#### Review



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# **Roots of Crops from the Window of a Forage Expert**

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Less known infos like the effect of wounding faba bean roots by high temperature, how maize roots climb up slopes, effect of cold on Medicago spp., effect of drought on soybeans, effect of active microbe species diversity in rhizosphereplant interface on complex interactions on roots, allelochemicals, axial water flow, gravitropism, fine and coarse roots, salt-responsive mechanisms, transport in root cells, phototropism, hormones, nutrient acquasition, hydrotropism and many other important physiologic processes attracting a forage crops academician's attention and interest were extracted from international studies and reviewed in this article.

### 1. Introduction

It was really interesting to read in the fresh study of Gao et al. (2020) that the forage crop alfalfa's roots are containing potential anticancer macromolecules in their tissues. Two new polysaccharides were purified from roots of alfalfa by these researchers. The conducted structural analysis showed that RAPS-1 was composed of rhamnose, xylose, arabinose, galacturonic acid, mannose and glucose. And RAPS-2 was composed of rhamnose, xylose, galacturonic acid, mannose, glucose and galactose. These two polysaccharides possesses superior antioxidant and anti-tumor activities (Gao et al., 2020). The hidden parts of forage crops and in general all crops and plants the roots - will probably help humanity to solve many accumulated problems of the world in the future. Because, it looks like the roots are living in

an environment of a highly diversified genetic soup of microorganisms. Root microbiome of model plant Arabidopsis thaliana indicates that its composition is strongly effected from location, inside section of the root, outside section of the root and soil type (Lundberg et al., 2012). Microbial diversity associated with roots of plants is enormous. Tens of thousands of species microbes are active in rhizosphere-plant interface. This complex community is referred as the second genome of the plant which is critical for plant health.

# 2. Interaction of Roots with Rhizosphere Microbes

In nature, plants are in a rich ecosystem with numerous and diverse microorganisms in the rhizosphere. Mycorrhizal fungi and nitrogen fixing symbiotic bacteria play important roles in plant performance by assisting mineral nutrition. An



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additional great progress has been made on composition of rhizospheric microbiomes and their dynamics in last decade. It is clear that plants also shape microbiome by root exudates. Bacteria developed various adaptations to survive in the rhizospheric environment (Jacoby et al., 2017).

Interaction of roots and beneficial bacteria in rhizosphere shapes the bacterial diversity. enhances plant growth and pathogen defense of plants. Plant growth promoting rhizobacteria shape cell division and differentiation to trigger changes in root system. Changing plant endogenous signaling pathways are included in this interaction. Many plant growth promoting rhizobacteria can phytohormones and effect produce plant development by molecules. Several fungi also have the same effects on roots which may be a part of a mechanisms conserved across kingdoms (Verbon and Liberman, 2016).

Plant roots determine carbon uptake and agricultural yield as a vegetation carbon pool of the World (Cabal et al., 2020). Decomposing fine roots is a large potential soil carbon source. Fine and coarse roots differ in morphology, nutrient concentrations, functions and decomposition mechanisms (Zhang and Wang, 2015). Vegetation type, fine root dynamics and rhizomorph dynamics influence soil respiration in addition to changes in temperature, light and humidity (Vargas and Allen, 2008). Plant roots are frequently experience local anaerobic stress which decreases level of ATP. But enhanced sugar delivery to the affected root part regenerate the needed ATP by anaerobic respiration (Cleland et al., 1994).

Allelochemicals released by plants play important roles in rhizosphere signalling, plant defence and stress responses. Plants use a variety of excreation mechanisms to release bioactive molecules into the rhizosphere (Weston et al., 2012).

Crop root systems can be defined by root length density, root length per soil layer of depth, sum of root length in the soil profile (total root length) or rooting depth (Ehlers et al., 1991). Winter wheat has a very productive root system. Tipically a wheat crop produce 1.5 t/ha roots with a total length of 300,000 km/ha when produced 20 t/ha total dry matter (Barraclough et al., 1991).

### **3. Interacting Network of Sensing Chemicals in Inner Tissue of Roots**

An important adaptation of plants for colonization of lands was gravitropic growth of

roots to reach water and nutrients by fixing theirself in the ground (Zhang et al., 2019). Terrestrial plant roots grow and explore underground by sensing many stimuli such as gravity, humidity, light, mechanical stimulus, temperature and oxygen. All of these stimuli are sensed in the root cap (Cassab et al., 2013). Roots exhibit gravitropism, phototropism and hydrotropism (Miyazawa et al., 2011).

The Cholodny-Went theory explains root gravitropism as a classical theory, basing on asymmetrical distribution of polar auxin transport carriers, auxin asymmetry following gravistimulation and generation of auxin response. But this classical model is inadequate to explain initiation of curvature, which occurs outside the region of most rapid elongation and is driven by differential acceleration rather than differential inhibition of elongation. Evidences indicates that there are two motors driving root gravitropism, one is not regulated by auxin (Wolverton et al., 2002).

Phytohormones regulate development and architecture of plant roots. Root cap synthesize Cytokinin (CK) to promote cytokinesis, vascular cambium sensitivity, vascular differentiation and root apical dominance. Young shoot organs produce Auxin (indole-3-acetic acid, IAA) to promote root development and induce vascular differentiation. Both CK and IAA regulate root gravitropism. CK and IAA hormones act together with ethylene to regulate lateral root initiation (Aloni et al., 2006). Whereas, strigolactones are secondary metabolites produced in plants for hormonal activity. In last decade, these compounds were shown to regulate shoot branching and leaf senescence, but now different researchers suggests that these hormones play important roles in root architecture (Matthys et al., 2016).

The plant hormone auxin regulates various developmental processes including gravitropism, root formation and vascular development (Bennett **Re-orientation** et al.. 1996). of Arabidopsis seedlings produces a fast. asymmetric release of auxin from gravity-sensing columella cells at the root apex. Gravitropic curvature in roots is mainly driven by the differential expansion of epidermal cells in response (Swarup et al., 2005). Gravity sensing in the root caps occurs mainly in the columella cells. After reorientation by the gravity field, root-cap amyloplasts sediment, that promotes the development of a curvature at the root elongation zones (Rosen et al., 1999). Plants use a special transport system made up of separate influx and efflux carriers to move plant hormone auxin between its synthesis sites to action sites (Marchant et al., 1999). Root gravitropism drives the relative distribution of plant roots in soil layers which probably influence the acquisition of soil resources such as phosphorus, too (Liao et al., 2004).

Deep root systems that extend into moist soil can significantly increase plant productivity (Watt et al., 2008). Plant root tips sense moisture gradient in soil and growing towards higher water potential named as root hydrotropism, which is needed by plants to survive when water is deficit (Chang et al., 2019). By hydrotropism, roots forage for water, a process depends on abscisic acid (ABA) (Dietrich et al., 2017). Root architecture and shoot parameters were determined under well watered and drought conditions under field conditions in three soybean cultivars by Fenta et al. (2014). A positive correlation was observed between nodule size, above-ground biomass and seed yield under well-watered and drought conditions.

As roots penetrate soil more, they enter a different environment where different resources (water and nutrients) are heterogeneously distributed in space and time. Many plant species react to this heterogeneity by changing their root development to colonize the resource-rich parts of soil. Roots have the ability to respond in complex ways by integration of multiple external signals, which may be a kind of behaviour (Forde and Walch-Liu, 2009).

Roots normally grow in dark, but if they exposed to light, roots bend to escape from light (root light avoidance) and reduce their growth (Silva-Navas et al., 2016). While gravitropism is the major tropistic response in roots, phototropism also help to orient growth of this organ in flowering plants. The interactions between tropisms can be important in determining the final form of plants and plant organs. In blue or white light, roots show negative phototropism, but red light trigger positive phototropism. In Arabidopsis, the photosensitive pigments phytochrome A (phyA) and phytochrome B (phyB) mediate this positive red-light-based photoresponse in roots (Kiss et al., 2003). Plant shoots typically grow opposite of gravity to access light, roots grow into the soil to absorb water and nutrients, but these gravitropic responses can be altered by developmental and environmental signals (Su et al., 2017). If maize roots placed on slopes in the dark, they climb up the slope. But if roots are illuminated, roots try to grow down along the gravity (Burbach et al., 2012). Based on studies on white mustard (*Sinapis alba*) seedlings, botanists thought that all roots are negatively phototropic. This "Sinapis-dogma" was changed a century ago, when it was shown that more than half of the tested 166 plant species does not behave like *S. alba* (53% displayed no phototropic response) (Kutschera and Briggs, 2012).

## 4. Root morphology

Watt et al. (2008) assessed root systems of wheat, barley and triticale in soils. 6% of deep roots were axile roots originated from the base of the embryo and 94% were branch roots. Selection for more deep penetrating axile roots and deep branches was found benefiting. Fageria (2005) conducted 10 greenhouse experiments to see the effect of root dry weight and root length on shoot yield of corn (Zea mays), rice (Oryza sativa), soybean (Glycine max), common bean (Phaseolus vulgaris) and wheat (Triticum aestivum). It was concluded that dry weight of roots is a good indicator for shoot dry matter accumulation prediction in annual crops. Shoot dry matter production efficiency (shoot dry weight/root dry weight) was in the order of common bean > soybean > wheat > upland rice > corn. Roots of legumes better in dry matter production efficiencies than cereals.

Increases in shoot density produce increases in root densities which result in an exponential decrease of erosion flow rates. Protection of the soil surface in the early plant growth stages is crucial with respect to the reduction of water erosion rates. Increasing the plant root density in the topsoil is a suitable erosion control strategy (Gyssels and Poesen, 2003). Mixtures, as an example, grass with alfalfa are preferred to alfalfa grown alone for soil and water conservation (Woods et al., 1953).

Additional to the mentioned factors, there are many other soil-related environmental factors influencing the growth and function of plant root systems like soil temperature, soil air, soil strength and soil nutrient supply to the developing roots and Quisenberry, (McMichael 1993) Soil temperature can influence roots in many ways. Under adequate soil moisture and nutrient availability, root length extension rates and root mortality rates increase with increasing soil temperature up to an optimal temperature, which changes among species. Root growth and mortality are seasonal in plants with a flush of growth in spring (Pregitzer et al., 2000). Low temperature is

a main factor limiting crop growth, development and production (Cui et al., 2019). Enhancement of cold tolerance is an important aspect in breeding forage legumes in view of increasing interest in extending the cultivation of these crops (Ratinam et al., 1994). Cold and low fertility of growing conditions are often associated with root adjustments to increase capture of deficient nutrient resources, but it is unclear if plants produce different type of fine roots in response to these conditions (Zadworny et al., 2017). Soil temperature influence not just its function but also above ground tissues of plants, too. In a study, it was observed that damaging of horse bean (Vicia faba L. minor) roots via rapid heating to above 80°C, induced an electric wave to the leaves within 25 s. This wave was then stimulated shoot respiration at a rate of up to 140-160% of its initial value within 70-80 s after the roots were heated (Filek and Kościelniak, 1997). Four plants, Poa sphyondylodes, Bromus inermis, Bromus sinensis and Elymus nutans were investigated during winter and spring for enzymatic activities by sampling approximately at 15 days interval during autumn and spring by Lian et al. (2001). Leakage of ions and enzymatic activities were found declined from September with the drop of temperature.

Salinity is a major stresses limiting agricultural productivity globally which roots are the primary site for salinity perception to transmit this signal to the shoot for salt response of the plant (Zhao et al., 2013). Adventitious roots form from any nonroot tissue during normal development (crown roots on cereals) and in response to stress (flooding, nutrient deprivation and wounding). They are also economically important (for cuttings and food production) (Steffens and Rasmussen, 2016).

Uptake of soil resources by root system is important but complex and challenging problem for agriculture, ecology and plant biology. Roots ineract with other organisms (mycorrhizas and Nfixing bacteria), release exudates to modify rhizosphere, uptake and transport nutrients as research interests by plant biologists. Improved understanding of the functional root architecture is required for efficient acquisition of soil resources and adaptation of plants to suboptimal soil conditions (Lynch, 1995).

### 5. Conclusions

Compared to huge research records based on aboveground plant organs, there is very little information subjecting roots and microbes relaated to them instead of its importance. Technological, methodological and sensor advances might be scanned in details to find more novel single or unified techniques and instruments to study roots and rhizosphere more fast and accurate to discover this hidden world. Compared to gaseous surrounding environment of aerial parts of crops, solid rhizosphere has a very huge contact surface area with plant cells and membranes. Rhizosphere also hosts ultra high diversity of microbes and chemicals from different groups. Hydroponic and aeroponic studies also might be searched and harmonised to develop a new approach to improve yields during these studies in parallel.

### References

- Aloni, R., Aloni, E., Langhans, M. and C.I. Ullrich. 2006. Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism. Annals of botany. 97(5), 883-893.
- Barraclough, P. B., Weir, A. H. and H. Kuhlmann. 1991. Factors affecting the growth and distribution of winter wheat roots under UK field conditions. In Developments in agricultural and managed forest ecology. (Vol. 24, pp. 410-417). Elsevier.
- Bennett, M. J., Marchant, A., Green, H. G., May, S. T., Ward, S. P., Millner, P. A. and K. A. Feldmann 1996. Arabidopsis AUX1 gene: a permease-like regulator of root gravitropism. Science. 273(5277), 948-950.
- Burbach, C., Markus, K., Zhang, Y., Schlicht, M. and F. Baluška. 2012. Photophobic behavior of maize roots. Plant signaling and behavior. 7(7), 874-878.
- Cabal, C., Martínez-García, R., Aguilar, A. de C., Valladares, F. and S. W. Pacala. 2020. The exploitative segregation of plant roots. Science. 370(6521), 1197-1199..
- Cassab, G. I., Eapen, D. and M. E. Campos. 2013. Root hydrotropism: an update. American journal of botany. 100(1), 14-24.
- Chang, J., Li, X., Fu, W., Wang, J., Yong, Y., Shi, H. and J. Li. 2019. Asymmetric distribution of cytokinins determines root hydrotropism in Arabidopsis thaliana. Cell research. 29(12), 984-993.
- Cleland, R. E., Fujiwara, T. and W. J. Lucas. 1994. Plasmodesmal-mediated cell-to-cell transport

in wheat roots is modulated by anaerobic stress. Protoplasma. 178(1), 81–85.

- Cui, G., Chai, H., Yin, H., Yang, M., Hu, G., Guo, M. and P. Zhang. 2019. Full-length transcriptome sequencing reveals the low-temperaturetolerance mechanism of Medicago falcata roots. BMC plant biology. 19(1), 1-16.
- Dietrich, D., Pang, L., Kobayashi, A., Fozard, J. A., Boudolf, V., Bhosale, R. and M. J. Bennett. 2017. Root hydrotropism is controlled via a cortex-specific growth mechanism. Nature plants. 3(6), 1-8.
- Ehlers, W., Hamblin, A. P., Tennant, D. and R. R. Van der Ploeg. 1991. Root system parameters determining water uptake of field crops. Irrigation Science. 12(3), 115-124.
- Fageria, N. K. 2005. Influence of dry matter and length of roots on growth of five field crops at varying soil zinc and copper levels. Journal of plant nutrition. 27(9), 1517-1523.
- Fenta, B. A., Beebe, S. E., Kunert, K. J., Burridge, J. D., Barlow, K. M., Lynch, J. P. and C. H. Foyer. 2014. Field phenotyping of soybean roots for drought stress tolerance. Agronomy. 4(3), 418-435.
- Filek, M. and J. Kościelniak. 1997. The effect of wounding the roots by high temperature on the respiration rate of the shoot and propagation of electric signal in horse bean seedlings (*Vicia faba* L. minor). Plant Science. 123, 39–46.
- Forde, B. G. and P. Walch-Liu. 2009. Nitrate and glutamate as environmental cues for behavioural responses in plant roots. Plant Cell and Environment. 32(6), 682–693.
- Gao, P., Bian, J., Xu, S., Liu, C., Sun, Y., Zhang, G. and X. Liu. 2020. Structural features, selenization modification, antioxidant and anti-tumor effects of polysaccharides from alfalfa roots. International journal of biological macromolecules. 149, 207-214.
- Gyssels, G. and J. Poesen. 2003. The importance of plant root characteristics in controlling concentrated flow erosion rates. Earth Surface Processes and Landforms: The Journal of the British Geomorphological Research Group. 28(4), 371-384.
- Jacoby, R., Peukert, M., Succurro, A., Koprivova, A. and S. Kopriva. 2017. The role of soil microorganisms in plant mineral nutritioncurrent knowledge and future directions. Frontiers in plant science. 8, 1617.
- Kiss, J. Z., Correll, M. J., Mullen, J. L., Hangarter, R. P. and R. E. Edelmann. 2003. Root phototropism: how light and gravity interact in shaping plant form. Gravitational and Space Biology Bulletin: Publication of the American Society for Gravitational and Space Biology. 16(2), 55-60.

- Kutschera, U. and W. R. Briggs. 2012. Root phototropism: from dogma to the mechanism of blue light perception. Planta. 235(3), 443-452.
- Lian, Z. R., Lin, Z. H. and C. G. Dong. 2001. Seasonal changes in enzymatic antioxidant system in roots of alpine perennial forage grasses related to freezing tolerance. Acta Ecologica Sinica. 06.
- Liao, H., Yan, X., Rubio, G., Beebe, S. E., Blair, M. W. and J. P. Lynch. 2004. Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. Functional Plant Biology. 31(10), 959-970.
- Lundberg, D. S., Lebeis, S. L., Paredes, S. H., Yourstone, S., Gehring, J., Malfatti, S., T. G. del. Rio. 2012. Defining the core Arabidopsis thaliana root microbiome. Nature. 488(7409), 86–90.
- Lynch, J. 1995. Root Architecture and Plant Productivity. Plant Physiol. 109.
- Marchant, A., Kargul, J., May, S. T., Muller, P., Delbarre, A., Perrot Rechenmann, C. and M. J. Bennett. 1999. AUX1 regulates root gravitropism in Arabidopsis by facilitating auxin uptake within root apical tissues. The EMBO journal. 18(8), 2066-2073.
- Matthys, C., Walton, A., Struk, S. M., Stes, E., Boyer, F. D., Gevaert, K. and S. Goormachtig. 2016. The Whats, the Wheres and the Hows of strigolactone action in the roots. Planta. 243(6), 1327–1337.
- McMichael, B. L. and J. E. Quisenberry. 1993. The impact of the soil environment on the growth of root systems. Environmental and experimental botany. 33(1), 53-61.
- Miyazawa, Y., Yamazaki, T., Moriwaki, T. and H. Takahashi. 2011. Root tropism: its mechanism and possible functions in drought avoidance. Advances in Botanical Research. 57, 349-375.
- Pregitzer, K. S., King, J. S., Burton, A. J. and S. E. Brown. 2000. Responses of tree fine roots to temperature. New Phytologist. 147(1), 105-115.
- Ratinam, M., Abd el Moneim, A. M. and M. C. Saxena. 1994. Variations in sugar content and dry matter distribution in roots and their associations with frost tolerance in certain forage legume species. Journal of Agronomy and Crop Science. 173(5), 345-353.
- Rosen, E., Chen, R. and P. H. Masson. 1999. Root gravitropism: a complex response to a simple stimulus. Trends in plant science. 4(10), 407-412.
- Silva-Navas, J., Moreno-Risueno, M. A., Manzano, C., Téllez-Robledo, B., Navarro-Neila, S., Carrasco, V. and J. C. Del Pozo. 2016. Flavonols mediate root phototropism and growth through regulation of proliferation-to-

differentiation transition. The Plant Cell. 28(6), 1372-1387.

- Steffens, B. and A. Rasmussen. 2016. The Physiology of Adventitious Roots. Plant Physiology. 170(2), 603–617.
- Su, S. H., Gibbs, N. M., Jancewicz, A. L. and P. H. Masson. 2017. Molecular mechanisms of root gravitropism. Current Biology. 27(17), R964-R972.
- Swarup, R., Kramer, E. M., Perry, P., Knox, K., Leyser, H. O., Haseloff, J. and M. J. Bennett. 2005. Root gravitropism requires lateral root cap and epidermal cells for transport and response to a mobile auxin signal. Nature cell biology. 7(11), 1057-1065.
- Vargas, R. and M. F. Allen. 2008. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytologist. 179(2), 460–471.
- Verbon, E. H. and L. M. Liberman. 2016. Beneficial microbes affect endogenous mechanisms controlling root development. Trends in plant science. 21(3), 218-229.
- Watt, M., Magee, L. J. and M. E. McCully. 2008. Types, structure and potential for axial water flow in the deepest roots of field grown cereals. New Phytologist. 178(1), 135-146.
- Weston, L. A., Ryan, P. R. and M. Watt. 2012. Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. Journal of Experimental Botany. 63(9), 3445–3454.
- Wolverton, C., Ishikawa, H. and M. L. Evans. 2002. The kinetics of root gravitropism: dual motors and sensors. Journal of Plant Growth Regulation. 21(2), 102-112.
- Woods, J. E., Hafenrichter, A. L., Schwendiman, J. L. and A. G. Law. 1953. The effect of grasses on yield of forage and production of roots by alfalfa-grass mixtures with special reference to soil conservation. 1. Agronomy Journal. 45(12), 590-595.
- Zadworny, M., McCormack, M. L., Żytkowiak, R., Karolewski, P., Mucha, J. and J. Oleksyn. 2017. Patterns of structural and defense investments in fine roots of Scots pine (*Pinus sylvestris* L.) across a strong temperature and latitudinal gradient in Europe. Global Change Biology. 23(3), 1218–1231.
- Zhang, X. and W. Wang. 2015. The decomposition of fine and coarse roots: their global patterns and controlling factors. Scientific Reports. 5(1), 9940–9940.
- Zhang, Y., Xiao, G., Wang, X., Zhang, X. and J. Friml. 2019. Evolution of fast root gravitropism in seed plants. Nature communications. 10(1), 1-10.

Zhao, Q., Zhang, H., Wang, T., Chen, S. and S. Dai. 2013. Proteomics-based investigation of saltresponsive mechanisms in plant roots. Journal of Proteomics. 82, 230-253.