants grown in dry soil than wet soils. Leaves of water stressed wheat plants showed decreased peroxidase activity, Lukicheva (1968) in his studies on the changes in enzymic activity under water stress on wheat leaves. In cowpea plant Takaoki (1968) observed that the catalase activity was highest at optimum soil moisture, if however, soil moisture level increased or decreased then the activity was supressed. In Sesamum seedlings the
enzymic activity fluctuated with time, Sesamum seedlings under desiccation, however, showed decline in catalase activity, Acharya (1968).

Many of the cellular enzymes occur in more than one form—isozymes and these isozymes change at different rates during desiccation of tissues. Succinic and glucose-6-phosphate dehydrogenase undergo quantitative change while malic dehydrogenase undergoes change in both quality and quantity. Peroxidase isozymes also showed marked changes after desiccation of the leaves as noted by Stutte and Todd (1969).

Under water deficiency in roots of Zea mays, Mir et al. (1970) observed a decreased rate of respiration and increase in cytochrome of oxidase activity. When mild to moderate stress was given to green barley leaves, a decline in level of phosphoenol pyruvate carboxylative was noted, Huffaker et al. (1970).

Wilson (1971) reported that in crested wheatgrass seedling amylase synthesis was not affected at low water potentials. However, in the same plant he observed that water potentials at -20 atm inhibited α-amylase. Maranville and Paulson (1972) observed in case of corn seedlings reduced protein synthesis during severe moisture stress condition, the loss of protein was not an account of increase protease activity. During mild stress protein
did not appreciably decrease, RNAse activity increase during severe stress.

According to Todd (1972) severe water deficits cause an overall decrease in enzyme level. Enzymes involving hydrolyzing or degradation remain at the same level or increase; they do not decrease until a severe desiccation has occurred. Enzyme associated with synthesis are decreased and levels of others rise as a result of water deficit. Enzymes which are stimulated by moderate water stress are α-amylase, Spoehr and Milner (1939) and ribonuclease Yi and Todd (1970) as mentioned in Todd (1972).

Bardzik et al. (1971) and Plaut (1974) reported inhibition of nitrate reductase activity under reduced soil moisture potential. Vora et al. (1974) reported depressed catalase and peroxidase activity of embryo axis and endosperm of Sorghum seedling under restricted moisture level.

Desiccation treatment depressed the catalase activity of wheat and sesamum seedling which rose again when the seedlings were revived, Acharya (1974), Acharya and Desai (1974). Low moisture level considerably depressed the catalase activity in embryo axis of Maize and gram and cotyledons of gram reported by Vora et al. (1975).
Nucleic acid metabolism:

Nucleic acids are known as the chief metabolites which decrease with a reduction of growth and increase with its resumption (Barskaya and Oknina, 1959; Tselniker, 1963) and an important role has been assigned to nucleic acid metabolism in adaptation of plants to adverse environmental conditions. Many workers studied the nucleic acid metabolism in plants under water stress. However, most of the data on the nucleic acid and water stress are available from the work of germinative seeds. Some of the data reported merit evaluation as it is likely that the data reported may be due to poor of analytical techniques, Hsiao (1973). A reduction in the total RNA content in the stressed tomato leaves was reported by Gates and Bonner (1959). But the leaves possessed the ability to incorporate $^{32}$P-labelled phosphate in RNA. They concluded that stress conditions lead to increase in the rate of destruction of RNA.

Kessler (1961) also reported decrease in RNA concentration per unit dry weight of tomato plants and this decrease was either due to increased RNA hydrolysis or due to reduced RNA synthesis. The incorporation of thymine-$^{14}$C in DNA was also considerably low in water stress plants, drought also enhanced RNase activity which resulted into enhanced decomposition of RNA. Treatment of
tomato plant with adenine reduced RNase activity as a result of which, RNA concentration increased. The adenine treated plants showed greater resistance to soil as well as atmospheric drought. DNA synthesis was also stimulated during early growth stages. Application of substances like caffeine, uracil, xanthin and uridine triphosphate enhanced drought resistance. Brouwer (1956) observed a cessation of the DNA synthesis in developing Vicia faba seeds when water dropped at the 75% of cotyledon fresh weight.

West (1962) observed an increase in RNA content of corn seedlings under water stress and there was quantitative reduction in the nucleotides. The nucleotide composition of RNA was altered in the droughted plants. The water stressed seedlings contained significantly higher ratio of guanosine monophosphate and uridine monophosphate to cytidine monophosphate and adenosine monophosphate. Kessler and Tishe (1962) gave explanation on the RNA metabolism during unfavourable conditions of the plants. They selected one drought tolerant plant (Olea europea) and another drought sensitive plant (Ligustrum sinensis). They observed that the resistance of the plant to unfavourable conditions was correlated at least partly due to either a higher (G + C) content of its RNA, or its capacity to synthesize (G + C)
rich molecules under the stimulus of a moderate water stress. In their opinion this might constitute a basic part of hardening reactions.

A decrease of nucleic acid content in the droughted wheat plants and an accumulation of intermediate products of nucleic acid metabolism was found by Ivanova (1965). Further, under severe wilting in addition to proteins, there was also decomposition of nucleoproteins. Satarova and Tvorus (1965) investigated the effect of high temperature and atmospheric drought on the RNA content and protein synthesis in potato. They observed an increase in the ammonical and amide nitrogen and a decrease in the content of protein. Plants hardened by temperature and by $\text{ZnSO}_4$ had more RNA than in the control plants especially after dry wind.

RNA is probably not affected by mild or moderate stress, Genkel et al., (1967) Stutte, (1968) West, (1966) However, in the leaves of sugarbeet, Shah and Loomis (1965) reported a significant decline in RNA and DNA, even under moderate stress. Ghazaleh and Bandershott (1967) observed higher DNA and RNA content in leaves of droughted sweet orange plants, than in plants under normal environmental conditions. Further they noticed fluctuations in the content of nucleic acids in bark tissue during the drought period of eleven weeks and this was attributed to the cambial activity.
In severely water stressed maize plants, Maranville (1967) found stimulated nuclease activity and a decline in RNA and DNA content and increase in free nucleotide,

According to Dove (1967, 1971) water stress directly affected RNase activity with a parallel or a preceding increase in soluble nitrogen content. There was also enhanced activity when excised leaf became yellow. He also found stimulated RNase activity in desiccated tomato leaflets. Water stress directly affected RNase activity at the cellular levels. When germinating seed were submitted to severe desiccation, there was no effect on mRNA if the prior imbibition was one day; if however, there was a period of three days of prior imbibition, the same desiccation treatment for two day altered or destroyed a majority of the mRNA, Chen et al. (1968).

According to Stutte (1968) the nucleotide composition of wheat RNA alone was not a criterion for determining the degree of drought resistance in wheat. When leaves and ears were treated with zinc and boron the biosynthesis of nucleic acids during drought was less reduced as compared to untreated plants, Vlasyuk et al. (1969). These elements supressed the activity of RNase during drought and as a result RNA content decreased with a lower rate in the plants. Increased RNase activity was associated with declined water content of plant tissue by Tvorus (1970). Activity of RNase
in many plant parts may be modified by cytokinin and ABA. Cytokinins repress RNase activity and ABA enhance it (DeLeo and Sacher, 1970; Leshem, 1971; Sodek and Wright, 1969; Srivastava, 1968 and Wyen et al., 1972). Both ABA and cytokinins have a role in the regulation of plant water balance (Mizrahi et al., 1970, 1972; Tal and Imber, 1971).

According to Del tour and Jacquard (1974) a drought sensitivity was related to the onset of nuclear DNA synthesis and genome duplication (Hsiao, 1970; Bewley, 1972 and Dhindsa and Bewley, 1976) reported the during desiccation of the drought tolerant moss Tortula ruralis, polysome levels substantially declined without stimulated RNase activity. They also observed that the ribosomes in the desiccated moss failed to complex with mRNA fragments.

Effect of the drought on the growth, ribosomal content, and water potential of the immature floral apex of wheat plant was investigated by Barlow et al. (1977). They observed cessation of elongation and differentiation of the floral apex at approximately $-12 \times 10^5$ pa (pascals). The polyribosomal content decreased from 50% of the total ribosomal to less than 10%. Elongation of expanding leaves was also severely inhibited. When the drought was continued, the water potential was also decreased. The exposed leaves died at about $-35 \times 10^5$ pa but the apex was still alive even at a water potential of $-60 \times 10^5$ pa and rewatering it eventually resumed growth.
Protein metabolism:

Proteins are the basic constituents of protoplasm and play a vital role in basic life processes. They are universally present in any cell. This is evidenced by the fact that the enzymes are the proteins, nucleic acids are conjugated with proteins to form nucleoprotein and the cytoplasmic membranes are also comprised of complex lipoproteins. Besides together lipids and carbohydrates, proteins are a chief source of energy. Proteins provide the carrier groups of enzymes and therefore, their metabolism plays paramount role in the physiological processes, Mothes (1956). Structural and medium component of protein is water, Klotz (1958). Any factor that reduces availabilities of water thus markedly influence structure and activities of enzymes. This has been adequately reviewed by Parker (1972).

An increase in soluble nitrogenous compounds of low molecular weight such as amino acids, ammonium and amide compounds and soluble protein has been reported under water deficit (Axelrod and Jagendorf, 1951; Roberts and Wood, 1951; Roberts, 1952 and Mothes and Engelbrecht, 1956).

According to Stocker (1960), there are two protein responses or phases in relation to drought. Phase one is the reaction phase and is characterised by decrease in protein content and formation of amino acids; in the second phase, i.e. the restitution phase, there is increase in protein content. Subsequently this postulate was also
supported by Chen et al. (1964). Proteins are adversely affected under water deficit (Satarova and Tvorus, 1965; Shah and Loomis, 1965; Thompson et al., 1966; Stutle and Todd, 1967, 1969; Saunier et al., 1968). On the other hand, Ghazaleh and Handschott (1967) reported no adverse effect of drought on concentration of water soluble proteins. That water deficit stimulates the hydrolysis of protein was shown by several workers. Thus, for example, Vozhenko and Shkol'nik (1963) found an increase in hydrolysis of proteins in the leaves of oat and barley under drought condition; there was accumulation of amino acids in the stem.

According to Kessler (1959), the deleterious effects of water stress on protein synthesis of plants may be due to a decreased supply of free amino acids from the amino acid pool, their defective incorporation into peptide chains or accelerated proteolysis. He further observed that under drought, RNase was freed, resulting in an enhanced decomposition of RNA and thereby impairing protein synthesis. Water stress impairs the protein synthesis; it also leads to proteolysis as reported by Zholkevich and Koretskaya (1959). In the opinion of Stocker (1960), the synthetic activities of the protease decreases and protein synthesis slows down under water stress. Vaadia et al. (1961) also reported decreased proteins during moisture stress.
Grinenko (1963) observed an increase in alanine and proline content in corn and sorghum under severe drought conditions. Fawcett (1965) observed a marked effect of environmental conditions like available moisture in the soil and its nutrient status on the protein content of wheat grain. Todd and Basher (1965) observed a destruction of the cellular components by hydrolytic enzymes, in droughted plants, but the crown which is the most drought tolerant part showed the least change in nucleic acids and protein.

In wilted excised leaf of a perennial grass, Kemble and Macpherson (1954) and in ladino clover leaves by Routley (1966) observed proline accumulation under water stress. Barnett and Naylor (1966) reported a continuous synthesis of amino acid in bermuda grass during water stress, but inhibition of protein synthesis and decline in protein level. Chen et al. (1964, 1968) observed a cyclic pattern of increase, decrease and restitution, in citrus leaves under water stress. Further, they reported inactivation of mRNA and subsequent inhibition of protein synthesis was resulted when wheat embryos were dehydrated during 24 and 72 hours of germination. Thompson et al. (1966) also reported a decreased synthesis of amino acids under moisture stress.
Genkel et al. (1967) observed a stimulated RNase activity under drought and other unfavourable conditions and this enhancement caused temporary break down of poly-somes which, in turn, reduced the rate of protein synthesis. According to Maranville (1967) the synthesis of protein was affected more than protease activity under water stress. The loss of protein was not detected during water stress. Drought changes the symmetry of cytoplasmic protein and increases the asymmetry, which after rewatering approximated that in controls indicating that macromolecular changes which occur during drought are reversible, Sedykh and Khokhlova (1967).

Petrie and Wood (1938) reported decreased protein synthesis with concomitant formation of amino acids under water stress. Ben-Zioni et al. (1967) reported decreased protein synthesis in water stress tobacco leaves. They also further reported reduction in leucine, incorporation under water stress. Later on Mir et al. (1970), Itai et al. (1968) also supported these findings.

Accumulation of total amino acids, glutamine, asparagine and mark increased in proline has been reported in the leaves of winter wheat, tobacco and rice under different water stress conditions, Palfi and Juhasz (1968).

Proline and asparagine favoured an increased in the relative hydration of protoplasm, there was less degree of
metabolic disturbance and also a partial normalization of aminoacid was maintain in these varities, Protsenko et al. (1968).

Genkel (1970) remarked that a high degree of resistance to drought is due largely to plant's ability to renew protein during the stress period. Todd et al. (1970) studied the protein fractions isolated from the wheat leaves subjected to the moisture stress. They reported degradation of protein to aminoacid in moisture stress leaves. Two major fractions were reported— one of very high molecular weights and second fraction was of low molecular weights. In the drought condition, the second fraction decreased markedly under the stress and the first fraction increased especially after recovery from drought. Hsiao (1970) reported decline in polysome levels in water stress tissues. In tissues subjected to the water stress, absisic acid increased, and it is likely that absisic acid may inhibit protein synthesis.

Proline accumulation under water stress was also reported by Singh et al. (1973). They found that barley plants subjected to water stress exhibited a rapid and considerable accumulation of proline. The number of membrane bound polysomes decreased in response to water stress, Armstrong and Jones (1973). Free protein contents of plants with the optimum supply of water is usually very low 0.2 to
0.6 mg/gram dry wt. During slow dehydration of the tissues, however, the free proline content rapidly rises and may reach a high level; therefore, a level of free proline has been considered as a reliable index of the degree of water deficit of tissues by Palfi et al. (1973). In their opinion, the proline test can also be applied for the diagnostic physiological drought due to salinization and cold. They have classified plants as proline accumulating and non-accumulating. Greenway et al. (1972) reported lower protein synthesis in maize root tips by mannitol and PEG. Mannitol had greater effect than PEG.

Dhindsa and Cleland (1975) observed a qualitative change in the types of protein produced by Avena coleoptile in water stress. There was also a quantitative reduction in the rate of incorporation of leucine into proteins. Similar changes were noted when osmotic mannitol and carbowax -4000 were used. Further Dhindsa and Cleland (1975a) and Mir et al. (1970) reported inhibition in total protein synthesis in various plant tissues under water stress. Dhindsa (1976) also reported inhibition of protein synthesis in water stress Avena coleoptile sections. Moreover, Dhindsa and Bowley (1976) studied the responses of drought in Tortula ruralis, and reported a decrease in fresh weight and inhibition of amino acid incorporation into protein and a decline in polysome with increasing water
stress; however, the ribonuclease activity increased. They further observed that during water stress ribosomes run off from mRNA and failed to reinitiate. Further Dhindsa and Bewley (1977) observed proteins were found to be stable during desiccation and subsequent rehydration, changes in membrane permeability, as indicated by the leakage of aminoacid, were observed during rehydration of desiccated moss and were dependent on the rate of desiccation.

Carbohydrate metabolism:

Carbohydrate metabolism as affected by moisture stress has been reviewed by several workers from time to time (Wadleigh and Ayers, 1945; Eaton and Ergle, 1948; Henrici, 1952, 1953; Sizakyan, 1954; Wager, 1954; Woodhams and Kozlowski, 1954; Mothes, 1956; Stocker, 1960; Evenari, 1962).

Water deficit lowers the starch content of the leaves with increase in hexose sugars (Iljin, 1957; Eaton and Ergle, 1948; Wadleigh and Ayers, 1945; Vasiliev and Vasiliev, 1936), but often changes in starch content were not compensated with changes in sugar content.

In droughted plants, reducing sugars were increased (Julander, 1945; Amer and Williams, 1958; Naidu, 1967 and Hodges and Lario, 1969). Decrease in synthetic activity and
increase in hydrolytic activity of enzymes invertase on sucrose. Under water deficit condition was reported by Genkel (1954). The decline in starch content and soluble carbohydrate under water stress may also be an account of decreased synthesis, Iljin (1957). Subbotina (1961) found that in cucumber, sugar also decreased as profound wilting caused a greater expenditure of sugar in energy processes. The sugars which accumulated in the leaf as a product of starch hydrolysis will be inactive. He also reported that decrease in starch content was an account of stimulated amylase activity in droughted plants. Vaadia et al. (1961) discussed the accelerated conversion of starch to sugars. Similarly, a four-fold increase in amylase activity was noted in cotton plant under water stress by Eaton and Ergle (1948). According to Vaadia et al. (1961) photosynthesis was less affected by water stress than growth. Reduction in sugar phosphates might result from reduced carbohydrate phosphorylation due to ATP shortage, Zolkevich and Rogacheva (1964). According to Tarchevskii and Siyanova (1963) drought changes the pathway of post-photosynthetic transformation of carbon, which was considered as an adaptive response of the droughted plants. They observed more labelled carbon in raffinose, proline, valine and malic acid under the influence of drought. Gates (1964)
noted that water stress causes increase in respiratory rate and these led to a degradation of starch level and enhancement in soluble carbohydrates and total sugars. Soil water deficit increased the level of sugar phosphate in plants of *Trifolium subterraneum*, Wilson and Huffaker (1964). They also suggested that the reduction in starch level in many species under water stress may also be on account of reduced level of UDPG. Water stress may interfere with energy utilization by uncoupling respiration and phosphorylation (Genkel, 1964; Zolkevich and Rogacheva, 1964) or from increased phosphatase activity as shown for chloroplasts isolated from water stressed plants, Mir and Poljakoff-Mayber (1966). Water stress adversely affected the movement of assimilates, Wardlaw (1967). Naidu (1967) observed more invert sugars in leaves of *Pennisetum* under water stress. Low water potential suppressed the synthesis of polysaccharides as reported by Hiller and Greenway (1968). According to Parker (1968) sugars increase in drought and the liquid water sugar mixture acts as a solvent as the cell dehydrates and thereby affords protection to tissues against dehydration.

Enzymatic hydrolysis of sugar decreased but that of starch increased during moisture stress. Acharya (1968) and Acharya and Chinoy (1975) reported increased amylase activity under water stress. Jani et al. (1968); Chinoy
(1969) and Jani (1969) reported an increase in the amylase activity in the desiccated barley seedling with a progressive decline in starch content resulting in a greater formation of sugars. A decline in starch content with an equivalent rise in reducing and nonreducing sugar as well as total carbohydrate was reported for loblolly pine under drought by Hodges and Lario (1969). They were of opinion that the decrease in carbohydrates was due to the decrease in the rate of growth of plants and not hydrolysis of starch. Jones (1969) also reported an inhibition of GA-induced synthesis of α-amylase in barley half seeds at a water potential above -20 atm. Maranville and Paulson (1970) observed no change in fructose and glucose concentrations on corn seedlings, subjected to three levels of moisture stress, however, there was much increase in sucrose concentration. Chlorophyll concentration decreased with increasing moisture stress. Chlorophyll a was more adversely affected than chlorophyll b. Sucrose and starch synthesis, as measured by 14C glucose incorporation were not changed by stress. Stimulated amylase activity under water stress was also reported by Vieira-da-Silva (1970). Stewart (1971) observed a faster decline in starch content of wilted leaves of bean with an increasing free sugars, which was mainly sucrose.
Vyas (1971) reported low activities of amylase and invertase enzyme and higher starch content in endosperm of seedling of barley under low moisture level. He also reported stimulated amylase activity under the water stress in the embryo axis of barley but a depression in invertase activity in embryo axis and as well as wilted leaves. There was increased concentration of non-reducing sugar in the embryo axis as well as in wilted leaves but lower amount in water-stressed endosperm. The invertase activity was considerably reduced in the embryo axis but was enhanced in water-stressed seedling especially earlier germination; low moisture level also decreased the reducing sugar concentration in both embryo axis and endosperm. Decline in glucose and sucrose in droughted Larrea divaricata leaves and this was not due to more respiration in the droughted plants. Pandya et al. (1973) found decreased amount of soluble sugars of seedlings of brown sarson under water stress induced by polyethylene glycol (4000). In peas drought decreased dry weight, relative turgidity, reducing sugars, sucrose and starch concentrations, ribulose, 1-5-diphosphate carboxylase activity and net photosynthesis in both drought susceptible, Alaska and drought resistant hardy varieties. Lee et al. (1974). Vora et al. (1974) reported depressed amylase and invertase activities of sorghum seedlings under low moisture
level. The sugars accumulated especially, in the embryo axis of water stressed seedlings, sugars declined during later period of germination, possibly through their oxidation. Vora et al. (1976) reported enhanced depletion of starch of the endosperm under various osmotica. The amylase activity of the embryo axis was enhanced by -3 and -5 NaCl, but it was depressed by -3 and -5 mannitol and PEG (6000). A depressed amylase activity by osmotica was noted for endosperm.

A number of workers have described a protective role to sugars against water deficit or drought. Sugars help in retaining turgidity and protoplasmic constituents, Maranville and Paulsen (1970), or by stabilizing proteins, Klotz (1958) and Parker (1972).

Sulfhydryl group in relation to stress:

Cecil (1963) had shown that sulfhydryl (SH) and disulfide (SS) groups are important in maintenance of structural integrity of protein. Levitt and his school (Levitt, 1962) have put forward a theory of protoplasmic resistance to cold and desiccation. They found an increase in titrable -SH with increasing cold hardiness. Levitt (1962) proposed the SH ≥ SS hypothesis of freezing injury. At a certain degree of tissue dehydration, SH and SS groups of adjacent protein molecule would approach each
other, chemical reactions take place and intermolecular SS bonds are formed either by an oxidation of two SH groups to SS and SH to SS intercharge reaction.

The SS bonds are covalent bonds which are far stronger than hydrogen and hydrophobic bonds, and are responsible for tertiary structure of the proteins. When thawing occurs and water reenters the protoplasm, pushing the protein apart newly formed SS bonds remain intact, but many of weaker hydrogen and hydrophobic bond will be broken by the stress and protein molecules would then unfold. If intermolecular SS bonds are sufficient, the unfolding would lead to denaturation of the proteins and death of the cell.

Increase in the protein SS in the desiccated leaf of cabbage was shown by Gaff (1966). It was a small increase and occur before injury in the case of soluble protein, but when the dehydration of the tissue was sufficient, it causing injury than their was a sharp rise in SS content in the structural protein. The formation of SS in the soluble proteins may be intramolecular and not directly injurious.

Levitt (1967) discussed relations of -SH level, ATP and amylase formation. The separation of S-S bonds during hardening resulted in an increase in -SH proteins and this is a likely source of increased water soluble proteins, but
the -SH levels decreased after an initial increase and went on to decrease as hardening proceeded, Levitt (1967).

\[ \text{SH} \xrightarrow{\text{reduced}} S - S \text{ are certainly complex.} \]

Morré (1970) has involved these changes in auxin growth effects as well as in protein stability under heat stress. Levitt’s theory was questioned by Mazur (1969), who pointed out that S-S bond formation is not ordinarily considered the cause of denaturation and is only one of the steps resulting in irreversible aggregation of a previously denatured protein.

Roberts (1969) has put forward a theory of hardening according to which new proteins substitute for already existent ones and he pointed out that isozymic forms of certain enzymes can be added or deleted when the cells are under certain circumstances.

**Effect of low temperature:**

Low temperature is one of the environmental factors that affects the distribution of plants. Cold injury an account of low temperature is one of the most limiting factor to the agriculture production. The subject of cold hardiness, therefore, has attracted many workers. It has been reviewed by time to time, (Parker, 1963; Levitt, 1966, 1967, 1969 and Olligh, 1967) as well as Alden and Hermann (1971) have reviewed extensively the various aspects of cold hardiness in plants. In this thesis some important
aspects of low temperature effects on plant growth are reviewed.

Protoplasmic changes: Tumanov (1967) discussed changes in physical properties of protoplasm during hardening and emphasized on the importance of gelling to the plant developing, against mechanical deformation, dehydration, and formation of intracellular ice by reducing mobility and orientation of water molecules.

Low temperature reduces speed of various cytoplasmic organelles and it also reduces formation of small vacuoles, Das et al. (1966).

Nucleus and nucleic acid: Changing in the staining characteristics of nuclei and nucleoli as well as physicochemical conditions of these organelles have also been reported under low temperature, Siminovitch and Charter (1958), Sergeeva and Polyakova (1964) and Das et al. (1966). The changes in nucleolus were ascribed a significant role in metabolic activities of the cells, because contraction of nucleolar vacuole may release substances, mainly RNA to cytoplasm, Das et al. (1966).

Several workers have observed varied responses of nucleic acids to cold treatment. Increase in nucleic acids was reported by Barskaya and Oknina (1959), no increase was reported by Siminovitch (1963). Li and Weiser (1963,
1969) found a constancy of nucleic acid at subfreezing temperature. Changes in the base contents of nucleic acid were reported by Kessler and Frank-Tishel (1962). They reported increase in guanine and cytosine in comparison to adenine and uracil and considered it as the basic part of cold hardiness processes in the plant. Their postulate was supported by the work of Jung et al. (1967); Shih and Jung (1968) and Li and Weiser (1969).

Khan et al. (1968) observed progressive increase in the synthesis of all nucleic acids with the increase in the length of the cold treatment of *Pyrus communis* seeds in the excised embryos. Correlation existed between the levels of the biochemical constituents and the degree of hardiness in the three peach cultivars as shown by Lasheen and Chaplin (1971). Gusta and Weiser (1972) and Babenko et al. (1971) also reported decrease in RNase activity during induction of cold hardiness respectively in Korean Boxwood leaves and in wheat. Brown and Sasaki (1972) observed a quantitatively decline of RNAs in *mimosa* epicotyls during induction of cold hardiness, but in hypocotyles, they remained relatively constant. Such decrease in RNase activity possibly indicates their role in regulation of RNA, protein synthesis during induction of cold hardiness. Brown and Bixby (1973) reported lowered RNase activity during induction of cold hardiness in epicotyl and hypocotyl
tissues of mimosa. They further reported decreased fresh weight.

Proteins and Amino acids: Parker (1963) has extensively investigated the protein metabolism of plants in connection of development of cold hardiness and resistance. Rise in water soluble protein level during development of frost hardiness and a fall in the spring with disappearance of frost hardiness was reported by Siminovitch and Briggs (1959, 1953).

The component of protein was also changed during cold hardiness. Increase in water soluble protein which associated the hardiness has also been reported by Johansson (1956), Vasil'yev et al. (1964), Coleman et al. (1966), Ghazaleh and Hendershott (1967). On the contrary, Henze (1959) observed more increase in protein, that were not water soluble than the water soluble ones. It has been observed that a rise in water soluble proteins during the development of frost hardiness, is on account of the break down of some of the more complex proteins and not from the synthesis of new amino acids and proteins, Drozdov and Sycheva (1965), while Wilding et al. (1960) observed that increase in protein content was both of the degradation of the complex protein and synthesis from free amino acid.

A net increase in amino acids in cabbage during hardening followed by decline in amino acids and increase
in water soluble protein was reported by Kohn and Levitt (1966). A fall in amino acid content probably indicated their utilization and synthesizing capacity in the water-soluble proteins. These changes in protein content associated with the changes in the nucleic acids are believed to affect the physical properties of cell protoplasm and enables the protoplasm to resist the stress from dehydration, which may be caused by intercellular freezing.

Application of purine and pyrimidine bases of nucleic acid imparted cold hardiness by influence of protein content, Jung et al. (1966, 1967).

Although amino acids changes during the development of frost resistance, According to Parker (1963) amino acids are poor indicators of protein levels and he doubts whether they play a role in frost hardiness. On the contrary, changes in amino acid content were positively correlated with frost resistance by Li et al. (1965). Qualitative changes in amino acids during cold hardiness were reported by Asen and Stuart (1958). In cold resistance proline also accumulates in large quantity, Teltscherova (1967).

Qualitative changes in protein as detected by electrophoresis occur at a time when cold hardiness took place in two woody species were reported by Craker et al. (1969). They further reported that proteins have been implicated in changes in membrane permeability to water,
bound water, protoplasmic elasticity and viscosity, enzyme stability, protoplasm maintains, sulfhydryl disulfide linkages and numerous enzyme-mediated metabolic changes during cold hardiness in plants.

**Enzyme activity**: According to Belkin and Perfil'eva (1962) resistance to cold involves changes in synthetic and hydrolyzing activities of entire enzyme systems. They observed a correlation between the intensities hydrolytic activity of invertase on sucrose and bark of apple branches and their resistance to frost. The changes in the enzyme system which in turn bring about metabolic changes during cold resistance were considered to be associated by hormonal actions by Van Huystee et al. (1965).

At a much lower temperature the enzymes became degraded and vitrified; and they lose their activity. Thus Sakai (1966) found that the most effective temperature for conversion of starch to sugar in willows was -3°C to -5°C. Below -20°C, such conversion did not occur, and frost hardening failed to take place. The water soluble enzymes were found to be active even after freezing -20°C but the enzymes which were bound in cellular structure were denatured, Ullrich and Heber (1961).

Hydrolytic activity of invertase was higher in the frost resistance varieties of wheat and rye and hydrolytic protease activity was increased at -8°C, Kolosha (1965).
According to Vasil'ev (1956), invertase enzymes absorbed on the proplasmic structures at room temperature, but at temperature below $+5^\circ C$, it is in the free state. Higher activity of oxidising enzymes at low temperature in cold resistant and thermophilic plants which were raised in soils at $10^\circ C$ to $12^\circ C$ than in plants grown in $20^\circ C$ to $25^\circ C$ was found by Korovin and Barskaya (1962). This was considered to be an adaptation to low temperature.

Alfalfa roots during hardening were found to form new isozymes with an increase in concentrations of soluble proteins and stimulated activities of catalase and peroxidase were found by Gerloff et al. (1967). Increase in peroxidase activity but decrease in polyphenoloxidase activity were observed in potatoes grown at a low soil temperature, Korovin and Barskaya (1962). They also observed no change in catalase activity. Sysoev and Krasnaya (1967) considered increase dehydrogenase activity as a frost-hardiness index in fully hardened wheat plants.

Carbohydrates: It is well known that during cold hardiness carbohydrates reserves are lowered. Starch decreased to minimum and sugar increased to maximum by Levitt (1956). During hardiness sugar complexes are changed and number of sugars are found, one of them is raffinose, which increases as frost hardiness developed, Parker (1963). This conversion is enzymatically brought about. The accumulation
of the reducing sugar at -18°C., which is the near lethal temperature to many wheat varieties, was attributed to an increase in hydrolytic activity by enzymes, cold resistance varieties had greater hydrolytic activity, Kolosha (1965).

Substances like sucrose are shown to retard growth of ice crystals and alter their pattern without depressing the point of ice nucleation any more than the freezing point, Parker (1963). This results in protection of proteins of membranes and enzymes from sudden loss of water with freezing. According to Ullrich and Heber (1957), sugars may also protect proteins directly by replacing some of the water of hydration more firmly through hydrogen bonding in structures sensitive to dehydration as water is removed to form ice. Protective compounds like sugars increase water holding capacity of the protoplasm. The increase in water-holding capacity of the protoplasm reduced mechanical deformation of the protoplasm when the cell was plasmolyzed by formation of extracellular ice as concluded by Samygin and Matveeva (1967). However, the ratio of bound sugar and protein did not increase significantly with the increase in the water soluble proteins in the autumn, Parker (1963).

The protective action of sugar may also serve as a source of energy development of cold hardiness, sugars must be distributed to sensitive sites in the protoplasm and vacuole. Sugars have to be distributed in such a way that
they must come in contact with sensitive sites. If they accumulate in vacuole, they may not be readily available for use by sensitive structure within the cytoplasm, as reported by Heber and Santarius (1964).

Single (1971) in a review showed several workers have shown a positive correlation between soluble carbohydrate content and frost resistance. Barta and Hodges (1970) observed that high rates of photosynthesis are also associated with cold hardening of wheat plants. The positive correlation between frost resistance and free proline, amino acids, \( \alpha \)-aminobutyric acid, soluble protein and total protein as reviewed by Single (1971).

**Presowing treatment and drought:**

Repeated wilting resulted in hardening of the plant tissue analogous to that observed at low temperature. On this basis, various workers involved the method of presowing treatment to induce drought hardiness, Genkel (1956) and Chinoy et al. (1966). The advantages or disadvantages of the pretreated method have been excellently reviewed by May et al. (1962) and Saxena (1974).

In the opinion of Genkel (1946, 1961) the presowing treatment affects the physico-chemical properties of the protoplasm; hydration of the colloids is enhanced. There is better viscosity and elasticity of the protoplasm. The bound
water rises and the rate of metabolism also increases. The root system also becomes stronger; these findings of Genkel were supported by the work of Petinov and Molotkovsky (1961). The yield of tomato was double under drought condition from plants raised from pretreated seeds, Genkel et al. (1966) investigated the effect of presowing treatment of the seeds of corn, tomatoes, and millet under condition of atmospheric drought. The pretreated plants had a normal course of reproductive process leading to the formation of crop. In the case of untreated plants under similar condition, there were small crops or no crop at all.

Hydration of colloids of maize plants from pretreated seed was more during the period of soil drought. Further, with potassium as a fertilizer, in addition of the pretreatment seed, the water retaining capacity of maize plant was more and the effect of drought hazard on the crop was less as reported by Shchukina (1965).

Mineral and salts are also used for pretreating the seeds; dilute solutions of the CaCl₂ were used for pretreating millet, oats, rye, barley, beet, pea, vetch, potato and successful results were obtained by May et al. (1962). Chinoy et al. (1965, 1967) used ascorbic acid to pretreated seeds of barley varieties; beneficial effects on growth and yield characters under drought and in the normal condition was observed. Increased drought tolerance of cabbage
sections by mercaptoethanol was found by Paricha and Levitt (1967). John and Jani (1968) reported beneficial effect of ascorbic acid pretreatment of three varieties of barley under drought and salinity. Pretreatment of paddy seeds significantly reduced the water requirement and the rate of transpiration was also reduced, Parija (1943), Parija and Pillay (1945). Repeated soaking and drying caused a favourable germination and seedling vigour which had a close relationship with enhanced water absorbing capacity probably due to amylase activity, Koller et al. (1962). Badalyan (1962) reported that of the pretreatment of wheat, beet and cotton increase the number of stomata per unit leaf area, greater leaf area, enhanced retained water capacity and increased in fresh and dry weights of the leaf of water stressed plants, as compared to the control. The pretreatment consisted water solution of super substrate with boric acid. The bound water content, yield of wheat and sugar content of beet were, also enhanced. Sintinikova (1960) observed that the pretreatment of seeds produced more dry matter content, total nitrogen and protein in plants.

Despite the favourable effects of pretreatment, pretreatment was not always beneficial as reported by workers from time to time. Thus for example Domanskii (1959) obtained reduced yield of spring barley from the pretreatment seeds. Jarvis and Jarvis (1964) found no increase
in the growth rate of sorghum grown from pretreated harden seeds in condition of drought. Jacoby and Oppenheimer (1962) observed increased resistant of water loss but not drought tolerance in the case of pretreated 'sooner' variety of sorghum. Salim and Todd (1968) tried water and dilute solutions of nine other compounds for pretreating seeds of wheat and barley varieties. They concluded that the response of pretreatment seemed to depend upon the variety used and therefore no generalized statement on the effect of pretreatment can be made.

Growth retardants which retard plant growth without causing harmful effects have also been tried (Halevy, 1962; Halevy and Kessler, 1963 and Martin and Lopushinsky, 1966) reported beneficial effect of growth retardants on the drought tolerance of various plants. CCC and B-995 increased ability of wheat plants to regenerate new shoots and rewatering after wilting reported by Plaut and Halevy (1966). Kharanyan (1967) observed water retaining capacity of the leaves considerably improved by CCC. When the soil was treated by CCC, the moisture retention was better than nontreated soil. Increase resistance of plants to drought by growth retardation, it was also observed by Sankhla (1968).

Kinetin was found to decrease, while ABA was found to increase the RNase activity of barley leaves with normal water balance. In the water deficit plants, however, kinetin stimulated RNase activity more than ABA, Arad et al. (1972).
It was suggested that under increased water deficit cell-water supercedes hormonal regulation in affecting RNase activity. CCC treatment enhanced germination of Brassica seeds under water stress imposed by PEG. Pandya and Khan (1973). Krishna Sastry and Udayakumar (1973) reported a decrease in fresh weight of cotyledon of cucumber but they observed increase in fresh weight by Benzyl adenine (BA) and suggested that BA promoted uptake of water under stress. Dehydrogenase activity, oxidative metabolism and $^{14}$C lucine incorporation in wheat seedlings were stimulated by pretreatment, Savino et al. (1976). GA treatment enhanced the seedling length, moisture content, nonreducing sugars and amylase activity of water stressed of Bajara seedlings Vora et al. (1975). GA stimulated the emergence of Paddy seeds at lower moisture content of the soil. The percentage germination was reduced as a moisture content was decrease as reported by Ulyamal (1976). Various growth regulators such as GA, CCC, MH and NAA, either by seed treatment and foliar application increased tolerance to NaCl of maize seeds Crawford and Huxter (1977).

Shah and Loomis (1965) observed that the sugarbeet leaves treated or sprayed with benzyl adenine had a reverse effect on reduced nucleic acid and protein in water stress plants.
Water deficits and hormone relations have been excellently, Livne and Vaadia (1972). Wright (1969), Wright and Hiron (1969) and Mizrahi et al. (1970) have considered abscisic acid as a regulator of physiological responses of plant under water stress.

Wright (1969) observed a rise in the levels of ABA in wilted leaves, which was in proportion to the degree of wilting.

When 0.1 M NaCl or 0.17 M mannitol was added to the nutrient medium of the roots, there was a substantial rise in amount of ABA, Mizrahi et al. (1970). Reid et al. (1969) found in water logged plants reduced level of GA in xylem sap.

Milborrow and Noddle (1970) observed that the rise in level of ABA was a de novo synthesis and not through release of bound form, when brief stress with -10 bars mannitol was given, indole acetic acid (IAA) oxidase activity increased. A moderate to a severe stress in the field also increased IAA oxidase activity, Derbyshire (1971). According to him, increased IAA oxidase activity reduced the auxin level in the water stress plants and retardation of growth during the stress may result from lack of auxin induced cell wall loosening in as well as from reduced turgor, while there are reports on water stress effects on auxin and GA levels the direct data, however, lacking.

The ABA content of the leaves increased between 3.0 and 4.5 times at the original content depending upon on the duration of the water stress given to wheat plant, Bengtson et al. (1977).