Implication of Different Tillage System on Root System Architecture and Their Environment

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Abstract

Root architecture serves as a promising target for efficient resource capture below the soil. Understanding its dynamics and performance under varying management practices is quite pivotal for the development of efficient cultivars in the era of resource crunch and vagaries of climatic scenarios. Because of the tedious methodology and time involvement, there is a limited study of root system architecture (RSA) performance under management practices; thus, in the present chapter, we reviewed the effect of varying tillage on root proliferation, resource capture, and its uptake. There is a presence of nutrient-specific transduction systems in roots for selectively absorb nutrients from the soil, and they modify as per the level of stress in the soil. This chapter also highlights how tillage alters both biotic and abiotic factors that, in turn, affect the root growth significantly. In addition, studies on the long-term effect of management practices on root dynamics/RSA are quite necessary for a complete understanding of resource capture and the pattern of its distribution in soil.

Keywords

Root system architecture · Tillage · Conservation agriculture · Carbon storage

23.1 Introduction

World agriculture is facing a greater challenge to produce more food and feed on diminishing natural resources, especially arable land, which is under an increasingly erratic environment. While arable land and water resources are dwindling by

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industrialization and urbanization, global capacities for food and feed production will increasingly have to compete with a growing need for energy and chemicals and the production of plants for purposes other than nutrition (e.g., clothing, housing, and biofuel). The only option left with us is to increase the crop productivity under the reduced nutrient and water inputs. Thus, it's inevitable to have a well-developed and efficient root system that can be brought through improved crop management and plant breeding. However, the study of plant roots is one of the most promising but least explored areas of research related to plant growth. The study of the root system is not new, with research papers going back in the literature over 100 years (Hanstein 1870; Janczewski 1874; Vines 1888; Pfeffer 1894; Nemec 1900).

Nevertheless, the aerial portions of plant species have received greater attention, probably because of their conspicuousness and easy access, while the underground portions have been neglected because of the difficulty of observing and sampling them and the disruption of root systems when they are removed from the soil. Roots play a vital role in connecting the plant to its environment and perform an essential function such as water and nutrient acquisition, plant anchorage, resource storage, and support of soil microbial communities (Bardgett et al. 2014). Root growth and development are highly plastic in response to the environmental condition and strongly determine plant performance and crop yield (Palta and Yand 2014).

Roots play a significant role in connecting the plant to the soil and thereby the soil to the atmosphere. The growth and development of aboveground plants depend on the acquisition of soil nutrients and water and so are closely associated with root morphology and physiology (Ju et al. 2015). Root interaction with the soil, the rhizosphere, symbiotic interactions with bacteria and fungi, exploitation of soil and increased surface by root hairs, and even more specific root characteristics such as Casparian bands in the endodermis, cellular characteristics of the root apex and the root cap all represent the basic knowledge of root biology (Ju et al. 2015). Regardless of long-standing observations and intensive research over generations, the root system architecture has mostly been ignored by mainline plant scientists and has remained "the hidden half" of the plant body (Waisel et al. 2002).

23.2 Root System Architecture

Soil is a heterogeneous medium with high spatial and temporal environmental variability at a wide range of scales, including those relevant to plant roots. The root system can be considered as an evolutionary response to such spatiotemporal variability in resource supply and associated constraints upon growth (Harper et al. 1991). Therefore, the extension of the root system in space and time is greatly governed by environmental conditions. The spatial configuration of the root system (number and length of lateral organs), so-called root architecture, vary greatly depending on the plant species, soil composition, and particularly water and mineral nutrient availability (Malamy 2005). Plants can optimize their root architecture by initiating lateral root primordia and influencing the growth of primary or lateral roots. The root system results from the coordinated control of both genetic endogenous programs by regulating growth and organogenesis and also the action of abiotic and biotic environmental stimuli (Malamy 2005; Hodge et al. 2009).

Root architecture addresses two important concepts: (a) the shape of the root system and (b) its structure. The shape defines the location of roots in space and the way the root system occupies the soil. Its quantification is generally achieved by measuring variables such as root depth, lateral root expansion, and root length densities. In contrast, root structure describes the variety of the components constituting the root system (roots and root segments) and their relationship (e.g., topology—the connection between roots; root gradients). However, root differentiation has important impacts upon structure–function relations (Clarkson 1996). The rhizosphere (i.e., the volume of soil around living plant roots that are influenced by root activity) (Hinsinger et al. 2005) is often simply thought of as a cylindrical shape around the root. However, this oversimplification does not account for integration at the root system level or for the inherent complexity of root systems that arise from the geometry, temporal dynamics, and heterogeneous aspects of roots. These complexities are incorporated into the concept of root architecture (Lynch and Brown 2001). Root geometry is complex because of the specific motion in space of each root, the relative locations between roots, and the possible overlapping of their zones of influence. The temporal dynamic comes both from the growth of the different root axes and from physiological processes associated with root segments (i.e., tissue differentiation), resulting in the temporal and spatial variability of function along the root axes. The diversity among roots within the root system and soil heterogeneity further increase this variability (Hodge et al. 2009). The spatial configuration of the root system i.e., root architecture, vary greatly depending on the plant species, soil composition, and particularly water and mineral nutrient availability (Malamy 2005). Plants can optimize their root architecture by initiating lateral root primordia and influencing the growth of primary or lateral roots.

Coupland and Johnson (1965) classified root systems architecture into (a) herringbone, comprising of the main axis and laterals only, or (b) dichotomous, where each lateral bifurcates. Much of the literature today uses Fitter's expansion of topological definition as an architectural trait (Fitter 1987, 1991). Taxonomically, most monocots have herringbone architecture, while most dicots have dichotomous architecture. More complex definitions of root architecture have also been proposed in which angiosperms are considered to have five distinct root types: tap, lateral, adventitious, basal, and collateral (Zobel 1986). While not commonly used in the studies of root architecture, this sort of classification can serve as a reminder that any changes in orientation, branching, elongation, and the relative distribution through the soil depth can give rise to a remarkable diversity of architecture (Bassirirad 2015).

Lynch (1995) quoted that the term "root architecture" may be used in various contexts to refer to distinct aspects of the shape of root systems. He further defined several terms related to the root system that delineates architecture from other terms (Table 23.1).

Roots can be defined as a continuum of root segments that vary in anatomy, morphology, and physiology, both spatially (different parts of the same root system)

Table 23.1 Important terminology in root system study

S. No.	Root-related terminology	Description
1.	Root morphology	It refers to the surface features of a single root axis as an organ, including characteristics of the epidermis such as root hairs, root diameter, the root cap, the pattern of appearance of daughter roots, undulations of the root axis, and cortical senescence. Anatomical features of a root related to cell and tissue organization are not usually part of architectural considerations
2.	Root topology	It refers to how individual root axes are connected to each other through branching. As in mathematical usage, root topology is stable to the deformation or rotation of the axes themselves and therefore is possible to measure on excavated root systems
3.	Root distribution	It refers to the presence (rather than the orientation) of roots in a positional gradient or grid. Typically, studies of root distribution are concerned with root biomass or root length as a function of factors such as depth in the soil, distance from the stem, and position between neighboring plants. Measurement of root distribution in agricultural and natural plant communities often includes roots of more than one plant or more than one species
4.	Root architecture	It refers to the spatial configuration of the root system, i.e., the explicit geometric deployment of root axes. Usually, studies of root architecture do not include fine structural details, such as root hairs, but are concerned with an entire root system or a large subset of the root system of an individual plant

Source: Lynch (1995)

and temporally (plastic changes, root aging), and perform multiple functions (Pregitzer et al. 2002; Wells and Eissenstat 2002). A schematic view of the typical root system is illustrated in Fig. 23.1. Among various root components, fine roots have been the focus of most research as it has been considered as critical for most root functions, including root elongation, nutrient and water acquisition, association with symbionts, and carbon exudation (Freschet and Roumet 2017). Detail of root traits contributing to plant functioning is described in Table 23.2. The root orders such as first, second, and third, generally, display thin, N-rich tissues that support mycorrhizal colonization and perform uptake of soil resource (Guo et al. 2008; Jia et al. 2013). In contrast, higher-order roots are thicker and longer-lived and generally perform transport and storage functions (Rewald et al. 2011). The first three order of the root is collectively known as absorptive roots, whereas higher-order roots (>3 order) may also be called as transport roots (Freschet and Roumet 2017).

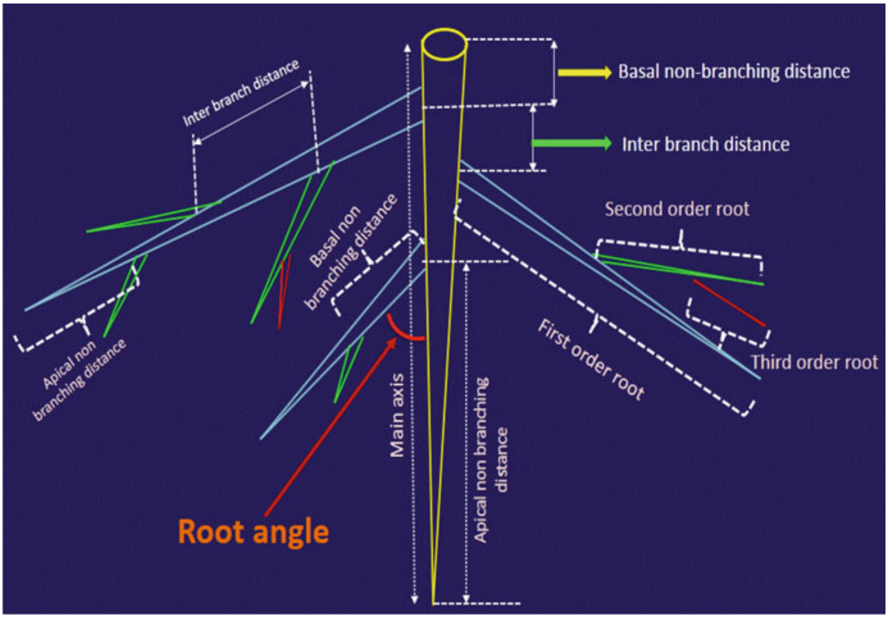

Fig. 23.1 A schematic view of the root system and its components

23.3 Methodology to Study of the Root System and Characterization

Agricultural crops usually need a well-developed root system in order to exploit deeper soil layers. They are then more resistant to periods of stress that often occur during growth and are more likely to yield well. Farmers should know what factors promote and impede root growth. With this knowledge, they can purposefully encourage root growth. Such help to the farmer is the ultimate aim of ecological research on roots (Schuurman and Goedewaagen 1965). Many techniques have been used to increase the accessibility of plant roots. Kolesnikov (1971) and Böhm (2012) summarize several methods of root studies. Some of them are (a) excavation methods, (b) monolith methods, (c) Auger methods, (d) profile wall methods, (e) glass wall methods, and (f) container methods. These methods are classical and still in use for root system characterization. However, with advancements in computing technology, a lot of innovative methods have been evolved with time. Recently, Paez-Garcia et al. (2015) reviewed strategies and approaches for root study in the field as well as in the laboratory. Those methods are presented in Table 23.3. Every method has its own advantages and disadvantages, which is well explained by Wasaya et al. (2018) and presented in Table 23.4.

Although phenotyping the field crop is becoming a focus of crop research, field-based phenotyping is largely subjected to a dispute (Chen et al. 2018). Not only the

Table 23.2 Plant function and associated root components

S. No.	Plant function	Root category	Root traits
1.	Soil exploration/ exploitation	Entire root	Specific root length, root vertical distribution, maximum rooting depth, root growth angle, branching intensity
		First three order of roots	Root mycorrhizal colonization, fine root mass fraction, branching intensity, root diameter
2.	Plant nutrient acquisition	Entire root	Nutrient uptake rate, N_2 fixation, mycorrhizal type
		First three order of roots	Nutrient uptake rate, specific root length, root mycorrhizal colonization, root hair length and density, root diameter, respiration rate
3.	Plant water acquisition	Entire root	Maximum rooting depth, root vertical distribution, root length density
		First three order of roots	Fine-root mass fraction, root cortex thickness, Specific root length, root diameter, root mycorrhizal colonization
4.	Carbon and nutrient conservation	Entire root/first three order of roots	Life span, root tissue density, root resorption
5.	Storage	Tap root/ rhizome/entire roots	Root diameter, element concentration.
6.	Anchorage, resistance to uprooting	Entire root	Root length density, maximum rooting depth, root tensile strength
7.	Penetration force in soil	First order of roots	Root diameter
8.	Penetration against herbivores	First three order of roots	Root mycorrhizal colonization, root phenolic concentration
9.	Penetration against pathogen	First three order of roots	Root mycorrhizal colonization

Adapted from Freschet and Roumet (2017)

interactions among plant genomics, field environment, soil, and crop management complicated the experimental design in the field, but also, in general, the objective of a field-based phenotyping task could be inconspicuous, due mainly to a poor definition of target traits. Some researchers even stated that phenotyping for field crops could never be possibly made because the plant phenotypes are infinite; they vary morphologically and molecularly over developmental time and in response to the environment (Chitwood and Topp 2015). The more we examine the root system, the more complicated their responses and interactions prove to be (Hodge et al. 2009).

Recent advancement of RSA-related phenome research has promoted the provision of a number of modern tools, many of which were resorted to computer science or image processing, e.g., DART (Le Bot et al. 2010), SmartRoot (Lobet et al. 2011),

Table 23.3 Strategies and approaches for root system architectural studies

S. No.	Plant cultivation system	Growth media	Descriptions
1.	Growth and luminescence observatory for roots	Soil (lab)	This method combines custom-made growth vessels and new image analysis algorithms to nondestructively monitor RSA development over space (2D) and time. The technique allows information on soil properties (e.g., moisture) to be integrated with root growth data. The system makes use of luminescence imaging of roots expressing plant codon-optimized luciferase
2.	X-ray computed tomography	Soil (lab and greenhouse)	Nondestructively visualizes opaque root structures by measuring the attenuation of ionizing radiation as it passes through the root. A series of projections are acquired and combined to reconstruct a 3D image of the root system
3.	Rhizophonics	Liquid media (lab)	Combines hydroponics and rhizotrons. System is made of a nylon fabric supported by an aluminum frame. The setup is immersed in a tank filled with liquid media. Allows nondestructive, 2D imaging of root architecture while simultaneously sampling shoots
4.	Clear pot method	Soil (greenhouse)	Uses transparent pots filled with soil or other potting media. Seeds are planted close to the pot wall to enable high- throughput imaging of roots along the clear pot wall. To prevent light exposure, the clear pot is placed in black pots while roots are developing
5.	Rhizoslides	Paper-based (lab, greenhouse)	The setup consists of a plexiglass sheet covered with moistened germination paper. Seeds are planted on the slit of the plexiglass. The system allows the separation of crown roots from embryonic roots
6.	Shovelomics	Soil (field-based)	Involves manual excavation of plants and separating roots from the shoots. Washed roots are then placed on a phenotyping board for root trait quantification. New algorithms allow the extraction of several root traits in a high-throughput manner
7.	Soil coring	Soil (field-based)	Uses a tractor-mounted, hydraulic soil corer to drive steel alloy sampling tubes into the soil. When combined with novel planting configurations (e.g., hill plots), this method allows for phenotyping deep-rooted crop varieties

(continued)

Table 23.3 (continued)

S. No.	Plant cultivation system	Growth media	Descriptions
8.	Rhizolysimeters	Soil (field-based)	Elaborate facility consisting of an underground corridor and concrete silos and pipes to house soil-containing soil cores for direct root observation
9.	Minirhizotrons	Soil (field-based)	A transparent observation tube permanently inserted in the soil. Images of roots growing along the minirhizotron wall at particular locations in the soil profile can be captured over time.

Source: Adapted from Paez-Garcia et al. (2015)

RootNav (Pound et al. 2013), RootTrace (French et al. 2009), RhizoScan (Diener et al. 2013), and Root System Analyser (Leitner et al. 2014). As these platforms are largely varied from one to another, cross-platform protocols are needed, paving the way for inter-platform exchanges of information, e.g., archiDART package (Delory et al. 2016) and RSML package. However, most of these RSA trait-analyzing platforms were still used for sub-root system-level parameters, i.e., geometrical or segmental level indices (Chen et al. 2018).

23.4 Root System Architecture and Water Uptake

Plant root systems perform many essential adaptive functions, including water and nutrient uptake, anchorage to the soil, and the establishment of biotic interactions at the rhizosphere. Changes in the architecture of the root system, therefore, can profoundly affect the capacity of plants to take up water and nutrients (López-Bucio et al. 2003). Three major processes affect the overall architecture of the root system. First, cell division at the primary root meristem (i.e., of initial cells) enables indeterminate growth by adding new cells to the root. Second, the formation of the lateral root increases the exploratory capacity of the root system, and third, the formation of root hair increases the total surface of primary and lateral roots. Alterations to any of these three processes can have profound effects on root-system architecture (RSA) and on the capacity of plants to grow in soils in which nutrient resources are limiting (López-Bucio et al. 2003).

There is much evidence that water availability can regulate root architecture. Del Bianco and Kepinski (2018) reviewed various studies on the root system and reported that water deficiency in the upper soil layer suppresses lateral root growth and root growth angle in *Arabidopsis* (Rellán-Álvarez et al. 2015) and crown root growth in *Setaria viridis* (Sebastian et al. 2016). Flooding, on the other hand, promotes adventitious root formation in rice and elongation in *Arabidopsis* (Lin and Sauter 2018). The genetic responses to drought and flooding are also very complex and involve variations in both the transcriptome (Janiak et al. 2016;

Table 23.4 Advantages/disadvantages of methods used for growing plants for root phenotyping

Growth environment	Advantages	Disadvantages	Examples
Laboratory	• It allows for easy and nondestructive visualization of RSA • It is easy to assess root growth • It does not require any washing of roots • It is time-saving as it does not require soil excavation as in the field • It is easily repeated under controlled conditions • It requires less resources • It gives a clear picture of all root types and RSA	• The root system architecture in laboratory-grown plants does not accurately reflect real-time field conditions • Controlled conditions also eliminate possible interaction with beneficial microbes due to the use of growth media other than soil as in field conditions • As plants are grown in controlled conditions, which prevents their exposure to environmental conditions, therefore, the physiological relevance of roots need further evaluation	EZ-Rhizo RootNav Root Reader 3D X-ray computed tomography SmartRoot
Greenhouse/ glasshouse	• Close to the field conditions as the medium used may be soil- or sand-filled pots • A large number of varieties can be evaluated in a shorter period of time • Easy to handle the experiments compared with the field • Less time is required for root washing as compared to the field	• Some roots may be destroyed during washing • RSA may be affected by the growth container • As plants are grown in controlled conditions, which prevents their exposure to environmental conditions, therefore, the physiological relevance of roots need further evaluation	Root Reader 2D WinRhizo
Field	• It gives a true picture or presentation of the root structure • It gives a clear physiological and practical picture as plants grow by facing all the environmental factors	• Roots form an extensive network which is difficult to excavate all the roots • Labor-intensive and time-consuming • Root excavation is very tedious and energy-intensive work • Washing of roots is also time-consuming • Destructive method as roots may be destroyed during excavation and washing • Problems may occur due to variability in the field or soil conditions	Shovelomics, DIRT WinRhizo X-ray computed tomography

Adapted from Wasaya et al. (2018)

Kwasniewski et al. 2016; Opitz et al. 2016) and the methylome (Chwialkowska et al. 2016), representing changes in gene expression over both short and longer timescales. Different cell types respond differently to water status (Opitz et al. 2016), although root hairs seem to be the prime site of water availability perception (Kwasniewski et al. 2016). Responses to variations in water availability involve auxin (Ma et al. 2017; Nakajima et al. 2017), cytokinin (Xu et al. 2016), H_2O_2 (Giuliani et al. 2005; Ma et al. 2017), ABA (Kong et al. 2016), and ethylene (Ali and Kim 2018). Flooding and drought can affect different crop species in distinct ways (Striker and Colmer 2017; Pavlović et al. 2018). In particular, structural differences, such as the number of xylem bundles (Prince et al. 2017; Considine et al. 2017) or crown roots (Gao and Lynch 2016) for drought and root porosity for flooding (Striker and Colmer 2017), are major components of such variation. From a molecular point of view, auxin has been revealed to be required for hydrotropism in pea and rice, but not in *Lotus japonica* (Nakajima et al. 2017).

Classical measures to characterize RSA include total root length, root surface area, and root volume. While total root length is related to the soil volume explored by the root system, root surface area is important for uptake and exudation mechanisms that occur across the root–soil interface, and root volume can be seen as a measure of carbon investment into a specific root structure. The number of branches (or the number of root tips) gives information about the degree of branching within a root system. Maximum rooting depth and maximum horizontal spread of the root system are negatively correlated and determine whether the root system is of steep and deep (Lynch 2013) or of shallow appearance, which has direct implications on root foraging, while deep-rooting plants can take up water from deeper soil layers and are thus advantageous in dry climates and during drought periods (Schnepf et al. 2018). The benefit of deep root systems in drought-prone environments has been demonstrated experimentally in rice (Steele et al. 2013), wheat (*Triticum aestivum*; Manschadi et al. 2010), maize (Hammer et al. 2009, 2010), legumes (Vadez et al. 2013), grapes (*Vitis vinifera*; Alsina et al. 2011), or trees (Pinheiro et al. 2005). However, other results seem to indicate that deep root systems are not always linked to an increase in yield. Experiments with chickpea (*Cicer arietinum*; Zaman-Allah et al. 2011a, b) and wheat (Schoppach et al. 2013) indicate that drought tolerance, especially in terminal drought conditions, can be linked to a conservative use of water throughout the season rather than deep rooting. In such cases, plants tailored for improved root length density at depth are likely to use too much water early in the season and reduce the reserve of water in the profile during the grain filling stage (Lobet et al. 2014).

Substantial variation in root architecture has been reported both among plant species (Kutschera 1960; Fitter and Stickland 1992; Bouma et al. 2001) and within genotypes of crop species (Liao et al. 2001; Sinha et al. 2017) in terms of traits such as depth of rooting, root elongation rate, root distribution at depth, xylem vessel diameter, root growth angle, and root-to-shoot dry matter ratio (Manschadi et al. 2010). The growth angle of root axes or root gravitropic response is a principal component of RSA, which has been strongly associated with temporal and spatial acquisition efficiency of soil resources. In common bean (*Phaseolus vulgaris* L.), for instance, the angle of basal roots is the major determinant of root architecture, while genotypes exhibiting a wider basal root angle appear to develop a shallower root system, which enhances topsoil foraging and thus phosphorous acquisition (Lynch and van Beem 1993; Nielsen et al. 1999; Liao et al. 2001; Lynch and Brown 2001). Likewise, Kato et al. (2006) demonstrated that the growth angle of nodal roots in rice (*Oryza sativa* L.) affects vertical root distribution and rooting depth, which are considered important traits for drought adaptation in upland rice. In wheat, Nakamoto and Oyanagi (1994) demonstrated significant genotypic variation in the angular spread of seminal roots in the Japanese germplasm and argued that deep-rooted wheat genotypes exhibit a narrower angle of seminal roots, while genotypes with a shallower root system tend to grow their seminal roots more horizontally.

Wasson et al. (2012) discussed the important strategies in the selection of RSA traits to increase uptake of stored soil moisture. These traits are (a) deeper root systems, (b) increased root length density in medium and deep soil layers, (c) reduced root length density in the topsoil, and (d) decreased resistance to water movement from soil to root by increasing root hair growth and xylem diameters (Fig. 23.2). However, Wasson et al. (2012) suggested these traits for the wheat crop, but these are applicable for most of the cereal crops for efficient uptake of soil water in rainfed conditions.

23.5 Root System Architecture Versus Nutrient Uptake

Worldwide, 60% of arable soils suffer from growth-limiting problems, with both deficiencies and toxicities of mineral nutrients (Cakmak 2002). Also, nutrient supply to the plants is frequently suffered from adverse soil conditions such as soil pH and redox state, which impact the phyto-availability of mineral nutrients and the concentrations of toxic elements in the soil solution (White and Greenwood 2013). Sparks and Benfey (2017) also stated that the amount of a nutrient that a plant will acquire depends on several factors, including the soil availability, the root system structural features, the plant stores of the nutrient, and the efficiency of nutrient uptake and utilization. However, it is not only the soil properties that affect the capability of soils to deliver nutrients. Soils also need to sustain root growth so that the growing plants can capture a sufficient proportion of the available nutrients and water (White et al. 2013; Schjoerring et al. 2019). Root size and architecture play a major factor in the nutrient uptake efficiency of plants (Fitter 1991; Bar-Tal et al. 1997). A plant's ability to explore the soil and to compete for soil resources is mainly dependent on the architecture of its root system (Lynch 1995). There is scientific consensus that root branching is subject to genetic control and influenced by biotic and abiotic factors. Therefore, manipulating RSA has emerged as a fundamental strategy to enhance nutrient and water acquisition, especially in low-input agricultural systems (Duque and Villordon 2019).

The contrasting availability of nutrients in time and space and their dependence on soil chemistry and microbiology entail trade-offs for root foraging strategies. For example, strategies to improve the capture of nitrate, which is highly mobile, often

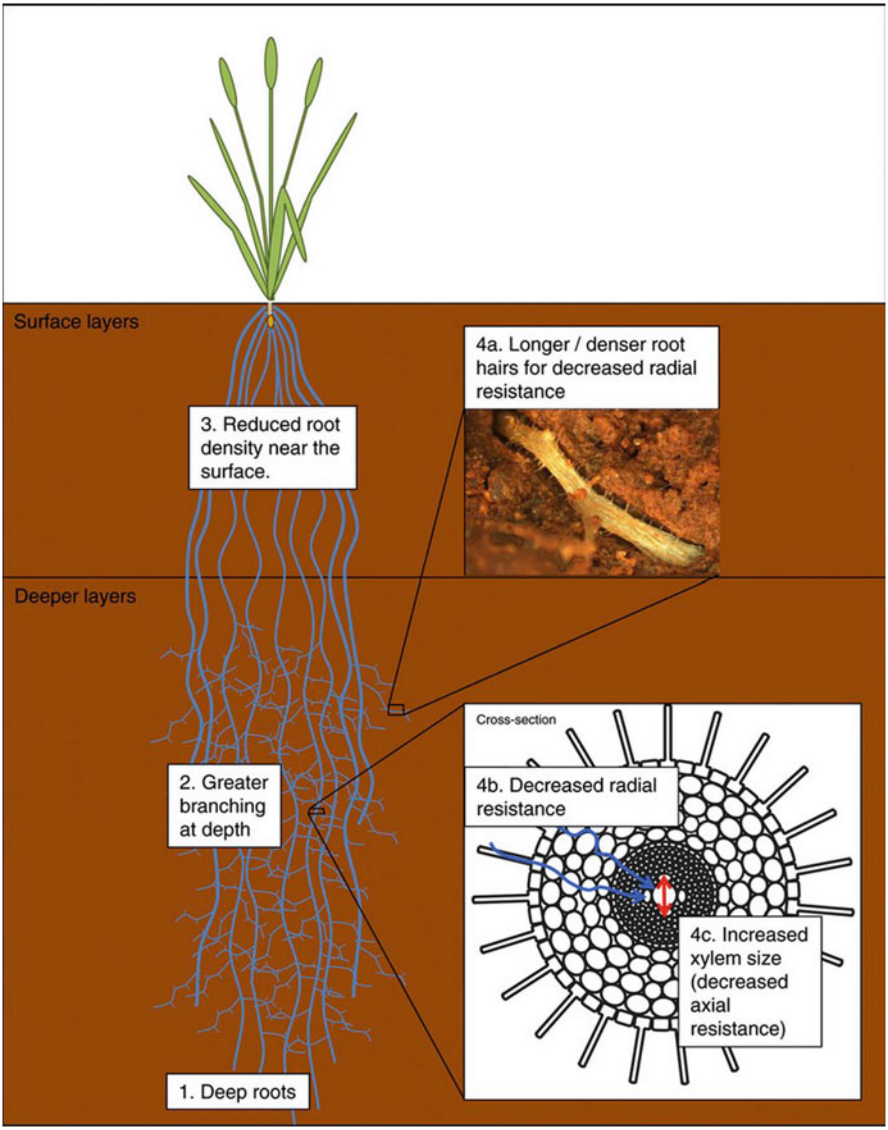

Fig. 23.2 Illustrating four desirable traits to increase deeper water uptake. (Adapted from Wasson et al. 2012)

incur trade-offs for the capture of phosphorous, which is relatively immobile. Further, the utility of strategies to improve nutrient availability via rhizosphere modification depends on whether the bulk soil is acid or alkaline (Hinsinger 2001). In soil, localized depletion of mineral nutrients by root limits continued resource capture (Barber 1984), necessitating continued exploration of new soil domains and intensifying interplant competition. Root phenotypes are the result of long and intensive selection for efficient and effective capture of soil resources, and efficient utilization of acquired nutrients has been subject to natural selection since the origin of life (Lynch 2019).

Nitrogen and phosphorus are among the elements considered most limiting to plant growth and productivity because they are often present in small quantities locally or are present in a form that cannot be used by the plant (Morgan and Connolly 2013). Plants are able to directly acquire nitrate and ammonium from the soil. However, when these nitrogen sources are not available, certain species of plants from the family Fabaceae (legumes) initiate symbiotic relationships with a group of nitrogen-fixing bacteria called rhizobia. These interactions are relatively specific and require that the host plant and the microbe recognize each other using chemical signals. The interaction begins when the plant releases compounds called flavonoids into the soil that attract the bacteria to the root. This form the bacteroids, which allow bacteria to enter the cytoplasm of cortical cells where they convert atmospheric nitrogen to ammonia, a form that can be used by the plants. (Limpens and Bisseling 2003; Ferguson et al. 2010; Morgan and Connolly 2013). Recently, Lynch (2019) presented the ideotype in terms of root system architectural parameters for efficient uptake of different nutrients. For example, the steep and deep root ideotype for improved N acquisition in maize consists of architectural, anatomical, and physiological traits. Architectural traits include steep root growth angles, few nodal roots, sparse lateral branching, and low architectural plasticity in response to environmental cues. Reduced root production is beneficial for N capture by reducing competition among root axes for internal (e.g., carbohydrate) and external (i.e., nitrate) resources (Postma et al. 2014). Guo et al. (2008) suggested an idiotypic root architecture for efficient N acquisition in maize that includes (a) deeper roots with high activity that are able to uptake nitrate before it moves downward into deep soil, (b) vigorous lateral root growth under high N input conditions so as to increase spatial N availability in the soil, and (c) strong response of lateral root growth to localized nitrogen supply so as to utilize unevenly distributed nitrate, especially under limited N conditions.

Unlike nitrate, which readily moves in soil toward the roots via both mass flow and diffusion, phosphate (Pi) is highly immobile. Mass flow typically delivers as little as 1–5% of a plant's P demand, and the amount intercepted by growing roots is only half of that (Lambers et al. 1998). The rest of all required Pi must reach the root surface via diffusion. Increasing Pi delivery to roots via mass flow can be achieved by enhanced transpiration rates, but this cannot have a major effect and would be at the expense of a plant's water use efficiency. Root interception of Pi can be increased by root proliferation, increased frequency and length of root hairs, a modified root architecture that enhances allocation to shallow soil horizons, and mycorrhizal symbioses. The diffusion of Pi toward the root can be increased by increasing the moisture content of dry soil or by increasing the Pi concentrations in the soil solution through the release of Pi from complexed, sorbed, or organic form of P Lambers et al. 2006). For efficient phosphorous acquisition, Lynch (2019) suggested two options to focus on (1) improving foraging in P-rich soil domains (i.e., the topsoil in

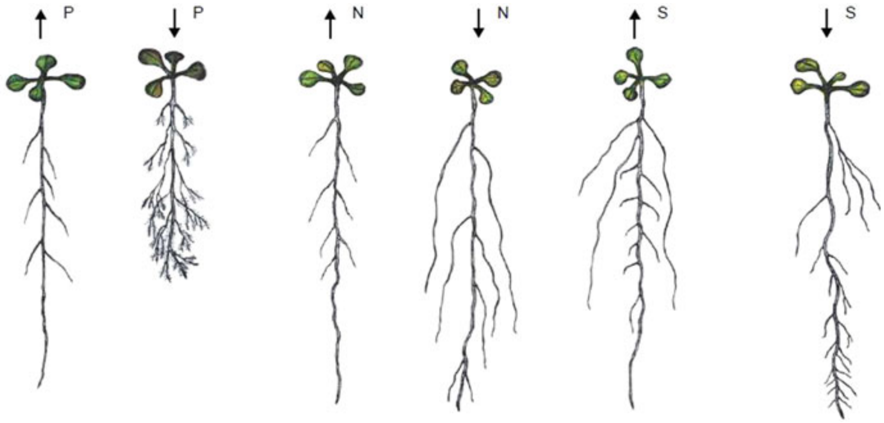

Fig. 23.3 Root system under the different nutrient concentrations. (Adapted from López-Bucio et al. 2003)

most agricultural soils) and (2) improving the exploitation of those domains through increased P solubilization. Topsoil foraging can be enhanced through greater production of axial roots, shallower axial root growth, angles, greater lateral root density, reduced root metabolic cost, and greater root hair length and density. Regarding the phosphorous solubilization in the rhizosphere, worldwide researchers showed the possibility of harnessing genetic variation in P-solubilizing exudates to develop P-efficient crop lines (Richardson et al. 2009). Natural and induced genetic variation for the production of these compounds is associated with P mobilization in vitro, but rigorous analyses have failed to show a benefit of such variation for P acquisition in a range of soils in the field, whether it be due to carboxylates (Pearse et al. 2007; Ryan et al. 2014) or phosphatases (George et al. 2008). This lack of response may be due to various factors, including limited spatiotemporal distribution of exudate production in root systems and their limited lifespan and mobility in the rhizosphere due to microbial metabolism and chemical fixation (Lynch 2019).

The ability of plants to respond appropriately to nutrient availability is of fundamental importance for their adaptation to the environment. Nutrients such as nitrate, phosphate, sulfate, and iron act as signals that can be perceived. The responses of root architecture to nutrients can be modified by plant growth regulators, such as auxins, cytokinins, and ethylene, suggesting that the nutritional control of root development may be mediated by changes in hormone synthesis, transport, or sensitivity. Recent information points to the existence of nutrient-specific signal transduction pathways that interpret the external and internal concentrations of nutrients to modify root development (López-Bucio et al. 2003). A study on the effect of various nutrient concentrations on the root system was published in "Current Opinion in Plant Biology" (López-Bucio et al. 2003). The following Fig. 23.3 is adapted from this study to understand the dynamics of the root system under the different nutrient concentrations.

23.6 Root System Architecture and Tillage System

Soil tillage has been a major farm operation of crop production for centuries. Tillage has been used to optimize edaphological conditions, such as soil water and soil temperature regimes (Somasundaram et al. 2018a), soil aeration, seed-soil contact, nutrient availability (Hati et al. 2015), bulk density, porosity, pore size distribution (Somasundaram et al. 2018b, 2019), and pest activity. Tillage aims to support seed germination, seedling establishment, plant, and root growth (Lal and Shukla 2004; Mehra et al. 2018). However, tillage operations are primarily aimed at loosening the soil (i.e., increasing porosity and reducing soil bulk density). The consequences of the soil interacting with equipment used for tillage and the timing of operations may result in soil compaction (Batey 2009; Reicosky 2003). Particle-to-particle or aggregate-to-aggregate contact affects the physical status of the soil matrix and its associated water, air, and temperature properties (Six et al. 2002). Furthermore, soil hardens upon drying act as a physical barrier to root development (Iqbal et al. 1998; Choudhary et al. 2015). The potential of plants to obtain water and mineral nutrients from the soil is primarily attributed to their capacity to develop extensive root systems (Guan et al. 2015). Huwe and Titi (2003) reports that tillage influences both biotic and abiotic processes, modifying structural properties such as cracks, aggregates, and pore continuity, as well as affecting soil aeration, temperature, and moisture levels. By greatly changing soil properties, tillage also greatly influences root growth. Mosaddeghi et al. (2009) conclude that the most important impact of tillage on crop development is achieved by affecting root development and function. Therefore, the root system serves as a bridge between the impacts of agricultural practices on soil and changes in shoot function and harvested yield.

Yeboah et al. (2017) found that no tillage with straw retention significantly decreased soil bulk density and boosted soil moisture content compared to conventional tillage with straw removed and no tillage with straw removed at the topsoil depth (0–30 cm), therefore, significantly affects the root length, root surface area, root diameter, and root volume through the 0–50 cm soil profile. The increased root morphological characteristics (root length, root surface area, root diameter, and root volume) under straw-amended soils, particularly in no-tillage (NT) system up to 50 cm soil depth, could largely be attributed to the decreased soil bulk density and the enhanced soil moisture, which promotes root proliferation during the growing season of wheat. At almost every growth stage, the root morphological characteristics in the top 50 cm soil depth under NT with straw retention were significantly greater than that under the NT and conventional tillage (CT) with straw removed treatment. In contrast, Guan et al. (2014) studied root development under three tillage systems, viz., no tillage (NT), plow tillage (PT), and rotary tillage (RT) in maize crop. The study showed that root biomass under PT and RT was significantly higher than under NT across 0–40 cm soil profile. Some other researchers also showed that maize roots are generally greater under PT than NT at all depths (Karunatilake et al. 2000; Sheng et al. 2012). Root length density (RLD) and root surface area density (RSD) are pertinent parameters for characterizing root systems (Amato and Ritchie 2002; Doussan et al. 2006). Guan et al. (2014) found that RLD in the uppermost soil profile (0–10 cm) showed no evident differences among tillage practices at the silking stage, but RLD under PT and RT was significantly greater than under NT at maturity. Similar findings were reported for tillage systems on chickpea by Muñoz-Romero et al. (2012), on maize by Karunatilake et al. (2000) and Mosaddeghi et al. (2009), and on spring wheat by Munoz-Romero et al. (2010). Qin et al. (2006) reported that RLD is significantly higher under NT than under CT (plow tillage) at a depth of 5 cm, whereas it is higher under CT than under NT in 10–50 cm soil profile.

Moreover, there is no difference in RLD between the tillage practices below 50 cm. Guan et al. (2014) found the RLD under PT was markedly higher than under NT in the 10–50 cm soil profile at silking and maturity stages, and there was no significant difference in LSD of 60–100 cm soil profile among tillage practices at maturity. RLD and RSD under PT and RT in the upper soil profile were high compared to under NT, which could be due to the existence of high soil compaction under NT. Mehra et al. (2018) used micro X-ray tomography (μXCT) to study the root phenotypes under the different tillage systems. Quantified root phenotypes over the plant growth stages show that the mean root volume was 9.6% higher in the top 20 cm of the soil in NT than CT practice. The vertical distribution of roots and root architectural measurements evaluated through μXCT indicated increased root length (8.7%) and root surface area (2.6%) under the CT system compared to NT. The higher root volume under the NT system could be related to the presence of higher mesopores in the top 20 cm soil, which have the ability to store more water and nutrients (Murphy 2014) than macrospores, thereby resulting in higher root volume in the NT system compared to CT.

It is universally accepted that soil bulk density is the highly dynamic soil attribute, affected prominently by the different management practices, including cropping systems and tillage management practices (Kushwa et al. 2016; Sinha et al. 2014a, b). A common response of the root system to increase in bulk density (BD) is a decrease in root length, concentrating roots in the upper layer, and decreasing rooting depth (Lipiec and Hatano 2003). The root elongation rate is decreased with the response to higher BD in cotton (*Gossypium hirsutum*) and peanut (*Arachis hypogaea* L.) (Taylor and Ratliff 1969), in pea (*Pisum sativum L.*) (Vocanson et al. 2006), in maize (*Zea mays* L) (Bengough et al. 2006), and in tomato (*Solanum lycopersicum*) (Tracy et al. 2012). Konopka et al. (2009) found that maize roots were more tortuous in compacted soil, with a greater branching density and shorter lateral roots. It has also been observed that moderate compaction of the seedbed may be beneficial for root growth and resource capture (Atkinson et al. 2009) and reduces the risk of lodging in cereals in light textural soils (Scott et al. 2005). Choudhary et al. (2015) determine the effect of soil compaction levels by varying the soil bulk density (BD) on rooting parameters of two contrasting chickpea cultivars in central India. The BD considered were (a) 1.2, (b) 1.4, (c) 1.5, and (d) 1.6 Mg/m^3 and rooting parameters studied were main axis length, number of nodes, number of primary roots, sum of the length of primary roots, root diameters, and root insertion angle. Results indicated that when BD was increased from 1.2 Mg/m^3 to 1.6 Mg/m^3, there was 59% and 45% reduction in root length of JG 11 and JG

130, respectively. On average, an increase in BD by 0.1 unit resulted in 19.34% and 19.11% decrease in the root main axis length of JG 11 and JG 130, respectively. The total number and length of primary roots were also significantly ($P < 0.05$) decreased by compaction levels. On average, the total primary root length decreased by about 66% in both the cultivars by increasing BD from 1.2 to 1.6 Mg/m^3. The same level of increase of BD resulted in 65% and 47% decrease in the number of nodal roots in JG 11 and JG 130, respectively.

Furthermore, it has also been observed that toward higher compaction levels, a small increase in BD resulted in a greater reduction in root architectural parameters. For example, an increase in BD from 1.2 Mg/m^3 to 1.4 Mg/m^3 resulted in 23% reduction in main axis length in JG 130, whereas further increase in BD from 1.4 Mg/m^3 to 1.6 Mg/m^3 resulted in 33% reduction in the main axis. Similarly, for JG 11, the same increase in BD resulted in 32% and 45% reduction in main axis length. At a higher compaction level, both the cultivars tend to increase its root diameter. An increase of 33% and 21% in root diameter was observed for JG 11 and JG 130 in response to an increase in BD from 1.2 to 1.6 Mg/m^3 (Table 23.5). It was observed that the angle became wider as the compaction levels increased. At higher compaction level, i.e., at BD 1.6 Mg/m^3, an angle of 60° was dominant in both cultivars, while a smaller angle of 40° was observed at lower compaction levels. As the BD levels increased from 1.2 to 1.6 Mg/m^3, the root angles also increased from 40° to 60°. Under the stressed condition, roots may have an optimum root angle to achieve the most efficient distribution and maximize the volume of soil explored for water and/or nutrient uptake (Lynch and Brown 2001; Tracy et al. 2012).

23.7 Impact of Root System Architecture/Pattern on Carbon Storage

Roots play a major role in carbon (C) storage in soil. Due to their rapid decomposition and turnover rate of fine roots, they provide primary input of organic C into the soil to the tune of 30–80% of the total (Steele et al. 1997; Brown 2002; Ruess et al. 2003; Howard et al. 2004). However, due to root biomass dynamics, production rate, monthly succession, seasonal rate of growth, architecture, and their pattern of proliferation, the rate of C storage mostly by fine roots varies greatly among different species. One of the most important factors dictating the decomposition of the fine roots is the C:N ratio, where evidence suggests that a low C:N ratio results in more decomposition of roots. Both abiotic and biotic factors affect the roots' decomposition and their transformation into the C stock of the soil. Moreover, the fine dynamics studies under different cropping systems and ecologies are very limited due to their tiresome methodology and the involvement of time. There is an urgent need to understand the root dynamics and production under a fluctuating environment for a better understanding of their contribution toward carbon storage in soil.

Table 23.5 Root architectural parameters of chickpea as affected by different levels of bulk density

	Main axis length (cm)		Number of nodes		Number of primary roots		Sum of length of primary root (cm)		Root diameter (mm)		Insertion angle[a] (degree)	
	JG-11	JG-130	JG-11	JG-130	JG-11	JG-130	JG-11	JG-130	JG-11	JG-130	JG-11	JG-130
BD-1	16.67a	17.00a	15a	16a	20a	23a	54a	57a	0.12b	0.19a	40 (30–65)	40 (30–65)
BD-2	11.33b	13.00b	12a	15a	15b	19ab	37b	36b	0.13ab	0.20a	40 (40–60)	40 (20–45)
BD-3	8.83b	9.17c	8b	14a	10c	17b	24c	25c	0.15a	0.20a	40 (40–70)	40 (30–80)
BD-4	3.77c	4.00d	7b	10b	7d	12c	18c	19c	0.16a	0.22a	60 (40–70)	60 (30–70)

[a] Angle presented as “mode.” *Value in parenthesis indicates range. BD1 = 1.2 Mg/m^3, BD2 = 1.4 g/m^3, BD3 = 1.5 Mg/m^3, BD4 = 1.6 Mg/m^3. Same letters (a, b, c, . . .) in a column indicate a nonsignificant difference between the treatments Choudhary et al. (2015)

23.8 Conclusions

In this chapter, we summarized behaviors of root system architecture proliferation under varying management conditions. Root system parameters found to be very sensitive to small changes in both biotic and abiotic factors that get changed due to the adoption of varying tillage options. Study of root system architecture on a long-term basis is quite necessary along with the aboveground plant component for better understanding of resource acquisition, nutrient cycling, carbon dynamics, and storage in soil.

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