PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol x(x): xx–xx
https://doi.org/10.14719/pst.4878

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REVIEW ARTICLE

Exploring root system architecture and its importance in solanaceous vegetables: A review

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OPEN ACCESS

ARTICLE HISTORY
Received: 30 August 2024
Accepted: 27 October 2024
Available online
Version 1.0 : 22 December 2024

Check for updates

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

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Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

CITE THIS ARTICLE
Indhumathi K, Sangeetha M, Saravanan KR, Deivamani M, Vennila MA, Sivakumar K. Exploring root system architecture and its importance in solanaceous vegetables: A review. Plant Science Today (Early Access). https://doi.org/10.14719/pst.4878

Abstract

The root system architecture (RSA) in solanaceous vegetables has become an exciting area of research, uncovering complex networks essential for plant development, nutrient absorption and resistance. This review delves into the comprehensive scope of research surrounding roots, shedding light on their dynamic nature and implications for agricultural practices. The Solanaceae family comprises various vegetables, including tomatoes, potatoes, peppers and eggplants, each with distinct root systems. Innovative methodologies have uncovered the complex and adaptive nature of these root systems. Roots of solanaceous vegetables have plasticity, reflecting their capacity to adjust to soil conditions, nutrient availability and stressors. From the taproot structures in potatoes to the fibrous nature of tomato roots, this review synthesizes findings to elucidate the mechanisms behind root development and responses to environmental stimuli. Furthermore, the symbiotic associations between solanaceous crop roots and soil microorganisms have attracted significant interest. Understanding the intricate interactions between root exudates, microbial communities and nutrient cycling opens avenues for sustainable agriculture, emphasizing the role of root architecture in fostering beneficial soil ecosystems. The implications of many research studies on RSA extend beyond academic interest and play a role in improving crop productivity. Understanding root system architecture enables breeders and agronomists to create cultivars with superior root characteristics, hence enhancing crop output, water-use efficiency and resilience to abiotic challenges. Nonetheless, certain gaps persist, requiring additional investigation. A deeper investigation into the molecular mechanisms governing root development in solanaceous vegetables, particularly under changing climate scenarios is important for future research.

Keywords

crop productivity; root stock; root system architecture; solanum; stress tolerance

Introduction

Roots play crucial roles in supporting plant growth and overall vitality. They facilitate the uptake of vital nutrients and water necessary for plant development, act as storage reservoirs for essential compounds, provide stability by anchoring plants in the soil and serve as interfaces for interactions with both harmful and beneficial organisms in the rhizosphere. Moreover, root growth and development adaptability in response to varying soil moisture and nutrient levels offer promising avenues for leveraging natural diversity to identify advantageous root traits that can significantly bolster plant productivity in agricultural settings (1-4). The comprehensive arrangement of all root components within a specific growth environment is collectively termed root system architecture (RSA). This RSA framework is highly dynamic and is profoundly influenced by external factors like soil moisture, temperature, nutrient availability and soil pH. Additionally, the diverse microbial communities surrounding roots profoundly influence how plants perceive and react to their surroundings (5, 6). Various root attributes equip plants with the capacity to respond dynamically, acclimate and flourish in diverse environmental conditions.

The grafting of vegetables has gained importance among horticultural scientists due to its robustness in plant growth, yield and tolerance against the incidence of pathogens, salinity and moisture stress. In solanaceous vegetables, a decrease in infection by the disease-causing organisms is reported due to grafting on various rootstocks (7-11). The ecological vulnerabilities of vegetables necessitate grafting with closely related species exhibiting relative tolerance. The RSA is altered due to environmental factors (12, 13). While grafting, the response behavior to salt tolerance in grafted plants is related to RSA. Root length, density, root hairs and root surface area determine salt tolerance. This is attributable to its function in ion and water absorption, which are the primary traits contributing to salt tolerance in grafted plants. However, in contrast to the substantial research on above-ground and physiological aspects, the relationship between RSA and abiotic stress tolerance requires further investigation (14). A stronger root system can support a long-season crop which is a priority. Hence, one important criterion is rootstock breeding for Solanaceous crops (8). The roots of tomato seedlings showed plasticity to salt stress (15). There is a higher level of correlation between root characteristics and the shoot parameters which shows the possible role of root architecture on salt stress tolerance. The suitable rootstocks for solanaceous vegetables are *Solanum torvum* Sw*, S. xanthocarpum* Sw*, S. mamosum* L*, S. integrifolium* Poir*, S. sisymbrifolium* Lam.*, S. toxicarium* Rich.*, and S. mammosum* L. (16-18).

Research on RSA in Solanaceous vegetables has gained considerable attention due to its significant implications for crop productivity, nutrient uptake, water efficiency and resilience to environmental stressors. Solanaceous vegetables, including tomatoes, potatoes, peppers and eggplants, exhibit diverse root structures that influence their adaptation to various soil conditions. This review gives an overview and review of studies focusing on RSA in these vegetables. Salient characteristics of Solanaceous vegetables, along with the details about RSA, are described in the following section:

Tomatoes (Solanum lycopersicum L.)

Root Morphology and Characteristics : Tomatoes have a fibrous root system characterized by both primary and adventitious roots. Many studies have been undertaken to assess the influence of root traits like root length, density, branching patterns, and depth on nutrient acquisition, particularly in phosphorus- and water-limited environments (15). Investigations into the genetic basis of root architecture have identified key genes and molecular pathways controlling root development. This knowledge has enabled the development of tomato varieties with improved root traits, enhancing their resilience and productivity under challenging conditions.

Potatoes (Solanum tuberosum L.)

Tuber Development : Root architecture studies in potatoes often focus on the relationship between root system development and tuber formation. Understanding the balance between root growth and tuber initiation is critical for optimizing yield (4). Research has explored potato root responses to biotic and abiotic stresses, including drought, pathogens and soil-borne diseases. Enhanced understanding of root traits related to stress tolerance aids in breeding efforts to develop resilient potato varieties.

Peppers (Capsicum spp.)

Root Efficiency : Investigations emphasize root traits associated with water and nutrient uptake efficiency. Studies often aim to identify genotypes with superior root systems capable of adapting to limited water availability and various soil types (13). Research also focuses on understanding the interactions between pepper roots and soil microbiota, elucidating how these interactions impact plant health and productivity.

Eggplants (Solanum melongena L.)

Root Structure and Soil Adaptation : Studies explore root traits governing eggplant adaptation to different soil conditions, such as saline soils or soils with varying moisture levels. Understanding root plasticity aids in developing varieties resilient to soil-related stressors. Investigations delve into the rhizosphere dynamics around eggplant roots, studying the influence of root exudates on soil microbial communities and nutrient availability (18).

In conclusion, studies on RSA in solanaceous vegetables cover a wide range of topics, from identifying genetic pathways controlling root development to comprehending physical features. These studies hold immense promise in developing crops with improved root systems, contributing to sustainable agriculture by enhancing productivity and resilience in diverse environmental conditions. However, ongoing research efforts remain crucial to further exploit the potential of root architecture studies for Solanaceous vegetable improvement.

Review of the earlier works

In recent years, there have been works related to RSA and their response to various rhizosphere environments (Fig. 1). There is variation among the species and genotypes in the root system characteristics and their response to soil features (19). Investigating root morphology and plasticity when faced with environmental changes helps to select genotypes that can manage abiotic stresses (20). Modification in root systems to their immediate environment for resource tapping and avoiding pathogen infestations can be exploited to a greater extent (21). Rootstocks hold considerable importance in adapting to soil-related factors, including water deficiency,

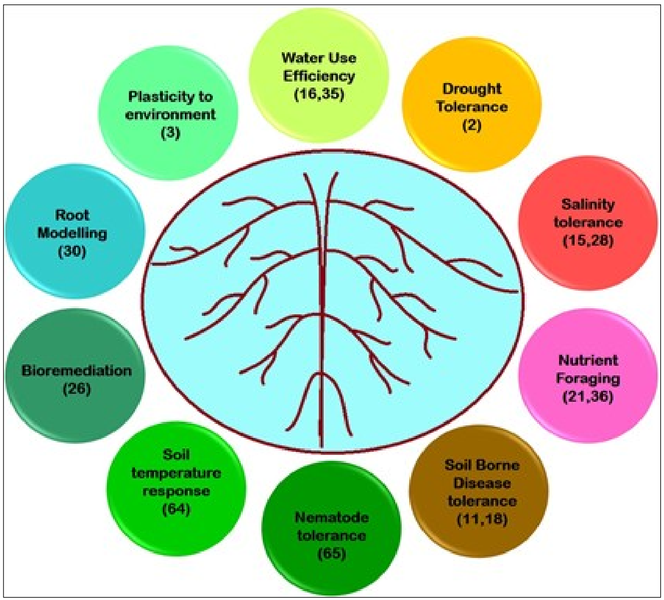

Fig. 1. Aims of root system architecture study by various workers.

high salinity, alkaline soils and disease susceptibility (19). There is a difference in the RSA of soybeans grown in the field and hydroponically. Soil characteristics have a strong influence on RSA. Root growth, growth period and rhizosphere size are restricted under controlled conditions than in field experiments. The RSA is influenced by plant genetics, soil environment characteristics and rhizosphere size (22).

The methods of high throughput root architectural phenotyping for beans and cowpeas were developed (23). The author mentioned that qualitative evaluation of the architecture of root grown up plants is tedious under field conditions. This type of work helps in selecting the useful root architectural phenotypes. Harvesting of roots is done at flowering time as the assessment at flowering reduces the differences in the phenology of root development (24). The root phenotypes are important as promising breeding targets for improving nutrient uptake and suggest the root system ideotypes for the efficient utilization of major and secondary nutrients (25). Root phenomic link with nutrient acquisition and utilization in amaranths has been studied (26). There is a positive correlation between the root traits and nutrient uptake. Even then, the traits are root length, root diameter and root volume. The topology and other structural characteristics and their interactions were not taken into account. The key function of the unseen partner, the root system of the rootstock, is still not understood. Through grafting, both scion and rootstock can influence the salt tolerance of grafted plants (27). There is flexibility in root growth and its traits in response to salinity (28).

Hydrogel-based transparent soil was used to mimic soil experiments while studying the root traits (29). The 3D imaging techniques are also being used for root phenotyping. There is software's where complete RSA viz. Smart root, Root Nav, Winrhizo, DIRT, etc. are used in root phenotyping. Though there are challenges in evaluating plant root systems, it is very important to elucidate RSA to understand plant's response to changing environments (30). Various methods for root phenotyping have been used by several works, both destructive and non-destructive (31). It is necessary to decide the experimental conditions before selecting a method. Soil core sampling is a classical root phenotyping method though it furnishes limited root system data (32). Shovelomics is being used for high throughput root phenotyping, especially in maize. It is digging out the root system washing and measuring numerous root traits for the larger population.

It is difficult to mimic the soil conditions artificially, and hence, the most common practice for root phenotyping is soil-filled tubes, flat cartridges and cultivation in regular soil (33). The author had given the docket of the software packages available for the root phenotyping experiments. It was reported that grafted tomatoes on rootstocks respond better to variations in soil salinity conditions (34). However, the authors have concentrated on shoot phenomics. The role of rootstocks is yet to be studied. The selection of grafting combinations with deep and vigorous root systems is emphasized (35). However, the use of roots as selection criteria is seldom followed. Rhizosphere is often simplified as the soil area surrounding the roots. However, it is an integration at the root system level and it is completed due to the geometry, temporal dynamics and heterogeneous aspects of roots. The root system complexity is due to its geometry, physiology and anatomy, influenced by various heterogeneous, environmental and soil factors.

The change in the RSA of wheat germplasm has been studied (36). The results revolved significant correlation of the root traits such as primary root length, total root length, total root surface area and root average diameter in the limited and non-limited phosphorous availability situation. They also report that in India, there is limited information on the RSA of what germplasm is being used in the breeding program. The rooting pattern of *Vetiveria* species *viz. V. nigritana*, *V. nirmondis*. *V. zizanioides* was studied and variation was found (37). The roots of *V. zizanioides* are much longer and thicker with less secondary branching and lesser lateral fibrous roots. The focus of that study is the analysis of root ideotypes for essential oil extraction or for environmental concerns.

The availability of potassium influences root architecture under moisture stress (38). The root projected area, maximum width and width-to-depth ratio reduced under water stress and K availability influenced the root depth under water stress. It was also found that the root gradient towards depth is inclined in reaction to water than to potassium. The implication of moisture stress on the RSA of cotton is well explained (39). They also reported the methods for studying cotton root systems under lab, field and greenhouse conditions.

Methods for Phenotyping Root Traits

Phenotyping root traits in the field poses significant challenges, limiting the comprehensive assessment of RSA features and their utility in breeding selection. The conventional field-based techniques are both labor-intensive and necessitate plot destruction for sample collection. Furthermore, soil heterogeneity across different field sites can substantially influence the RSA of field-grown plants, confounding genetic and environmental interactions. To overcome these limitations, alternative approaches involve assessing roots in plants cultivated under controlled conditions. Methods employed to evaluate plant root architecture must accurately depict root growth, mitigate the impact of environmental factors altering root development, possess sufficient throughput for phenotyping numerous genotypes routinely screened in breeding programs and facilitate the translation of root phenotypes from controlled environments to field conditions. Several software tools, such as RootScan, DART, GiARoots, RootNav, Rhizo, Root Reader, Root System Analyzer, Root Reader 3D and RooTrak, have been developed to capture root images and extract quantitative data (40-48).

Analysis of root images is pivotal for root phenotyping strategies; the choice of plant cultivation method significantly influences the effectiveness of image analysis tools. The selection of the plant cultivation system decides whether the objective is to answer fundamental root developmental queries or to conduct high-throughput root trait selection for breeding purposes. For studying root development, methods often involve gel-based media, soil-filled containers and rhizotrons offering controlled conditions to analyze RSA features and genetic-environmental interactions. Conversely, high-throughput root selection methods range from assessing seedlings on germination paper to excavation of field-grown plants. Each method possesses distinct advantages and disadvantages. For instance, gel-based systems permit non-destructive real-time imaging but might lack physiological relevance. Soil-filled containers allow more realistic root imaging but have limitations in throughput and resolution. Laboratory and greenhouse-based methods such as GLO-Roots, X-Ray Computed Tomography and clear pots offer controlled environments but lack the interspecific competition seen in field conditions (Table 1). Meanwhile, methods like shovelomics, soil coring and rhizolysimeters maintain physiological relevance but involve destructive assays. Ultimately, the choice of plant culturing method for root imaging depends on various factors, including the specific root trait of interest, sampling timescales, infrastructure capabilities and associated costs.

Prospects

Reports of previous works showed that grafting is essential for overcoming salinity stress tolerance in Solanaceous vegetables. Understanding the role of the root system of the rootstocks morphologically, anatomically and physiologically under salinity is essential for further rootstock breeding. The studies in root systems are mostly physiological and anatomical and hence, the morphological changes, i.e., root phenomics, have to be studied. Studies on the root characteristics are done mostly in cereals and staple crops and not in horticultural crops (Fig. 2). Grafting has been done to enhance the efficiency of the plant response for nutrient use efficiency, biotic and abiotic stress, crop productivity and crop duration. Abundant studies have been carried out on the shoot systems traits such as plant height, branching, leaf characteristics, flowering phenology and fruit characteristics, i.e. both morphologically and physiologically. However, root system characteristics such as root length, root spread, root volume, topology and growth dynamics have not been focused on enough. Hence, it is very essential to study the root phenes of the solanaceous vegetables in comparison to the rootstocks, which is the basis for further rootstock breeding programmes.

Workers have reported that the solanaceous rootstocks used for grafting showed relative tolerance to salinity compared to crops on their roots (49-52). But it is expressed in terms of growth, yield and physiological parameters of the shoot and rarely that of roots. It is expected that this increased tolerance is due to the rootstocks and their role needs to be investigated. Research indicates that the wild solanaceous rootstock population has heritable differences in root phenes to mitigate salinity stress. (53). The data on the root geometry, viz., position of root segments in rhizosphere, root system depth, width and volume root length, number of different types of roots and the root dynamics of the wild *Solanum* rootstocks shall be obtained. This will help assess the robustness/plasticity of the rootstocks used for the grafting of solanaceous vegetables.

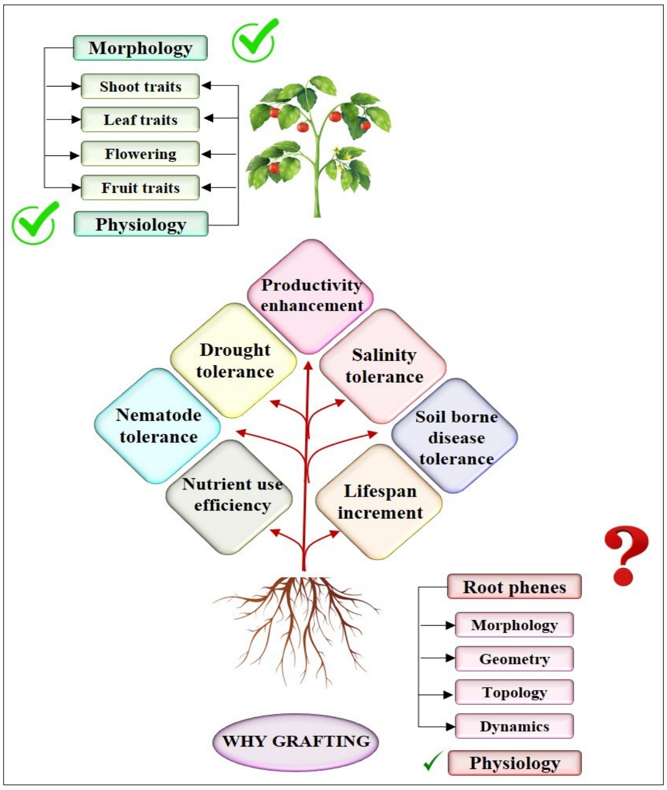

Fig. 2. Research gaps in grating studies of Solanaceous vegetables.

Table 1. Technology & software used for Root system architecture study

Technology	Software used	Crops	Reference
Mini rhizotron	GiA Roots EZ-Rhizo	Potato Tomato	(56) (58)
Rhizotubes	DART Scanner & physical measurement	Chillies & *Solanum* sp. Brinjal	(59) (60)
Root columns	Win RHIZO	Tomato	(61)
Aeroponics	Win RHIZO	Potato	(62)
Field-level root excavation	Physical measurement	*Solanum carolinense* L.	(63)
Field study	X-ray micro-computed technology	Tomato	(64)

This will be helpful in the identification of the root phenotypes of wild *Solanum* species with improved stress tolerance which will intensify the scope of grafting in Solanaceous vegetables. By identifying root phenes involving various morphological, geometrical and topological characteristics of the root system and its dynamics, we will have a clear idea of the plasticity or robustness of the root system. This will be helpful in the identification of characteristics improving the tolerance or resistance of the particular genotype in response to any disease incidence, best infestation, salinity, drought, etc. Correlation studies in response to stress will help in developing 'Root ideotypes', which can be a criterion for the selection of comparatively more efficient rootstocks in the seedling stage itself reducing the time taken for the breeding programme. This will be the primary step in the roots of the breeding program and also lead to the development of root ideotypes which will be the next milestone in the production of solanaceous vegetables (Fig. 3).

Commercially important solanaceous vegetables, such as potatoes, tomatoes, eggplants and chillies, are subject to a variety of biotic and abiotic stressors that hinder their successful production (54). Untiring works were done in overcoming the limiting factors and one of the major and viable technologies being commercially exploited is grafting. The rootstocks are proven to be successful in overcoming problems such as root nematode, soil-borne diseases, drought and salinity. Salinity is a major limiting factor for the glycophytes will perform better under lesser salt concentrations (55). Most of the studies concentrate on the above-ground traits, such as shoot growth and yield parameters, in searching for sources of salinity tolerance. Recent works focus on the nutrient uptake efficiency of roots based on their dynamics (56). Knowledge about the dynamics and architecture of the root system is very important for improving water efficiency with future limited water resources as it is based on the root traits (57).

Understanding the biology of the root system is essential for the efficient utilization of resources, as it is the key player in sustaining crop productivity, which is within the limits of various biotic and abiotic factors. In recent decades, extensive work has been done in exploring the RSA of crops and being used in the breeding programme. But the work on the RSA of the horticulture crops is comparatively meagre, especially in India. It becomes crucial to study the root characteristics to exploit them to the maximum extent in breeding programs aiming at resource acquisition and the efficient trade-off between the rootstock and scion.

The scope of vegetable grafting will be extended by the chances of crop improvement through rootstock breeding. Correlation studies in response to salinity will help in developing 'Root ideotypes', which can be a criterion for the selection of comparatively more efficient rootstocks in the seedling stage itself, reducing the time taken for the breeding program.

Conclusion

This article on the RSA of solanaceous vegetables revealed that roots are essential for increasing crop yield and for comprehending the intricate interactions between environmental and genetic variables that shape root characteristics. This exploration of RSA holds immense significance, particularly in the context of plant breeding and agricultural practices. The challenges associated with phenotyping root traits in the field have led to the development of alternative approaches involving controlled cultivation conditions and advanced imaging techniques. These methods, facilitated by innovative software tools and standardized data formats, offer avenues for comprehensive root trait analysis, aiding in the selection of desirable traits for breeding programs. The choice of plant cultivation methods, whether in controlled environments or field conditions, significantly impacts the accuracy and relevance of root imaging and subsequent analysis. Each method presents unique advantages and limitations, emphasizing the importance of selecting an approach aligned with the specific goals of the study, whether it is useful for understanding fundamental root developmental processes or conducting high-throughput trait selection for breeding purposes. As Solanaceous vegetables play a crucial role in global agriculture and food security, understanding and optimizing their root systems is fundamental for improving crop productivity, resilience to environmental stresses and resource utilization efficiency. The collective efforts in exploring and deciphering the complexities of RSA in these plants pave the way for enhanced crop management practices and the development of resilient varieties tailored to meet the challenges of a changing environment. Continued research, collaboration and innovation in the realm of root system studies will be pivotal in unlocking the full potential of Solanaceous vegetables, ensuring sustainable agricultural practices and addressing the evolving demands of a growing global population.

Acknowledgements

The authors are thankful to KVK, Papparapatty and the Directorate of Extension Education, Tamil Nadu Agricultural University, Coimbatore, for the technical support.

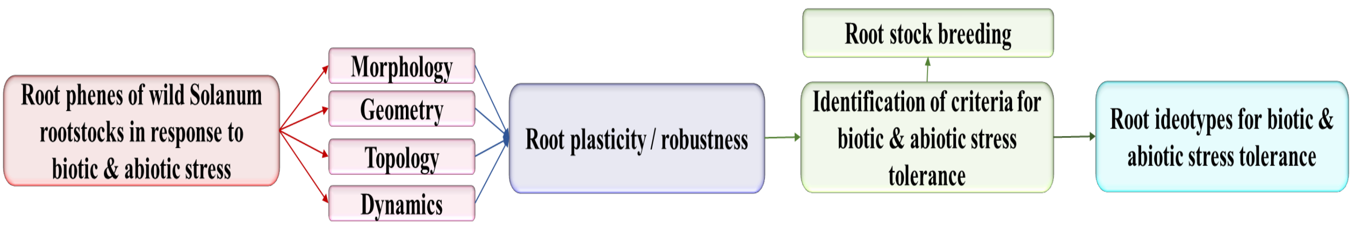

Fig. 3. Future thrust in studying the roots system architectural traits.

Authors' contributions

KI contributed to the collection of articles and formulated the concept. MS prepared the draft for the review. KRS and MD compiled the references. MAV and KS corrected and revised the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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