

This approach could give greater impetus to the sorghum crop improvement program. In the tropics, photosensitive sorghum grows very tall in the rainy season and often produces a large number of leaves and a few productive heads. To avoid this, photoinensitive sorghum are generally preferred.

As yield is the primary goal of the breeder, optimum growing conditions are essential for the expression of a crop's full genetic potential. Significant yield improvement has been achieved in different crops, but only under high input situations. In these favorable environments, the potential yield is determined during the early stage of inflorescence development and the panicle meristem is capable of producing the optimum number of florets to their full genetic potential. This is simultaneously substantiated by the optimum photosynthetic efficiency of the leaf attained during the vegetative stage. Nevertheless, it is very difficult to provide congenial growing conditions in most semiarid regions of the world. Often, crops are prevented from expressing their full genetic potential. The productivity of the panicle is drastically reduced due to several unfavorable environmental conditions like lack of water, low nutrients availability, salinity, high temperature, etc. Therefore, major research efforts need to be directed to screen genotypes which could express their optimal genetic potential under unfavorable field conditions.

In substantiation of this, under water stress situations, the growth and development of panicles is affected to an extent by the intensity of water stress at different stages of development. Under severe water stress when cell division is of paramount importance, spikelet differentiation tends to stop but under moderate stress situation, differentiation may be delayed not suspended. Under severe water stress, failure of stem and internode elongation leads to poor or no exertion of the panicle. There could be a drastic reduction in floret number, thereby impairing the final productivity of the panicle and crop. Water stress affects the germination of pollen and growth of pollen tubes on stigmas. During grain development, water stress affects the sustained growth rate of grain. This ultimately leads to poor seed setting and filling of the grain and drastic reduction in seed size. It also has a direct effect on seedling establishment (Chapter-3). Therefore, drought avoidance trait with its capability to complete panicle development and anthesis within a short span of time is an adaptive mechanism. Lines could be selected from the group which express better panicle growth. These could be incorporated in the crop improvement program.

A full understanding of the reproductive apex and its interaction with environmental factors could provide some clues for the selection of cultivars and genetic improvement of the crop.

The maximum yield is determined by the potential of a crop variety and its adaptation to a particular environment. At present, breeders look for a dwarf plant with a compact panicle. However, in a tropical environment, compact panicle provides a favorable environment for the infestation and disease, like grain moths and earhead bugs. A lax panicle provides less opportunity for the development of the biotic stress. The focus of research should be to increase grain number per panicle and grain weight rather than evolving a dwarf plant prone to infestation. An ideotype in sorghum needs to be formulated for better adaptation in the environment.



## ROOT DEVELOPMENT AND GROWTH

### INTRODUCTION

Physiologists are more interested in the above ground portions of plants which play the central role during photosynthesis in plant metabolism. Very little attention is given to studies on the growth and function of root systems. This is partly due to the unavailability of an efficient technique for the extraction of roots from the field. Considerable variation in the expression of the size of roots occurs under different environmental conditions (Russell, 1977). Due to the difficulties involved, most research endeavors concerning root studies are conducted in greenhouses, growth chambers, rhizotrons and a few are based on observations in the field (Kaigama *et al.*, 1977). It is not possible to make a complete analysis of the growth and function of either roots or shoots unless the interrelationship between them and their behaviour in edaphic systems is taken into account (Russell, 1977).

Different techniques have been adopted to study root development in different crops. In sorghum, soil cores are taken from the field with the help of tubes to study depthwise distribution of roots and to correlate the relationship between root and the above-ground portion of the plant at different morphological development stages. Root morphogenesis and early growth have been done mostly in hydroponic culture (Blum *et al.*, 1977 a,b), sand culture (Nour and Weibel, 1978), and glass house pot culture (Hackett, 1973). Böhm (1977) described and compared different methods of root observation, both destructive and nondestructive in a natural environment in mini-rhizotrons. The use of clear tubes buried in the soil, or mini-rhizotron, has been described by different authors (Waddington, 1971; Böhm, 1977). Böhm (1977) stated that mini-rhizotrons required less time for data collections compared to other methods. Other methods have been adopted for the study of root system in different crops (Newmann, 1966; Marsh, 1971; Tennant, 1975; Voorhees, 1976; Sanders and Brown, 1978; Foale and Upchurch, 1982).

An endoscope introduced into a transparent tube and placed into the soil before sowing has been used for direct observation of root distribution and intensity of root colonization (Martens and Clauzel, 1982).

The root system of sorghum plants grown in soil measured at 9, 14 and 17 days from sowing indicate the low average diameter of the root number and the very high extension rate. Sorghum appeared to maintain a stable relationship between the overall number, length, surface area and volume of its root (Hackett, 1973). In sorghum, both under irrigated and non-irrigated conditions a rapid penetration



of root was observed early in the growing season (Kaigama *et al.*, 1977). Traces of roots were observed at depths of 140 to 150 cm 6 weeks after emergence. A greater proportion of total root dry weight accumulated at deeper depths in non-irrigated than in the irrigated sorghum, but the rate of dry matter accumulation of both roots and tops was higher in the irrigated treatment. Response of sorghum plant rooting to irrigation timing showed that daily irrigation resulted in as rapid and as deep a root penetration as did less frequent irrigation (Merrill, 1976). In this study, root length and dry weight yield were 20 to 30% higher under daily irrigation. Merrill and Rawlins (1979) also reported that increases in root length and root dry matter were larger under irrigated rather than under non-irrigated conditions. A video recording system in mini-rhizotron has been developed by Upchurch and Ritchie (1983) for observations of root systems and densities at different depths, which gives good correlation with those determined by soil sampling.

Studies on root and shoot development by Heatherly (1975) in silt loam soil in Missouri indicate that root density in the 0-30 cm soil region reached maximum at 5 weeks after planting and then remained relatively constant until 2 weeks before maturity, declining rapidly afterwards. Below 30 cm the time of maximum root density occurred 2 to 4 weeks later. More than 80% of the root mass was located in the top 30 cm of soil. Depth-wise distribution of dry matter at maturity has been investigated by several researchers (Bloodworth *et al.*, 1960; Teare *et al.*, 1973). Sorghum root could reach a depth of 150 cm or more (Miller, 1974; Nakayama and van Bavel, 1963; Lavy and Eastin, 1969; Mayaki *et al.*, 1976; Kaigama *et al.*, 1977). Lateral extension of the root over 2 m from the crown was reported by Lavy and Eastin (1969). Different reports indicate that more than 80% of sorghum roots are concentrated within 30 cm below the surface (Bloodworth *et al.*, 1960; Nakayama and van Bavel, 1963; Stone *et al.*, 1973; Saint-Clair, 1977; Jordan *et al.*, 1979 a,b; Thomas *et al.*, 1979). Burch *et al.* (1978) reported that the early maturing variety (Ruse) of sorghum approached maturity, its root distribution decreased in soil layers below 10 cm depth whereas in other varieties (Bragg), which matured 2 weeks later, maintained a deep root system and continued to deplete water down to 120 cm. Deep penetration of some roots could be related to drought resistance and that drought resistance could be improved by selecting genotypes with deeper roots. The more drought resistant cultivars were stated to have heavier roots, greater root volume and higher root/shoot ratio than the drought susceptible lines (Nour and Weibel, 1978).

The seminal root arises with the emergence of the radicle through the coleoptile. The seminal root is mainly responsible for the establishment of seedling. Crown roots develop from the basal stem nodes and provide anchorage to the plant by spreading laterally before growing downward. Blum *et al.* (1977) reported that the early maturing sorghum genotypes initiated the adventitious roots earlier than the later maturity genotype. This character may be useful as a selection criterion for improved crop establishment. Jordan *et al.* (1979 a,b) reported that the seminal root of sorghum seedlings growing under field conditions usually deteriorates as the crown root system become established. They reported that in field situations the appearance and rate of elongation of crown roots are influenced

by available soil water in the upper layer, usually limited under rainfed situations.

Studies on root systems of some Senegalese and American sorghum cultivars indicated that the former produced lower root weight than the American ones, and they showed better balance between root and shoot (Saint-Clair, 1977). This trend may be associated with adaptation to semiarid or dry environments. About 84% of the root weight were found to be located in the first 25 cm soil layer. Myers (1980) reported that the maximum root dry weight occurred at about the time of anthesis and argued that total root length and root mass were reliable criteria for root measurement. Genotypic differences in root development are desirable in sorghum (Blum *et al.*, 1977 a,b; Nour and Weibel, 1978; Jordan *et al.*, 1979 a,b; Jordan and Miller, 1980).

Root clipping has no significant effect on root growth and shoot growth. Compensatory growth within the existing root member was capable of maintaining root length and volume, but not root dry weight when crown roots were severely reduced (Jordan *et al.*, 1979 a,b). Under mulching systems root growth viz. root length, number of adventitious roots, volume of roots, dry weight of roots were found superior when compared to the control, both at flowering and harvest (Palanivel and Ramanathan, 1981).

Sorghum root growth is influenced by soil physical properties (Baligar and Nash, 1978). Germination and emergence of sorghum were delayed in finer aggregates. An increase in clay content reduced root growth, but an increase in aggregate size increased root elongation. Better root growth was observed in a sandy to sand-loam texture than clay to clay-loam texture (Baligar and Nash, 1978). Hewitt and Dexter (1979) concluded that smaller aggregates offer better nutrient availability per unit length of root. Deep ploughing before sowing increased root density and water use efficiency (Chopart and Nicou, 1976). Warsi and Wright (1973) reported that increasing nitrogen levels from 0 to 160 kg/ha increased root growth, specially during the early stages. Myers (1980) in a comprehensive review of the literature on root in grain sorghum states that most of the work has concentrated on mineral absorption using radioactive trace techniques (McClure and Harvey, 1962; Nakayama and van Bavel, 1963; Lavy and Eastin, 1969), and water use (Blum and Naveh, 1976). Hemsath and Muzurak (1974) studied the growth of seminal roots at an early seedling stage and found elongation positively correlated to the water potential of the soil which indicates the effect as that of soil resistance. The effects of partial and complete removal of the primary seminal root of sorghum during the first 6 days of growth after germination were investigated by Chotib *et al.* (1976) by growing seedlings in modified Hoagland's solution. No significant differences were found in various growth components between the untreated controls and plants with induced defective primary root systems. Damage occurring 1 or 2 days after primary root emergence is compensated by the rapid appearance and growth of adventitious roots due to the availability of seed reserves. A vigorous primary seminal root is not a requirement for normal growth of the hybrid sorghum.

A strong coordination between shoot and root characteristics has been reported in sorghum (Bhan *et al.*, 1973; Jordan *et al.*, 1979 a,b; Wright *et al.*, 1983). Mirhadi



*et al.* (1979) reported that there was some relationship between the growth of internodes and rooting behavior in sorghum plants: with the emergence of the 2 leaves on the plant, one of the lower internodes reaches its maximum length. At this time, root primordia began to elongate from the base of the internode. A similar phenomenon was observed in lower internodes of corn plants (Kobayashi and Mizutani, 1970).

The total number of primordia and elongated roots increased with high water content, but the increase was higher after a ten-day drought, once the leaf had emerged (Mirhadi and Kobayashi, 1979). There was no significant difference between control and wilting treatments at all growth stages for the number of roots. Teare *et al.* (1973) reported that water stress was apparently responsible for reduced activity of nitrate reductase, which eventually reduced the ratio of protein to amino acid.

González-Rodríguez (1989) established a model in a quantitative estimation of root growth in sorghum, both under irrigated and non-irrigated conditions. The number of first and second order roots could be predicted from the branch length of the seminal roots since constant rates were observed. Root dry weight and length were strongly associated with leaf area and shoot dry weight.

Many studies have dealt with the distribution pattern of roots in different profiles, but they have not taken into account the whole root system and its components, which is only possible in solution cultures, sand cultures or in microtome sections. Very few attempts have been made to study the whole root system of sorghum, pearl millet and other cereals in soils. The following account is based on the study (unpublished) by the author to investigate the development of the whole root system under different conditions. The results are discussed in the light of available literature.

## DEVELOPMENT OF THE ROOT SYSTEM

After emergence, the radicle elongates to give rise to the seminal root. The mesocotyl elongates from the base of the radicle and the mesocotyl roots emerge from the coleoptile node (Fig. 6.1). Sorghum has a fibrous root system, and mesocotyl roots increase in magnitude when seeds are planted deep in the soil.

Two types of root are generally identified in sorghum: seminal roots which arise directly from or below the germinating seed, and the adventitious or mesocotyl roots that arise from the axis between the node of the coleoptile and the base of the radicle (Fig. 6.2a). At later stages, about 30 days after emergence, crown roots arise from stem above ground (Fig. 6.2b). However, from the standpoint of physiological function both types of roots function in a complementary manner (Williams, 1962). Injury to the seminal root can lead to enhanced activity of nodal roots. The root system in sorghum is similar to that of other cereals. As growth advances, both adventitious and nodal roots develop branched secondary roots which in turn develop tertiary roots and so on. On the basis of the stage of development and their function, the root systems of sorghum could be distinguished into their constituent components. The following observations

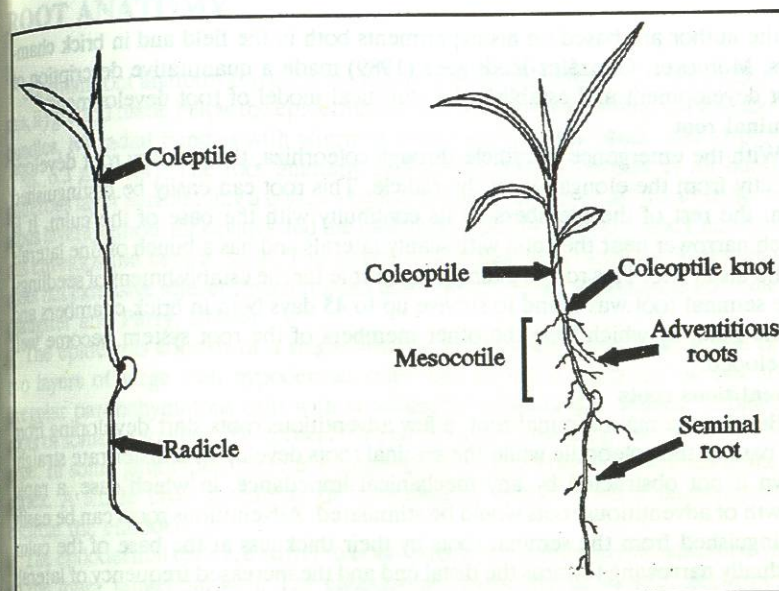


Fig. 6.1 Development of primary roots.

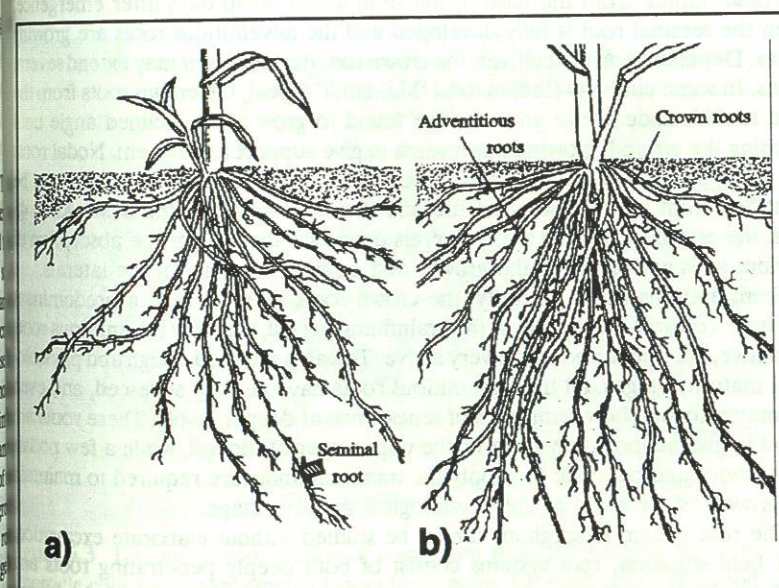


Fig. 6.2 Root system of sorghum in the field (a) at panicle initiation stage, (b) at boot stage.



by the author are based on his experiments both in the field and in brick chambers. Moreover, González-Rodríguez (1989) made a quantitative description of root development and established a statistical model of root development.

#### Seminal root

With the emergence of radicle through coleorhiza, the primary root develops directly from the elongation of the radicle. This root can easily be distinguished from the rest of the members by its continuity with the base of the culm. It is much narrower near the culm with scanty laterals and has a bunch of fine laterals at the distal end. This root is mainly responsible for the establishment of seedlings. The seminal root was found to survive up to 45 days both in brick chambers and in the field, by which time the other members of the root system become well developed.

#### Adventitious roots

Besides the main seminal root, a few adventitious roots start developing from the base of the coleoptile while the seminal roots develop at a faster rate straight down if not obstructed by any mechanical impedance, in which case, a rapid growth of adventitious roots would be stimulated. Adventitious roots can be easily distinguished from the seminal roots by their thickness at the base of the culm, gradually narrowing towards the distal end and the increased frequency of laterals from the base to the distal ends. About 30 days after emergence, the activity and growth of adventitious roots becomes predominant. The adventitious roots are found to be quite active up to anthesis and start senescing thereafter.

#### Nodal or crown roots

These initiate from the base of the stem about 30-40 days after emergence when the seminal root is fully developed and the adventitious roots are growing better. Depending on the cultivar, the crown root development may extend several nodes. In some cultivars (Indian local 'Maldandi' types), the crown roots from the third to fifth node above ground were found to grow at an inclined angle until reaching the ground, growing downwards to give support to the stem. Nodal roots are green above ground and send profuse laterals while in the soil; they can be identified from by their stout nature and the few laterals at the base. After a few days, the crown roots send many laterals deep into the soil for the absorption of nutrient as is evident from the growth and meristem activity of the laterals.

From anthesis up to maturity, the crown roots seem to take a predominant support function. Towards the middle of the grainfilling period, very few adventitious roots are active, but major nodals are very active. Towards the hard dough and physiological maturity stages, all the adventitious roots have already senesced, and even the major nodals show symptoms of senescence at deeper levels. These roots are found to give support only towards the upper layer of the soil, while a few nodals may survive and continue to supply the minimum moisture required to maintain the growth of the plant at the physiological maturity stage.

The root system in sorghum cannot be studied without elaborate excavation. In a field situation, root systems consist of both deeply penetrating roots and shallower horizontally extending roots, depending on irrigated and rainfed cultivars. Under irrigated conditions, horizontally extending roots are profuse while in rainfed soils, roots penetrate deeper.

## ROOT ANATOMY

Sorghum root anatomy is typical of monocots. It is composed of i) outer epidermis, ii) ground tissue below the epidermis, iii) endodermis surrounding the vascular bundles, iv) radial bundles with alternate xylem and phloem bands, and v) pith (Figs. 6.3 and 6.4). The root anatomy of *Sorghum bicolor* consists of an outer peridermal layer surrounding a cortex which is composed of outer soil parenchymatous layers without air cavities and the innermost layer, the endodermis. Endodermis envelops the central stele. The anatomy of nodal roots is similar to seminal roots but extensive sclerenchyma regions develop in both the hypodermis and stele (Sangster and Parry, 1976a).

The epidermis consists of a single layer of cubical cells subtended by one or two layers of large oval hypodermal cells. The cortex is made up of oval to irregular parenchymatous cells with considerable inter-cellular spaces. In older roots of some genotypes, the cortical cells elongate to assume a plate-like appearance. In some genotypes, there is a single layer of thick-walled exodermis in the cortex. A single layer of cubical or brick-shaped cells of cortical parenchyma encircle the endodermis.

The endodermal cells are barrel to boat-shaped and are thickened with suberin on the inner tangential wall. The endodermal thickening varies with genotype. Silica crystals are present in the endodermal cells; their shape and size vary with cultivar and with the age of root (Figs. 6.5-6.8). Silica crystals are absent in some genotypes. The pericycle below the endodermis is composed of one or more layers

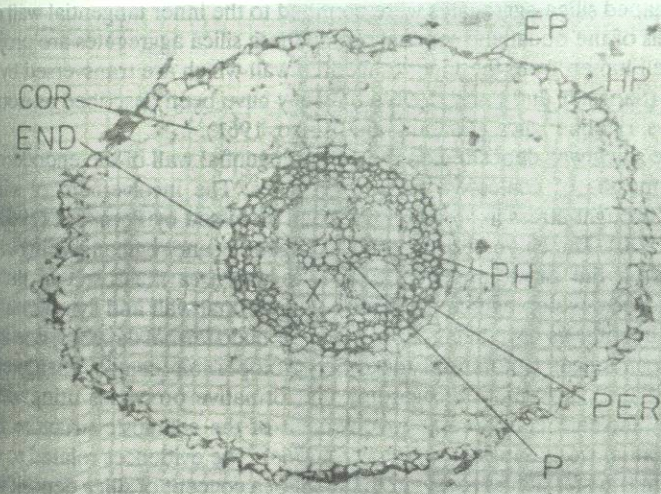
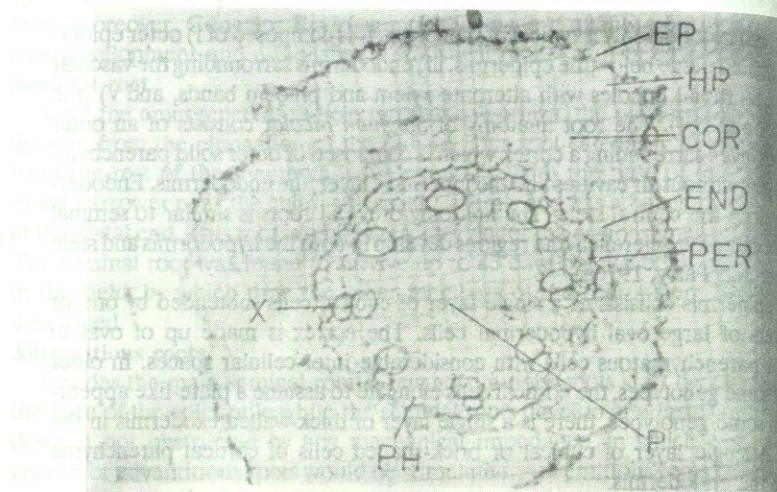


Figure 6.3 Transverse root section of a sorghum genotype showing the pattern of cortical cells and arrangement of vascular bundles. EP-epidermis, HP-hypodermis, COR-cortex, END-endodermis, PER-pericycle, X-xylem.

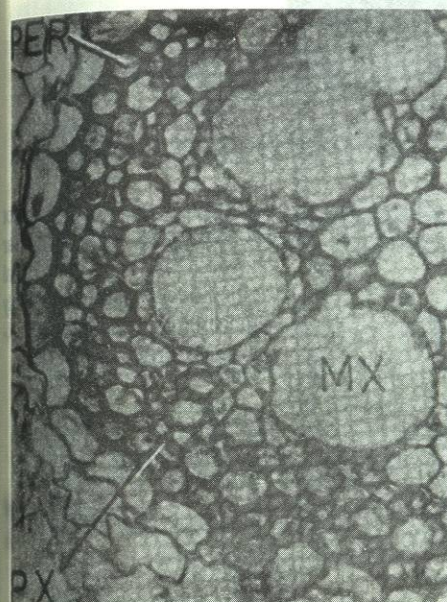




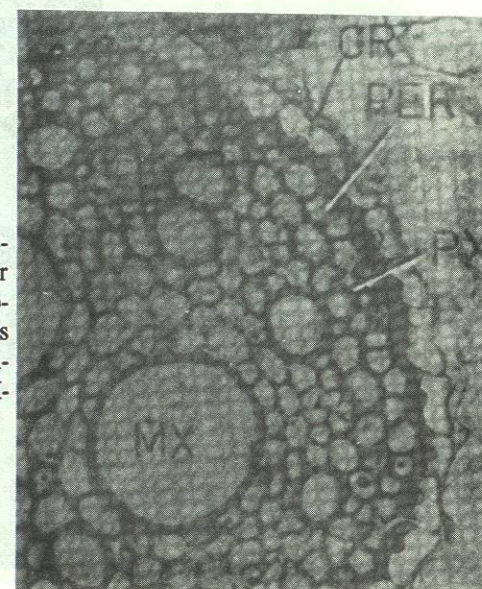
**Figure 6.4** Transverse root section of another genotype showing the pattern of epidermal cell, cortical cell and vascular bundles. EP-epidermis, HP-hypodermis, COR-cortex, END-endodermis, PER-pericycle, X-xylem and PH-phloem.

of thickwalled sclerenchyma cells of which generally the outermost layer is highly lignified. Lignification varies in different genotypes. Solid silica deposits occur as domeshaped silica aggregates were confined to the inner tangential wall of the endodermis of the nodal and seminal roots. These silica aggregates are projected into the cell lumen from the inner tangential wall which are transversed by xylem pit canals (Sangster and Parry, 1976 a,b). They have been described as isotropic, amorphous, opaline silica (Lanning and Linko, 1961).

Opaline silica was deposited on the inner tangential wall of the endodermis as spherical masses of coalesced primary particles. The involvement of silica in particular drought stress in sorghum has been discussed by Ponnaiya (1960) and Doggett (1970). The characteristic serial arrangement and regular spacing of silica aggregates on the inner tangential wall is regarded as the result of the physical forces developing over the entire endodermal wall and cytoplasmic face. Two hypothesis have been put forward for endodermal deposits, one involving physicochemical factors and the other protoplasmic control (Sangster and Parry, 1976 a,b). Information regarding the formative processes using electron microscopy indicate considerable involvement of the cellulosic structure of the inner tangential wall (Sangster and Parry, 1976c). The evidences related to water and nutrient transfer across roots are in favour of a concept of silica deposit within the endodermis of sorghum by direct cytoplasmic involvement. Silicon is deposited on the inner tangential walls of the endodermis. In addition, discrete evenly distributed deposits varying in size partly fill the lumen of these layers. Some exhibit a number of smaller protrusions. These lumen deposits show protrusions



**Figure 6.3** Transverse root section of CSH1 showing the thickening pattern of the walls of endodermal cells and pericycle. Endodermal silica crystals were not observed. PER-pericycle, PX-protoxylem, MX-metaxylem.



**Figure 6.6** Transverse root section of IS-148, a sorghum cultivar showing highly thickened endodermal cell wall and silica crystals in the endodermal cell cavity. CR-silica crystal, PER-pericycle, MX-metaxylem.



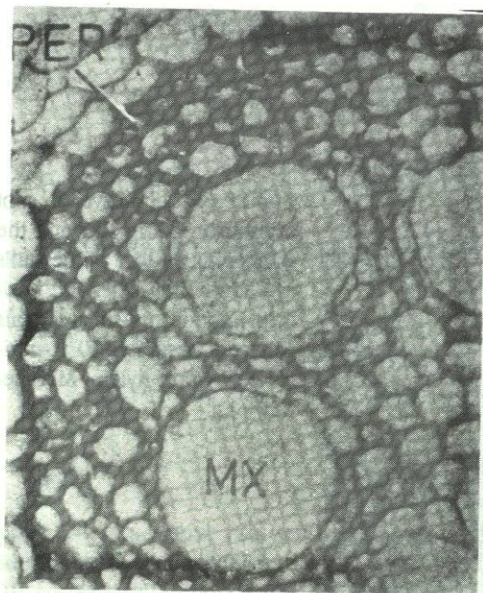


Figure 6.7 Transverse section of *Dobbs*, a cultivar showing thickened endodermis, silica crystal and thickened pericycle. PER - pericycle, MX - metaxylem.

Figure 6.8 Transverse root section of IS-301 showing highly thickened pericyclic cell and absence of silica crystals.

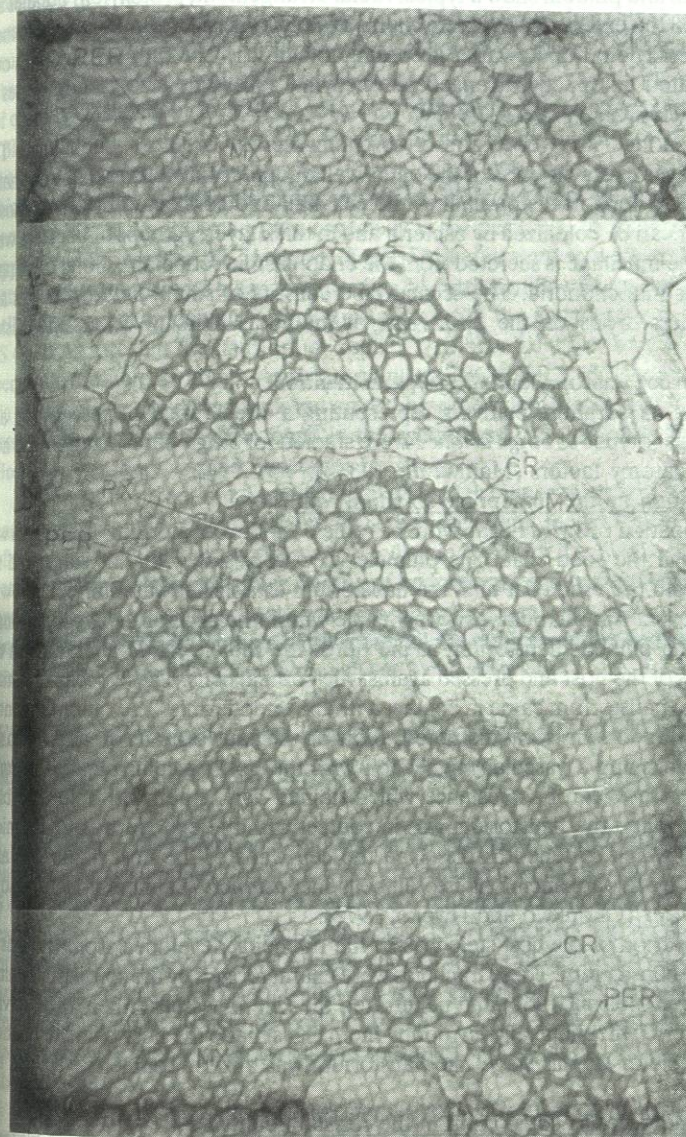
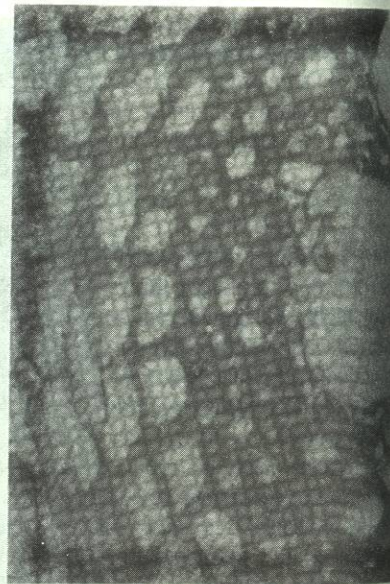


Figure 6.9 Transverse root sections of sorghum genotypes showing the pattern of cell wall thickening of the endodermis, pericycle and xylem vessels, and orientation and size of silica crystals.