A Review on Response of Root System Architecture and Root Phenotypic for Biotic And Abiotic Stress

Arega Wole Damena[1, *]

[1]Department of Plant Science (M Sc. In crop and irrigation agronomy), Mekdela Amba University College Of Agriculture and Environmental Science

Abstract

Root is has great role for plant adaptation and productivity of the agricultural crops as well as other plants by exploiting the soil resource thus, important for plant growth and development or main growth factors. Root system architecture is made up of structural features which exhibits great role in response to environmental stress, and critical to plant growth and development with sufficient root growth. Root system architecture has a central role in crop plants' response to abiotic (soil microorganisms) and abiotic stresses like water stress, mechanical impedance. Root morphology can be affected by nutrient availability, osmotic stress, salinity, and light. Phenotyping root is one of the drought management tools as roots are more prone to drought conditions and play a significant role in the plant's life by extracting soil resources from deeper soil layers to carry on several metabolic functions in the plant's body and its phenotyping helps to understand different root traits. Understanding interactions between roots and their surrounding soil environment is important to increase root growth, which can be improved through root phenotyping. In addition, knowing of the development and architecture of roots, as well its plasticity, holds thus great role for stabilizing the productivity under suboptimal conditions in the root environment

Introduction

Plant roots play a significant role in plant growth by exploiting soil resources via the uptake of water and nutrients [72]. Roots are essential for plant adaptation and productivity, but are less studied due to the difficulty of observing them during the plant life cycle [34]. Roots are essential for plant productivity and serve a variety of functions, such as water and nutrient uptake, forming symbioses with other microorganisms in the rhizosphere, anchoring the plant to the soil, and acting as storage organs. The different interactions of a root with its environment depend on its organization and structure, from the cellular to whole-plant level. The root contains a stele, comprised of the xylem, the phloem, and the pericycle [67]. Much of the research on root traits has thus far focused on the most common cereal crops and model plants. As cereal yields have reached their yield potential in some regions, understanding their root system may help overcome these plateaus [34].There is great potential to use the wide genotypic and agronomically induced

diversity of root systems and their exuded chemicals to influence rhizosphere biology to benefit crop production [57].

Root system architecture (RSA), made up of structural features like root length, spread, number, and length of lateral roots, among others, exhibits great plasticity in response to environmental changes, and could be critical to developing crops with more efficient roots [34]. Root system architecture (RSA) is an important developmental and agronomic trait, which plays vital roles in plant adaptation and productivity under water-limited environments. A deep and proliferative root system helps extract sufficient water and nutrients under these stress conditions (74).Since roots grow underground, they are the first to sense abiotic stresses and adjust their genetic program for post-embryonic development to survive the stress [43]. Plant roots obtain water and nutrients from the soil, which is a complex system with intrinsic properties, abiotic and biotic interactions.

The main functions of root systems are also explored including how roots cope with nutrient acquisition from the heterogeneous soil environment and their ability to form mutualistic associations with key soil microorganisms (such as nitrogen fixing bacteria and mycorrhizal fungi) to aid them in their quest for nutrients [28].Plants growing in soil develop close associations with soil microorganisms, which inhabit the areas around, on, and inside their roots. These microbial communities and their associated genes collectively termed the root microbiomeare diverse and have been shown to play an important role in conferring abiotic stress tolerance to their plant hosts [27].

Root morphology can be affected by nutrient availability [24], osmotic stress [19], salinity [22] and light [33]. A plant's final phenotype is highly dependent on external signals, and the level of plasticity can facilitate responses to stresses [50].Phenotyping root is one of the drought management tools as roots are more prone to drought conditions and play a significant role in the plant's life by extracting soil resources from deeper soil layers to carry on several metabolic functions in the plant's body and its phenotyping helps to understand different root traits [72].Root traits such as fine root diameter, specific root length, specific root area, root angle, and root length density are considered useful traits for improving plant productivity under drought conditions[72].Root development is controlled by auxin and cytokinin signaling [49] and is modulated by external stimuli through other hormones and alterations in auxin or cytokinin sensitivity [30].So that, understanding interactions between roots and their surrounding soil environment is important, which can be improved through root phenotyping [72].Finally, the main objective of this seminar paper is to review the response of root system architecture and root phenotypic for biotic and abiotic stress.

Literature Review

Root growth and development

Roots are axial multicelular structures of sporophytes of vascular plants which usually occurs underground, have strictly apical elongation growth, and generally have gravitropic responses which range from positive gravitropism to diagravitropism, combined with negative phototropism [55]. Root growth regulation, and its response to changing environmental conditions, is a highly complicated process that is controlled at many different levels by complex actions of gene networks in both time and space [35]. Root growth relies on a specific set of signals involving hormones, nutrients and carbon supply [37]. They generated a fractal-based model for root development that accounts for specific interactions between ethylene levels, nitrogen availability and energy supply.

Root System Architecture (RSA)

Root system architecture (RSA) refers to the spatial configuration of the root system or the explicit deployment of root axes [43]. Under poorly understood genetic control, RSA exhibits plasticity and responds to external environmental conditions such as soil moisture, nutrients, temperature, pH, and microbial communities [4]. The study of RSA is important for agricultural productivity because most soils have uneven distribution of resources and/or localized depletions that make spatial distribution of the root system an important determinant of a plant's ability to exploit these resources [43].Roots are essential for plant productivity and serve a variety of functions, such as water and nutrient uptake, forming symbioses with other microorganisms in the rhizosphere, anchoring the plant to the soil, and acting as storage organs. The different interactions of a root with its environment depend on its organization and structure, from the cellular to whole-plant level. The root contains a stele, comprised of the xylem, the phloem, and the pericycle [66].

General Root functions in the heterogeneous soil environment

The main functions of a root system are anchorage and uptake of water and nutrients. In trees and other woody species, extensive belowground structures whose main role is to provide support rather than nutrient acquisition are required but in smaller plant species anchorage occurs largely as a secondary function of root growth and development in soil [28]. The overall form or 'architecture' of the root system is also important for anchorage and water-nutrient uptake. Root system architecture is very varied among different plant species but within species architecture is flexible and can alter as a result of prevailing soil conditions. This flexibility arises due to the modular structure of roots which enables root deployment in zones or patches rich in moisture or nutrients [28].

Physiological and genetic determinants of root growth and architecture

A major difference between plant and animal development is that positional information rather than cell lineage determines cell fate in plants [65]. Post-embryonically, plant development is essentially driven by stem cells localized in apical regions of shoots and roots, and referred to as apical meristems. This particular characteristic allows plants, which are sessile organisms, to adapt their morphology and organ development to the encountered 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 on water and mineral nutrients availability [45]. Plants can optimize their root architecture by initiating lateral root primordia and influencing growth of primary or lateral roots. The root system results from the coordinated control of both genetic endogenous programs (regulating growth and organogenesis) and the action of abiotic and biotic environmental stimuli [45]. The interactions between these extrinsic and intrinsic signals however complicate the dissection of specific transduction pathways. Such complex traits likely depending on multiple genes may be analyzed through quantitative genetics via the identification of quantitative trait loci (QTL) linked to root architecture [19]. Understanding the molecular mechanisms governing such developmental plasticity is therefore likely to be crucial for crop improvement in sustainable agriculture. The embryonic root apical meristem (RAM) specification occurs very early in embryo development [6]. The RAM constitutes the stem cell niche that eventually produces all below-ground organs, including lateral roots [58].

Phytohormonal regulation of the root system: Auxin as a major player

The different stages of root development are controlled and regulated by various phytohormones with auxin playing a major role [40]. In roots, auxin is involved in lateral root formation, maintenance of apical dominance and adventitious root formation. Auxin also plays a major role in lateral root initiation and development. Lateral root development can be divided in different steps: primordium initiation and development, emergence, and meristems activation. Auxin local accumulation in Arabidopsis root pericycle cells adjacent to xylem vessels, triggers lateral root initiation by re-specifying these cells into lateral root founder cells [17]. All these developmental events require correct auxin transport and signaling. Furthermore, it is also involved in the growth and organization of lateral root primordia and emergence from the parent root [36].Indeed, mutants or transgenic lines with elevated auxin biosynthesis and endogenous levels of IAA display significant increased root branching [64]. Auxin transport into the regions where lateral root initiate also seems crucial for the regulation of root branching [11].

Roots Bridging the Yield Gap

Breeding efforts to improve crop yield are in general focused on aboveground, shoot-related phenotypes, whereas the roots as 'hidden half' of the plant are still an under-utilized source of crop improvement [12,69]. Trials aimed to select for new cultivars with improved crop yield are in general performed under optimal nutrient concentrations, which has often led to selection for smaller and less plastic roots [73]. Moreover, modern cultivars develop in general faster and the earlier initiation of shoot sinks stimulates the investment of biomass into the shoots rather than into the roots. Modern wheat cultivars indeed have smaller root sizes and root:shoot ratios than older ones [70]. Given the crucial role roots play in the establishment and performance of plants, researchers have started 'the second green revolution' to explore the possibility of yield improvements through optimization of root systems [42]. Because water and nutrients are not evenly distributed in the soil, the spatial arrangement of the root system is crucial for optimal use of the available resources. This spatial arrangement of the root and its components is referred to as root system architecture (RSA). Length, number, positioning, and angle ofroot together determine RSA. These traits determine the soil volume that is explored.

In addition, the root surface area depends on root hair development and root diameter. The ability to adjust RSA is an important aspect of plant performance and its plasticity to a large variety of abiotic conditions [67]. Root development is guided by environmental information that is integrated into decisions regarding how fast and in which direction to grow, and where and when to develop new lateral roots [45]. The limits of root system plasticity are determined by intrinsic pathways governed by genetic components [51, 66, 25, 30]. Understanding the development and architecture of roots, as well its plasticity, holds thus great potential for stabilizing the productivity under suboptimal conditions in the root environment [12, 75].

Plant–Microbe Interaction

In light of growing concerns over the threat of water and nutrient stress facing terrestrial ecosystems, especially those used for agricultural production, increased emphasis has been placed on understanding how abiotic stress conditions influence the composition and functioning of the root microbiome and the ultimate consequences for plant health. However, the composition of the root microbiome under abiotic stress conditions will not only reflect shifts in the greater bulk soil microbial community from which

plants recruit their root microbiome but also plant responses to abiotic stress, which include changes in root exudate profiles and morphology [27].

The bacterial and fungal members of the root microbiome can establish commensal, pathogenic, and beneficial associations with their host [53].A large body of evidence highlights the beneficial services provided by the root microbiome, particularly its importance in maintaining plant productivity by contributing to plant biotic and abiotic stress resistance and resilience via many mechanisms [53, 68].

Root response to biotic and abiotic stress

Root response to micro-organisms

Though root systems are genetically determined they can be strongly influenced by a wide range of abiotic and biotic factors, including the presence of soil microorganisms. In some cases the effect upon root growth and morphogenesis are clearly evident with the formation of visible novel organs (e.g. root nodules in the Rhizobium-legume symbioses), while in others the impact upon roots are much less evident [28].

Pathogenic fungi and cyanobacteria-invaded coralloid roots

Pathogenic fungi reduce plant growth and affect root architecture [28]. In tomato plants infected by Rhizoctoniasolani, the root system is characterized by the scarcity of short adventitious roots and the emergence of many short laterals, leading to a more branched root system [60]. R. solani and Pithium sp. have been shown to induce a more monopodial type of branching pattern, with fewer orders of branching than uninfected controls in tomato and Medicago sativa, respectively [60]. Coralloid roots are characterized by dichotomous branching, forming coral-like shapes. Their development begins with the formation of young roots named precoralloids that, when mature, are invaded by cyanobacteria located between the cells of the root cortex [15]. Coralloid roots infected by cyanobacteria are surrounded by a pronounced layer of mucilaginous material, where cyanobacteria occur as short hormogonial filaments, the infective units of the Nostoc species involved in the symbiotic association [26]. Hormogonia penetrate the roots through breaks in the dermal layer and reach, through a cortical channel, the cyanobacterial zone, which is the structural and physiological site of the CycasCyanobacteria symbiosis.

Legume nodules and Ectomycorrhizal (ECM) roots

Nodules are specialized root organs in which symbiotic bacteria (Rhizobia) are able to convert atmospheric nitrogen into ammonia as a nitrogen source. Establishment of the Rhizobium-legume symbiosis depends on a molecular dialogue: flavonoids excreted by host plant roots induce the expression of bacterial nod genes, which encode protein involved in the synthesis and excretion of specific lipochitooligosaccharide signalling molecules called nod factors, that in turn are recognised by host legumes [2, 59]. Responses to nod factors by root hairs include: altered ion fluxes and plasma membrane depolarisation, calcium spiking, root hair deformation (due to changes in the actin cytoskeleton), and early nodulin gene expression.

In cortical cells, nod factors induce nodulin gene expression and cell division leading to nodule primordium formation [2]. In legumes Rhizobia induce two types of nodules: determinate and indeterminate [15]. The latter are the most commonly formed on temperate legumes by Rhizobium

species, while the former are induced by Bradyrhizobium (the name is associated with the slow growth of these bacteria) on tropical legumes. Nodule formation is a multistep process. Rhizobia move to roots by positive chemotaxis in response to root exudates. The bacteria then infect the host roots via root hairs, or via wounds and lesions, or through spaces occurring around root primordia or adventitious roots. In the case of root-hair infection, the attachment of Rhizobia leads to root hair curling, Rhizobia then enter the root by invagination of the plasma membrane, and induce formation of an infection thread, a growing tube with cell wall material filled with growing bacteria [59]. Rhizobia move down the infection thread towards the root cortex, where cell division leads to the production of nodule primordia, functioning as a meristem [2].

In pea, the genes controlling nodule morphogenesis have been identified for plant tissue colonization and differentiation of bacteria into bacterioids and for the development of nodule tissue [10]. The genetic system controlling nitrogen-fixing symbiosis development in plants likely evolved from the system controlling AM symbiosis [10]. Rhizobia obtain carbon compounds, especially malate, from their host and in turn perform nitrogen fixation at the centre of the nodule in a microaerobic zone surrounded by a layer of very closely packed cells with few air spaces.

Ectomycorrhizal are formed by mutualistic interactions between soil fungi and the roots of woody plants. In Ectomycorrhizal plants, roots usually have very few, or no, root hairs and tend to be short and thick. Within the root, hyphae always remain apoplastic and can colonize the epidermal (angiosperms) and the cortical cell (gymnosperms) layers, forming the Hartig net, a complex branched structure, which mediates nutrient transfer between fungus and plant [66]. The most evident root modifications are the early formation of lateral roots and a dichotomy of the apical meristems in a number of species. External hyphae extend out of the depletion root zones, to explore the soil substrate and are responsible for the nutrient capture and water uptake of the symbiotic tissues. The fungi may also acquire nutrients from more complex organic substrates, but large differences between different species and even among strains of the same fungus exist in accessing these complex substrates [56]. The structure of ectomycorrhizal is essentially determined by the fungal species rather than the host plant, however there is considerable variation in the degree of host specificity among species and even among strains of ectomycorrhizal fungi [38].

Plant growth promoting rhizobacteria (PGPR)

Root system structure is also influenced by other beneficial soil micro-organisms such as the root colonizing "Plant Growth Promoting Rhizobacteria (PGPR). PGPR's affect root architecture by increasing total root length and branching as a consequence of hormone production and improved plant mineral nutrition [9]. In turn, these changes to the root system architecture likely impact upon microbial dynamics in the rhizosphere through altered rhizodeposition including changes in signalling molecules released [3].Plants with different root system structure and physiology, are differently dependent upon mycorrhization [18] while, in turn, colonisation by mycorrhizal fungi may impact upon root system structure [9].

Root response to abiotic stress

Different researchers reported that how roots respond to abiotic stresses, including nutritional limitations, elemental toxicities, waterlogging and physical constraints. Soil acidity affects more than 30 % of arable

land and continues to limit agricultural productivity globally. Aluminium and manganese toxicities are largely responsible for poor plant growth but nutrient deficiencies also contribute. Many species have evolved strategies to cope with these stresses, and Rao et al.,[54] comprehensively review the adaptive changes in root structure and function that provide protection from these hostile soils. They encourage further breeding strategies to select for additional root traits. Liska et al. [41] demonstrate how exposure of roots to air, or to toxic metals such as cadmium, influences the development of suberin lamella. Suberin is a wax-like cell-wall polymer that provides a barrier to the movement of water and solutes. They find that suberin is preferentially deposited on the side of the root exposed to these treatments, presumably as a means of protecting the plant from these stresses.

Phenotypic screens for single, abiotic soil constraints, such as those in the studies summarized above, can reveal the genetic and physiological basis of tolerance mechanisms. Similar studies have identified many new membrane transport proteins that regulate the uptake of nutrients and the exclusion of toxic ions through specific root exudates [63]. The next step will be to combine these treatments and score performance with the multiple stresses encountered in the field. This will accelerate progress towards improving agricultural production and provide management options for forestry and natural systems [57]. Soil is the most complex of all environments containing liquid, gaseous and solid phases, the ratios of which can change depending on the prevailing conditions.

Mechanical impedance

Roots are subject to mechanical impedance when the force required to displace soil particles as the root grows increases. As a result, root diameter behind the root tip increases and root elongation decreases with increasing soil strength. Compaction is another major soil constraint that affects root penetration and final rooting depth. Popova et al., [52] studied the effect of soil strength on elongation rate and diameter of maize (Zea mays) roots and finally revealed that how final root shape and tortuosity in compacted soil results not only from mechanical deflections but also from tropic responses via touch stimuli.

Water stress

Generally, water is believed to be available for plant uptake at matric potentials greater than -1.5 MPa (the wilting point of many mesophytic plants), but root growth can be severely slowed by potentials greater than this value [7]. Schenk and Jackson [62] surveyed the literature on root system sizes for individual plants from deserts, scrublands, grass. Plant lands and savannas all with ≤ 1,000 mm mean annual precipitation. They found that maximum rooting depth showed a strong positive relationship with mean annual precipitation for all plant growth forms, except shrubs and trees. Moreover, maximum rooting depth for all growth forms tended to be shallowest in arid regions and deepest in subhumid regions, which was thought to be the result of more restricted water infiltration depths in areas with lower precipitation. These results appear to contradict the widely held view that rooting depth increases in drier environments. However, as Schenk and Jackson [62] state, the distinction between relative and absolute rooting depths is critical. Thus, for a given canopy size herbaceous plants do have deeper maximum rooting depths in drier environments, but as canopy size increases so too does the absolute rooting depth. However, the relationship is not simply due to increased plant size as above– and below–ground allometrics also change with climate. Moreover, depths at which plants have 50% or 95%

of their total root biomass are significantly deeper in drier than in humid environments [61]. Water availability is not the only abiotic factor that influences rooting depth, soil texture, organic horizon size [61] and plant species composition will also dictate the rooting depth achieved.

Remodeling of the Root System during Salt Stress

Nutrient availability and salinity of the soil affect the growth and development of plant roots (Kawa et al., 2016). Salt has a distinct effect on root growth [22]. Although, low salt concentrations up to 50 mM can promote plant growth in Arabidopsis [29], higher salt concentrations have severe negative effects. Both primary and lateral root growth is inhibited during salt stress [29]. In addition, lateral root number specifically decreases in the root zone developed after exposure to salt stress [29]. Most studies show no effect of salt stress on lateral root density, indicating that the decrease in number of lateral roots is related to the inhibition of primary root growth [29]. Within seconds after exposure to salt stress, plant signaling is activated.

In addition, mature cell length is smaller in salt stressed roots. Quiescence is induced by abscisic acid (ABA), which is rapidly up-regulated under salt stress due to the decrease in osmotic potential [16,23]. ABA in general inhibits both gibberellin (GA) and brassinosteroid (BR) signaling [20] and stress-induced reduction of growth has been shown to benefit the plant [1]. Galvan-Ampudia et al.,[21] showed that plants can specifically redirect growth away from higher salt concentrations, a response called halotropism. This response was observed in Arabidopsis, tomato and sorghum seedlings, both on agar media and in soil. Similar to gravitropism, auxin redistribution is central in regulating halotropism. Endocytosis of PIN2, an auxin efflux carrier, at the side of high salt concentrations, redistributes auxin in the root [21]. Part of the salinity response is also triggered by osmotic stress and shows overlap with drought responses.

Most crop species are highly sensitive to salinity. Tomato serves as a model crop that is widely used to study how salt tolerance can be enhanced in crop species. For a wide range of vegetables, including tomato, grafting is a very effective way to increase crop resistance to biotic and abiotic stresses, without affecting above ground characteristics. For several salt sensitive commercial tomato cultivars, grafting onto rootstocks of more tolerant cultivars has positive effects on productivity when exposed to high salinity [47]. The Na^+/K^+ levels in the shoot (scions) indicated that the tolerant rootstocks prevented Na+ reaching the shoot, illustrating the importance of the root system for salt tolerance. Unfortunately, only little is known about RSA development of crops during salt stress. In rice, rye, and maize inhibition of root length has been observed under high salinity [48].

Root Phenotyping for Drought Tolerance

Among various environmental stresses, drought is one of the serious stresses which has a significant but negative impact on crop yield. To manage drought, different tools are used to enhance crop yield under drought scenarios. Roots are the main organs to respond, perceive and maintain crop yield under drought conditions. Plant root systems are essential for adaptation against different types of biotic and abiotic stresses. Apart from genotyping quantitative traits, phenotyping has been a major challenge for plant breeders to improve abiotic stress tolerance in crop plants. It includes genetically complex traits that are extremely difficult to measure, and would be ideal to assist plant breeders for using in breeding program (Sharma et al., 2016). Roots have been evolved to be responsive and extremely adaptive to the local

environment, their morphology, growth and physiology are closely related with plant genotype and growth medium properties. For example, elongation rate and number of lateral roots can be decreased by high soil water content or soil density and this can also be associated with shoot growth reduction [7]. The type of root distribution required for different crops depends on the target environment, as abiotic stresses experienced by roots have a significant effect on the crop yield [5,71]. Strong root development is essential for survival of seedlings in soils which undergo rapid surface drying, while sufficient moisture remains available in deeper soil layers.Therefore, good understanding about plant responses to abiotic stresses might be helpful in the selection of more resistant crop varieties [12].

Conclusion and Recommendation

Root is very important plant part for plant adaptation and productivity of the agricultural crops as well as other plants by exploiting the soil resource through the uptake of water, air (oxygen) and nutrients thus, important for plant growth and development or main growth factors. Root system architecture is made up of structural features which exhibits great role in response to environmental stress, and critical to plant growth and development with sufficient root growth. Root system architecture has a central role in crop plants' response to abiotic (soil microorganisms) and abiotic stresses like water stress, mechanical impedance. Besides, the main importance of root systems include how roots cope with nutrient acquisition from the different soil environment and their ability to form mutualistic associations with key soil microorganisms. Root development is guided by environmental information that is integrated into decisions regarding how fast and in which direction to grow, and where and when to develop new lateral roots. Root morphology can be affected by nutrient availability, osmotic stress, salinity and light.

Phenotyping root is one of the drought management tools as roots are more prone to drought conditions and play a significant role in the plant's life by extracting soil resources from deeper soil layers to carry on several metabolic functions in the plant's body and its phenotyping helps to understand different root traits. Understanding interactions between roots and their surrounding soil environment is important to increase root growth, which can be improved through root phenotyping. In addition, knowing of the development and architecture of roots, as well its plasticity, holds thus great role for stabilizing the productivity under suboptimal conditions in the root environment.

Reference

1. Achard, P., Cheng, H., De Grauwe, L., Decat, J., Schoutteten, H., and Moritz, T., 2006. Integration of plant responses to environmentally activated phytohormonal signals. **Science** 311, 91–94. Doi: 10.1126/science. 1118642.

2. Amor BB, Sidney L, Shaw SL, Oldroyd GED, Maillet F, Penmetsa RV, Cook D, Long SR, Denarie J and Gough C., 2003. The NFP locus of Medicagotruncatula controls an early step of Nod factor signal transduction upstream of a rapid calcium flux and root hair deformation. **Plant Journal,**34:495–506. Doi:10.1046/j.1365-313X.2003.01743.x.

3. Bais HP, Weir TL, Perry LG, Gilroy S and Vivanco JM., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. **Annual Review of Plant Biology** 57:233–266. Doi:10.1146/annurev.arplant.57.032905.105159.

4. BaoY., Aggarwal P., Robbins N.E.,SturrockC.J., Thompson M.C., and Tan H.Q., 2014. Plant roots use a patterning mechanism to position lateral root branches toward available water. Proc. Natl. Acad. Sci. U.S.A. 111, 9319–9324. Doi:10.1073/pnas.1400966111.

5. Batey, T., 2009. Soil compaction and soil management–A review. **Soil Use Management**, 25, 335–345.

6. Benfey PN, Scheres B., 2000. Root development. **Current Biology** 10: R813–R815, Doi: 10.1016/S0960-9822(00)00814-9.

7. Bengough AG., 2003. Root growth and function in relation to soil structure, composition, and strength. In: de Kroon H, Visser EJWEcological studies, vol. 168: root ecology. Springer-Verlag, Berlin-Heidelberg, pp 151–171.

8. Bengough, A.G., McKenzie, B.M.,Hallett, P.D., Valentine, T.A., 2011. Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. **Journal of Experimental Botany**, 62, 59–68.

9. Berta G, Sampò S, Gamalero E, Massa N and Lemanceau P., 2005. Suppression of Rhizoctonia root-rot of tomato by Glomusmosseae BEG12 and Pseudomonas fluorescens A6RI is associated with their effect on the pathogen growth and on root morphogenesis. **Europian Journal of Plant Pathology**111:279–288, Doi: 10.1007/s10658-004-4585-7.

10. Borisov AY, Danilova TN, Koroleva TA, Kuznetsova EV, Madsen L, Mofett M, Naumkina TS, Nemanki TA, Ovchinnikov ES, Pavlova ZB, Petrova NE, Pinaev AG, Radutoiu S, Rozov SM, Rychagova ST, Shtark OY, Solovov II, Stougaard JS, Tikhonovich IA, Topunov AF, Tsyganov VE, Vasil'chikov AG, Voroshilova VA, Weeden NF, Zhernakov AI and Zhukov VA., 2007. Regulatory genes of garden pea (Pisumsativum L.) controlling the development of nitrogen-fixing nodules and arbuscularmycorrhiza: a review of basic and applied aspects. **Applied Biochemical Microbiology** 43:237–243, Doi: 10.1134/S00036 83807030027.

11. Casimiro I, Marchant A, Bhalerao RP, Beeckman T, Dhooge S, Swarup R, Graham N, Inzé D, Sandberg G, Casero PJ and Bennett P., 2001. Auxin transport promotes Arabidopsis lateral root initiation. **Plant Cell** 13:843–852.

12. Den Herder, G., Van Isterdael, G.,Beeckman, T., and De Smet I., 2010. The roots of a new green revolution. **Trends Plant Science** 15, 600–607. Doi: 10.1016/j.tplants.2010.08.009.

13. Den Herder, G., Van Isterdael, G.,Beeckman, T., and De Smet, I., 2010. The roots of a new green revolution. **Trends Plant Science15**, 600–607. Doi: 10.1016/j.tplants.2010.08.009.

14. Den Herder, G., Van Isterdael, G., Beeckman, T., De Smet, I. The roots of a new green revolution. **Trends Plant Science**. 2010, 15, 600–607.

15. Douglas AE., 2002. Symbiotic interactions. Oxford University Press, Oxford

16. Duan, L., Dietrich, D., Ng, C. H., Chan, P. M. Y., Bhalerao, R., and Bennett, M. J., 2013. Endodermal ABA signaling promotes lateral root quiescence during salt stress in Arabidopsis seedlings. **Plant Cell** 25, 324–341. Doi: 10.1105/tpc.112.107227.

17. Dubrovsky JG, Sauer M, Napsucialy-Mendivil S, Ivanchenko MG, Friml J, Shishkova S, Celenza J and Benkova E., 2008. Auxin acts as a local morphogenetic trigger to specify lateral root founder cells. ProcNatlAcadSci USA 105:8790–8794, Doi:10.1073/pnas.0712307105.

18. Fitter AH.,2004.Magnolioid root-hairs, architecture and mycorrhizal dependency. **New Phytology.** 164:15–16, Doi:10.1111/j.1469-8137.2004.01193.x.

19. Fitz Gerald JN, Lehti-Shiu MD, Ingram PA, Deak KI, Biesiada T and Malamy JE, 2006. Identification of quantitative trait loci that regulate Arabidopsis root system size and plasticity. **Genetics** 172:485–498. Doi: 10.1534/genetics. 105.047555.

20. Gallego-Bartolome, J., Minguet, E. G., Grau-Enguix, F., Abbas, M., Locascio, A and Thomas, S. G., 2012. Molecular mechanism for the interaction between gibberellin and brassinosteroid signaling pathways in Arabidopsis. Proc. Natl. Acad.Sci.U.S.A.109,13446–13451.Doi: 101073/pnas.1119992109.

21. Galvan-Ampudia, C. S., Julkowska, M. M., Darwish, E., Gandullo, J., Korver, R. A., and BrunoudG., 2013. Halotropism is a response of plant roots to avoidasalineenvironment.**Current Biology**23,2044–2050.Doi:10.1016/j.cub.2013. 08.042.

22. Galvan-Ampudia,C.S.,andTesterink,C., 2011. Salt stress signals shape the plant root.**Curr. Opin. Plant Bioloy,** 14,296–302, Doi:10.1016/j.pbi.2011.03.019.

23. Geng,Y.,Wu,R.,Wee,C.W.,Xie,F.,Wei,X.,Chan,P.M.Y.,2013.Aspatiotemporalunderstandingofgrowt hregulationduringthesaltstressresponsein Arabidopsis.**Plant Cell**25, 2132–2154, Doi:10.1105/tpc.113.112896.

24. GiehlRF,Gruber BD and vonWiren N., 2014. It'stimetomakechanges:modulation of root system architecture by nutrient signals. **Journal of Experimental Botany** 65: 769–778.

25. Gifford,M.L.,Banta,J.A.,Katari,M.S.,Hulsmans,J.,Chen,L. andRistovaD.,2013. Plasticity regulators modulate specific root traits in discrete nitrogen environments.PLoSGenet.9:e1003760. Doi:10.1371/journal.pgen.1003760.

26. Grilli-Caiola M., 2002. Cycad coralloid roots housing cyanobacteria. In: Seckbach J (ed) Symbiosis: mechanisms and model systems. Kluwer Academic Publishers, Dordrecht, pp 399–409.

27. Hartman Kyle and Susannah G Tringe, 2019. Interactions between plants and soil shaping the root microbiome under abiotic stress.**Biochemical Journal**, 476, 2705–2724 https://doi.org/10.1042/BCJ20180615.

28. Hodge Angela, Graziella Berta, Claude Doussan, Francisco Merchan, and Martin Crespi, 2009.Plant root growth, architecture and function. **Plant Soil** 321:153–187.Doi. 10.1007/s11104-009-9929-9.

29. Julkowska, M M., Hoefsloot, H. C. J., Mol S., Feron R., de Boer, G J., and Haring, M. A., 2014. Capturing Arabidopsis root architecture dynamics with ROOT-FIT reveals diversity in responses to salinity. **Plant Physiology**166, 1387– 1402, Doi:10.1104/pp.114.248963.

30. Jung JK and McCouch S., 2013. Getting to the roots of it: genetic and hormonal control of root architecture. **Frontiers of Plant Science** 4: 186.

31. Jung,J.K.,andMcCouchS., 2013.Gettingtotherootsofit:geneticandhormonal control of root architecture. **Front. Plant Science** 4:186,Doi: 10.3389/fpls.2013. 00186.

32. KawaDorota, Magdalena M. Julkowska, Hector Montero Sommerfeld, Anneliekter Horst, Michel A. Haring and Christa Testerink, 2016. Phosphate-Dependent Root System Architecture Responses to Salt Stress. **Plant Physiology**, Vol. 172, pp. 690–706.

33. Kellermeier F, Armengaud P, Seditas TJ, Danku J, Salt DE and Amtmann A., 2014. Analysis of the

root system architecture of Arabidopsis provides a quantitative readout of crosstalk between nutritional signals. **Plant Cell** 26: 1480–1496.

34. Khan M. A., Dorcus C.Gemenet and Arthur Villordon, 2016. Root System Architecture and Abiotic Stress Tolerance: Current Knowledge in Root and Tuber Crops. **Frontiers in Plant Science**, Volume 7 | Article 1584.

35. KoevoetsIko T., Jan HenkVenema, J. Theo. M.Elzenga and Christa Testerink, 2016. Roots Withstanding their Environment: Exploiting Root System Architecture Responses to Abiotic Stress to Improve Crop Tolerance. **Frontiers Plant Science** 7:1335,Doi: 10.3389/fpls.2016.0133.

36. Laskowski M, Biller S, Stanley K, Kajstura T and Prusty R., 2006. Expression profiling of auxin-treated Arabidopsis roots: toward a molecular analysis of lateral root emergence. **Plant Cell Physiology** 47:788–792, Doi:10.1093/pcp/pcj043.

37. Le Deunff E, Lecourt J and Malagoli P., 2016. Fine-tuning of root elongation by ethylene: a tool to study dynamic structure-function relationships between root architecture and nitrate absorption. **Annals of Botany** 118: 607–620.

38. Le Quere A, Schutzendubel A, Rajashekar B, Canback B,Hedh J, Erland S, Johansson T and Anders Tunlid A., 2004. Divergence in gene expression related to variation in host specificity of an ectomycorrhizal fungus. 12:3809–3819,Doi:10.1111/j.1365-294X.2004.02369.x.

39. Lemanceau P, Offre P, Mougel C, Gamalero E, Dessaux Y, Moënne-Loccoz Y, Berta G., 2005. Microbial ecology of the rhizosphere. In: Bloem J, Hopkins DW, Benedetti A Microbiological methods for assessing soil quality. CABI Publishing, Wallingford, pp 228–230.

40. Leyser O., 2006. Dynamic integration of auxin transport and signalling. **Current Biology** 16:R424–R433.Doi: 10.1016/j. cub.2006.05.014

41. Liska D, Martinka M, Kohanova J and Lux A., 2016. Asymmetrical development of root endodermis and exodermis in reaction to abiotic stresses. **Annals of Botany**118: 667–674.

42. Lynch, J. P., 2007. Turner review no. 14. Roots of the second green revolution. **Australia Journal of botany**, 55, 493–512.Doi: 10.1071/BT06118.

43. Lynch,J., 1995.Rootarchitectureandplantproductivity.**Plant Physiology**.109, 7–13, Doi:10.1104/pp.109.1.7.

44. M. WattA,B, J. Kirkegaard, and J. B. Passioura, 2006. Rhizosphere biology and crop productivity-a review. **Australian Journal of Soil Research**, 44, 299–317.

45. Malamy JE., 2005. Intrinsic and environmental response pathways that regulate root system architecture. **Plant Cell Environment.**28:67–77, Doi:10.1111/j.1365-3040.2005.01306.x.

46. MalamyJ.E., 2005.Intrinsicandenvironmentalresponsepathwaysthatregulate root system architecture. **Plant Cell Environment** 28, 67–77, Doi: 10.1111/j.13653040.2005.01306.x

47. Martinez-Rodriguez,M.M.,Estan,M.T.,Moyano,E.,Garcia-Abellan,J.O., Flores, F. B., and Campo J. F., 2008. The effectiveness of grafting to improve salt toleranceintomatowhenan"excluder"genotypeisusedasscion.**Environmental Experiment of Botany**63,392–401, Doi:10.1016/j.envexpbot.2007.12.007.

48. Ogawa, A., Kitamichi, K., Toyofuku, K., and Kawashima, C., 2006. Quantitative analysis of cell division and cell death in seminal root of rye under salt stress. **Plant Production Science,** 9,56–6,

Doi:10.1626/pps.9.56.

49. Petricka JJ, Winter CM, and BenfeyPN.,2012. Control of Arabidopsis root development.**Annual Review of Plant Biology** 63: 563–59.

50. Pierik R, and Testerink C 2014. The art of being flexible: how to escape from shade, salt, and drought. **Plant Physiology** 166: 5–22.

51. Pigliucci, M., 2005. Evolution of phenotypic plasticity: where are we going now? TrendsEcol.Evol.20, 481–486, Doi:10.1016/j.tree.2005.06.001

52. Popova L, van Dusschoten D, Nagel A, Fiorani F and Mazzolai B., 2016. Plant root tortuosity: anindicator ofroot pathformation insoil with differentcomposition and density. **Annals of Botany,** 118: 685–698.

53. Raaijmakers, J.M., Paulitz, T.C., Steinberg, C., Alabouvette, C. and Moenne-Loccoz, Y., 2009. The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. **Plant Soil,** 321, 341–361.

54. Rao IM, Miles JW, Beebe SE and Horst WJ.,2016. Root adaptations to soils with low fertility and aluminum toxicity. **Annals of Botany,** 118: 593–605.

55. Raven, J. A, and Edwards, D., 2001. Roots: evolutionary origins and biogeochemical significance. Journal of Experimental Botany.**Supply 1**:381-401.

56. ReadDJ and Perez-MorenoJ., 2003.Mycorrhizasandnutrientcycling in ecosystems–a journey towards relevance. **New Phytology**, 157:475–492, Doi:10.1046/j.1469-8137.2003.00704.x.

57. Rich SM, Watt M., 2013. Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. **Journal of Experimental Botany,**64: 1193–1208.

58. Sabatini S, Heidstra R, Wildwater M and Scheres B., 2003. Scarecrow is involved in positioning the stem cell niche in the Arabidopsis root meristem. **Genes Development,** 17:354–358, Doi:10.1101/gad.252503.

59. SadowskyMJ.,2005. Soil stress factors influencing symbiotic nitrogen fixation. In: Wernerand D, Newton WE Nitrogen fixation in agriculture, forestry, ecology and the environment. Springer, The Netherlands, pp 89–10.

60. Sampo S, Avidano L and Berta G., 2007. Morphogenetic effects induced by pathogenic and non-pathogenicRhizoctoniasolaniKühn strains on tomato roots. **Caryologia**, 60:1–20.

61. Schenk HJ and Jackson RB 2002b. The global biogeography of roots. **Ecological Monogr**, 73:311–328.

62. Schenk HJ and Jackson RB., 2002a. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. **Journal of Ecology, 90**:480–494 Doi:10.1046/j.1365-2745.2002.00682.x.

63. Schroeder JI, Delhaize E and Frommer WB, 2013. Using membrane transporters to improve crops for sustainable food production. **Nature,** 497: 60–66.

64. Seo M, Akaba S, Oritani T, Delarue M, Bellini C, Caboche M and Koshiba T., 1998. Higher activity of an aldehyde oxidase in the auxin-overproducing superroot1 mutant of **Arabidopsis thaliana**. **Plant Physiology,** 116:687–693,Doi: 10.1104/ pp.116.2.687.

65. Singh MB and Bhalla PL., 2006. Plant stem cells carve their own niche. **Trends Plant Science,**

11:241–246,Doi:10.1016/j.tplants. 2006.03.004.

66. Smith SE and Read DJ, 2008.Mycorrhizal symbiosis, 3rd Edn. Academic Press, London.

67. Smith, S., and De Smet, I., 2012. Root system architecture: insights from Arabidopsis and cereal crops. **Philos. Trans. R. Soc. B Biol. Sci.** 367, 1441–1452. Doi:10.1098/rstb.2011.0234.

68. Tkacz, A. and Poole P., 2015. Role of root microbiota in plant productivity. **Journal of Experimental Botany** 66, 2167–2175, https://doi.org/10.1093/jxb/erv15

69. Wachsman, G., Sparks, E. E., and Benfey P. N., 2015. Genes and networks regulating root anatomy and architecture. **New Phytology,** 208, 26–38, Doi: 10.1111/nph.13469.

70. Waines, J. G., and Ehdaie, B., 2007. Domestication and crop physiology: roots of green-revolution wheat. **Annual Botany,** 100,991–998, Doi:10.1093/aob/mcm180.

71. Wang, Y. and Frei, M., 2011. Stressed food–The impact of abiotic environmental stresses on crop quality. **Agricultural Ecosystem and Environment**, 141, 271–286.

72. Wasaya Allah, Xiying Zhang, Qin Fang and Zongzheng Yan, 2018. Root Phenotyping for Drought Tolerance: A Review. **Agronomy**, 8, 241, Doi: 10.3390/agronomy8110241.

73. White, P. J., George, T. S., Gregory, P. J., Bengough, A. G., Hallett, P. D., and McKenzie, B. M., 2013. Matching roots to their environment. **Annual Botany**. 112, 207–222, Doi:10.1093/aob/mct123.

74. Ye Heng, Manish Roorkiwal, Babu Valliyodan, Lijuan Zhou, Pengyin Chen, Rajeev K. Varshney and Henry T. Nguyen, 2018. Genetic diversity of root system architecture in response to drought stress in grain legumes- review paper. **Journal of Experimental Botany,** Vol. 69, No. 13 pp. 3267–3277, doi:10.1093/jxb/ery082.

75. Zhu, J., Ingram, P. A., Benfey, P. N., and Elich, T., 2011. From lab to field, new approaches to phenotyping root system architecture. **Current Opinion Plant Biology** 14,310–317, Doi:10.1016/j.pbi.2011.03.020.