Chapter 3

GROWTH OF ROOTS

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INTRODUCTION

The growth, development and function of plant roots in relation to plant productivity has been very difficult to evaluate, especially in natural field situations. Weaver (1926) and co-workers stated over 50 years ago that "An exact knowledge of the root development of crop plants, of their position, extent and activity as absorbers of water and solutes at various stages of growth is of paramount importance to a scientific understanding of plant production." The accumulation of this knowledge becomes more important as more crops are grown under adverse conditions and the need for production efficiency increases.

This portion of the treatise on cotton physiology will concentrate specifically on providing a general overview of root growth and development in cotton, methods of measurement, some factors affecting cotton root growth, and root/shoot relationships that affect productivity.

THE ANATOMY OF THE COTTON ROOT

The cotton root system as described by Brown and Ware (1958), Hayward (1938), and Tharp (1965) consists of a primary or 'tap' root which may grow for several days after germination without branching. When branching does occur the lateral root primordia develop generally about 12 cm behind the primary root apex with tertiary roots developing about 5 cm behind the secondary root apex (Mauney, 1968). If the primary root happens to become injured, there generally is an increase in the number of secondary roots one of which may take over and act as the primary root.

The anatomy of the cotton root has been described in some detail by Hayward (1938) and others (Spieth, 1933; Baranov and Maltzev, 1937). In general, the epidermis of the cotton root is a single layer of cells surrounding the cortex which is made up of spongy parenchyma cells usually 10-12 cells thick. The endodermis is another single cell layer that encloses the stele which consists of a cell layer called the pericycle as well as the xylem and phloem elements along with other parenchyma cells in the central part of the stele. The xylem elements are arranged into distinct bundles usually in a tetrarch (four separate bundles) with the younger protoxylem located at the outer radii and the older metaxylem near the center

of the stele. Hayward (1938) states that it is possible for the primary root to be a pentarch with five distinct vascular bundles present. Recent work by McMichael *et al.* (1983) confirms this in several cotton strains (Figure 1). They also de-

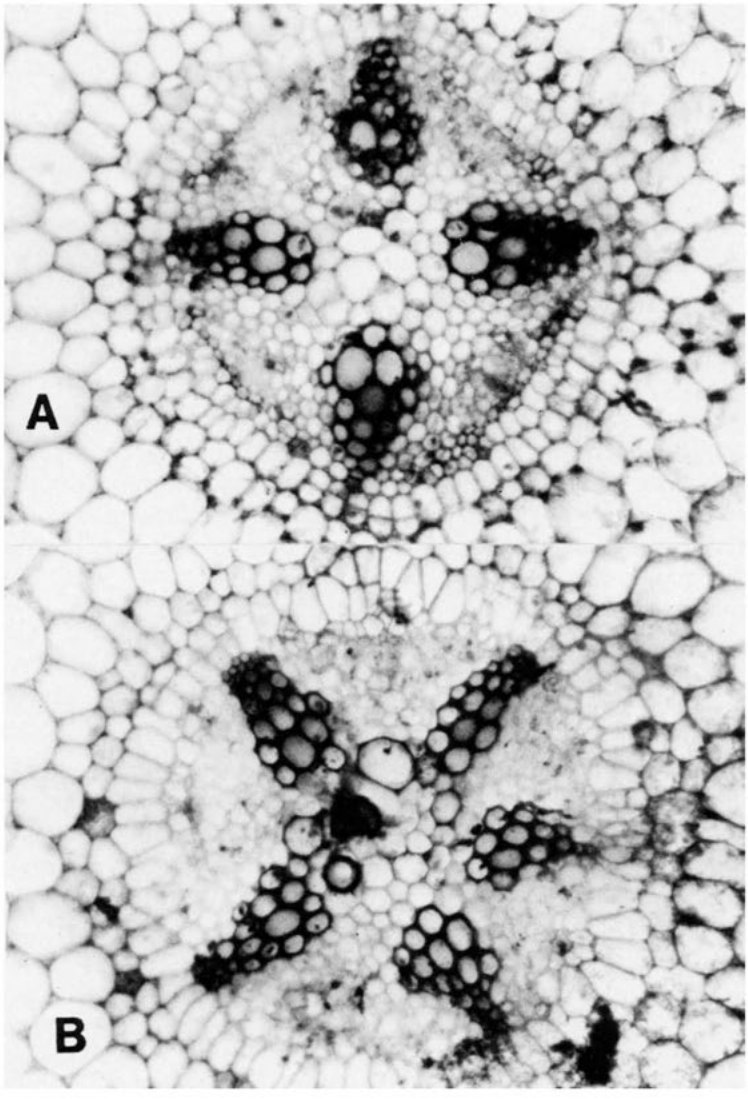

Figure 1. Xylem pattern in primary roots of *G. hirsutum* cv. DPL-16 (A) and *G. hirsutum* cv. T25 (B). The tetrarch arrangement (A) is typical of cultivated cottons. The pentarch arrangement (B) has been found in drought tolerant types. (X100)

scribed a hexarch pattern in some primary roots of other cotton strains. They suggested that the number of vascular bundles in cotton may be an inherited trait of some importance in determining differences in root morphology that have been observed.

The protophloem is located between the radii of the vascular bundles and eventually gives way to formation of the sieve tubes and companion cells. As the root grows and secondary thickening takes place, the epidermal and cortical cells disappear while the pericycle remains to protect the mature root. During the seedling stage rings of sieve tubes and xylem vessels are formed along the outer edges of the stele as one moves along the root toward the junction of the hypocotyl and as the root ages (Speith, 1933).

METHODS FOR MEASURING ROOT GROWTH IN COTTON

In recent years measurement techniques have been described for investigating root growth and development in cotton as well as other crops, particularly in field situations. In addition, screening techniques for accurate evaluation of genetic diversity in root growth have been developed. Rapid technological advancements in related fields such as engineering, soil physics, and plant physiology have made it possible to accurately estimate root growth and development, and scientists have become more aware of the importance of root activity to plant productivity. It is therefore important to discuss the methods used to evaluate the growth of root systems to give some idea how specific problems associated with root research may be approached.

Bohm (1979) and Heen (1980) described a number of methods that have been and are currently being used to evaluate plant root systems in both the greenhouse and field situations. They also describe several techniques for washing roots from soil samples and make recommendations as to which techniques may be most useful in helping to answer specific questions. Bohm (1979) groups and classifies the various methods for studying root growth. These range from the more tedious and time-consuming excavation, monolith, and auger methods to such techniques as root observation laboratories (rhizotrons), other glass wall methods, and more indirect methods such as radioactive tracers. Each method, as Bohm (1979) points out, has certain advantages and disadvantages depending on the research objective and the resources available. Excavation methods, for example, are not only extremely labor intensive, but also require that a large amount of field plot area be disturbed and rendered unusable for similar studies for a number of years. The glass wall methods, on the other hand, allow root studies to be conducted in somewhat natural, undisturbed situations in the same area for repeated seasons. Greenhouse methods for studying root systems range from growing plants in small pots and washing out the roots to growing plants in much deeper and larger diameter containers to simulate the volume of soil a plant might occupy in a field environment.

Since it is impractical to discuss in detail here all of the methods for measuring root growth, I will briefly outline two methods we are currently using in our laboratory to measure root growth in cotton both in the greenhouse and in the field.

The greenhouse method we are using to evaluate differences in root growth in different cotton germplasm is similar to that described by Reicosky (1972). Large polyvinyl chloride (PVC) tubes 20 cm in diameter and 180 cm long are first cut into sections 15 cm long to a total length of 1 m and into 30 cm sections for the remaining length of the tube. The tube is then re-assembled and the seams of each section taped with heavy duty tape. A 2 cm window is also cut into each section and re-taped to facilitate periodic sampling of the soil in each section for water content. One end of the tube is covered with a wire mesh screen and the assembly is placed in a larger diameter container. The space remaining in the container is filled with coarse gravel to maintain the tube in a free-standing upright position. Coarse gravel is placed in the bottom of each tube to a depth of 4-6 cm to insure proper drainage. Each tube is filled with soil and packed to a known bulk density. Water is applied to fill the profile to 'field capacity'. Seeds are planted and the plants thinned to one plant per tube when the plants reach the first true leaf stage. The treatments for a particular experiment are imposed when the plants reach the desired stage of growth. Root samples are collected at various times during the experiment by removing the tape from each section and slicing through the bottom of the section with a metal cutting tool to obtain only the volume of soil and roots contained in that section. The roots in each section are washed free of soil and the total root length and root length density determined by the methods described by Newman (1966). The total dry weight of the roots in a particular section as well as the total profile is measured. The tubes may then be re-assembled and used again in other experiments.

The method we are using to evaluate the growth of cotton roots in the field involves the use of a glass wall observation tube called a minirhizotron (Bohm, 1979). This technique was first proposed by Bates (1937) as a less costly alternative to the glass wall observation trenches. Waddington (1971) and Bohm (1974) also described this technique. The method basically consists of drilling or augering a hole in the soil to the desired depth (usually 1.5 to 2 m in our studies). The diameter of the hole is only slightly larger than the diameter of the tube to be inserted to insure a good contact between the tube and the soil with minimum air gaps. We have been using 10 cm diameter tubes in our studies that are installed in the row at approximately 30 degrees from the vertical to prevent roots from striking the soil-glass interface and growing down the tube as might be the case if the tubes are installed vertically. Waddington (1971) and others used glass tubes for their minirhizotrons, but more recently Plexiglas tubes have been substituted for the glass tubes (Sanders and Brown, 1979). We are currently using Plexiglas tubes for the minirhizotrons in our cotton studies. The tubes are etched with a grid

system before being inserted into the soil. The grid not only indicates depth but also serves as the system for measurement of root length and root length density by counting the number of roots crossing the horizontal transects of the grid.

Waddington (1971) used a fiber-optic technique for observing root growth in the minirhizotrons. Bohm (1974) later used a mirror attached to a pole equipped with a light source to observe root growth in his system. Recently Sanders and Brown (1979) utilized a fiber-optic technique by attaching a 35-mm camera to a fiber-optic scope allowing photographs of the roots intersecting the transparent walls to be taken and later evaluated using an image analysis system. We are using a borescope apparatus equipped with a light source and a low-light sensitive television camera to record the images of each section inside the tube on video tape. The tape is replayed in the laboratory and intersections of roots in each scene are counted on a Newman (1966) grid superimposed on a television monitor. This technique allows measurements to be made on total root length and root length density in cotton throughout a profile during the entire season in a relatively natural undisturbed field situation.

THE DEVELOPMENT OF THE COTTON ROOT SYSTEM

The general development of the cotton root system has been described by Balls (1919), Baranov and Maltzev (1937), Collins and Warner (1926), Pearson (1974), Brown and Ware (1958), Hayward (1938), and Taylor and Klepper (1978). The depth of penetration of the primary root and the formation, number, and depth of penetration of lateral roots may vary according to the variety of strain, soil type, soil water content, and other soil and plant related factors. The influence of some of these factors on root growth will be discussed later, but in general the primary root may penetrate to depths of over three meters under some conditions (Balls, 1919a) while the lateral roots may remain fairly shallow—less than one meter (Hayward, 1938). Thus the root distribution within a soil profile (usually expressed as cm of root per cubic cm of soil or root length density) may vary considerably depending on the conditions to which a particular plant is subjected. The rate of root elongation in soil may range from as much as six cm per day (Taylor and Ratliff, 1969) to considerably less than one cm per day depending on the conditions. The lateral roots extend outward from the taproot sometimes to a horizontal length of over two meters (Taylor and Klepper, 1978). The total root length continues to increase as the plant develops until the maximum plant height is achieved and fruit begins to form (Taylor and Klepper, 1974, 1978; Pearson and Lund, 1968). The root length then begins to decline as plant height stays the same and older roots die.

The total volume of soil explored by a cotton root system for water and ions, hence the development of root density, is related to the ability of the root system to produce secondary roots. The more fibrous the root system the greater the potential for increased rooting density. The lateral root primordia arise from the

cambial region of the stele and are arranged in rows along the primary root. The number of rows correspond to the number of vascular bundles present in the stele (Brown and Ware, 1958). McMichael *et al.* (1982) presented evidence to indicate that those cotton lines that possess five or six vascular bundles also have the potential for producing five and six rows of lateral roots respectively. If the number of lateral roots are increased due to the increased number of primary root vascular bundles, it is possible for those plants to have a greater root density, explore a greater soil volume, and have increased capacity for water and nutrient uptake up to some maximum density necessary to deplete the soil profile. It is interesting to note that roots with an increased number of vascular bundles also should have an increase in the amount of phloem present and thereby an increased potential for movement of material into the system to promote root growth.

The genetic control of root growth in cotton has been alluded to (Taylor and Klepper, 1978), but little work on the evaluation of available cotton germplasm for differences in root growth or specific rooting patterns has been conducted. The evaluation of several exotic photoperiodic strains of cotton for several characteristics including taproot growth and lateral root development was conducted by Quisenberry *et al.* (1981) using 35-day old greenhouse grown plants. They found significant differences in the taproot length and the number of lateral roots between a number of the strains. They suggested these differences may be associated with differences observed in adaptation to drought conditions. McMichael *et al.* (1982) evaluated a number of the exotic cotton strains for differences in root development using other techniques. They evaluated the growth patterns of the taproot and the lateral roots of young seedlings that were growing under constant temperatures in small polyethylene growth pouches filled with nutrient solution. The taproot length, lateral root length, and number of laterals were measured daily for seven days. The results showed significant differences as found by Quisenberry *et al.* (1981) in older plants. This technique allowed a large number of entries to be evaluated over a relatively short period of time. Additional studies need to be conducted on genetic differences in rooting patterns and the inheritance of specific traits associated with root development and plant productivity.

SOME FACTORS AFFECTING COTTON ROOT GROWTH

Most of the factors that directly affect root growth in cotton are soil related (Pearson, 1974; Carson, 1974) although above ground processes in the plant such as photosynthesis, fruiting, and development of leaf area interact to influence root development. For the purposes of this portion of the discussion, only soil related factors will be mentioned.

SOIL TEMPERATURE

The temperature of the soil is generally lower than that of the air and less subject to rapid fluctuations during the season (Nielsen, 1974). The temperature

at which roots of most plants exhibit maximum growth rates is lower than that for aerial organs. It appears from several different studies that the optimum soil temperature for cotton root growth is somewhere between 28C and 35C (Pearson, 1970; Bloodworth, 1960; Letey, 1961; Taylor, 1972). When the soil temperature deviates significantly from the optimum a number of things may occur. At low temperatures root growth is reduced and less branching occurs (Brouwer and Hoagland, 1964). Water uptake is also reduced (Nielson, 1961) and nutrient uptake is altered (Nielsen and Humphries, 1966). Christiansen (1963) states that subjection of cotton roots to low temperatures may cause death of the root cortex tissue. Guinn and Hunter (1968) reported a buildup of sugar in plant roots exposed to low temperatures.

The exposure of cotton roots to temperatures higher than the optimum also has an adverse effect on growth. More branching seems to occur (Nielsen, 1974) and enzymatic activity and metabolism is reduced (Nielsen, 1974). Taylor (1983) and Arndt (1937) indicate that the overall rate of cotton root elongation is reduced at high temperatures. Thus, the changes in root growth and activity as a function of temperature may have an effect on both root length and root length density, but, as Taylor (1983) points out, reliable field data to determine to what extent this occurs is generally lacking. This information is important, however, since there are many problems with things such as stand establishment in much of the cotton growing areas of the country which are affected by the low soil temperatures at planting time (Wanjura, 1972; and Chapter 36).

SOIL STRENGTH

The growth of cotton roots through compacted soil layers such as plow pans or through areas of very high bulk densities may present severe problems in many soils where cotton is grown. Taylor (1974) gives an excellent review of the effects of changes in soil strength on the growth of root systems of cotton as well as other crops.

In general, studies with penetrometers (devices used to measure soil strength) have shown that as the soil resistance increases root elongation rates decrease (Grimes, 1975; Taylor and Ratliff, 1969; Grimes, 1972; Pearson, 1970). Since differences in soil strength are closely related to soil water content (Taylor and Ratliff, 1969; Grimes, 1972), the decrease in root growth and penetration into lower depths of a profile could mean that there would be less total water available to the plant. This could also mean that the plant would extract water from only a very limited area of the total soil volume (Grimes, 1972).

Changes in root morphology also may occur when plants are grown in soil with high strength characteristics. Taylor (1963) found that cotton grown in soil of high strength had roots with small diameters (<0.9 cm) which contributed to significant yield reductions. Mathers (1967) found that xylem and phloem cells were much smaller in cotton roots that were grown in soil with restricted layers than roots that had not been subjected to high strength layers. The manifestation

of these responses in root growth in high strength layers has been suggested by some to be hormone mediated (Russell and Goss, 1974).

Many of the effects of changes in soil strength on root growth are not documented. In some cases roots may find their way through the high strength layer by means of worm holes or cracks so that differences in top growth may not be evident (Taylor, 1983).

SOIL AERATION

The concentrations of the soil gases, particularly oxygen and carbon dioxide, or the balance of the levels of the two in the soil may significantly reduce or enhance root development.

In general, the soil air is about 20 percent oxygen, 79 percent nitrogen, and <1 percent carbon dioxide at a depth of about six inches (Stolzy, 1974). These concentrations may vary considerably - to <5 percent oxygen and as much as 20 percent carbon dioxide. Cannon (1925) reported oxygen concentrations of 7-8 percent in the soil he was studying. Clements (1921) stated that the carbon dioxide levels in the soils in his experiments ranged from <1 percent to 15 percent depending on the conditions.

The concentration of the soil atmosphere is influenced by a number of factors including soil temperature and soil water content. Cannon (1925) reported that temperature had an effect on soil atmosphere composition by its direct influence on the partial pressures of the gases. Russell and Appleyard (1915) stated that the oxygen concentration in a waterlogged soil fell to as little as 2 percent with little change in the carbon dioxide level. Similar results have been reported elsewhere (Stolzy, 1974).

Cotton roots respond to changes in the composition of the soil air. Their growth does not seem to be hindered by carbon dioxide levels that significantly reduce root growth in other plant species (Kramer, 1969). Cotton roots do seem to be highly sensitive to changes in oxygen concentrations. The elongation of the taproots was reduced when they were exposed to 5 percent oxygen levels for a short period of time and were killed within three hours after the soil air was purged of oxygen (Huck, 1970). These results are not suprising since oxygen is required for root respiration and growth. Whitney (1941) studied the effects of changes in the composition of the soil air on water absorption by a number of crops including cotton. He concluded that water uptake was reduced by either the toxic effects of carbon dioxide reducing root cell permeability, or the reduction of respiration due to the low oxygen levels, or an interaction between the two effects. The latter is likely to be the case under most field situations.

SOIL WATER

The changes in water content of the soil affects the growth and productivity of plant tops via changes that occur in absorption of water by plant roots to replace transpirational water losses and maintain plant turgor for growth. Soil water

content also may have a direct effect on the growth rates and distribution of roots within a soil profile. There have been excellent reviews and articles written dealing specifically with the absorption of water by plant roots, the resistances encountered as water moves along the water potential gradient to the leaves, and interactions between water and nutrient uptake by roots (Russell, 1977; Taylor and Klepper, 1978; Newman, 1974; Taylor and Klepper, 1975; Gardner and Ehlig, 1962; Rose and Stern, 1967; Gardner, 1964; Hillel *et al.*, 1975). The reader is referred to these works for more in-depth study of these subjects. This portion of the discussion will be limited to the more direct effects of changes in soil water on the overall growth rates and distribution of cotton roots.

The distribution of cotton roots may be altered by changes in soil water content, particularly as the soil dries out (Taylor, 1983). Rooting depth may be increased in drying soil (Klepper, 1973) while root elongation rates may be significantly decreased (Taylor, 1983). Taylor and Klepper (1974) also show that root density in cotton decreases as soil water content decreases. There may or may not be significant alterations in root activity as the soil dries since root proliferation may occur at lower depths to maintain water uptake rates and the growth of plant tops (Browning, 1975; Taylor and Klepper, 1974). Root densities may decrease to 0.2 cm per cubic cm and still be effective in water extraction (Jordan, 1983). Taylor and Klepper (1971) have shown that the water extraction per unit root length in cotton does not change with depth so that a root may be as effective, for example, in extracting water at 100 cm as it would be at 10 cm. McMichael (1980) observed that the root length density increased significantly at the lower depths and decreased at the upper soil layers (<30 cm) in several commercial cottons during a period when the soil was allowed to dry. The root length density of plants in irrigated plots was always greatest in the upper part of the soil profile (<30 cm). He also observed that total root length reached a peak about 80-85 days after planting when maximum plant height was achieved. Taylor and Klepper (1974) noted that root length did not increase in a soil layer when the water content of that layer fell below 0.06 cubic cm/cubic cm or a soil water potential of about -1 bar. They also showed that when a dry soil was rewatered both plant height and root length resumed growth and continued to increase.

Thus, changes in soil water content and soil water potential may change rooting patterns and may or may not change root activity in relation to top growth if the changes in soil water status are gradual so that the root systems can adapt to the changing environment.

ROOT-SHOOT RELATIONSHIPS

The root and shoot environment interact with growth processes in a plant to modify the genetic potential of the plant and influence productivity. The relation between root growth and shoot growth is therefore very complex and depends on many factors acting simultaneously within the plant system. Aung (1974), in his

extensive review of root-shoot relationships, emphasizes this complexity and views the plant as an integrator of many environmental influences.

In general, root growth in cotton (namely total root length development) increases as the plant develops until fruiting begins (McMichael, 1980). The total root length reaches a peak at peak plant height and reproductive growth commences. There is a linear increase in the shoot-root ratio, however, up until that time. Eaton (1931) and Eaton and Joham (1944) in earlier studies, showed that the defruiting of cotton plants caused an increase in the size of the root system as well as the carbohydrate content of the roots. Crowther (1934a; 1941) showed also that nitrogen and water applications to cotton plants stimulated the growth of the above-ground parts of the plant but suppressed root growth.

The root-shoot ratio is generally reduced, as stated above, as reproductive growth occurs since the overall growth rate of the roots is reduced (McMichael, 1980; Aung, 1974). McMichael and Quisenberry (unpublished) observed similar results in fruiting and non-fruiting lines of cotton they investigated. The shoot-root ratio may also be altered by the influence of factors other than fruiting such as changes in soil temperature, soil moisture, and alteration in the top growth such as changes in total plant leaf area (Aung, 1974; Russell, 1977). Russell (1977) also points out that the control mechanisms for partitioning of dry matter into roots or shoots may be hormone mediated since evidence for the role of plant hormones in promoting or inhibiting growth processes has been documented in recent years. Regardless of the actual control mechanisms conditions favoring early root growth are desirable to establish a root system capable of supporting the growth of the above ground portion of the plant during periods of stress or other adverse growing conditions.