DISCUSSION

The experimental results reported here helped us to understand the effects of water stress and its alleviation by rewatering on the physiology of two varieties of *Gossypium hirsutum* L.

The water status of soil and plants are interdependent (Kramer, 1959). The depletion of soil water content induced water stress in both varieties (LRA 5166 and MCU 9) of cotton and the magnitude of the deficit in both soil and plant increased with the days of stress (Figs. 1 and 2). Rewatering increased the water status of both soil and plants. Though the same trend of water status was maintained by both the varieties, the magnitude of deficit varied. The variety LRA retained more relative water content than MCU under both stress and recovery periods (Fig. 2).
The retention of water content by the variety LRA could be for the avoidance of severe water deficit. The variety MCU survived at low water content (Table 1). This water retention characteristics of varieties revealed the differential mechanisms of drought resistance in the two varieties of cotton. Naidu and Bhagyalakshmi (1973) showed that the relative turgidity in drought resistant varieties of sugarcane decreased very rapidly during water stress, compared to the less resistant types. The drought tolerance is the ability to survive reduction in water content and the drought avoidance is the ability to prevent reduction in water content (Turk et al., 1980). Based on this concept it is reasonable to identify the mechanisms in MCU as drought tolerance and in LRA as drought avoidance. This concept is further supported by the biochemical parameters studied.

Root/shoot ratio in terms of dry matter of both the varieties increased as the duration of stress increased and no marked change was noted in the control plants (Fig. 3). This is in accordance with the earlier reports (Hoffman et al., 1971; Hsiao and Acevedo, 1974; Jones and Turner, 1978; Sharp and Davies, 1979; Meyer and Boyer, 1981; Aggarwal and Sinha, 1983; Blum et al., 1983; Gupta et al., 1984). They ascribed these changes to the osmotic capacity of the roots. Quisenberry et al. (1981) concluded that root morphology and root growth potentials appear to be important traits in the adaptation of cotton to conditions where limited soil-water availability is
a major constraint on plant growth. Bielorai et al. (1983) pointed out that under extreme water deficits, cotton leaf growth slows down, and the excess of photosynthates is translocated primarily to the roots, resulting in an increase in the root-top ratio.

During revival period, the root/shoot ratio gradually decreased (Table 2). This shows an adaptive feature of the change in root/shoot balance that occurred during stress as suggested by Aggarwal and Sinha (1983). They reported that when growth under stress was restricted, the maize plant invested its accumulated solutes in roots which could explore more soil volume and provided the shoot with required support. Once stress was relieved, the condition became favourable for shoot growth, dry matter accumulation became more in shoot than in root. In the present study, root/shoot ratio was higher in LRA than in MCU under both stress and revival period compared to respective controls (Table 2).

Water stress is reported to reduce growth by reducing leaf area (Boyer, 1970; Acevedo et al., 1971; McCree and Davis, 1974; Meenakshï, 1980; Karamanos et al., 1982; Blum et al., 1983; McCree, 1986). Leaf area is considered as an excellent indicator of photosynthetic capacity of a plant (Miller et al., 1956; Beg and Turner, 1976). Jordan (1970) and Turner et al. (1986) observed the gradual decrease in cotton leaf area in water stressed conditions. In the present study also, the same
trend was noticed (Fig. 4). Upon rewatering, a recovery to 74% in MCU and 69% in LRA was noticed (Table 3). Acevedo et al. (1971) and Cutler and Rains (1977) have reported full recovery only for a brief stress period. Bielorai and Hopmans (1975) reported only a partial recovery under long stress. Significant recovery of leaf area was observed only in the MCU variety.

Moursi et al. (1978) found that no significant changes of chlorophyll in terms of dry weight and an increase of chlorophyll in terms of leaf area in cotton plants. But in the present study, the content of chlorophyll (in terms of dry weight), especially chlorophyll-b decreased under water stress conditions (Fig. 5). Reduced chlorophyll formation during water stress has been attributed to the reduction of protochlorophyll synthesis (Virgin, 1965; Alberte et al., 1975; Makhmudov, 1983). Upon resumption of the normal watering regime, chlorophyll levels recovered quickly in MCU (Table 4).

Photosynthetic sensitivity of cotton to water stress has been reported by Moreshet et al. (1979) and Krieg (1983). In the present studies, reduction in photosynthesis especially in MCU was noticed under water stress conditions (Fig. 6). This could be attributed primarily to reduced photosynthetic area (Fig. 4) and chlorophyll pigments (Fig. 5). After rewatering of water stressed cotton plant, the photosynthesis was in general
lower than that of the unstressed plant (Fig. 6). Similar trend was reported by Pallas et al. (1967) in cotton. In the present study, in 3 days recovered MCU, a total recovery was observed (Table 6). Total recovery was reported in cotton (Jones, 1973) and Soybeans (Bunce, 1978b). But a partial recovery in cotton plant has been reported by Bielorai and Hopmans (1975) and they attributed the failure of stomata to reopen fully as a reason for lack of full recovery of photosynthesis.

Quick revival of chlorophyll content, leaf area and photosynthesis in MCU, even with low water content in leaf tissues justifies drought tolerance mechanism of MCU variety as suggested by Levitt (1956) and Turk et al. (1980). On the other hand, LRA showed drought avoidance mechanism by maintaining higher water content and slow recovery of leaf area, chlorophyll and photosynthesis.

Sugars (reducing, non-reducing and total) accumulated during water stress and depleted upon recovery (Fig. 7; Table 7). Cutler and Rains (1978) reported that in cotton, during water deficit, reduction in the cellular enlargement without parallel reduction in the intensity of carbohydrate source, could be accounted for sugar accumulation. Accelerated conversion of starch to sugars during water stress has been reported by many workers (Eaton and Ergle, 1948; Parker, 1968; Vieira da Silva, 1968). Jacobsen et al. (1986) reported that the synthesis and activity of amylase was higher in the water stressed barley
leaves. In the present study also, the amylase activity was found to be very high in the stressed plants (Fig. 9). This could be the reason for the higher accumulation of sugars. When the roots of cotton plants were subjected to an osmotic stress, soluble sugars accumulated in the leaves and were proportionally decreased in the roots (Vieira da Silva, 1968).

Among the two varieties studied, MCU showed higher content of reducing sugars (Table 7) associated with the higher amylolytic activity (Fig. 9). Decrease in starch levels may be due to reduced photosynthesis (Fig. 6) and increased hydrolysis (Table 8) as also was suggested by Kozlowski (1964). The accumulation of sugars could protect the protoplasm from coagulation and desiccation and the higher concentration might prevent visible wilting for a long time (Levitt, 1972). In the revived MCU variety, the content of reducing sugars depleted quickly as compared to LRA (Fig. 7). Corresponding decline in the activity of amylase was noted in both the varieties (Fig. 9).

Drought resistant variety has been found to have higher sugar content than susceptible ones (Vaadia et al., 1961; Maranville and Paulsen, 1970; George, 1978; Meenakshi, 1980; Kathiresan, 1983). Highest concentration of total sugars in the drought resistant types was mostly due to the marked predominance of non-reducing sugars (Murty and Srinivasulu, 1968; Ramakrishnayya
and Bhattacharjee, 1973). In the present investigation, the variety MCU showed higher accumulation of total and non-reducing sugars (Fig. 7) and therefore reasonably MCU could be considered as more drought resistant than LRA.

The respiration was enhanced in both varieties of cotton plants subjected to mild stress conditions of 3 and 6 days after withholding water and it declined under severe stress (9 days—Fig. 10). Similar pattern was also reported by earlier workers (Upchurch et al., 1955; Brix, 1962; Kaul, 1966). Decrease in respiration due to water stress could be evidenced by loss of dry matter (Table 2) as also suggested by Brown and Thomas (1980). Respiration in MCU was less affected than LRA during water stress and the same variety revealed quick recovery (Table 9). Even though respiratory activity improved upon rewatering, the rate was lower than that in unstressed plants. The respiration rates per unit dry matter for stressed cotton and beans were the same for the plants which had not undergone stress (Brown and Thomas, 1980).

Energy content in terms of oxycalorific value was found to be lowered with the intensity of stress and improved upon rewatering (Fig. 11). A similar decrease in energy content was noticed under water stress conditions of Capsicum annuum (Venkatanarasimhan, 1984). In the present study MCU retained
relatively high energy value (Table 10), which might indicate the potential for higher productivity in this variety even under stress conditions, as energy content refers to productivity (Hunt, 1966; Odum, 1971).

Research on protoplasmic drought resistance in cotton based on the structural hypotheses of Iljin (1953) and Souza et al. (1984) demonstrated that drought destroyed the structural organization of the cells through membrane disruption, leading to membrane leakiness. This is confirmed in the present study of the electrolyte leakage that increased under stress conditions (Fig. 12). Among the two varieties studied, MCU seems to have more stable membrane as revealed by the low leakiness compared to LRA (Table 11). During recovery, the electrolyte leakage dropped in both the varieties (Fig. 12), suggesting the recovery of the stability in membrane structure. This is in accordance with the results of Shcherbakova and Kacperska-Palacz (1980) in winter rape, who found that dehydration followed by restoration of tissue turgidity caused a decrease in the leakage of electrolytes.

Water stress was found to enhance the activity of acid phosphatase in cotton varieties studied (Fig. 13). Similar trend was reported by many workers (Vieira da Silva et al., 1974; Vieira da Silva, 1976; Pham Thi et al., 1982). They also linked the acid phosphatase with drought resisting potential
of plant species. When acid phosphatase activity under stress was compared in MCU and LRA, it was noted that the variety MCU was having lower activity of the enzyme (Table 12). It seems that MCU as more drought resistant than LRA following the contention of Dassa et al. (1985) who pointed out that the activity of acid phosphatase was higher in the more drought sensitive varieties of pearl millet.

Water stress triggers the peroxidase activity in both the varieties of cotton studied (Fig. 14; Table 13). Similar observation was made in maize (Petinov and Malysheva, 1960), wheat (Stutte and Todd, 1969), bean (Alekseeva and Ramazanova, 1973), paddy (Dwivedi et al., 1979; Mohandas, 1979; Biswas and Choudhuri, 1984), Vigna (Mukherjee and Choudhuri, 1983). The increased activity of peroxidase may be attributed to the increased availability of substrates like $H_2O_2$ due to water stress (Mukherjee and Choudhuri, 1983).

Buffer soluble protein content gradually decreased in both the varieties as the intensity of water stress increased (Fig. 15). Reduction in the protein content due to water stress had been reported by many workers (Hsiao, 1973; Levitt, 1980b; Kramer, 1983; Biswas and Choudhuri, 1984; Joshi, 1985). The accelerated protein breakdown as well as the reduced rate of protein synthesis are the principal factors attributed to the
decreased protein content during water stress (Barnett and Naylor, 1966; Hsiao, 1970; Barlow et al., 1977; Cooke et al., 1980; Bewley and Larsen, 1980, 1982). The decrease in the protein content and a corresponding accumulation of total free amino acids were discussed by many workers (Palfi, 1968; Stewart, 1973; Meenakshi, 1980; Tan and Halloran, 1982; Fukutoku and Yamada, 1984). In the present study also a similar relationship was observed (Tables 14 and 15). The major source of energy in the form of ATP, required for protein synthesis is obtained from respiratory and photosynthetic phosphorylations (Levitt, 1980b). The reduction in the protein synthesis noted in the two varieties of cotton plants under water stress conditions, associated with reduction in respiratory and photosynthetic rate could therefore be attributed to reduced supply of ATP due to its decreased production.

Shiralipour and West (1984) pointed out that protein synthesis was rapidly reinitiated in maize when water stress was released and that these proteins were especially rich in proline. In the present study, among the two varieties, higher depletion of protein content was noticed in LRA than in MCU during the stress period (Table 14). Correspondingly higher accumulation of total free amino acids was also observed in LRA variety (Table 15). The recovery of protein content was
found to be of the order of 20% in both the varieties (3 days recovery - Table 14).

A gradual accumulation of free amino acids was noticed in both cotton varieties as the duration of stress increased, and declined as the stress was relieved (Fig. 16). Accumulation of total free amino acids during water stress has been reported by many workers (George, 1978; Levitt, 1980b; Meenakshi, 1980; Kramer, 1983; Hooda and Sheoran, 1984; Stephen and George, 1985; Becker and Fock, 1986b). The reason for the increased content of free amino acids could be due to the accelerated proteolysis as well as decline in the rate of protein synthesis (Jager and Mayer, 1977; McMichael and Elmore, 1977; Meenakshi, 1980). Since protein synthesis decreases in stressed plants, demand for amino acids slows down and they accumulate (Hsiao, 1973). Besides, de novo synthesis of amino acids may also lead to their accumulation as suggested by Meenakshi (1980) and Rhodes et al. (1983).

In the present investigation, among the two varieties LRA showed a higher quantity of total free amino acids during the water stress period than MCU 9 (Table 15). But during one day recovery period, MCU retained higher content of free amino acids than LRA (Fig. 16). Upon rewatering, in both the varieties, the content of free amino acids depleted and attained the control value on the 3rd day of recovery (Table 15). This supports the earlier findings of McMichael and Elmore (1977) in cotton.
Several hundred fold increase in the free proline content was noticed during stress period and the content depleted upon rewatering in both the varieties (Fig. 17). Increased free proline content during water stress was reported in cotton by earlier workers (George, 1978; Janagoudar et al., 1983). Among the two cotton varieties studied, MCU showed higher spurt in free proline accumulation than LRA (Table 15). This was associated with the lower water status of the variety (Fig. 2). For instance in MCU, the RWC was only 46% (of control) on 9 days of stress with 3162% of proline accumulation as against 56% RWC and 2357% proline in LRA.

The cause of proline accumulation during water stress has been suggested to be mainly due to protein hydrolysis (Palfi, 1968; Stewart, 1973), or due to de novo synthesis of proline (Singh et al., 1972; Lawlor and Fock, 1977; Bogges and Stewart, 1980). Proline may serve as a source of energy and nitrogen during immediate post-stress metabolism (Wang, 1968; Oaks et al., 1970; Singh et al., 1972; Savitskaya, 1976; Blum and Adelina, 1976).

It is generally considered that a high carbohydrate level is required for the accumulation of proline (Carceller
and Fraschina, 1980). The variety MCU accumulated higher content of sugars (129% of control as against 108% in LRA) (Table 7) and proline (3163% of control as against 2358% in LRA) (Table 15) during 9 days stress period. Stewart (1972) observed in bean plants, a higher level of carbohydrates and a slow depletion of proline during recovery. Similar trend was noticed in the present study in MCU variety (Tables 7 and 15). The high carbohydrate content in MCU could be attributed to the active photosynthetic process when compared with LRA (Fig. 6).

Accumulation of free proline in leaves as an adaptive mechanism for drought tolerance has been reported in Bermuda grass (Barnett and Naylor, 1966), barley (Singh et al., 1972); sorghum (Sinha and Rajagopal, 1975), sunflower (Srinivasa Reddy and Krishna Sastry, 1977; Kathiresan, 1983), cotton (George, 1978), paddy (Meenakshi, 1980). In the present study, MCU showed a remarkable accumulation of free proline (Table 15) suggesting its efficient adaptive mechanism for drought tolerance. Shiva Raj (1985) suggested that proline accumulation in maize cultivars may be related to better recovery resistance.

The revival studies of water stressed plants showed a fast depletion of the stress-accumulated proline (Routley, 1966; Thakur and Rai, 1981; Sano and Kawashima, 1982; Aloni
and Rosenshtein, 1984). This decrease has been attributed to the fast depletion to the rapid oxidation of proline and frequent transport of proline to the site of oxidation (Stewart et al., 1977). It was suggested that the variety which accumulated higher proline during stress, recovered more rapidly upon relief of stress (Sinha and Rajagopal, 1975; Blum and Ebercon, 1976). Contrary to this, in the present study, the variety MCU, though accumulated higher proline, recovered slowly upon rewatering (Fig. 17). Janagoudar et al. (1983) suggested that cotton variety which maintains high proline even after the alleviation of stress is considered to be superior in drought resistance over the variety which does not maintain such high levels. According to this contention, the variety MCU is superior over LRA in drought resistance ability. The latter one showed fast depletion of proline during recovery (Table 15).

The total nitrogen in both the varieties of cotton showed an initial increase, followed by a decrease during severe stress (9 days - Table 16). This trend is in accordance with the earlier reports (Wadleigh and Ayers, 1945; Stocker, 1960; Chen et al., 1964; Routley, 1966; George, 1978; Meenakshi, 1980; Bharambe and Varade, 1982). This increase may be due to increased translocation of nitrogen from different regions of the plant to the leaves as suggested by Chen et al. (1964) in citrus. The data on insoluble nitrogen content of cotton under stress conditions also show a similar pattern of change (Table 16).
Soluble nitrogen content also showed a steady increase in the water stressed plants of both the varieties, MCU and LRA (Fig. 18). Similar pattern was also reported by George (1978) in cotton cvs. MCU 5 and GS 23. Consequently the total free amino acids also showed an increasing trend (Fig. 16). McMichael and Elmore (1977) also reported in cotton plant that an increase in soluble nitrogen reflected in total free amino acids. In the present study when the two varieties (MCU and LRA) were compared, the content of soluble nitrogen and total free amino acids was found to be lower in MCU under stress conditions, but higher under stress alleviation periods, while the reverse trend occurred in LRA (Figs. 16 and 18).

Content of insoluble nitrogen was higher in MCU than that of LRA under both water stress and revival conditions (Table 16). During water stress period, the trend of insoluble nitrogen was in line with that of buffer soluble protein and total nitrogen content (Figs. 15 and 18). However, upon re-watering the content of total nitrogen and insoluble nitrogen revived quickly in MCU variety (Table 16). A casual relationship between the slow recovery of chlorophyll levels in LRA (Table 4) and the behaviour of leaf nitrogen content (Table 16) in this cultivar seemed possible. Similar relationship was reported in maize genotypes (Sanchez et al., 1983).

Nucleic acid content decreased in both the varieties of cotton subjected to water stress (Figs. 19 and 20). Among
the nucleic acids, changes in RNA content were more significant than those of DNA (Table 17). Depletion of nucleic acid during water stress has been reported by earlier workers (Chinoy et al., 1974; Meenakshi, 1980; Khan and Garg, 1981). Gates and Bonner (1959) attributed this depletion to the failure of the stressed leaves to synthesize nucleic acid or to its excessive destruction or to the cessation of chromosomal multiplication. This was also attributed to the increased RNAase or RNA polymerase activity (Kessler, 1961; Dove, 1967; Genkel et al., 1982; Biswas and Choudhuri, 1984). The decrease in the nucleic acid especially RNA reported in the present experiment is also paralleled with the corresponding decline in the content of buffer soluble protein (Fig. 15). For instance in MCU 9, the RNA was 80% (of control) on 9 days of stress with 70% protein content, as against 64% RNA and 54% protein in LRA 5166 (Tables 14 and 17). Since protein synthesis takes place on polyribosomes and depends on DNA and RNA molecules, the disturbance in the protein metabolism as a consequence of water stress must depend on the preceding changes in nucleic acid metabolism (Kessler, 1961; Deltour and Jacqmard, 1974; Levitt, 1980b; Meenakshi, 1980).

Among the two varieties studied, RNA and DNA contents depleted fast under stress period in LRA compared to MCU (Table 17), but quick recovery was noticed in MCU compared to LRA.
The present studies showed that water stress lowered the content of minerals like sodium, calcium, magnesium, phosphate and iron in cotton varieties (Figs. 22, 24, 25). This is in accordance with the observations made by earlier workers (Wadleigh and Richards, 1951; Meenakshi, 1980; Clark, 1981; Bharambe and Varade, 1982; Hocking, 1982). On the other hand it was found that potassium was the only inorganic cation which increased in content with the development of water stress (Fig. 23). Accumulation of potassium during water stress was observed by many workers (Viswanath, 1977; Versan and Phillips, 1978; Munns et al., 1979; Turner, 1979; Meenakshi, 1980; Jones et al., 1980; Turner and Burch, 1983; Jadhov and Karadge, 1985). Christerson (1976) found an increase in drought hardiness in pine seedlings due to increased potassium content and it influenced the desiccation tolerance of cytoplasm through the colloidal property or the metabolisms of carbohydrates and proteins. Pitman and Cram (1977), Pitman (1981) and Flowers and Yeo (1986) have assigned a key role of K⁺ as turgor generators in cells. Rajagopal (1985) pointed out that K⁺ reduces transpirational losses and increases water-use efficiency in crop plants. Adequate levels of K⁺ in paddy were associated with its survival after a period of water stress (Rena et al., 1978).

In both the varieties of cotton, the accumulated potassium depleted upon rewatering (Fig. 23). Janagoudar et al. (1983) also reported a gradual increase in the K⁺ content of cotton Bhagya variety, under water stress condition and a fall after
24 h of rewatering. Wilson and Ludlow (1983) reported a rapid fall in the $K^+$ concentration after rewatering, which attained the control value within 7 days in the dry leaves of green panic, buffel and speargrass.

The variety, MCU 9 which showed a higher accumulation of potassium (Table 19) can be considered to be more drought resistant following the contention of Sanandachari (1978) in sugarcane varieties. The same variety also maintained high $K^+$ content during the recovery period (Fig. 23). The high level of $K^+$ in MCU was found to be associated with that of free proline (Fig. 17). For instance, 9 days stress resulted in an accumulation of 147% (of control) $K^+$ and 2950% of free proline in MCU as against 129% $K^+$ and 1970% free proline in LRA. Similar relation has been shown in cucumber (Udaiyakumar et al., 1976), paddy (Meenakshi, 1980), groundnut (Shashidar et al., 1981), cotton (Janagoudar et al., 1983) and prosomillet (Jadhav and Karadge, 1985). The presence of $K^+$ appeared to promote transformation of glutamine and alanine to proline (Tang et al., 1985).

Sodium accumulated under mild water stress conditions (3 and 6 days) in both the cotton varieties. The concentration remained higher in the revived LRA variety (Fig. 22). Similar observation was made by Wilson and Ludlow (1983) in green panic. The key role of sodium besides $K^+$ in maintaining turgidity of
plant cells has been well established (Raschke, 1979; Cram, 1976).
Hooda and Sheoran (1984) reported an accumulation of Na$^+$ ions
in wheat, maize, sorghum and bajra. Under severe stress condi­
tions (9 days) cotton varieties depleted the sodium (Table 19).

Calcium concentration decreased in both the varieties
of cotton with the subsequent increase in levels of plant water
stress (Fig. 24A; Table 19). Similar observation was made in
maize (Medriski and Wilson, 1960), paddy (Meenakshi, 1980),
soybean (Karlen et al., 1982), cotton (Bharambe and Varade,
1982). Meenakshi (1980) has attributed the decrease in the
concentration of Ca$^{++}$ to the reduced rate of its translocation
to the aerial parts during severe stress period. It is interesting
to note similar trends of Ca$^{++}$ and membrane integrity during
water stress. Variety LRA revealed lower membrane integrity
by showing high electrolyte leakage (Table 11), and the same
variety had low concentration of Ca$^{++}$ (Table 19). For instance
in LRA, the electrolyte leakage was 173% (of control) on 9 days
of stress with 59% calcium as against 154% electrolyte leakage
and 81% calcium in MCU. Chari et al. (1986) discussed the possible
role of Ca$^{++}$ in inducing membrane stability and maintenance
of higher water status in groundnut and cowpea plants.

Water stress reduced the concentration of magnesium
in both varieties of cotton and improved upon rewatering (Fig.24B;
Table 19). Gradual decrease in the concentration of Mg$^{++}$ under water stress condition was also reported in corn (Jenne et al., 1958), maize (Medrinski and Wilson, 1960), soybean (Karlen et al., 1982), speargrass (Wilson and Ludlow, 1983) and cotton (Bharambe and Varade, 1982). As Mg$^{++}$ is the major component of chloroplast, a similar trend of Mg$^{++}$ and chlorophyll (Fig. 5) was noticed in the stressed cotton plant. Variety MCU showed lower contents of total chlorophyll (Table 4) and magnesium (Table 19). For instance in MCU 9, the total chlorophyll was 75% (of control) on 9 days of stress with 78% of Mg$^{++}$ as against 83% total chlorophyll and 86% Mg$^{++}$ in LRA 5166. However, during recovery, the improvement of Mg$^{++}$ and chlorophyll was more rapid in MCU than in LRA.

Phosphate concentration decreased with increase in levels of plant water stress in both varieties of cotton (Fig. 25A; Table 19). Similar trend was reported in tomato (Greenway et al., 1969), Trifolium subterraneum (Wilson and Huffaker, 1964), Litchi chinensis (Nakata and Suehisa, 1969), paddy (Meenakshi, 1980), cotton, sorghum and soybean (Sharpley and Reed, 1982), cotton (Bharambe and Varade, 1982). The decreased concentration of phosphate was attributed to decreased translocation and inhibition of its uptake (Dunham and Nye, 1976; Meenakshi, 1980; Bharambe and Varade, 1982). Phosphate concentration improved upon rewatering in both the varieties of cotton (Table 19). Wilson and Huffaker (1964) observed recovery during 24 h of rewatering in Trifolium subterraneum.
Water stress reduced the concentration of iron in both the varieties of cotton (Table 19). Iron nutrition was adversely affected only in LRA 5166 by increased duration of stress (Fig. 25B). Lower concentration of iron under water stress condition was also reported in paddy (Meenakshi, 1980). Pitman (1980) has pointed out that uptake of iron is reduced in plants in response to low soil water potential.

Changes in the content of organic acids during water stress period and its alleviation varied in the two cotton varieties studied (Table 20). In general, the organic acids did not differ qualitatively in response to water stress but there was a marked quantitative difference. This is in conformity with the earlier findings of Ergle and Eaton (1949, 1951), Sadykov et al. (1959) and George (1978) in cotton and Meenakshi (1980) in paddy. Under water stress condition, depletion of total organic acids was observed in both the varieties of cotton (Fig. 31). This finds support from the earlier works of Kaul (1966) in wheat; George (1978) in cotton and Ford (1984) in tropical legumes. Higher content of fumaric, lactic, succinic, aconitic and citric acids were noted in MCU than in LRA subjected to both stress and its alleviation treatments.

The concentration of aconitic acid increased gradually under water stress condition and decreased upon rewatering in
MCU variety (Table 20), whereas a reverse trend was noticed in LRA. Accumulation of aconitic acid in the drought resistant variety (GS 23) and a reverse condition in the drought susceptible one (MCU 5) were reported in cotton (George, 1978). Aconitate, an important trivalent organic anion, was reported to accumulate in response to water stress in maize (Lawlor and Fock, 1978), sorghum and sunflower (Jones et al., 1980) and paddy (Meenakshi, 1980). Aconitic acid might be involved in the osmotic adjustment of tissues suffering from water stress, as polyvalent ions are believed to be potentially more effective as osmotic agents than equimolecular concentration of monovalent ions (Jones et al., 1980). Tartaric acid concentration increased with increase in the level of water stress in both the varieties of cotton (Fig. 28B). This is in accordance with the earlier reports of Meenakshi (1980) in paddy. In both varieties of cotton, the concentration of tartaric acid depleted upon rewatering (Table 20).

A fall in citric acid and rise in malic acid were observed in both varieties of cotton (Figs. 29, 30). This is in accordance with the earlier reports of Ergle and Eaton (1949) and George (1978) in cotton; Kaul (1966) and Prasad et al. (1982) in wheat, Meenakshi (1980) in paddy and Becker and Fock (1986a) in maize. The interconversion of citrate to malate could not be ruled out as suggested by Ergle and Eaton (1949) in water stressed cotton plant. Among the two varieties, MCU was found to be more efficient in retaining higher amount of organic acids.
George (1978) identified the drought resistant property of GS 23 cotton variety by its ability to maintain a steady level of organic acidity during water stress and consequent pH alteration resulting in minimum damage to the enzymatic machinery of the system.

The most important physiological mechanism enabling plants to tolerate stress is the lowering of osmotic potential, termed as osmoregulation or osmotic adjustment (Hsiao et al., 1976; Turner et al., 1978). Any loss of water from cells during water stress will lead to solute concentration by increasing solutes within the cells and correspondingly resulting in lowered osmotic potential (Jones and Turner, 1980). Sugars, potassium, organic acids and amino acids are known to be important osmoregulators (Dhindsa et al., 1975; Cutler et al., 1977; Cutler and Rains, 1978; Kluge, 1976; Munns et al., 1979; Munns and Weir, 1981; Jones et al., 1980, 1981; Meyer and Boyer, 1981; Turner and Burch, 1983; Morgan, 1984; Nunez, 1984; Flowers and Yeo, 1986). The accumulation of osmoregulators play a significant role in maintaining a potential gradient for water uptake (Slatyer, 1957) and the turgor potential of plants subjected to severe water stress (Hsiao et al., 1976; Jones and Turner, 1978; Jenson, 1981).

The two varieties of cotton studied in the present investigation, MCU 9 and LRA 5166, showed the accumulation of
osmoregulators such as sugars, amino acids particularly proline, potassium, organic acids especially malic acid (Figs. 7, 17, 23 and 29). Such an accumulation of osmotically active solutes plays an important role in maintaining a favourable water balance in the two varieties. Similar results in cotton genotypes have been reported by others (Cutler et al., 1977; Cutler and Rains, 1978; George, 1978). Between the two varieties studied, MCU is more efficient in accumulating osmotic solutes even in low water status of the plant. This strongly supports that the variety MCU 9 has a better drought resistance mechanism compared to LRA.