Chapter 6

STRESS RESPONSE
IN COTTON ROOT SYSTEMS

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INTRODUCTION

The development of the root system of the cotton (*Gossypium hirsutum* L.) plant is under genetic control but may be modified by environmental factors. The root system is an integral part of the "soil-plant" environment and as such provides the means for both water and nutrient absorption as well as the production of key plant hormones such as abscisic acid, cytokinins, and certain gibberellins. Also, part of this environment, the root system is subjected to a myriad of influences such as different soil properties as well as soil micro-flora and fauna that act alone or in combination to impact root development and plant productivity.

Since cotton has a taproot system, the extensibility of root development is dependent on the initiation and growth of the lateral or secondary roots. Therefore, these roots can extend outward from the taproot to a distance of over two meters (Taylor and Klepper, 1974). These roots also remain fairly shallow (less than one meter deep, Hayward, 1938). The lateral roots are formed from the cambial layer of the taproot and are arranged in a row according to the number of vascular bundles present in the primary root. The depth of root penetration depends on a number of factors, but in general the taproot can reach depths of over three meters and can elongate at a rate from less than one to over six centimeters per day. In general, the root system continues to grow and increase in length until young bolls (fruit) begin to form (Taylor and Klepper, 1974), at which time root length declines as older roots die. New roots continue to be formed past this point but the net result is a decline in total length (Hons and McMichael, 1986).

The concept of root stress in cotton as the plant develops, as will be discussed in subsequent sections of this chapter, centers generally around the impact of soil conditions on root system performance and growth, since roots grow in the soil matrix and are subject to factors that change in the soil environment. One particular aspect of cotton root development, however, that might be categorized as strictly root stress, would be the infection of roots by plant pathogens such as Verticillium wilt (*Verticillium dahliae* L.), and other pathological organisms. Although these organisms live in the soil, they can have a more direct effect on root system growth as contrasted to other soil factors such as water and nutrient stress

Therefore, the overall objectives of this chapter are to discuss individually some of the major soil factors that influence root development, how these factors affect plant productivity in gen-

eral, and the extent of genetic variability in the response of cotton to soil (root) stress. A more in-depth presentation of the factors that impact cotton root development is discussed in the chapter by McMichael *et al*. (2010) on growth and development of root systems.

STRESS RESPONSES IN COTTON ROOT SYSTEMS

There are many different kinds of stress that can influence root development in cotton. As indicated earlier, most of these stress factors originate as a result of changes that occur in the soil surrounding the roots that indirectly impact root function as well as root growth. Each of these factors will be discussed in terms of how they affect cotton root development with the realization that the interactions between these factors are extremely important in determining the final result.

Water Stress and Root Water Relations

The water content of the soil can have a significant influence on rooting depth and rooting density and therefore on function of cotton roots (Klepper *et al.*, 1973). Root activity can also change as the soil dries since root proliferation may occur at lower depths to maintain water uptake rates (Klepper *et al.*, 1973). Recently, McMichael and Lascano (2010) demonstrated the occurrence of "hydraulic lift" in cotton roots where water is transmitted to the roots in the drier upper soil layers through the root system. The water moves from the wetter lower layers to the upper layers to maintain the viability of the roots in the drier layers to reduce overall root stress. In general, soils with a small water-holding capacity have deeper roots while those with a larger capacity have shallow roots (Glinski and Lipiec, 1990). McMichael (unpublished data) showed that rooting densities of cotton increased significantly at lower depths and decreased in upper soil layers in several commercial cotton cultivars when the upper soil profile dried. Klepper *et al.* (1973) also observed that the rooting patterns of cotton in a drying soil shifted as the soil dried. Initially more roots were in the upper layers, but as a result of the death of the older roots in the upper soil levels due to the soil drying and production of new roots at the lower depths, the rooting density increased with depth. Cotton plants grown in uniformly moist soil did not show this reversal. Malik *et al.* (1979) also showed that emergence of cotton roots from soil cores of different water contents into a soil zone where water was freely available to the roots increased as the soil dried.

The root/shoot ratios also increased as the water content increased due to an absolute increase in root weight with shoot weight not being affected. Changes in water distribution as a result of irrigation practices can also impact the growth of cotton roots. Radin *et al*. (1989) noted that long irrigation cycles tended to trigger more rapid deterioration of the root system during periods of heavy fruiting above the normal net reduction in root growth as fruit develops. This trend was slow to be reversed. Carmi *et al.* (1992) observed that in cotton irrigated with a drip system a shallow root system with a high percentage of the roots less than one millimeter in diameter were concentrated around the emitters which resulted in a strong dependence on a frequent supply of water for continued growth. In other studies, Carmi *et al*.

(1993) also showed that the capability of more mature cotton plants to adjust rooting patterns to large changes in water distribution was slow and that preferential root growth relative to shoot development did not occur in response to progressive soil drying in their case. Carmi and Shalhevet (1983) also observed that dry matter production by cotton roots was less severely inhibited than shoots under decreasing soil moisture. This implies that changes in the root dry weight/root length relationships can change in response to changes in soil moisture. In terms of water extraction, Taylor and Klepper (1975) observed that water uptake in cotton was proportional to the rooting density as well as the difference in water potential between the root xylem and the bulk soil. Jordan (1983) showed that rooting densities may decrease to as low as 0.2 cm/cm^3 and still extract water. Taylor and Klepper (1974) showed that root length did not increase in a soil layer when the water content fell below 0.06 cm^3/cm^3 which was equivalent to a soil water potential of -0.1 MPa. In other work, Taylor and Klepper (1971) also observed that water extraction per unit length of root was greater in wet soil and decreased exponentially with soil water potential. In general, they found that deep roots were as effective as shallow roots in extracting water. Interactions between soil water status and soil temperature can also influence the function of cotton roots. Radin (1990) showed that the hydraulic conductance of cotton roots declined at cooler temperatures which would affect water uptake. Bolger *et al*. (1992) also showed that conductance decreased when the root temperatures were reduced from 30°C to 18°C. These results would suggest that under certain conditions the water uptake by cotton roots may decrease as a result of low soil temperatures even though water was not a limiting factor. Oosterhuis (1981) showed that root hydraulic conductivity was decreased by mild water deficit. The importance of the water relations of cotton roots *per se (i.e.,* axial vs. radial water flow and cell water relations) is certainly not to be overlooked in any discussion of the impact of water on root development. Oertli (1968) has provided an excellent review of water transport through the root systems of plants and soil-root interactions. Since much of this information is directly related to other factors mentioned in this chapter, a more comprehensive rendering is included in the next discussion on osmotic adjustment.

Most of the studies on the water relations of cotton have focused on the whole plant (e.g., Ackerson *et al*., 1977). Field research using mini-rhizotrons has shown that non-irrigated cotton had a deeper root length than irrigated cotton (McMichael, 1990; Keino *et al*., 1994). Furthermore, only non-irrigated cotton showed cultivar differences in root length density (Keino *et al*., 1994). These results suggested that cotton cultivars express large differences in root length distribution under water stress, and therefore, deep rooting cultivars should be selected within environments where water is limiting. Carmi *et al*. (1992) showed that a shallow and restricted root system resulted in strong dependence of the plants on frequent and sufficient water supply, such that temporary minor changes in irrigation affected plant water status and productivity. However, a shallow root system allowed maximum flexibility for using irrigation to quickly and efficiently affect plant water status and influence processes which determine productivity. In the last ten years there have been a number of new methods introduced to measure the water relations of roots. In cotton, thermocouple psychrometers have been used to measure root water potential (Oosterhuis, 1987; Yamauchi *et al*., 1995) and osmotic potential (Oosterhuis, 1987). The vapor pressure osmometer has also been used to

record osmotic potential (Ball and Oosterhuis, 2004) in excised roots. There are few reports on the nature of the osmotica in cotton and the importance of proline (McMichael and Elmore, 1977) and glycine betaine.

Root resistance accounts for a significant fraction of the hydraulic resistance in most plants (e.g., Fiscus, 1983). Radial root resistance is usually substantially higher than the axial resistance (Yamauchi *et al.*, 1995). Hydraulic conductivity in cotton roots is reduced under conditions of water-deficit stress (Oosterhuis and Wiebe, 1980). Methods to measure cotton root hydraulic conductance were compared by Yang and Grantz (1996) with the reverse flow and transpirational methods appearing to have more physiological validity than the root exudation method. There have been reports of oscillations of 30 to 50 minutes in apparent hydraulic conductance in cotton plants (Passioura and Tanner, 1985), which is similar to the oscillations in stomatal conductance of cotton leaves (Barrs, 1971). Water deficit decreased cotton root pressure by 51% compared to a well-watered control, but had no effect on the exponential pressure-flux relationship (Oosterhuis and Wiebe, 1986).

Osmotic adjustment, or osmoregulation, is a plant mechanism for drought tolerance and the maintenance of water (ψ_w) potential gradients (Wyn Jones and Gorham, 1983). Osmotic adjustment involves the active accumulation of osmotic (e.g. sugars, organic acids and mineral ions) in the cytosol during periods of water deficit or salt stress to lower the osmotic potential (ψ_s) (Munns and Termaat, 1986). The lowered ψ_s response to decreasing ψ_w allows for the maintenance of pressure potential (ψ_p) for turgor (Hsiao, 1973). Turgor maintenance under water stress allows continuation of growth, although at a reduced rate in comparison to optimal conditions (Sharp and Davies, 1979). Osmotic adjustment may be an important mechanism in plant tolerance although some crops do not undergo adjustment (Morgan, 1980; Oosterhuis and Wullschleger, 1988). Osmotic adjustment is a well accepted phenomenon in higher plants (Morgan, 1984). The occurrence of osmotic adjustment, however, is not universal. Varying degrees of adjustment will depend on the nature of the applied stress, and also on the crop or species, cultivar, organ, and developmental age of the organ (Morgan, 1984; Turner and Jones, 1980). In cotton, as in most other crops, research on osmotic adjustment has focused on the leaves (Ackerson, 1981; Ackerson and Herbert, 1981; Cutler and Rains, 1977, 1979), and there are few reports of adjustments in the water relations of cotton roots in response to water stress (Oosterhuis and Wullshleger, 1987a). Cotton appears to have a greater ability to osmotically adjust to water stress than most other major row crops (Oosterhuis and Wullschleger, 1988) (Table 1). The magnitude of osmotic adjustment in cotton was greater in leaves (0.41 MPa) than roots (0.19 MPa), although the percentage change was greater in roots (46%) than leaves (22%) (Oosterhuis and Wullschleger, 1987a). The authors related this to the drought tolerance and survival capabilities of cotton. There is only one reported study of the role of osmotic adjustment with the growth of a root system in droughted field plants (Ball *et al.*, 1994). This study showed only a small, limited amount of osmotic adjustment in the roots of field-grown cotton and a substantial adjustment in the leaves in agreement with Oosterhuis and Wullschleger (1987a). Osmotic potential of leaves varies diurnally (Hsiao, 1973), independently of daily cycles of leaf hydration. Therefore, leaves can maintain turgor during the daytime at the same level as during the night (Acevedo *et al.*, 1979). Radin *et al.* (1989) inter-

preted the diurnal cycling of osmotic potential in cotton as an indication of a "sink-limited" condition within the plant during the boll development period. However, there have not been any similar studies on cotton roots. There is only a small range of genetic diversity of this trait in commercial cotton cultivars (Oosterhuis *et al.*, 1987), although Nepumeceno *et al.* (1998) recently reported significant drought tolerance in an Australian commercial cultivar, CS-50. However, a more substantial range of osmotic adjustment exists in the primitive landraces and wild types of cotton (Oosterhuis *et al.*, 1987). However, the role of osmotic adjustment in a cultivar bred for production as an annual crop may be quite different from that of osmotic adjustment in a perennial wild type. Osmotic adjustment has been favored as a trait offering potential for manipulation in the breeding of drought resistant crops (Sharp and Davies, 1979; Morgan and Condon, 1986; Turner, 1986). Work in Australia on wheat (*Tritium aestivum* L.) (Morgan and Condon, 1986) and sorghum (*Sorghum bicolor* L.) genotypes (Ludlow and Muchow, 1988; Ludlow *et al.*, 1989) has shown increased yield in high osmotic adjusting phenotypes. The yield increase in sorghum of nearly 30% over low adjusting phenotypes was related to deeper rooting resulting in more carbon fixation and increased harvest index. A clear yield advantage from osmotic adjustment in cotton has not been demonstrated. The role of osmotic adjustment in maintaining root growth, allowing water uptake longer in drying soil, has been emphasized by Acevedo and Hsiao (1974). The premise that osmotic adjustment allows for turgor maintenance and increased root growth at low water potentials implies that the plant will be able to exploit a greater and deeper soil volume for water. The role of the root system during drought is receiving current research attention as a possible sensing organ and in root-to-shoot ratios. Jones and Turner (1978) cautioned that the capacity to tolerate drought may be attributed to factors other than plant water relations, such as rooting habit, conductance of water through the xylem, and desiccation tolerance.

Table 1. Magnitude and percentage osmotic adjustment in response to water stress by various crop plants. (From Oosterhuis and Wullschleger, 1988).

| Crop | Osmotic adjustment | | | |
	Magnitude		Percentage[z]	
	Leaves	Roots	Leaves	Roots
	------------(MPa)------------		------------(%)------------	
Cotton	0.41a[y]	0.21a	22.4	46.3
Sorghum	0.31a	0.19a	25.1	37.1
Sunflower	0.17b	0.16a	13.9	25.2
Wheat	0.08c	0.03b	6.6	4.4
Soybean	0.05c	0.00b	4.0	-0.8

[z] Percentage osmotic adjustment refers to the percentage decrease in osmotic potential compared to the well-watered control.

[y] Means within columns followed by the same letter are not significantly different at the 5% level of probability.

Soil Temperature

The temperature of both the soil and air can have a significant influence on the growth of cotton root systems. Most research has shown that in general, the growth of cotton roots increases with increasing soil temperature until an optimal temperature is reached beyond which growth declines. Early work suggested that the optimal soil temperature for the growth of cotton roots was approximately 35°C (Bloodworth, 1960; Lety *et al.*, 1961; Pearson *et al.*, 1970; Taylor *et al.*, 1972). Pearson *et al.* (1970) showed that root elongation increased to a maximum of 32°C and then declined sharply as soil temperature increased in 80-hour-old seedlings. Research by Bland (1993) in controlled environment experiments showed that the rate of cotton root growth increased with the rate at which the soil warmed. His experiments indicated that the root system grew at progressively lower rates of elongation as the rate of soil warming was reduced from isothermal conditions. In research on the growth of roots of cotton seedlings at various soil temperatures, McMichael and Burke (1994) showed that the optimal temperature for root elongation may depend on the level of available substrate or stored seed reserves. They suggested that the measured root length at 10 DAP (days after planting), for example, represented a composite of both narrow and broad metabolic temperature responses. Analysis of mitochondrial electron transport showed that the temperature optimum for root metabolism at 10 DAP (days after planting) for example, was lower than that obtained from the measure of accumulated root growth during the same time period. Kaspar and Bland (1992) indicted that changes in soil temperature can affect growth of a number of root system components. For example, low temperatures generally reduced cotton root branching (Brower and Hoagland, 1964), while higher temperatures approaching the optimum tend to increase branching (Nielsen, 1974). The uptake of water by roots is reduced at low temperature (Nielsen, 1974) while higher temperatures result in increased uptake. Bolger *et al.* (1992) demonstrated that the hydraulic conductance of cotton roots declined as the root zone temperature decreased below 30°C and that conductance at 18°C averaged 43% of that at 30°C. Differences in the response of different root types to temperature were also apparent. Research conducted by Arndt (1945) indicated that the cotton taproot may be more adapted to adverse soil temperatures than subsequent branch roots at least until the taproot had developed to approximately 10 cm in length. Later work on seedling development of a number of exotic cotton strains grown in hydroponics showed similar results (McMichael *et al.*, 2010) (Fig 1.). Steiner and Jacobsen (1992) also noted differences between two cotton cultivars in their sensitivity to soil temperature. When the root temperature was low (20°C), root growth was reduced regardless of the temperature of the air (McMichael and Burke, 1994). The root-shoot interaction in response to temperature may be related to changes in source-sink relationships. Guinn and Hunter (1968), for example, showed changes in carbohydrate levels in shoots and roots in response to temperature with a build-up of sugars occurring at low root temperatures. The successful emergence and initial growth of cotton seedlings is important for the establishment of healthy and improved productivity. Wanjura and Buxton, (1972 a, b) showed that when the minimum soil temperature at planting depth dropped from approximately 20°C to 12°C, the hours required for initial seedling emergence increased from 100 to approximately 425 hours. In many cotton-growing areas the soil temperature can be significantly lower than the optimum when seeds are planted thus impacting the final yield. Therefore the

development of cultivars that possess a root system that can grow and function at low temperatures could improve plant performance. However, since the exact mechanism(s) of the response of cotton roots to temperature are not known, further research, perhaps in the molecular area, is needed to elucidate the nature of the response.
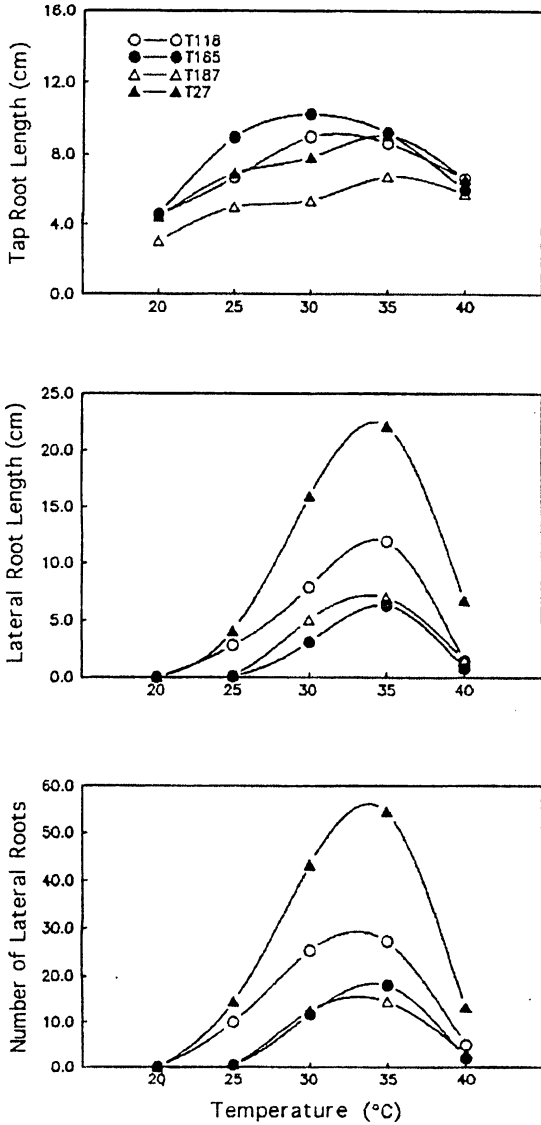
Figure 1. The influence of temperature on the growth of primary (tap) roots and lateral roots of 10-day-old cotton seedlings of four exotic strains of cotton. (From McMichael *et al.*, 2010)

Salinity

Cotton is a relatively salt tolerant species, but growth can still decline when the plant is exposed to saline stress. Germination and emergence (El-Zahab, 1971) and seedling growth (Zhong and Lauchli, 1993) are particularly salt-sensitive. Salinity generally reduces root growth (Silberbush and Ben-Asher, 1987), but there have been reports of mild salinity enhancing root growth (Jafri and Ahmad, 1994; Leidi, 1994). The ions Na^+, K^+, Ca^{2+}, Mg^{2+} and Cl^- are the common constituents involved in high salinity and altered plant growth and root expression. Primary root growth of cotton seedlings was severely inhibited by high concentrations of NaCl in the growing medium, but supplemental Ca reduced Na influx and improved root growth (Cramer *et al.*, 1987; Zhong and Lauchli, 1993). The protective effect of supplemental Ca on root growth under high salinity has been associated with improved Ca status and maintenance of K/Na selectivity (Cramer *et al.*, 1987) and improved cell production (Kurth *et al.*, 1986). Obviously high soil salinity can cause effects similar to water-deficit stress on plant growth (Kramer and Boyer, 1995). The degree of salinity influences the plant's ability to osmotically adjust to the altered water potential gradient between the soil solution and the plant root. According to Zhong and Lauchli (1993), cotton is a relatively salt tolerant plant, but can be very sensitive to salt conditions in the seedling stage. Water stress and ion toxicity are most likely the result of high salt conditions that reduce plant growth. Cramer *et al*. (1987) observed that the growth of the taproot of cotton seedlings was reduced in the presence of NaCl but that the effects could be countered somewhat by the addition of Ca to the growing media. Zhong and Lauchli (1993) found that the elongation of the taproot of cotton seedlings was reduced by 60% over the control plants when the roots were exposed to 150 mol / m^3 NaCl. The addition of Ca increased the elongation rate to within 80% of the controls. They also observed that the growth zone (the region of root cell elongation) of the taproot was shortened by the increased salt content of the media. Kurth *et al*. (1986) showed that the rate of cell production declined in cotton roots in the presence of high salt and that the shape of the cortical cells were affected. Reinhardt and Rost (1995d) also observed that high salt reduced the width and length of metaxylem vessels in cotton seedlings which increase with plant age. These changes in root morphology along with changes in osmotic relationships as a result of high salt, can result in a significant reduction in root growth and root activity to reduce plant productivity.

Pathogens

The presence of soil-borne pathogens can impact the growth and function of cotton root systems. Pathogens such as *Phymatotrichopsis omnivera* are common agents that cause root rot in cotton (Rogers, 1937). Domsch *et al*. (1980) have indicated that cotton seedlings may be more resistant to attack by this organism than older plants due to a reduced carbon content of the root bark. An increase in the carbon content of the roots due to loss of branches and fruit tends to reverse this effect. King and Presley (1942) reported that a disease of cotton that was characterized by a swollen taproot and internal black rot of the vascular tissue was found in Arizona in 1922.

The organism was identified as *Thielaviopsis basicola* and was found to be most damaging to the cotton root system in the seedling stage. Rothrock (1992) later showed an interaction of this organism with soil temperature, soil water, and soil texture on the infection of cotton roots. Burke and Upchurch (unpublished data) observed that cotton plants grown at low temperatures in the absence of pathogens had increased lateral root production even at the low temperatures (13°C). Other studies have shown that infection of cotton roots by nematodes may impact the growth and development of the plant (Kirkpatrick *et al.*, 1991). These authors indicated that the effects of the infection were similar to water stress. The hydraulic conductivity was reduced and drought resistance was increased.

Recently Liu (1995) demonstrated the effect of VAM (vesicular arbuscular mycorrhizae) on *Verticillium wilt* in cotton. His data indicated that when the cotton roots are colonized by VAM, the incidence of *Verticillium* is reduced resulting in improved yields.

Genetic Potential

The growth of the root system of cotton is under genetic control (McMichael *et al.*, 1987) but may be modified by the environment as discussed in previous sections of this chapter. McMichael (1990) has shown variability for root weight in a number of exotic cotton accessions. Variability in root/shoot ratios was also observed in these studies. Earlier, McMichael *et al.* (1985) showed genetic differences in the number of vascular (xylem) bundles in cotton taproots and suggested that variability in lateral root production was associated with the differences in vascular arrangement. Later research indicated this to be the case (McMichael *et al.*, 1987; Quisenberry *et al.*, 1981). McMichael *et al.* (unpublished data) also found genetic differences in the response of cotton seedlings to changes in temperature. Quisenberry *et al.* (1981) found differences in older plants in lateral root production as well as taproot growth. It was further suggested by McMichael *et al.* (1985) that the observed increase in the vascular system and enhanced lateral root production could lead to improved water status of the plant in drought conditions since the potential for additional water uptake and utilization might be possible. Work by Cook and El-Zik (1992) suggested that cotton genotypes having deep roots and increased lateral root production would be more drought resistant based on the variability in root traits. Oosterhuis and Wullschleger (1987b), however, were unable to show significant improvement in hydraulic properties of the plants with the increased vascular arrangement. In field studies, Hons and McMichael (1986) showed that water extraction patterns from fallow rows of a 2x2 skip row pattern were significantly less than cotton planted in every row. This suggested that there was not sufficient rooting density in the cultivar used to use the additional water in the fallow rows. This led Quisenberry and McMichael (1996) to use a more extensive skip-row planting technique to show significant, differences in rooting potential in a number of cotton genotypes by measuring differences in yield as a function of the ability of the plant root systems to extract water. This approach can be utilized to rapidly evaluate genetic differences in root development under field conditions.

Genetic Variability for Improving Root Growth

Genetic variability in a number of root parameters in cotton has been shown to occur across a range of environmental conditions. Quisenberry and McMichael (1996) indicated that genetic differences in rooting potential was related to plant productivity and that an increase in potential (primarily increases in root branching and distribution) could result in increases in yield of cotton under conditions of a drying soil profile. Greenhouse studies conducted using twenty-five cotton genotypes ranging from exotic accessions to commercial cultivars showed significant variability in the dry weights of root systems of sixty day-old plants (Table 2). The variability was greater in the exotic accessions than in the commercial cultivars (McMichael and Quisenberry, 1993). McMichael *et al*. (1985) showed that the increased root xylem (vascular bundle) arrangements in the taproot of some of the exotic cotton accessions resulted in a significant increase in total vessel cross-sectional area and an increased number of lateral roots. This increase suggested an overall decrease in axial resistance to water flow in the root system which may be associated with characteristics of drought tolerance in plants with the increased xylem vessels. Oosterhuis and Wullschelger (1987a) supported the finding that increased water flux was associated with increased xylem cross sectional area. However, an increased number of vessel elements in the xylem of the primary root did not result in any apparent decrease in axial resistance to water flow. The increased number of lateral roots associated with increased vascular bundles resulting in increased xylem vessels may be important characteristics associated with drought tolerance in plants with the increased xylem vessels which may lead to improved yields.

SUMMARY

The growth and development of the root system of cotton has been shown to be genetically controlled, but subject to modifications by a wide range of both above and below-ground environmental conditions. The overall productivity of the plant is, therefore, influenced by the integrated response of the roots to environmental stimuli. In this chapter we have briefly touched on how the cotton root system initiates and grows as well as discussed a number of major factors that influence root development. We have also presented some strategies for enhancing root growth in cotton such as taking advantage of genetic variability. Since current techniques are readily available and can be incorporated into most cotton research programs, future work should not neglect the importance of taking into account the development of the root system in evaluating cotton growth and productivity. As molecular biology continues to make inroads into our understanding of plant development and presents the possibilities for genetic engineering of plant growth processes, the opportunity also exists for manipulating the growth and development of the root system. These advances coupled with the new concepts of precision farming for example, may provide the means for maximizing cotton root system function for maximum plant productivity.

Table 2. Mean root dry weights averaged over experiments for 25 cotton genotypes grown in the greenhouse. Plants were 60 days old at time of harvest. (From McMichael and Quisenberry, 1992).

Genotype	Root dry weight (g)
T184	3.95
T141	3.86
T252	3.30
T283	3.12
T1	3.11
T171	3.08
T256	3.07
T461	2.83
T25	2.80
T115	2.79
T15	2.74
T1236	2.73
T185	2.47
T80	2.45
T45	2.36
Paymaster 145	2.16
Deltapine 61	2.15
G. herbaceum	2.15
Coker 5110	2.05
T151	2.03
T50	2.01
Tamcot CAMD-E	1.91
T169	1.87
Pima S-5 (*G. barbadense*)	1.77
Lubbock dwarf	1.63
LSD (0.05)	0.47

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