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Understanding Root Biology for Enhancing Cotton Production

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Abstract

Cotton is an important commercial crop grown in India. It occupies an area of about 12.7 million hectares and is grown both in irrigated as well as rainfed tracts. In such situations, roots are very important organ for plant growth and development, since they act as anchors, providing mechanical support, and chemical extractors for the growing plant. Root length density sets the proportion of water uptake both under wet conditions and dry soils. Cotton plants with efficient root system capture water and nutrients from soil having these features of longer tap root. It is widely accepted that breeding efforts on aboveground traits are not sufficient to the necessary yield advantage. Shifting the emphasis to analyzing the root system would provide an additional means to enhance yield under changing climatic condition. Belowground image analysis studies point to the importance of root system architecture for optimizing roots and rhizosphere dynamics for sustainable cotton production. In this review, we describe the cotton root biological context in which root-environment interactions providing an overview of the root growth morphology species wise, phytohormone action that control root growth, root anatomical significance in drying soils, biotic and abiotic stresses involved in controlling root growth and environmental responses.

Keywords: root architecture, root diseases, stress conditions, root growth, cotton

1. Introduction

Cotton is one of the most important fiber crops cultivated worldwide. India has the largest cotton acreage approximately 12.7 million hectares and is now the second largest cotton producing country in the world with 312 lakh bales (each of 170 kg) [1]. Cotton cultivation in India encounters with several environmental factors like, abiotic stresses such as drought, flooding, salinity, heat waves and extreme events that limits cotton productivity and projected climate changes could increase their negative effects in the future [2]. Plant root system represents an important interface through which plants respond to various environmental factors. The interface between the environment and plants is multifaceted, with temporally and spatially dynamic processes affecting the signals that growing cells grasp [3]. Taproot systems like in cotton plants are composed of a primary root (the taproot) and lateral roots that emerge from this primary root. The depth of the primary root; the periodicity of lateral root patterning [4], growth rate, and root tip angles of the lateral roots define the potential volume of soil that can be explored and foraged for soil

resources by the root system. The sessile nature of plants has made them extremely sensitive toward the constant flux of surrounding environmental factors. Root architecture is intimately interwoven with and shaped by the availability of soil resources. Strategies for enhanced resource acquisition have recently focused on root traits with the targeted approach for efficient utilization of water and nutrients. [5] proposed that quantification of root traits should focus on phenes, which are defined as the smallest quantifiable phenotypic elements that cannot be divided further. These traits can be computed automatically from root images. The role of the root system under soil moisture stress is receiving much focused research attention recently and which signify importance of root traits such as root length, root-to-shoot ratios, rooting habit, conductance of water through the xylem vessels, and drought tolerance. The depth of root penetration depends on a number of environmental factors, but in general the taproot can reach depths of over three meters and can root cells elongate one to six centimetres per day. In general, the root system traits such as root length continues to thrive upto young boll formation [6], at which time root length declines as older roots die. New roots continue to be formed but overall decline in total length [7]. Roots constitute a critical organ and functionally associated with crop architecture, lodging resistance, drought resistance and yield potential [8]. Due to low heritability and complexity of root system, breeding for root traits has been relatively slow associated with its expensive, labor intensive methodology and time-consuming phenotyping [9]. So far, no report has explored the developmental behaviour of seedling root traits with molecular markers in upland cotton.

2. Root architecture in cotton

Cotton is one of the taproot crop, where the root system consists of tap root, lateral root, branch root, hair root and root hairs. Cotton production systems are exposed to several abiotic stresses during the growing season. In general, plant root zone expansion is a highly desirable outcome of crop production. Roots are a plant's lifeline to water and nutrients that directly impacts cotton productivity. Cotton is grown under stressful conditions that can limit water and nutrient availability throughout the growing cycle. Access to water and nutrients is especially critical to production of the highest quality fiber [10]. Root system architecture is constituted an assemblage of root phenes which determine the temporal and spatial distribution of roots in the diverse soils and the ability of the plant roots to absorb water and essential nutrients from the soil [5]. Cotton plant has a taproot that grows fast and reaches to a depth of 20–25 cm even before seedling emergence. The total depth of root system usually reaches about 2.5 meter depending upon soil physical traits such as soil moisture, soil aeration, soil temperature and genetic potential of variety [11].

In general *G. arboreum* genotypes can withstand dry spell, intermittent and terminal drought conditions in rainfed cotton cultivation due deep tap root system [12]. Cotton is grown in India on soils of varying depths in rainfed tract of central region. In India more than 95 percent of area is covered by Bt-hybrids and in some area Bt-hybrids have been found to have shallow roots (30 cm) due to early onset of reproductive phase. Synchronized boll development in Bt plants altered source-sink relationship and led to early crop maturity [13]. Due to hard-pan of the soils or surface irrigation during early seedling stage impacts early root development. Lack of proper phenotyping strategy for root traits and low heritability for root traits are the most important constraints. There is need to exploit existing genetic variability for root traits. Selection for and incorporation of increased seedling vigour and rapid root system establishment traits may be included into future cotton varieties to improve drought tolerance [11].

The studies on characterization of genetic diversity for root traits in cotton crop with respect to abiotic stresses is very scanty due to inherent challenges in sampling intact roots from the field condition [11]. Therefore, existence of variability for root traits among available cotton germplasm/cultivar in response to environmental stresses indicates the possibility of selecting best genotype to withstand future change climatic scenario. Extensive research has shown that water uptake into plant roots occurs primarily in response to water potential gradients between bulk soil and the root interior. Hence, traits like osmotic adjustment of roots offers potential for manipulation in the breeding of drought resistant plants [14]. In cotton, morphological adaptive response to excess water has been seen as formation of adventitious root and hypertrophied lenticels. Formations of shallow or deep roots are some of the differential strategies adopted by growing plants to adapt to their environments. Root length density sets the magnitude of water uptake both under irrigated and rainfed soils. Thus, root responds to the altered root architecture that may further impact soil properties by decreasing the development of secondary roots. With the help of modern phenotypic tools to understand root system, studies on adaptive root system architecture can be one of the breeding strategies to incorporate into modern cultivar with taking advantage of available genetic variability [11].

3. Development of root systems

Cotton have vertical tap roots [15]; secondary and tertiary roots originates from the tap roots [16] having a single layer covering of epidermal cells surrounded by root cortex. The Arrangement of xylem is either tetrarch or pentarch and the endodermis cells surround the stele and pericycle cells of roots [17]. The secondary roots can grow up to two meters [6]. Lateral roots are mostly shallow [18] and are formed by a taproot cambial cell. Their radial arrangement depends on number of vascular bundles (four or five) in primary root [19, 20]. Vascular bundles also have a direct correlation with taproots and number of lateral roots [21]. Functional significance of root size is determined by length, surface area, diameter, and volume of roots [22]. These traits determine growing plants nutrient uptake efficiency under low nutrient conditions [23]. Root growth and distribution is closely linked with nutrient and water uptake from the soil as most of cotton roots are present in 0–60 cm depth. Adequate nitrogen (N) supply may enhance the root biomass. However, application of N in sodic soils reduces the root parameters such as density, volume, and surface area of cotton roots [24]. Soil temperature of 35°C is optimal for cotton root growth [25]. Soil water status also influences the root development. Soils with less water holding capacity have deeper roots than soils with high water holding capacity [26]. Type of irrigation also affect the cotton root growth as heavy irrigation water supply affects the root system more rapidly during reproductive stage than normal reduction in root growth during boll development [27].

4. Root traits for phenotyping

Root traits can be used as reliable selection criteria for drought tolerance in cotton [28]. Several studies revealed that introgression of root traits has been successfully enhanced crop productivity [29]. Maintaining of cell tissue turgor reinforced by superior water mining through roots has also been shown to enhance photosynthetic carbon assimilation and finally water use efficiency. Aquaporins, the water channels through the cell membrane are gaining significance as a possible

mechanism to enhance water uptake and transport [30]. They assume significance in the scenario of drought tolerance as they actively involved in the regulation of hydraulic conductivities for a better water uptake, CO₂ transport as well as tight cell osmoregulation across cell membranes under water stress [31]. More profuse (higher root length density) and deeper root systems in the soil is often proposed as desirable characteristics for drought adaptation [11, 31]. Mild and initial-stage drought stress enhanced root length in cotton, but long-time water deficit reduced the root activity [32]. Nevertheless, drought tolerant genotypes having large root system coupled with a low $\Delta^{13}\text{C}$ could be the best donor parent for breeding for abiotic stress tolerance in cotton [33].

5. Root disorder: soil compaction

Generally, compaction is considered to be detrimental to plant root growth; however, usually not all parts of a root system are exposed to the same degree of compaction under field conditions, and the capacity of unimpeded parts of the root system for compensatory growth may result in only the distribution of roots being changed and not the total length. Compacted soils will have lower root densities and be inefficient absorbers of water and nutrients. Nutrient deficiencies that may show up due to restricted rooting and soil compaction. When soils are compacted, bulk density increases and the number of larger pores decreases, leading to increased resistance (soil strength) to root growth. Roots growing into compacted soil must displace soil particles, so that the rate of root elongation decreases as soil strength increases. In soil without significant compaction, roots will grow through soil pores and rapidly extend into the profile. Taylor and Ratliff [34] showed that root elongation rates in cotton (*Gossypium hirsutum*) decreased with increasing soil strength. Fine-textured soils physical conditions often limit root penetration and thus effect on water translocation due to the development of hardpans. Cotton roots become unable to take advantage of high water holding capacity of fine textured soils. Such soils required deep tillage for breaking of hardpans below the surface of soils [35]. Low aeration is very common in clayey soil that is caused due to heavy and frequent irrigations, waterlogging, and soil compaction due to heavy machinery that restricts the root proliferation and optimal nutrient uptake. Soil compaction on the other hand significantly decreases cotton productivity because of its deep-rooted nature. Soil compaction can be reduced by deep plowing and by cultivating deep-rooted cover crops, which penetrate compacted soil zone besides creating channels.

Early season moisture stress to cotton plants can be the cause of a deeper root system [36]. During this time, the greatest root deepening is attained; however, lateral roots carry on growing throughout the rooting zone; therefore, the maximum size of the roots may not be achieved till 90 days of sowing [37]. Moreover, cotton has a deep root system with low density of roots in the surface layer of soils where availability of nutrients is high. Therefore, the rooting system makes cotton crop more dependent on the subsoil for nutrition. Soils with smaller particles have less pore space and bind water more tightly owing to capillary forces. This effect is quantified by the soil matric potential, which is affected by compaction and drying. In Vertisol soil, wetting and drying cycles in soil cause swelling and shrinking, respectively, which induce cracks that can extend deep into the soil. Models of soil chemical and physical properties (such as matric potential, hydraulic conductance, and hardness) need to be designed that enable prediction of such properties based on image data [38]. These data can be integrated into plant physiological models such as SimRoot to predict the effects of the soil environment on root physiology [39]. The distribution of water in the soil is generally determined by influence of

gravity. But the porosity of the soil and the presence of hardpans and macropores influence overall the rate of bulk flow [40]. Some nutrients, such as nitrogen, follow similar principles as water because they do not bind tightly to clay particles in soil. Phosphorus is present at very low levels in about 70 percentage of agricultural soils and in chemical forms that are unavailable to the plant [41].

6. Root morphology of cultivated cotton species

6.1 Root study of cultivated cotton species

Improving of yield and maintaining yield stability of cotton crop, under normal as well drought stress conditions, is very much essential for the ever-increasing global population. India is the only country where all the four cultivated cotton species are being cultivated in rainfed conditions. India experiences drought like situation or gaps in rains during most critical cotton crop growth period in such areas every year. Various other factors, such as high temperature, flood, low light, pests and diseases and nutrients deficiency affects cotton production severely. Environmental factors, such as drought stress affect growth, productivity, and fibre quality of cotton [42, 43]. Deep root systems and more profuse root length density in the soil are often considered as selection criteria for drought adaptation trait. Luo et al. [32] reported that mild and early stage drought stress enhanced root length in cotton, but at later stage reduced the root activity as compared to water sufficient plants. Riaz et al. [44] established genotypic variability for root/shoot parameters under water stress in cotton (*G. hirsutum*). This has provoked to study the growth of plant and understand root architecture of cotton species under laboratory conditions.

Laboratory experiment was conducted at ICAR-Central Institute for Cotton Research, Nagpur in a newly designed rhizotron made of transparent acrylic resin sheets to understand root architecture of intact plants of cultivated cotton species. Transparent acrylic resin sheets filled with soil media facilitate the study of root systems of intact cotton plant seedlings grown in a rain out shelter. This method eliminates destructive root sampling and makes possible continuous observations and periodic tracing of undisturbed root systems of the seedlings. Megha et al. [45] evaluated *G. hirsutum* genotypes for water stress by slanting glass plate technique. The present rhizotron assembly was constructed using two transparent acrylic resin sheets of sizes, 2.44 x 1.22 m (**Figure 1**). The soil media of one inch thick was sandwiched between two transparent acrylic resin sheets in an aluminium framework having four compartments for root observations. The two plants of each cultivated cotton species, *G. arboreum* (Phule Dhanwantari), *G. hirsutum* (NH 615), *G. barbadense* (ND 3B) and *G. herbaceum* (Jayadhar) were sown in each compartment at a distance of 30 cm. The experiment was repeated in *kharif* 2017 and 2018 season with normal watering at field capacity. The periodic observations of root and shoot growth were recorded until plant matures at 60 days. The 60 days old seedlings were taken out to study the root growth parameters and density. The composition of the soil was a sterilised mixture of sand, soil, vermicompost and FYM in 1:2:1:1 ratio. The chemical properties of the soil media used for the experiment was 7.33 pH, 0.47 EC, 0.67% OC, 332.5% N, 21.73% P, 8.73% S, 0.82% Zn, 1.58% Fe, 1.78% Cu, 7.69% Mn and 1.33% B.

The results of the experiment revealed that root growth of *G. arboreum* and *G. hirsutum* was more and faster than the root growth of *G. barbadense* and *G. herbaceum* (**Figure 2**). The dry matter accumulation in shoot and root system also shows same trends. The initial root growth was faster till 35–40 days, a stage of squaring cotton plant followed by slow growth towards 50th day making a sigmoid pattern of



Figure 1.
Acrylic resin sheet rhizotron assembly for seedling roots showing of four cultivated Cotton species.

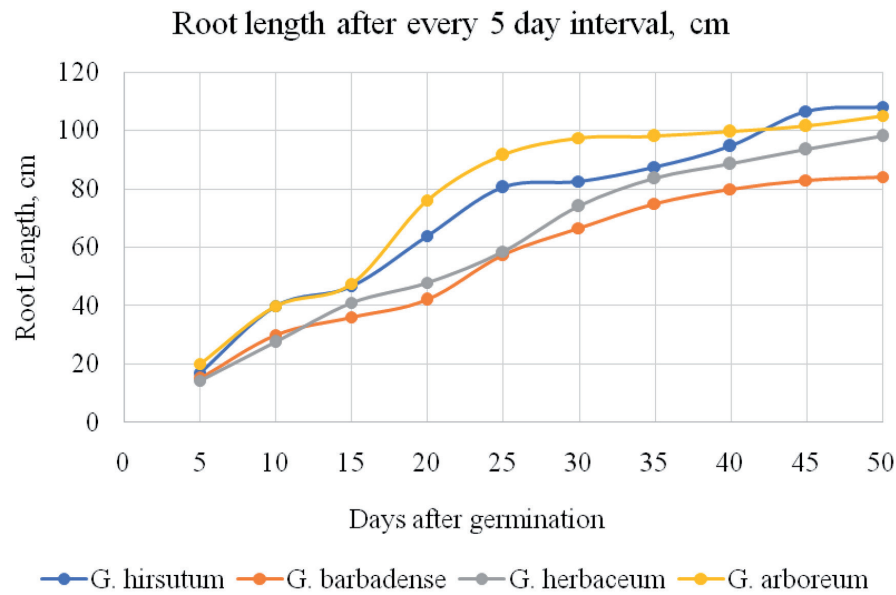


Figure 2.
Root length after every 5 days interval of cultivated cotton species.

roots growth. The secondary lateral root initiation takes places just below the crown and same pattern sequentially follows from top to bottom of root. The cap portion and 20–25 cm above remain devoid of lateral roots during pre-flowering growth period. Generally, the root growth after flowering is declined over the period of time. The root density was highest in first 30–45 cm depth. Reduction of root length density at 42 and 70 days after emergence has been reported by Plaut et al. [46]. Cotton root growth follows a typical sigmoidal curve and continues to grow up to flowering [6]. The tap root first tries to penetrate the soil as long as it can in the first week of its growth. Due to its tap root system, the development of lateral roots and overall root density depended on the available soil volume of water and nutrients. The growth of course roots serves as function of anchorage and typically establish overall root system architecture, controlling ultimate rooting depth, and the ability of plants to grow into compacted soil layers [47]. The number of lateral roots produced depends on the number of xylem poles in the taproots of cotton seedling [48]. As the number of vascular bundles increased, high branching intensities of lateral roots also increased in 7-day-old seedlings of exotic cotton [21]. The root architecture, growth and density can be visually seen in the **Figure 3**.



Figure 3.
Root growth of four cultivated cotton species after 60 days after sowing.

Shoot Growth: After 60 days of sowing the plants were taken out of frame to study the shoot and root length, stem thickness, shoot and root dry weight and their ratios. The aerial growth was good in all the species and the fresh weight was highest in *G. hirsutum* (1.6 kg) followed by *G. barbadense* (1.2 kg), *G. arboreum* (0.4 kg) and *G. herbaceum* (0.4 kg). The stem thickness was highest in *G. herbaceum* followed by *G. hirsutum* and lowest was in *G. barbadense* (**Figure 4**).

Root Growth: Similarly, the below ground root growth was robust in all the species (**Figure 3**). The root growth was good in all the species and the fresh root weight was highest in *G. hirsutum*. The root thickness from crown to 35 cm was highest in *G. hirsutum* and *G. arboreum*. However, the crown portion was thickest in case of *G. herbaceum* and uniformly thinnest and tapering at later root growth among all the species (**Figure 5**). Root thickness was more uniform upto 15 cm and was tapering afterword in *G. barbadense*.

Root: Shoot Ratio: Root system is a key trait of interest in relation to acquisition of soil resources towards development of remainder of the plant, either relative to leaf area, shoot, or whole plant size. Accordingly, root: shoot ratio changes with plant growth and development in addition to shifting in response to limiting resources above versus below ground. Among all the cotton species, root biomass or root dry weight remained highest in case of *G. barbadense* with dry root: shoot ratios of 0.81 followed by *G. hirsutum* (0.64), *G. herbaceum* (0.59) and *G. arboreum* (0.48) (**Figure 6**). More profuse (higher root length density) and deeper root systems

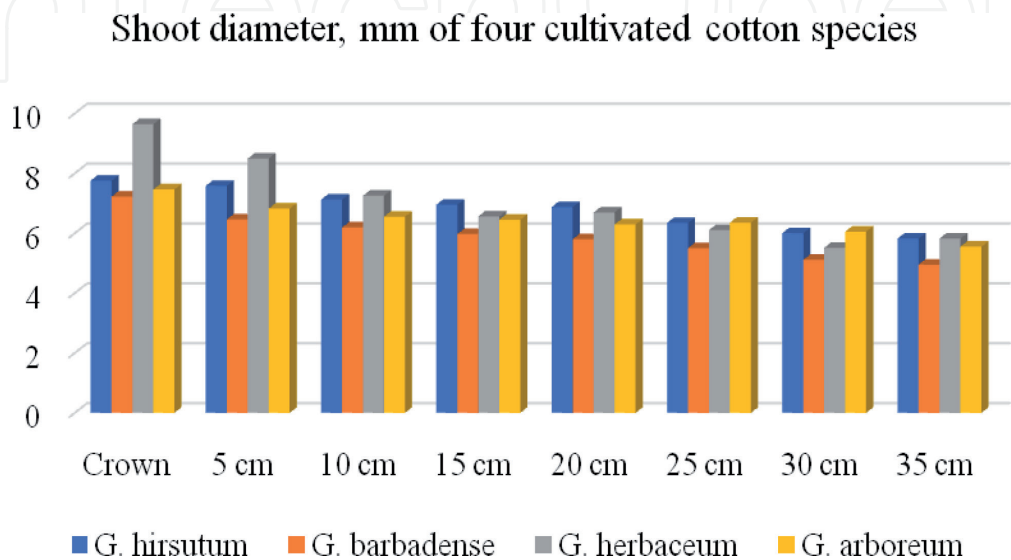


Figure 4.
Shoot/Stem thickness after 60 DAS from crown level upward (mm).

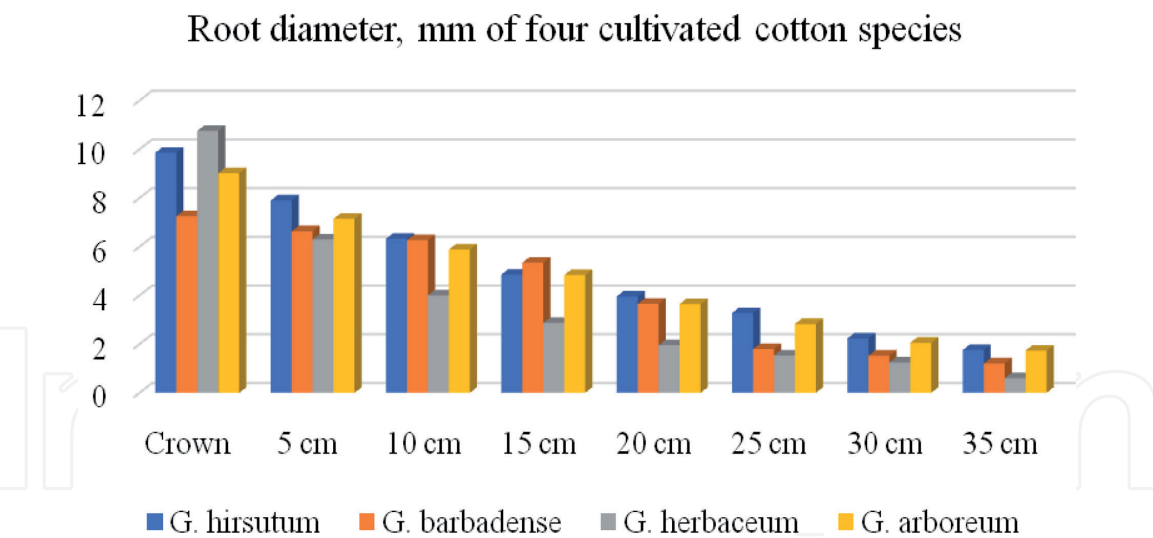


Figure 5.
Root thickness after 60 DAS from crown level downward (mm).

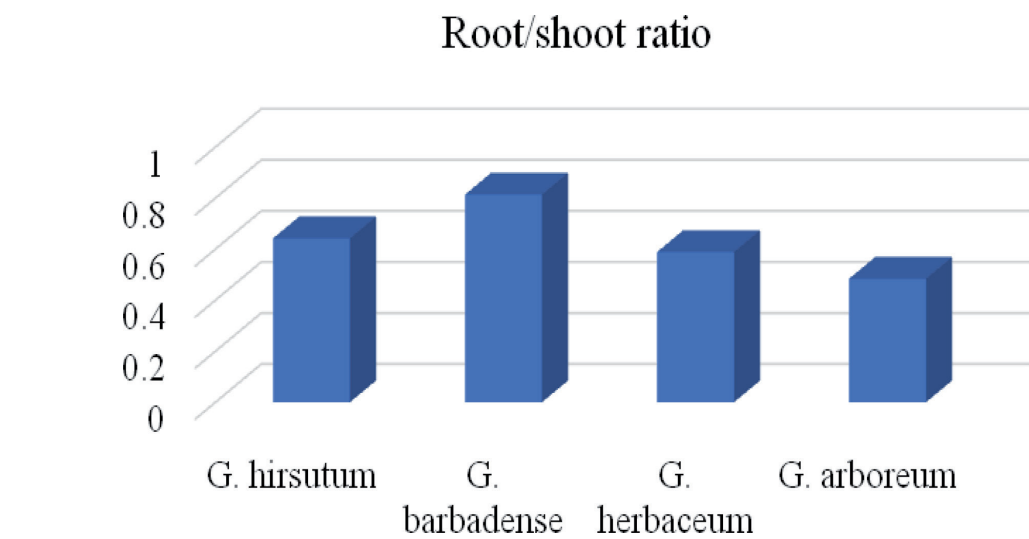


Figure 6.
Dry root/shoot ratio after 60 DAS.

in the soil are often proposed as desirable characteristics for drought adaptation. McMichael and Quisenberry [49] showed significant variability in the dry weights of root systems of sixty-day-old plants of twenty-five cotton genotypes ranging from exotic accessions to commercial cultivars.

6.2 Root growth and development under abiotic stresses

6.2.1 Drought

In most of crop plants drought stress is perceived initially by the root, which continues to grow underneath the soil even though shoot growth is inhibited under water deficit conditions [50]. Root temporal and spatial growths in soil matrix are closely linked with aboveground shoot traits. Water stress affects more to the growth of lateral roots than the growth of primary root, mainly by suppression of the activation of the lateral root meristems [51]. Increased root length in the soil under drought stress helps to get water from deeper soil layer [52, 53]. An increase in root density in soil layer (70–180 cm) in drying soil profile shown in cotton by [54]. More profuse (higher root length density) and deeper root systems in the soil

are often proposed as desirable characteristics for drought adaptation [11, 31]. Luo et al. [32] described response of mild drought stress at initial-stage enhanced root length in cotton, but long-time water deficit induced the root activity as compared to control plants. In another study, biotech cotton plants were more tolerant to drought stress, with a better efficient root system than in wild type [55]. Similarly, the transgenic cotton plants harbored *Arabidopsis* that enhanced drought tolerance 1/homodomain glabrous 11 (AtEDT1/HDG11) gene had well-developed roots in addition to other drought-tolerant features [56].

Roots sense the edaphic water stress, transmit chemical signals to the above ground portion ie.shoots, and maintenance of root growth despite reduced water availability through water foraging [57]. The transpiration rate and stomatal conductance of plants are reduced during water deficit, and they are stimulated by chemical and hormonal signalling before hydraulic signalling in the roots. Various phytohormonal signalling molecules such as auxin and cytokinin are produced in the roots and play a crucial role in shoots during the drought stress in plants [10].

The water content of the soil can have a significant influence on rooting depth and root length density and therefore on the overall function of cotton roots [54]. McMichael and Lascano [58] demonstrated presence of “hydraulic lift” phenomenon in cotton roots where water is transported 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 high water holding capacity have shallow roots and with low water holding capacity have deeper roots [26]. Klepper et al. [54] reported change in root morphology under drying soil. Initially more roots were in the upper soil profile, but as a result of the death of the older roots in the upper soil layer due to the soil drying and production of new young roots at deeper layer results in increased rooting density with depth. Radin et al. [27] reported that long duration irrigation cycles makes more rapid deterioration of the root system during periods of boll development. Carmi et al. [59] showed that subsurface irrigation such as drip have more profuse growth of roots within one millimeter in diameter of size concentrating nearer to emitters site. Carmi and Shalhevet [60] reported that dry matter production in root is less affected than shoot growth under drying soil condition. In other studies, changes in rooting growth pattern based on maturity of cotton plants and availability of water distribution and in response to progressive drying soil [61]. 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 [62] 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. Taylor and Klepper [6] showed that both deep roots and shallow roots were effective in extracting water from the soil. Radin [63] showed that the hydraulic conductance of cotton roots declined at cooler temperatures which would affect water uptake. Oosterhuis [64] reported under mild drought stress in cotton decreased activity of root hydraulic conductance, influence on axial and radial movement of water and overall impact of water on root development. Field study on root traits using mini-rhizotrons has shown that rainfed cotton had tendency to grow at deeper depth than irrigated cotton [65, 66].

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 under low rainfall regions. [67] reported significant role of osmotic adjustment with the growth of a root system in drought stress condition under field. In cotton, drought stress limits root development, shoot traits and fibre quality [68]. Drought affects the root growth which in turn may leads to reduced biomass accumulation in cotton. Cotton undergoing water deficit explores

moisture and nutrients by deeper root penetration [69]. Cotton showed some adaptations toward drought stress effect with increased root length and decreased shoot length; the enhanced root/shoot ratio indicates water assimilation and enhanced drought tolerance [68]. The capacity to form a greater number of lateral roots increased root surface area for water absorption which is desirable traits for drought adaptation [70]. Drought treatments reduced the GA content of roots; upon rewatering GA content and CAT activity increases [71]. Overexpression of GhNAC2 suppressed the ethylene pathway and activated the ABA/JA pathway which leads to longer roots, larger leaves, and hence higher yield in cotton under drought [72]. ABP9 gene was introduced into *Gossypium hirsutum* L and its over expression confers drought tolerance in cotton by better root systems, higher germination, reduced stomatal aperture, and stomatal density [73]. Abdelmoghny et al. [74] described the analysis of gene expression of fourteen drought stress related genes under water stress indicated that both ABA dependent and ABA independent mechanisms operate differentially in studied genotypes for drought tolerance. The *G. hirsutum* genotype IC325280 exhibited ABA mediated expression of stress responsive genes. Molecular basis of drought tolerance in IC357406 and IC259637 genotypes could be attributed to ABA independent pathway. Based on morpho-physiological and biochemical screening, the genotypes IC325280 and IC357406 were identified to possess efficient root traits.

6.2.2 Waterlogging

Waterlogging creates a hypoxic condition [75] and cotton is most susceptible to O₂ deficiency [76]. Moreover, waterlogging causes reduction in cotton yield [77] due to reduced plant growth and nutrient uptake [78]. The excessive water-logging particularly with younger plants is responsible for root damage due to lack of oxygen, yellowing of leaves due to gaseous hormone ethylene production or poor nutrient uptake and wilting of plants, increased square abscission and shorter internodes [79]. Excess water in waterlogged soil promotes the fruit and boll shedding in cotton due to hypoxia in the root zone. Invitro studies show that root apices must be at or above the critical oxygen pressure for normal root growth and extension [80]. The O₂ concentration threshold value below which root expansion begins to decline depends on the critical oxygen pressure for respiration, which in turn is influenced by the characteristics of the tissues through which O₂ must diffuse the O₂ affinity of oxidases [81]. In field-grown cotton, root growth is a function of O₂ consumption in the soil by roots and microbes [82]; growth inhibition starts under mildly hypoxic (O₂, 10%) conditions. Short term exposure of cotton plants to transient (2–3 min) anoxia caused transitory cessation of tap root elongation but it resumed activity as the O₂ supply was normalized. But continues exposure for example 3 h of anoxia resulted in complete death of the terminal apices of cotton roots [83]. Armstrong and Drew [81] proposed that inhibited energy production in reduced oxygen supply condition of root, inhibits cell division which results into deterioration in absorption of water and nutrients from the soil. Zhang et al. [84] also demonstrated that despite up-regulation of fermentative genes, waterlogging also induces oxidative damage to cotton root tissues.

In a comprehensive study by Davies et al. [85] reported waterlogging tolerance of different plant species confirmed that primary tolerance mechanisms reside in roots not in shoots. The root system plays a pivotal role in root-shoot communication to waterlogging through mechanism of (i) Water and nutrient uptake from soils and supply to the aboveground organs; (ii) Synthesis of endogenous hormones regulating plant response to hypoxia. Root structural traits and processes strongly

depend on edaphic factors. Root internal cellular arrangement impacts shape and growth of cortical cells, path lengths, tissue level oxygen demands and radial losses, and shape of the root apical region [86]. Within a single root axis of a plant, root apices and the stele are potentially anoxic while the outer cortical tissues may continue to be aerobic [87]. Factors controlling these tissue-specific and genotypic variations in O_2 status are not well understood in cotton, where phenotypic variation in anatomical features such as radial dimensions and biophysical characteristics of roots cells might yet be exploited. Initiation of morphological adaptation like adventitious root primordia is controlled by an interaction with production of gaseous hormone ethylene [88]. Ethylene accumulation also triggers various cellular adaptive traits such as cortical cell senescence, root porosity and secondary growth of phelloderm in dicot species [89].

Eudicotyledons species such as cotton do not display the same widespread tendency to form aerenchymatous roots as that of monocots [90]. However, there are other potential adaptations to submergence tolerance, with cotton enhancing survival in short-term deficient oxygen supply by developing lenticels [91]. Parawilt or sudden wilt in the cotton field are noticed under drought conditions that are followed by heavy rains or irrigation. In studies at ICAR-CICR, Nagpur, Gotmare et al. [92] reported genotypic differences were observed in terms of morphological adaptations such as lenticel and adventitious root formation when cotton plants subjected to waterlogged conditions. Agronomic practices such as sub-soiling prior to planting to improve root development and increase sufficient soil O_2 is necessary for root development [93].

6.2.3 Salinity

Cotton is relatively salt tolerant and can tolerate salinity up to 7.7dS m^{-1} [94] beyond that growth declines when the plant is exposed. Germination and emergence [95] and seedling growth [96] are most salt-sensitive stages of cotton. Salinity induces nutrient imbalance by high accumulation of ions such as Na^+ and Cl^- with lower concentration of K^+ , Mg^{2+} , and Ca^{2+} ions. Salinity also caused altered growth and root expression. Cramer et al. [97] observed that the growth of the taproot of cotton seedlings was reduced in the presence of NaCl but that the effects could be alleviated by the addition of Ca^{2+} to the growing media.

The elongation of the taproot cotton seedlings was reduced to 60 percentages when roots were subjected to 150 mol/m^3 NaCl salinity stress, Zhong and Lauchli [96]. Salinity stress causes morpho-physiological alterations in cotton by reducing the leaf and root weight, root growth, proline, and chlorophyll contents, stomatal conductance and net photosynthesis [98]. Salinity usually reduces the root growth due to inhibition of root length and reduction in number of secondary roots [99]. Leidi [100] demonstrated that high salinity stress condition constrained the growth of primary root length and under mild salinity stress also inhibited the length of secondary roots. Plant growth heavily relies on ionic influx in the root system along with their translocation toward shoot part. With the increase in the salinity, root growth reduced significantly in different soils but the suppression in root growth, fresh and dry weight was more in clay and loam soils [101]. Salinity has decreased root length and delayed secondary root growth have been reported [97]. Sodium is also a competitor of calcium to limit its uptake by cotton roots [102]. Cotton is salt tolerant, but its vegetative growth is severely affected on saline soil. Shoot is more sensitive to salt than roots. Reinhardt and Rost [103] showed that high salinity stress reduces cellular structural features such as root width and length of metaxylem in cotton growing seedlings which increase with increase in plant growth.

These altered 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.

6.2.4 Heat stress

Cotton are photosynthetically more tolerant to drought and heat that requires a mean minimum temperature of 12–15°C and mean maximum temperature of 20–30°C for better growth [104]. The minimum temperature for seed sowing is 15.5°C [105] and optimum temperature of 35°C for root growth and development [106] for irrigated, while thermal kinetic window (TKW) is 23.5–25°C for rainfed cotton. The lowering of temperature from 30 to 18°C causes reduction in hydraulic conductivity of roots, resulting in reduced proliferation of roots [107]. Cotton root growth is maximum at day/night temperatures of 30/22–35/27°C and rise in temperatures to 40/32°C alter root distribution pattern resulting in limited downward extension of roots [108, 109]. Generally, abiotic stresses such as heat and drought stress restricted the root growth, plant height, boll development, and fiber quality. The root growth is faster at initial stages than shoot growth. McMichael and Burke [106] reveal that soil with a temperature range of between 20 and 32°C is suitable for proper root growth and development. The elevated root temperature between 35 and 40°C affects the root hydraulic conductivity, affect nutrient uptake, reduce hormone synthesis and translocation in different part of the plant [110, 111]. It is well established that the site of cytokinin originates in roots and the most sensitive process in growth and development of plants [112]. As compare to shoot temperature, root temperature are more critical because of less adaptable to extreme temperature variations [113]. Bolger et al. [107] also showed that conductance decreased when the root temperatures were reduced from 30–18°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.

7. Plant hormones: the actions that control root growth and development

Phytohormone auxin is a small tryptophan derivative that induces a battery of developmental responses in plants. But auxin rarely acts alone. Cytokinin, an adenine derivative is required for vascular patterning, and hormonal signalling that pattern the root vasculature in crop plants [114]. During drought stress abscisic acid (ABA) plays a crucial role as a signalling molecule from its production site (roots) to the leaves for closure of stomata [115]. The root system of crop plants is altered by intrinsic developmental signals and diverse environmental cues. Trigger for to activate internal and external environmental cues on phytohormones to regulate the formation of a highly plastic and adaptive root system [116], which sustains the growth of plants even in unfavorable conditions. Several recent studies on hormonal regulation suggest that cross-talks among different hormones are essential for the regulation of root development, and auxin plays a central role in these processes. Although two phytohormones, auxin and cytokinin are the key regulators of root development have been extensively studied, the roles of other phytohormones still need to be further characterized to give us a full view of root development. Hormones appear to control root growth by regulating cell division and/or expansion [117, 118]. Phytohormone regulate root growth processes such as cell proliferation, differentiation or expansion in distinct tissues. New studies have highlighted a new target zone for hormonal regulation is transition zone found between the zones of proliferating and expanding root cells. Jasmonic acid (JA)

promotes lateral root formation by directly inducing the auxin biosynthesis and/or modulating PIN2 accumulation on the plasma membrane [119]. A growth retardant mepiquat chloride (MC), a gibberellin synthetic growth inhibitor regulates the plant growth upon soaking seeds or foliar spraying of leaves. Response of MC on cotton plants results into shorten internode elongation, reduce main stem nodes, and decrease plant height, leading to more compact plant architecture and increase numbers of lateral roots. Over view of phytohormones involve in root structure and function regulation shown in **Table 1**.

The major areas of PGR research are to improve defoliation characteristics and control rank growth in cotton. Roots play an essential role in plant growth by acquisition of water and nutrients from the soil. Endogenous hormone auxin, which is transported and regulated by auxin efflux transporters, has been reported as a

Hormone	Production site	Transport	Site of Action	Reference
Auxin (IAA)	Shoot meristem	Xylem & Phloem	Root meristem, dynamic regulation of root meristem size.	[120]
Absciscic acid (ABA)	Roots	Xylem & Phloem	Regulate root growth and LR branching	[115, 121, 122]
Cytokinins (CK)	Root tips & Developing seeds	Xylem & Phloem	Cell enlargement, amount of CKs reaching the shoot will reflect the extent of the root system	[98, 123]
Gibberellins (GAs)	Root meristem	Xylem & Phloem	Endodermis of the root elongation zone	[124]
Ethylene	Tissues undergoing senescence or ripening	Moves by diffusion from its site of synthesis	Adventitious root formation	[125]
Brassinosteroids (BRs)	Root	Xylem	Lateral root development epidermis	[126–128]
Strigolactones (SLs)	Root	Xylem	Shoot branching regulation, positive regulators of primary root elongation and negative regulators of adventitious root formation	[127, 129, 130]
Jasmonic acid (JA)	Plasma membrane	Xylem & Phloem	Promotes lateral root formation	[119]
β -Cyclocitral (β -carotene-derived apocarotenoid)	Endogenous root compound	-	Promote cell divisions in root meristems and stimulate lateral root branching	[131]
Karrikins (KARs) smoke-derived butenolides	Root ligand	-	Root hair elongation, root density,	[132]

Table 1.
An overview on the phyto-hormones involved in the regulation of root meristem size and the pivot of root growth.

positional cue for root cell type determination [133]. Comparative gene analysis of *G. hirsutum* and *G. arboreum* indicated that PIN1–3 and PIN2 may play an important role in root development. GhPIN1–3 and GhPIN2 are required for cotton root development, which can be further used in breeding programs to selecting genotypes that are lodging-resistance [133]. The current studies showed that the majority of cotton PIN genes contained auxin response elements (AuxREs) and salicylic acid responsive elements in their promoter regions, which can be up-regulated by exogenous hormone treatment [134].

8. Mechanism that determine the root structure and architecture and soil resource acquisition: eg. Nitrogen

Plant nutrient absorption and uptake is the process successfully executed by young roots, especially by the root hairs. The absorption of water through roots is always in a continual state of flux and further, the uptake of water by the cells generates a pressure known as turgor. Root system architecture plays a critical role for crop growth by providing above ground mechanical support and controlling water and nutrient acquisition. Lateral roots, the major part of the root system in terms of root length and number, have crucial physiological capacities for water and nutrient uptake, and serve as the primary interface in response to heterogeneous soil environments. Lateral root initiation originates from asymmetric cell division of xylem pole-pericycle cells induced by auxin-accumulation [135].

Efforts to increase flowering and boll retention cannot be realized unless the plant has the ability to supply sufficient nutrients to these sinks to cater their demands. Alteration of root: shoot (i.e. higher root: shoot) ratios could potentially benefit the plant by providing a larger root mass to meet the needs of the above-ground biomass. The total plant root length continues to increase as the plant develops from seedling to until the maximum plant height is achieved and boll begin to form [6, 136]. The root then begins to decline as plant height enter into reproductive phase and older roots die. Synchronization of plant root activity with boll production is critical both in variety and Bt-hybrids [13]. Increased root activity during the later stages of boll filling is important for supplying needed nutrients and water to the developing cotton boll, but prolonged activity can hamper with late-season vegetative growth at cut out stage near to or following defoliation and problem of regrowth after application of harvest aids.

Plant root growth is closely linked with shoot growth, both of which are affected by N availability in the soil. In addition, roots in the surface soil were more strongly affected by availability N than roots distributed in the deeper soil layers. Root trait such as total root length, total root surface area, and root biomass in the top soil layer (0–15 cm) was significantly correlated with shoot and boll biomass. Next, 60–75 cm layer, total root length, total root surface area, and root length were significantly positively correlated with seed cotton yield. The application of a moderate level of N markedly increased total shoot biomass, boll biomass, and seed cotton yield [137]. Nitrogen plays an important role in plants root and shoot communications during plant growth and is critical for maximizing crop productivity [138].

Insufficient N fertilizer application causes premature senescence, while excessive application causes excessive vegetative growth and increases soil pollution. Root growth is significantly affected by N fertilization; especially low N levels enhanced root elongation [139, 140]. Zhang et al. [141] suggested that N can affect the distribution of roots in the soil. Iqbal et al. [142] showed that for improving N use efficiency in cotton the morphological characteristics of the root system is an important feature.

Luo et al. [143] demonstrated that cotton root activity in the soil at a depth of 40–120 cm was significantly correlated with canopy photosynthetic rate and significantly affected by nitrogen levels. N-sensitive period of cotton growth are flowering and boll period [144]. Root length and surface area are important traits for describing root system architecture [145]. Moderate available N could improve assimilate transport from source to sink, which could increase biomass in the fruiting parts [146]. The modulation of root development by N availability has great agricultural importance and its understanding provides the basis for improvement of cultivars with better root architecture. Recent studies demonstrated that arginine is the precursor of nitric oxide in roots catalysed by nitric oxide synthase [147], and nitric oxide plays a key role in the lateral root formation. In *Arabidopsis* reduced activity of arginase may increase synthesis of nitric oxide contents in roots and therefore resulted into improved formation of the lateral roots in transgenic plants. Wang et al. [73] reported use of CRISPR/Cas9-mediated editing of arginase genes in cotton in upland cotton R18, orthologous arginase genes (GhARG), Gh_A05G2143 and Gh_D05G2397, in the A and D chromosomes. CRISPR/Cas system was efficient in producing targeted mutations in the selected genes which improved lateral root system under both sub-optimal nitric conditions consequent adaptation of cotton on a different type of soils [70].

9. Root cellular anatomical significance in plant growth and development

9.1 Anatomical

McMichael et al. [17] showed that the increased root xylem cells in radial cellular fashion in the vertical taproot of few exotic cotton germplasms resulted in a significant increase in total xylem cross-sectional area and number of lateral roots which may be associated with drought tolerance in plants with the increased xylem vessels. Oosterhuis and Wulfschelger [10] supported the finding that increased water flux was associated with increased xylem cross sectional area. Elevated number of xylem cell files in the primary root did not contribute to the decrease in axial resistance to water movement. The increased number of lateral roots cells 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. The root tip grows by adding new root file cells along the axis and enlarging at the tip, forming the tap root. The root tip produces a tap root of 12 to 20 cm by the time cotyledons emerge from the soil [148]. Lateral roots initiate inside the tap root tissue and grow horizontal into fresh soil for nutrient and water uptake. Because these young lateral roots proliferate near the surface in warm, nutrient rich soil, they are critical for seedling vigour. The origins of lateral roots are from cambium of the tap root and are arranged in radial fashion depend upon the number of vascular bundles present in the primary root. Crop roots are the main organs that primarily sense and respond to the biotic as well as abiotic stresses [88]. A high number of lateral roots would increase the total root surface volumetric area of the plant that may potentially improve the overall growth, fiber length, yield, and stress tolerance against severe conditions. Therefore, genetic engineering of root traits especially lateral roots makes cotton plants to enhance yield and fibre contents but will also make cotton crop tolerant to abiotic stresses [73].

9.2 Root tip border cells and pathogens

The number of border cells that can be produced daily by a given root is conserved at the plant family level, and can range from a dozen for tobacco to ten thousand for cotton. During cell differentiation of root system, the border cell production of tap roots, branch roots and secondary roots are identical [149]. Current evidences and results have suggested that border cell production in different plant species is tightly regulated process including cotton and govern by endogenous and environmental cues [149]. Upland cotton (*Gossypium hirsutum*) discharges 8,000–10,000 root border cells per 24 hours. The cotton root tip surrounding border cells can diffuse after dissolved in liquid water for 30 sec, showing one days' accumulation of border cells (~10,000) surrounding the tip. Border cells of cotton specifically attract zoospores of *Pythium dissotocum* (Root Rot), which germinate, penetrate and kill the cells within two minutes. The chemotactic behavior of zoospores of *Pythium dissotocum* and *Pythium catenulatum* were attracted to border cells of their hosts, *Gossypium barbadense* and *G. hirsutum* but unresponsive to non-host plant species [150].

9.3 Root diseases of cotton

Other than abiotic stresses faced by cotton plants during cotton root development, however, biotic stresses that might be categorized as 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 edaphic factors such as water and nutrient stress. King and Presley [151] reported that a disease of cotton that was characterized by a swollen taproot and internal black rot of the vascular tissue was found in USA (Arizona) in 1922. The plant pathogenic fungus was identified as *Thielaviopsis basicola* and was found to be the most damaging to cotton root system in the seedling stage that causes black root rot. Detailed study of black root rot infection of cotton roots and their interaction with edaphic factors were showed by [152].

Cotton *Verticillium* wilt caused by *Verticillium dahlia* fungus during seedling stage of crop growth that causes significant yield losses in most of cotton growing areas [153]. *V. dahliae* is a soil-borne pathogen, which infects the plants through root system causing stunted growth, wilting and defoliation, thus incurring 15–70 percentage yield losses [153, 154]. Liu [155] reported the effect of VAM (vesicular arbuscular mycorrhizae) on *Verticillium* wilt in cotton. The data indicated that when the cotton roots are colonized by VAM, the incidence of *Verticillium* is reduced resulting in improved yields.

9.3.1 Root rot

The root rot disease caused by *Rhizoctonia solani* Kuhn and *Rhizoctonia bataticola* (Taub) Butler is among the most serious diseases of cotton at seedling and growth stages in all the cotton growing region of India. However, the disease is more prominent in the north India including Panjab, Haryana, Rajasthan and western regions of Uttar Pradesh. The pathogen attacks both *G. hirsutum* and *G. arboreum* species of cotton. The disease first occurs in June on seedling stages and becomes severe during July months in North and central India. The fungal hyphae are septate and relatively thick in size. *R. bataticola* produces pycnidia, known as *Macrophomina phaseolina* (Maubl.) Ashby. The sexual stage of *R. solani* is *Thanatephorus cucumeris* (Frank) Donk which produces basidia and basidiospores (sexual spores). The soil

moisture of 15–20 percent and temperature range of 35–40°C is most favourable for the pathogen infection. The vast diversity has been reported in *R. solani* and *R. bataticola* isolates with host range of more than 400 hosts for *R. bataticola* and more than 150 hosts range for *R. solani* [156].

Complete wilting of the affected plants and drooping of leaves from top to bottom with sudden wilting is the characteristics symptoms of root rot disease (**Figure 7**). In the field, diseased may occur in isolated spots and later develops into more or less in circular patches. Earlier symptoms appear on roots including main roots and brown to black discoloured infection on the roots with sore-shin and the diseased plants can be easily pulled out from the soil (**Figure 8**). The germinating seedlings and young seedlings are attacked by the pathogen to hypocotyl causing



Figure 7.
Diseased cotton plants showing black discolored infection on the roots with sore-shin.



Figure 8.
Cotton root rot disease.

black lesions, stem girdling and finally death of the seedling. Generally, roots of affected plants shreds and become yellowish in colour as compared to disease free plants. In case of severe infection, higher numbers of dark brown coloured sclerotia bodies are seen on the stem or on the shredded bark. Similarly, microsclerotia may be observed on roots and stems in case of *R. bataticola* (*M. phaseolina*). The disease is mainly soil-borne and the pathogen can survive in the soil as microsclerotia (*R. bataticola*) and/or sclerotia (*R. solani*) for many years in the field. The secondary infection spread through sclerotia and/or microsclerotia which are disseminated by cultural operations, irrigation water, and farm implements [157].

It was observed that the disease progressed faster in *G. arboreum* as compared to *G. hirsutum*. It is also noticed that there is no clear relationship between soil moisture and soil temperature in relation to root rot incidence. However, there was increased root rot incidence in case of increase or decrease levels of soil moisture. This is due to the facts that causal agents (variants) are involved in root rot disease with different fungal biology and favourable condition at particular infection stages of pathogens [158].

Seed dressing with recommended fungicides is an important strategy for the management of root rot and seedling diseases with any one of the fungicides i.e. Fluxapyroxad 333 g/l FS, Tetraconazole 11.6% w/w (12.5% w/v) SL, Carboxin 37.5% + Thiram 37.5% DS and Thiram 75% WS at the recommended doses. It was observed that biocontrol agents *T. harzianum*, *T. viridae* and *G. virens* proved effective against *R. bataticola*. Development and screening of resistance varieties are very important for the management of root rot diseases. Whereas, integrated disease management practices including resistant varieties bioagents, crop rotation with non-host crops, deep tillage during summer, FYM, amendments with organic matter and fungicides are the key factors in the management of root rot disease of cotton [159].

Other studies have shown that infection of cotton roots by nematodes may impact the growth and development of the plant with infections similar to water stress. This conditions favours reduction in hydraulic conductivity and increases drought resistance in plants [160].

9.3.2 Plant parasitic nematodes

Root-knot nematodes (RKN): Plant parasitic nematodes, especially root-knot nematodes (RKN), are the hidden enemy of crops. The estimated overall annual yield loss of world's major crops due to damage by phytoparasitic nematodes has been reported to the extent of 12.3% [161]. The national loss due to plant parasitic nematodes in 24 different crops in monetary terms has been worked out to the tune of 21068.73 million rupees [162]. Amongst all, the root-knot nematodes *Meloidogyne incognita* is the most pathogenic species with a host range spanning over 300 plant genera in India. In field crops the yield losses due to root-knot nematode are estimated to be in the range of 10–27% [162, 163]. Nematode problems are exacerbated in the tropics as climate conditions are ideal for nematode development and are now compounded by agricultural practices as monoculture of susceptible cultivars that favour population development and thus crop damage. Plant parasitic nematodes cause losses in cotton crop by feeding on roots and are also involved in diseases complexes resulting in yield reduction. About 10% of agricultural production worldwide is lost due to nematode damage. The nematode infection causes stunting, yellowing, chlorosis, mid-day wilting, reduced boll size and reduction in lint percentage. The nematode infected plant roots are shorter with fewer roots and root hairs. Appearance of patches of stunted plants in field is indicative of nematode damage. These patches grow in diameter every year in nematode infected fields.

The root knot nematode, *Meloidogyne incognita*, of cotton is one of the most important plant parasitic nematode and has been reported on Bt cotton in north



Figure 9.
 Roots of cotton infected with *Meloidogyne incognita* showing heavy root galling on entire root.

India (**Figure 9**). On national scale cotton crop losses ranging between 12.3–20.8% have been attributed to *M. incognita* [164]. Amongst six races of *M. incognita* documented so far [165], only race three and four are known to attack cotton. Race diversity of *M. incognita* across India has been recorded and race two, three and five have been reported predominantly on different crops in Maharashtra [166–168]. Race three is reported from Karnataka and Tamilnadu on cotton [169] while race four has been recorded on cotton from north India [170]. The root knot nematode produces galls on roots and its size varies with the host species. Comparatively smaller galls are produced on cotton roots. Root-knot nematode *Meloidogyne incognita*, a sedentary endoparasitic nematode, is an obligate parasite. During invasion, the nematode secretes enzymes including CAzymes, cellulases, xylases, expansins, chorismate mutase, proteases, galactouronase, pectate lyase etc. which have diverse functions ranging from softening of plant cell walls to inducing differentiation of host root cells into multinucleate giant cells that form a permanent feeding site. Feeding cells are important organ of nematode for successful attachment and development. Nematodes increase demand on plant energy resources while reducing the supply and prevent plants from getting enough water and plant food. Symptoms of nematode injury on cotton root can get expressed on above ground plant parts as weakened plant condition, leaf chlorosis, less ability to tolerate adverse conditions, reduced boll size and reduced lint percentage. Root knot nematode is also involved in disease complex with *Fusarium*. The intensity of *Fusarium* wilt increases in nematodes infected fields. The reniform nematode (*Rotylenchulus reniformis*) is another dominant species causing damage to cotton in central and south India. Pericycle and phloem tissues of cotton roots are damaged by immature female of reniform nematode.

9.4 Belowground data revolution

The improvement of belowground plant efficiency has potential to further increase crop productivity. However, hidden half i.e., plant roots studies are challenging, due to its underground nature and difficult to screen. Several tools for identifying root anatomical features and image analysis software have been proposed (**Table 2**). However, the existing tools are not fully automated and require significant human effort to produce accurate results [202–204].

1.	Fully automated reconstruction software	Ez-Rhizo	[171]
		Rhizo scan	[172]
		Dynamic Root	[173]
		Root Reader 3D	[174]
		GrowScreen Root	[175]
		Root Track	[176]
		Root Trace	[177]
		NM Rooting	[178]
		REST	[179]
		DIRT	[180]
		GIA Roots	[181]
		GLO-RIA	[182]
		Root Scape	[183]
		RhizoVision	[184]
2.	Semi- automated reconstruction software	Root Nav	[185]
		Root System Analyzer	[186]
		Smart Root	[187]
		Root Reader 2D	[188]
		DART	[189]
3.	Database	GRooT	[190]
		sROOT	[191]
		FungalRoot	[192]
		Fun ^{Fun}	[193]
		MycoDB TraitAM	[194, 195]
		FRED	[196]
		TRY	[197]
		TropiRoot	[198]
		Open Traits	[199]
		CLO-PLA	[200]
		Rhizopolis	[201]

Table 2.
List of root system architecture image analysis tools and database.

10. Conclusions

Studies of cotton root biology bring challenges and opportunities to understand the intimate interaction between plants and their environment. Root systems use a variety of mechanisms to adjust growth dynamics to local conditions, such as uneven distributions of nutrients and water. These signals are integrated using different systemic signals such as phyto-hormonal at the whole-plant and root system levels to adjust root and plant growth accordingly. The complexity of soil-root interactions in a highly heterogeneous environment calls for the use of computational models to help integrate the different underground soil processes. However, despite major advances made in plant–soil-microbe interaction, large gaps remain in understanding root biology.

11. Challenges

1. Nutrient acquisition (N, P, K) under changing environmental conditions through roots.
2. Characterization of Root system architecture (RSA) which is an important trait for genetic improvement of nutrient acquisition from nutrient limiting soils.
3. One major challenge will be to reconcile the optimal root architectures, for example, N and P acquisition in one root system. Since the optimal RSA is also related to the carbon status of the plant, planting density, and temperature.

12. Future perspectives

1. Identification of root system ideotypes for important abiotic stress conditions such as drought and salinity is necessary to facilitate breeding efforts focused on root traits.
2. Understanding how plants integrate signals from different nutrients at different concentrations and locations within the root system will require developing new methods to capture these complex interactions.
3. The modification of soil parameters, as well as microbial or plant engineering are strategies developed to engineer the rhizosphere. Thus, rhizosphere engineering may ultimately reduce our reliance on agrochemicals by replacing their functions.

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