REVIEW OF LITERATURE

Literature on the modulation of various processes of plants under water stress conditions, is reviewed hereunder.

Drought is the most important environmental constraint to world agricultural production (Jamaux *et al.*, 1997). Drought is simply defined as 'prolonged dry weather' but however a more working definition would be the "inadequacy of water availability, including precipitation and soil moisture storage capacity, in quantity and distribution during the life cycle of the crop to restrict expression of its full genetic yield potential" (Khanna-Chopra and Sinha, 1998).

Plant water deficit occurs when the rate of transpiration exceeds water uptake, this may be due to excessive water loss, reduced absorption or both. The absorption depends on soil moisture, aeration, size and distribution of root system and largely on the rate of transpiration. The rate of transpiration on the other hand, is determined by the solar radiation, wind, humidity and leaf structure and stomatal opening. As these factors vary depending on the season of the year and the time of the day, it is to be expected that water stress is recurring, albeit temporary event in the life cycle of every plant. The degree to which a particular water deficit influences the plant depends on the nature of the plant characteristics that influence water uptake by the plant, the rate of transpiration and the response of the plant to the water deficit generated.

Water deficit elicits a complex of responses beginning with stress perception, which initiates a signal transduction pathway(s) and is manifested in changes at the cellular, physiological and development levels. Cellular water deficit can results changes in solute concentration, cell volume and membrane shape, disruption of water potential gradients, loss of turgor and denaturation of protein. The ability of the whole plant to respond and survive cellular water deficit depends on whole- plant mechanisms that can integrate the cellular responses (Bray, 1997). The maintenance of internal water levels is an important mechanism for survival of plants during water stress. It is the degree to which the plant can withstand the water deficit without perceptible growth inhibition and yield loss that constitutes its drought tolerance.

Tolerance and sensitivity towards a particular stress depends on the genetic and biochemical make up of plant species (Dubey, 1994). It is well documented that various environmental stresses cause an important modification in gene expression in plants (Vierling, 1991).

Resistance to water deficit occurs when a plant withstands the imposed stress, and may arise from either tolerance or a mechanism that permits avoidance of the situation. Whole-plant mechanisms can contribute to the avoidance of water deficit during the plant's life cycle, and avoidance can also occur at the cellular level. The response depends on the species and genotype, the length and severity of water loss (Fig.) the age and stage of development, the organ and cell type, and the subcellular compartment. A stepwise gradual adaptation to increasing intensity of water stress allows biochemical and structural modifications of cellular membranes and maintenance of membrane fluidity, which is prerequisite of the acquired tolerance (Stewart 1989).

Fig. Responses to water deficit in relation to the extent and rate of water loss (Bray, E.A. 1997)

The response of the plant is dependent on the extent and rate of water loss. A slow rate of loss may permit acclimation to the water deficit and limit the extent of injury, while a rapid rate of loss may preclude acclimation. The same water deficit in a sensitive species and a resistant species may not trigger the same response. The triangles indicate the extent (relative length of vertical axis) and time (relative length of horizontal axis) of each parameter.
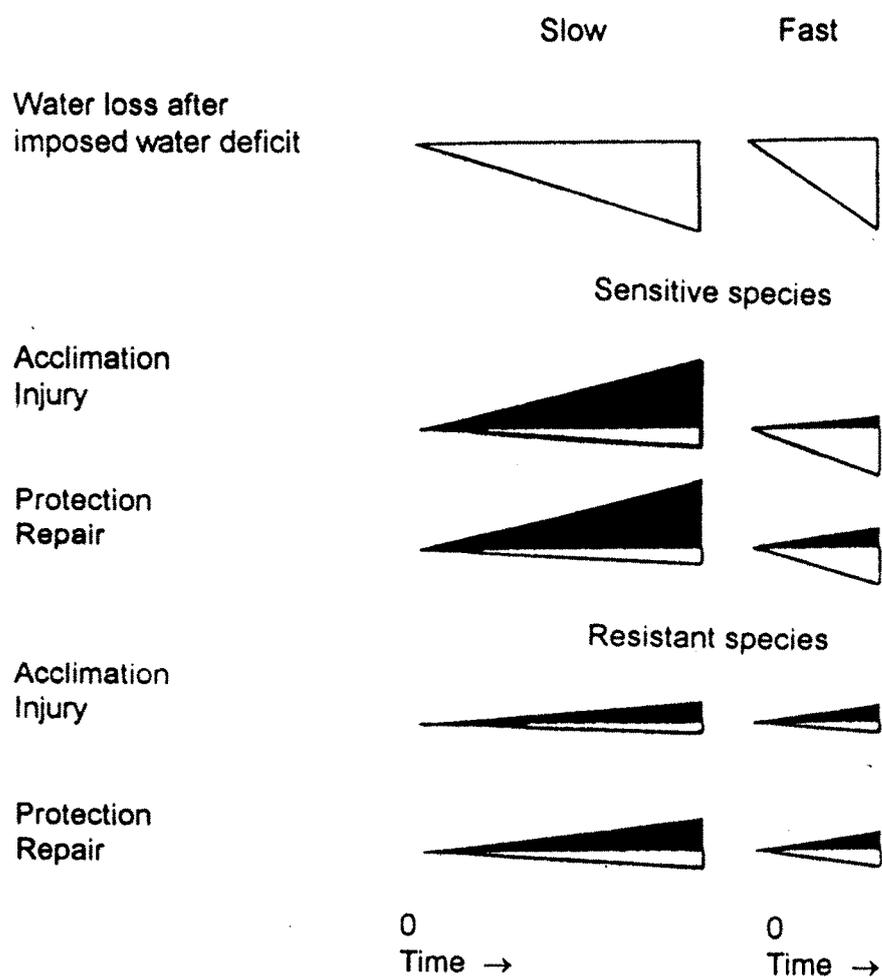
Most higher plants are exposed to varying degrees of water stress at some stage in ontogeny. The type of water stress may vary from small fluctuations in atmospheric humidity and net radiation in more mesic habits to extreme soil water deficits and low humidity in arid environments. The performance of plants under moisture stress is highly dependent upon the maintenance of favourable plant water status. The response of the plant to water stress is not same at all stages of growth. Several morpho-physiological and biochemical responses of plants to water stress have been described by Sinha (1986).

Water deficits affect many aspects of plant growth including the anatomy, morphology and physiology. The quantity and quality of plant growth depends on cell division, cell enlargement and differentiation and all are affected by water stress with a differential reduction depending on the sensitivity of the process (Barlow *et al.*, 1980). Water stress results in the reduction in leaf expansion and consequently declined leaf area has been reported for several crop plants (Boyer 1970a; Begg and Turner, 1976; Takeda *et al.* 1978; Sobrado, 1986, Sinha, 1986; Turner *et al.*, 1986; Randall and Sinclair, 1988; Masle and Passioura, 1988; Premachandra *et al.*, 1989; Serpe and Mathews, 1992; Schultz and Mathews, 1993; Kumar and Elston, 1993; Feng *et al.*, 1994). Further, it was also reported that relative leaf expansion rate (RLER) was always smaller in stressed plants compared to controls, indicating that reduced leaf growth accounted for lowering the leaf area during drought conditions (Sobardo, 1986).

Alterations in dry mass accumulation during water stress were reported by several workers. A significant inhibition in dry mass yield under drought stress

was noticed in cotton (Jordan, 1970), in Oat (Vora and Patel, 1977), in bean (Jaeger and Mayer, 1977), in barley (Hanson *et al.*, 1977), in red kidney bean, in field bean (Farah, 1981), in rice (Turner *et al.*, 1986), in cocoa, in *Echinochloa* Sp. (Denis and Susan, 1989), in groundnut (Kulkarni *et. al.*, 1988), in *Vigna sinensis* (Biswas *et al.*, 1989), in peach (Steinberg *et al.*, 1990) and in alfalfa (Schubert *et al.*, 1995).

Decrease in leaf moisture content as a result of water stress was reported (Lawlor, 1973; Yadav and Bhatt, 1989). Thus, it is evident from the preceding reports that water stress affects relative leaf expansion rate, dry mass accumulation and leaf moisture content. It was noticed that very often drought tolerance has been correlated with the genotypes showing lesser degree of inhibition with respect to above parameters. Water stress is also known to influence strongly the rate of root elongation and the number of growing roots in several plant species. The extent and pattern of root development are closely related to the plant to absorb water and hence are of great significance in drought tolerance.

Modulation in growth rate of plant is one of the most sensitive plant responses to water stress (Hsiao, 1973). The reduction in growth is common phenomenon in plants under water stress conditions (Gupta *et al.*, 1985; Hussain *et al.*, 1990; Leopold, 1990; Schultz and Mathews, 1993; Pratibha *et al.*, 1994 and Schubert *et al.*, 1995). It has been shown that plant growth depend on cell division, cell enlargement and cell differentiation and all are affected by water

stress with a differential reduction depending on the sensitivity of the process (Barlow *et al.*, 1980).

Shoot and Root Growth

A decrease in height of the plant under water stress conditions was reported in wheat (Lawlor and Wilford, 1973), *Lotus scopanis* (Nilsen and Muller, 1981); in cow pea (Khalil and Mandurah, 1989), in peach (Jerie and Irvine, 1989), in *Vicia faba* (Hussain *et al.*, 1990), in pea (Arvind Kumar *et al.*, 1990), in *Prosopis chinensis* and *Dalbergia sissoo* (Pandey *et al.*, 1994), in alfalfa (Schubert *et al.*, 1995) and in *Acacia nilotica* (Pokhriyal *et al.*, 1997). Boyer *et al.* (1985) reported that water deficits limits soybean stem growth by reducing water uptake and wall extension.

Davies *et al.*, (1994) reported that roots subjected to drying soils may produce a non-hydraulic (hormonal) signal which carries an important effect on shoot growth and development, irrespective of the plant water status.

Water stress is known to influence various root attributes such as root size, morphology, depth, density and hydraulic conductance (Passioura, 1982). The extent and pattern of root development are closely related to the ability of the plant to absorb water and hence are of great significance in drought tolerance.

A few field and laboratory studies suggest that water stress induce an absolute increase in the depth and weight of roots in some foliage sp. Extensive root development was observed in drought hit soils when compared to soils are having more moisture content (Keyes and Grien, 1980). Deep and dense root

system enables the plant to tolerate drought by maintaining water uptake and higher water potential (Passioura, 1974). White and Castillo (1988) reported that the drought tolerant bean geno- types extend their roots than sensitive genotypes under drought environments. In general, extensive root systems are effective in postponing dehydration especially in deep soils.

Narayan and Misra (1989) recorded deeper penetration of root under moisture stress and concluded that the depth of root penetration can provide a useful selection criterion for wheat breeding under drought tolerance. Root penetration through compacted soil layers or hard pans has been recognised as an important breeding objective for drought improvement in rice (Hanson *et al.*, 1990).

Baldry (1973) reported that the root growth of wheat reached a maximum between -5 and -10 bars soil water potentials and ceased by -25 bars. Other investigators have confirmed that root growth is restricted/marked reduction under severe moisture stress (Taylor and Klepper, 1974; Christie, 1975; Hurd, 1976; Ramanjulu, 1996). There were also reports stating that water deficit decreases the root growth (Roberts, 1976; Deans, 1979; Jerie and Irvine, 1989; Aravindkumar *et al.*, 1990 and Pandey *et al.*, 1994).

Water deficits reduce the stands of plants. In general, shoot growth is reduced more than root growth because more severe water deficits develop in the shoots and probably persist longer.

Thus, root shoot ratios are generally increased by water stress. Increased root to shoot ratio was reported in cotton (Malik *et al.*, 1979), in *Vigna sinensis*

(Biswas *et al.*, 1989) and in *Prosopis chilensis* (Pandey *et al.*, 1994). Increase in root to shoot ratio may be an adaptive response to drought (Passioura, 1974) and conserve water which may be an adaptation for drought survival (Kramer, 1969; Hisago, 1973).

In contrast, O'Toole and Cruz (1980) reported an increase in shoot to root ratio in rainfed in low land rice cultivars under mild water stress. Similarly, increased shoot to root ratio was reported in safflower (Gupta *et al.*, 1985) and in soybean.

Fresh weight and dry weight

During water stress condition the alteration of fresh weight and dry weight were reported by several workers. A significant reduction in fresh and dry weight was noted in wheat (Lawlor, 1973), in oat (Vora and Patel, 1977), in barley (Hanson *et al.*, 1977) in horse gram (Padmavathi, 1989), in mulberry (Ranjitha Kumari, 1991), in potato (Hener and Nadler, 1995) and chick pea (Singh *et al.*, 1997).

A significant inhibition in drymass yield under drought stress was noticed in field bean (Farah, 1981), in groundnut (Kulkarni *et al.*, 1988), in *Vigna sinensis* (Biswas *et al.*, 1989) in peach (Steinberg *et al.*, 1990), in alfalfa (Schubert *et al.*, 1995), in sweet potato (Chowdary and Varma, 1997) and in mulberry (Ramanjulu *et al.*, 1998a). Singh and Singh (1986) reported that drought sensitive varieties of sugar cane showed more reduction in dry matter than drought tolerant varieties under water stress conditions.

Leaf area

Leaf growth is the most sensitive and the first plant organ affected by water deficit. Water stress results in the reduction in leaf expansion and consequently declined leaf has been reported for several crop plants (Turner *et al.*, 1986; Randall and Sinclair, 1988; Premachandra *et al.*, 1989a; Serpe and Mathews, 1992; Schults and Mathews, 1993; Kumar and Elston, 1993; Peng *et al.* 1994; Rao and Wright, 1994; Singh *et al.*, 1997), in mulberry (Ramanjulu *et al.*, 1998). Kumar and Elston (1997) observed a substantial differences in leaf expansion at different growth stages. Crop cultures with more erect and narrow leaves are considered to be an adaptive trait to water stress conditions (Blum, 1980).

Thus, it is evident from the preceeding reports that water stress affect leaf area, relative growth rate, relative leaf expansion rate, dry mass accumulation. It was noticed that, very often drought tolerance has been correlated with the geno types showing lesser degree of inhibition with respect to above parameters.

Leaf water potential

A decline in plant water potential as a result of drought stress has been documented in several plant species. Water stress also caused a decrease in leaf water potential in wheat (Barlow *et al.*, 1977; Manns *et al.*, 1979), in barley (Hanson *et al.*, 1977), in rice (O' Toole and Cruz, 1980), in cotton (Ackerson, 1981), in populus (Mazzoleni and Dickmann, 1988), in *Echinocloa* sp. (Deris and Susan, 1989), in *Lupinus* (Jensen *et al.*, 1980), in alfalfa (Irigoyen *et al.*, 1992; Schubert, *et al.*, 1995), in maize (Premachandra *et al.*, 1989; Brown *et al.*, 1995),

in apple (Wang *et al.*, 1995), in tomato (Torrecillas *et al.*, 1995), in citrus (Save *et al.*, 1995), in chick pea (Singh *et al.*, 1997), in potato (Heuer and Nadler, 1998), in mulberry (Ramanjulu *et al.*, 1998), stated that the two basic parameter, which describe the degree of the plant water deficit are the water content expressed as relative water content (RWC) and water potential in the cell.

Relative Water Content (RWC)

The RWC are less accurate when compared to leaf water potential, it is still valid and useful in understanding plant water status. Decrease in leaf RWC as a response to water stress has been well known (Jensen, 1981; Denis and Susan, 1989; Naidu *et al.*, 1990), *Brassica carinala* (Uprety and Tomar, 1993), in Sorghum (Nagy *et al.*, 1995), in Cassava (Sundaresan and Sudhakaran, 1995), in Chick pea (Singh *et al.*, 1997), in Cotton (Nepomuceno *et al.*, 1998) and *Ziziphus mauritiana* (Clifford *et al.*, 1998), in Mulberry (Ramanjulu *et al.*, 1998) suggested the plants that are able to retain high relative water content during drought stress are considered as tolerant ones to dehydration.

Ramanjulu and Sudhakar (1997 and 1998) reported that tolerant mulberry genotype showed a smaller decrease in RWC than the sensitive one during water deficits. Similar reports were made for many plant species during water stress conditions (Sairam, 1994; Neagz *et al.*, 1995).

The review presented above pointed that the water relation during water stress were distributed. However, the extent of decrease depends on the severity, duration and plant species ability to tolerate.

Proteins

Protein as an important organic nitrogenous constituents of plants, would be expected to play a role in the compensatory mechanisms of plant species during stress conditions. Environmental stress could evoke compensatory metabolic changes through modification and modulation of the quantity and quality of proteins. Protein synthesis is closely related production of new tissues, which is the principal sink for N_2 compounds and it is declined during stress. Under water stress, decreased amount of protein was observed in *Hordeum vulgare* (Dungey and Davies, 1982) in maize and wheat (Luna *et al.*, 1985), in alfalfa (Halim *et al.*, 1989; Irigoen *et al.*, 1992), in rice (Jha and Singh, 1997) and in potato (Heuer and Nadler, 1998).

Proline

Proline accumulation, a general response to various environmental stresses such as drought (Aspinall and Paleg, 1981; Ramanjulu *et al.* 2000), salinity (Giridara Kumar *et al.*. 2000; Sudhakar *et al.*, 1993; Stewart and Lee, 1974; Lutti *et al.*, 1999; Aziz *et al.*, 1999; Guerri, 1998), heavy metal (Alia and Saradhi 1991), low pH (Anon, 1973), pathological conditions (Meon *et al.*, 1978) and high temperature. Kemble and Macpherson (1954) reported the liberation of amino acids in rye grass during wilting and further observed that proline was the only amino acid which occurred in excess of expectation and this excess was very large. The accumulation of free proline as a consequence of water stress has been documented by several investigators in different plant species (Barnett and Naylor, 1966; Levitt, 1972; Hsiao, 1973; Aspinall and Paleg, 1981, Karamanos *et*

al., 1983; Yadava and Bhatt, 1989, Cyr *et al.*, 1990; Naidu *et al.*, 1990; Badiani *et al.*, 1990; Voetberg and Sharp, 1991, Sarkar, 1993; Raggi, 1994; Good and Zaplachinski; 1994; Ober and Sharp, 1994; Sundarasan and Sudhakaran, 1995; Kavi Kishore *et al.*, 1995; Mattioni *et al.*, 1997; Clifford *et al.*, 1998).

The accumulation of proline in stressed tissues has been attributed either to enhanced proline synthesis (Barnett and Naylor, 1966; Harda *et al.*, 1986) or inhibiton of proline oxidation (Steward and Lee, 1974; Stewart and Boggess, 1978; Huang and Cavalieri, 1979) or impaired protein synthesis (Hsiao, 1970; Morilla *et al.*, 1973).

The survival value of proline accumulation during water stress was contested by Hanson *et al.* (1977), who suggested that high proline levels in water stressed leaves was essentially a symptom of injury and hence might not represent a true index of drought tolerance. Similarly, others considered enhanced proline levels as merely an effect of stress rather than a cause of tolerance (Boggess *et al.*, 1976; Hanson and Nelson, 1978; Bogess, 1980; Sarkar, 1993).

Antioxidative enzymes

The over production of active oxygen species such as superoxide, hydrogen peroxide and hydroxyle radicals results from the exposure of plants to different environmental stimuli. Increased formation of active oxygen species has been associated with the development of injury symptoms resulting from diverse stress conditions including chilling (Fadzillah *et al.*, 1996); drought (Smirnoff, 1993).

Antioxidants can be divided into three general classes including (1) lipid soluble and membrane-assoicates tocopherols; (2) water soluble reluctance, ascorbic acid (ASA) and glutathione; and (3) enzymes such as superoxide dismutase, catalase, paroxidase, ascorbic peroxidase and glutathione reductase (Foyer, 1993).

Peroxidase

An ascorbate peroxidase is a specific involved in the remove of chloroplastic H_2O_2 (Asada and Badger, 1984), Smirnoff and Cumbes (1989) and Price and Hendry (1987) reported the activity of ascorbate peroxidase was not significantly increased in water stressed barley and wheat. Similarly the activity of ascorbate peroxidase was largely unchanged in both moss species of drought tolerant *Tortula ruraliformis* and drought sensitive *Dicranella palustnis* (Seel *et al.*, 1992).

Moran *et al.*, (1994) showed an enhanced activity of peroxidase in pea plants subjected to water stress. In contrast, Irigoyen *et al.* (1992) reported a severity dependent inhibition in the activity of peroxidase in the leaves of alfalfa.

Catalase

It has been reported that the water stress could affect the activity of Catalase (Mukherjee and Choudhuri, 1981a,b). A decline in catalse activity under water stress conditions was documented by several investigators (Mukherjee and Choudhuri, 1983; 1985; Quartaeci and Navari, 1220, 1992). Declined activity of catalase has also been shown in *Vigna* seedlings (Mukherjee and Choudhuri,

1981b), in rice seedlings (Goyal 1987), in moss species (Seel *et al.*, 1992) and in pea plants (Moran *et al.*, 1994) under water deficits. The water stress severity dependent differential response in respect of catalase activity was reported by Irigoyen *et al.*, (1992) in alfalfa plants, where the mild drought stress inhibited the catalase activity and the catalase activity was highly stimulated under moderate water stress conditions.

Goyal (1987) reported a relatively higher degree of declined catalase activity in drought susceptible rice cultivar (Jaya) than in drought tolerant cultivar (N-22) under water stress condition. Similarly, Seel *et al.*, (1992) showed that the drought sensitive mass *Dicranella palustris* recorded in relatively higher magnitude of inhibited catalase activity than in drought tolerant moss *Tortula ruraliformis* under drought stress. In contrast, Van Rensburg and Kruger (1994) showed increased activity of catalase in four tobacco cultivars in response to water stress. Lodh *et al.* (1972) observed increased catalase activity in drought sensitive rice cultivars but not in the drought tolerant cultivars.

Malondialdehyde

Malondialdehyde content which is one of the decomposition product of biomembranes showed greater accumulation under drought stress. These results are in agreement with reports by several investigators under drought (Baisak *et al.*, 1994), salinity (Dionisio Sen *et al.*, 1998; Gassetti, 1994; Giridhara Kumar *et al.*, 2000, Sreenivasulu *et al.*, 1999), heavy metal (Ram Devi *et al.*, 1998).

From the literature cited above, it is clear that the considerable research effort has been made towards the identification of plant species and genotypes of

crop plants that are tolerant drought. Though a few investigators concentrated on the physiological and biochemical studies in Mulberry to water stress (Veeranjineyulu and Ranjitakumari, 1989; Ramanjulu and Sudhakar, 1997; Ramanjulu *et al.* 1994 a,b,c; 1999 and 2000), a little is known about the physiological and biochemical aspects of drought tolerance of high yielding mulberry cultivar, ANANTHA, RFS-175. In the present investigation, therefore, an attempt is made to understand the physiological and biochemical responses of mulberry cultivar Anantha, RFS-175 along with certain selected varieties, namely S-30, S-34, RFS-135 and M-5 to water stress.