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Adaptive Mechanisms of Root System of Rice for Withstanding Osmotic Stress

Afsana Hannan, Md. Najmol Hoque, Lutful Hassan and Arif Hasan Khan Robin

Abstract

Being one of the major cereal crops, rice has a great effect on food security of the world population. But worldwide rice production faces severe threat due to a combination of factors like uncontrolled human rise, limited agricultural land and increasing environmental stresses. Coping with this situation is an urgent call for meeting the challenge. For overwhelming rice production by battling with this condition, scientists and researchers try their best to develop such rice varieties which can adapt to adverse climatic conditions. But, the majority of the research efforts are given on above ground parts of rice to make it stress tolerant. Root, one of the major parts of plant, remains unnoticed although it has immense possibility of adaptation under stress conditions. Fruitful and efficient utilization of limited resources are possible through healthier and competent root systems. Selection and breeding of rice genotypes with extensive root systems may contribute to more efficient use of soil nutrient resources and this ultimately influences the yield stability of rice.

Keywords: *Oryza sativa* L., root system, osmotic stress, adaptive mechanisms, lateral roots

1. Introduction

Rice is such an agricultural commodity that covers the third-highest worldwide production making it one of the most important cereal crops [1]. With its wide geographic distribution extending from 50°N to 35°S, rice is expected to be the most vulnerable cultivated crop to changing climates in future [2, 3]. Rice production is dwindled mainly because of biotic and abiotic stresses due to the complexity of interaction between the stress factors and various molecular, biochemical and physiological phenomena affecting plant growth and development [4, 5]. To battle with these situations, development of adaptive rice varieties is one of the best strategies. Since aboveground parts are often taken into consideration for making stress tolerant varieties, root study remains backward in this aspect. Roots, the hidden portion of the plant have not yet been much focused. Because exploring the root traits of the plant are much more difficult compared to its above-ground traits. But when it comes to the fact of studying the optimal developmental plasticity system and characteristic features of plant growth, the root system is given the first priority [6].

Root system is the site of water and nutrient uptake from the soil, a sensor of abiotic and biotic stresses, and a structural anchor to support the shoot. The root system communicates with the shoot, and the shoot in turn sends signals to the roots [7]. Soil type, moisture and nutrients all strongly influence the architecture of the root system [8–10]. Recently it has been emphasized that root architectural traits play a decent role for the adaptation of crop varieties under different abiotic stresses [11, 12]. Root interaction with changing environment is a complex phenomenon that differs with genotypes and intensity of stress [13–17]. For that, different species and also genotypes under the same species may respond contrarily under stress conditions and show different magnitudes of tolerance or susceptibility to stress. These diversities can be exploited by plant breeders to improve stress tolerance in plants. Scientists assume that selection for yield will indirectly select for varieties with the optimum root system. But the fact is, more directed selection for specific root architectural traits could enhance yields for different soil environments [18]. As by 2035, a predicted 26% increase in rice production will be essential to feed the rising population [19], it is imperative to develop high yielding rice cultivars with efficient root systems for better exploitation of natural resources under stressed conditions.

2. Progress in root study of rice under osmotic stress

2.1 Reasons why root study has become the topic of interest

Being the hidden half of the plants, the root system performs several functions like water and nutrient acquisition, mechanical support to the plant and storage of reserve assimilates [7]. In plant, roots are the first organ for sensing the water limitation and the roots are also the signal transmitter to other plant parts through xylem sap and phytohormone which is known as one of the most important root-shoot stress signal mechanism [20–23]. Development of the root system is a major agronomic trait and proper architecture in a given environment permits plants to survive in water and nutrient deficit conditions and gives the ability to utilize minimum resources efficiently [6].

Crop loss in rice production has become severe now-a-days due to abiotic stresses. Therefore, having a clear knowledge about the architecture and development of roots of rice toward optimizing water and nutrient uptake has become crucial for exploitation and manipulation of root characteristics for enhancing yield under unfavorable conditions [24, 25]. In general, root study comprises the study of the entire root system or a large portion of the plant's root system [26, 27]. To understand the functional characteristic of root system and the necessity to exploit heterogeneous environment, root architecture study has become crucial in plant productivity as root system architecture is strongly linked with plasticity to the plant through which plant can alter its root structure according to its heterogeneous environment [26].

2.2 Root system architecture of rice

Elongation and branching are the mode of plant root growth. Local environmental conditions, physiological status of the plants and the type of root determine the magnitude and direction of root elongation [6]. Root system architecture (RSA) is thus the three-dimensional geometry of the root system including the primary root, branch roots, and root hairs [6, 26, 28, 29]. Topological, distributional and morphological features combine to form the root system architecture [8, 26, 30]. Topology denotes the branching pattern of individual roots including features like

lengths and diameters, number of roots originating from a node, root insertion angles, magnitude and the altitude of root [31, 32]. Measures of the spatial distribution of roots simplify the dissection of root systems [26]. Root morphology refers to the external features of a root axis and may include properties of roots hairs, root diameter and trend of secondary root emergence. Acceleration or inhibition of primary root growth, increment of lateral roots (LRs) and a rise in root hairs and also the formation of adventitious roots are the ways of modification of root system architecture. The primary root is formed during embryogenesis. This primary root produces secondary roots those in turn produce tertiary roots [6, 33]. Root system architecture has proved to be a critical factor in plant survival, contributing to water and nutrient acquisition efficiency and competitive fitness in a given environment [34]. Composition of soil specially water and mineral nutrients availability and plant species have impact on root architecture [6].

Monocot cereals have a complex fibrous root system consisting of an adventitious root (ARs) bunch. Adventitious roots originate from the shoot or subterranean stem. This type of root is sometimes referred to as a nodal or crown root [35]. Root systems of rice plants (*Oryza sativa* L.) comprise numerous nodal roots of relatively short length: a mature rice plant usually has several hundreds of nodal roots, most of which are less than 40 cm in length [36]. Rice (*Oryza sativa* L.) is a model cereal crop with seminal roots that die during the growing period [36]. Thus, lateral roots and adventitious roots are the key determinants of nutrient and water use efficiency in rice [37].

Several embryonic and postembryonic roots including the radicle, the embryonic crown roots, the postembryonic crown roots, the large lateral roots (L-type), and the small lateral roots (S-type) [38] form the rice root systems (see **Figure 1**). Lateral rice roots can appear on any primary root, including embryonic and crown roots, and can be classified into two main anatomical types [39]. Numerous small lateral roots (S-type) are thin with determinate growth that can be formed from large lateral roots (L-type) and they never bear any lateral roots. Whereas large lateral (L-type) roots are few in number, thinner compared to primary roots that show indeterminate growth. Additionally, lateral elongation of small lateral roots and downward elongation of large lateral roots indicate non-responsiveness of the small lateral roots to gravity. Higher orders of branching can also be observed in the large lateral roots of the crown roots that emerge at later growth stages [40].

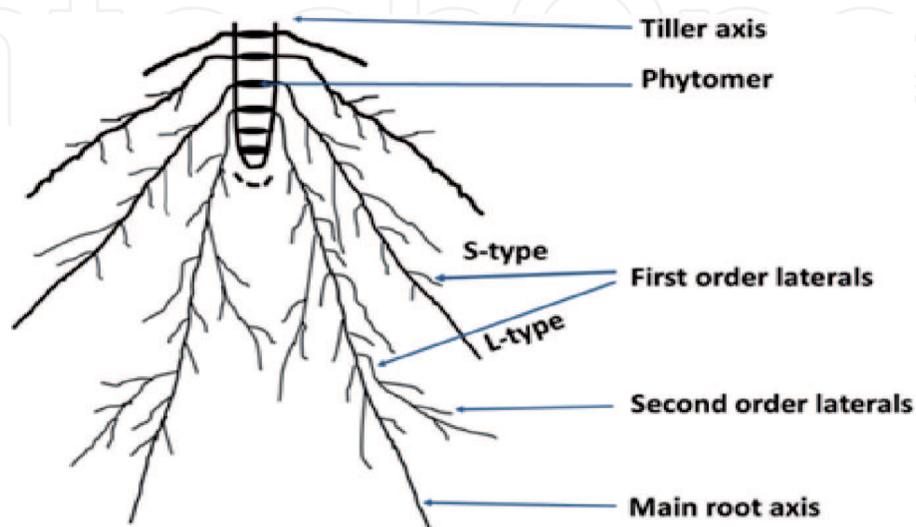


Figure 1. A typical root system architecture at the tiller axis of *Oryza sativa* L. Black disks indicate individual root bearing phytomer with progressive development chronologically from top to downward. Root hairs form on main axis and all the lateral roots [41].

These small and large lateral roots exhibit differential growth and lateral root bearing pattern signifying unlike purposes for these two types of lateral roots [37].

2.2.1 Phytomer concept

The concept of a phytomer was established around 6–7 decades ago [40, 42]. Clear knowledge about phytomer is required for better understanding of plant development and architecture. Many higher plants, including rice, are composed of successive stem segments called phytomer [43–45]. Each phytomer consists of an internode of the stem with one leaf, one tiller bud and several adventitious (nodal) roots [36]. The phytomer concept has long been recognized among grass scientists [46, 47]. The coordinated development of stem, tiller bud, and adventitious roots in each phytomer corresponds to the phyllochronic time in rice [43, 44, 48]. This indicates that genotypic variation in root-and-shoot growth can be ascribed to the variation of stem and adventitious root development at the phytomer level [49].

Detailed study of root morphology and architecture at the phytomer level become more obvious with the attainment of new knowledge about segmental architecture of poaceous crops [50–53]. As the higher plant structure is formed by the repetitive unit of plant growth called phytomer [54], so phytomer formation, its growth and senescence ultimately determine development of plant canopy [47]. Therefore the phytomer components have become the interest of the plant breeder.

2.2.2 Lateral roots

Root axes of rice plants serve functions of anchorage and typically establish overall root system architecture [55]. The lateral roots are the functionally active part of the root system involved in nutrient acquisition and water uptake. The size, type and distribution of lateral roots eventually decide the ultimate length and surface area of an individual root and finally of a whole tiller. Understanding morphology of the lateral roots is therefore important to develop rice cultivars with an efficient root system [11, 56].

In rice, there are two types of lateral roots; long and thick roots, and short and slender roots [57–59]. It has been designated that the first type as L-type and the latter as S-type [60]. The L-type lateral roots are usually long and thick and are capable of producing higher-order lateral roots, whereas S-type ones are short, slender, and non-branching. In rice plants, these two types of lateral roots are visually distinguishable. The L-type lateral roots show basically identical tissue arrangement with seminal and nodal roots, whereas S-types are anatomically different wherein their vascular systems are simplified [35].

In rice plants, the observed average diameter of S-type lateral roots (first-order) that were produced on mature nodal roots of a one-month-old plant was 80 μm , whereas that of L-type roots was almost double that, i.e., 159 μm . Average length was 7.6 mm for S-type and about 30 mm for L-type. The S-type laterals were almost similar in length, and only very few S-type laterals exceeded 10 mm in length. The L-type laterals varied greatly in length and some of them elongated to more than 300 mm [60]. The small laterals are less effective in water and nutrient uptake than even root hairs [61].

The changes in lateral root development were triggered by changes in water status in the root zone, and these developmental changes were induced by genetic [62, 63] and environmental factors. With regard to the environmental factors, it is shown that phenotypic plasticity promoted lateral root development and that nodal root production was the key trait that ensured stable growth of rice plants grown under changing soil moisture levels [64]. As far as the literature explored,

developmental morphology of the individual roots with special reference to different lateral root branches was not studied in detail, probably due to lack of the most appropriate tools and methods [11].

2.2.3 Root hairs

Root hairs are tubular-shaped cells that arise from root epidermal cells called trichoblast; they are thought to increase the absorptive capacity of the root by increasing the surface area [65]. Root hairs contribute as much as 77% of the root surface area of the cultivated crops, forming the major point of contact between the plant and the rhizosphere. Root hair is a long and narrow tube like structure originating from a single cell through tip growth (the deposition of new membrane and cell wall material at a growing tip). For being the major water and nutrient uptake site of plants, root hairs form a progressively significant model system for development studies and cell biology of higher plants [66]. Root hairs had the highest contribution toward total length and surface area of an individual root whereas main axis and first order laterals mostly contributed root volume [11].

Root hairs are localized for many water channels [67], phosphate [68], nitrogen [69], potassium [70], calcium [70], and sulfate transporters [71], all of which are beneficial to water and nutrient uptake by plants [72]. There is significant inter- and intra-specific variation exists for root hair traits, and this has been linked to P uptake. Plants with longer, denser root hairs exhibit greater P uptake and plant growth in P-deficient soils [73–75]. So, the root hair traits, especially root hair length can be exploited in breeding for improved nutrient uptake and increased fertilizer use efficiency [76]. Considerable researches support an important role for root hairs in P attainment [73–75, 77, 78]. Root hair length and root hair density (which is usually correlated with root hair length) have clear value for the acquisition of P and probably other diffusion-limited nutrients such as K and ammonium [79].

Usually root hair traits have a low heritability and their expression is influenced by soil type resulting in lack of research in this field [6, 80, 81]. It has been proposed that plasticity in root epidermis development as a response to a variety of environmental conditions might reflect a function of root hairs in sensing environmental signals, after which plants adjust themselves to the stress conditions, such as by increasing nutrient acquisition and water uptake or by helping to anchor the plant to the soil [82–87]. Root hair elongation increases root surface area. Root surface area increment is a common phenomenon when the plants are subjected to the stress condition like salinity, drought or other abiotic stresses [79, 88–91].

2.3 Research progress of rice root study till date under osmotic stress

Plants recurrently face several stresses like salinity, drought, submergence, low temperature, heat, oxidative stress and heavy metal toxicity while exposed to the nature. Growth and grain production in cereals is often limited by these stresses under field conditions. All these stresses either directly or indirectly impose osmotic stress to plants that ultimately affect the final yield of rice. Root is the first part which can sense these stresses better than other plant parts. So researchers prioritize the fact of understanding the root adaptive responses of plants upon osmotic stress. In the last 30 years, comprehensive studies have been performed focusing on architecture and developmental morphology of roots and their genetic and molecular basis [11]. Morphological and anatomical development of the rice root system was thoroughly reviewed [92] whereas the mystery of root length was also reviewed [93]. A recent study highlighting the growth, development and genetic reasons of root morphology and function of crop plants was provided by [94]. An outstanding study

on root system architecture and its molecular and genetic background also greatly contributed to the relevant literature recently [37]. The physiological background of root branching was also studied [7, 33]. The root parameters that are focused by the studies comprising root anatomy, plant height, root-shoot ratio, length, diameter, density, surface area and volume of root, root elongation rate, root branching, expansion of root regarding tiller development, maximum root depth, distribution pattern of root in soil column, root hydraulic conductivity, hardpan penetrability, all of which possess innumerable functional implication [95]. Roots of large diameter show greater penetration ability [96–98] and branching [8, 99] because of having larger radii of xylem vessel and poorer axial resistance to water flux [100].

2.3.1 Plasticity of root traits under drought

Water is essential for survival and plant growth. As a sessile organism, plants constantly encounter water deficit, which is the most severe environmental stress limiting plant growth and productivity in natural and agricultural systems [101, 102]. Thus, water stress tolerance has been a fundamental scientific question in plant biology.

Plants have evolved complex adaptive mechanisms that enable them to survive drought conditions. Over more than five decades, researchers have identified osmotic adjustment, antioxidant protection, and stomatal movement as key adaptive mechanisms for survival where both osmotic adjustment and reactive oxygen species (ROS) are involved in this plastic development process [103]. To cope with the changing water status in the growing environment, plants have evolved various adaptive mechanisms by which plants can modify root allocation and root system architecture to obtain more water [104].

Numerous studies have provided evidence to show that when plants are subjected to water stress, root growth is strongly inhibited, although root development is less sensitive to water stress than that of shoots [105–107].

Root system architecture is regulated by osmotica [108]. The osmotic potential of the soil alters the depth of the root system, its overall mass, the rate of root elongation and the number of lateral roots in many plants, including *Arabidopsis* [8, 9, 107, 109, 110].

Root length, root dry weight, and root production are limited by drought stress [111, 112]. Roots are the significant plant part which increase plant adaptability power to soil water deficits by maintaining water uptake under dry conditions [113]. Root and other root components such as root hair, root-shoot ratio, and root length are found to be decreased in drought sensitive varieties. But the resistant varieties which possess tolerance capacity against drought showed increase in root hair, high root to shoot ratio and root length [114]. Roots are considered as the most efficient plant organ which helps plant to uptake water and minerals from the soil and during drought stress. Root proliferation and changes in root parts occurs to take more water from deeper regions of the soil [25]. Different types of changes are observed in root growth of drought resistant rice varieties such as a deeper and highly branched root system than drought- sensitive varieties [115]. Plant also extends its roots for more nutrients (such as phosphorus) and water uptake which results in more root to shoot ratio [116]. In recent years breeding for developing larger and more efficient root systems has become the hotspot in research in some crops such as rice, as there is a relation between root system size and tolerance to water stress [81, 117].

The change in lateral root development, i.e. in the plasticity of the root system, exhibited under water deficit conditions may play an important role in drought stress tolerance [35]. From an agronomical view, the knowledge about lateral root development is useful for breeding varieties with drought stress tolerance [118].

2.3.2 Modification of root system components under submergence stress

The importance of root system structure is particularly recognizable when its significance in relation to its function is clearly identified. The significance of root system structure in nutrient and water uptake was stressed in previous study [119].

Under waterlogged conditions, the plant roots have to function in anaerobic soil, and there are at least two morphological adaptations that roots exhibit in response to anaerobiosis, i.e., development of new adventitious roots [120, 121] and superficial rooting (i.e., the concentration of new root growth in the upper layers of the soil) [122]. Nodal root production (increase in number) continued to take place, however, in the sense that when adventitious roots in the lower nodal position of the plant's stem die due to waterlogging injury, new adventitious roots appear at the next highest nodal position. There appears to be a direct relationship between the death of older adventitious roots and the development of new ones. Progressively waterlogged plants generally show smaller root system size than those grown in a well-drained condition. It is considered that the turgor pressure affects the cell elongation and growth of plants [123, 124]. Aerobic cultivars of rice have greater ability for plastic lateral root production than irrigated lowland cultivars under transient moisture stresses [125].

2.3.3 Plasticity of root traits under salinity stress

We have a little understanding of the responses of roots and root hairs to salinity stress and their function in stress tolerance. The efficient root system can either avoid or lessen the osmotic stress. Usually, growth, morphology, and physiology of the roots alter first under salinity stress and the whole plant is then affected. Therefore, the responses and characteristics of the roots under saline conditions are of primary importance for plant salt-tolerance [126]. It is supposed that root morphology affects salt accumulation around the roots impeding uptake of water from saline areas. Modification of root morphology has a big potential to develop crop salt tolerance [127]. Root hairs have higher sensitivity to salt than other root traits and shoots [128]. Environmental factors also regulate the root hair development [128]. The development of root epidermal cells has great plasticity where the differentiation programs can be switched from one to another in response to external factors [17]. Plasticity in development of root epidermis as a response to a variety of environmental conditions might reflect a function of root hairs in sensing environmental signals, after which plants adjust themselves to the stress conditions [82, 84–87, 129].

Root hair growth and development and their physiological role in response to salt stress are largely unknown [128]. The development of root epidermis cells has great plasticity where the differentiation programs can be switched from one to another in response to external factors [17]. Root hairs have higher sensitivity to salinity than do roots and shoots [128]. Systematic study on root hair plasticity induced by salt stress and the possible role in plant adaptation/tolerance to salinity is still lacking [128]. Usually root hair traits have a low heritability and their expression is influenced by soil type resulting in lack of research in this field [6, 80, 81].

2.4 Varietal differences in rice root morphological characteristics

Earlier many scientists had reported root morphology and its distribution were greatly varied based on genotypes of plant species [13–16]. There is widespread evidence that root architecture and different root characteristics of many crop species varies among genotypes [14, 130–133]. In a few quite recent studies, the importance

of studying root architectural traits has been emphasized for the adaptation of the crop varieties to various abiotic stress conditions. Genotypic variation has a significant role in adapting the adverse environmental and edaphic effects [14]. Inter- and intra-species variations in root architectural traits are very useful to breed the crops for root features optimum for diverse environmental conditions [134–136].

Root anatomical and morphological traits have been well studied in rice [92]. Varietal differences in root morphological characteristics such as length and thickness have been reported in cultivated rice (*Oryza sativa* L.) in various studies [11, 14, 41, 137]. In general, the roots of upland rice cultivars are thicker and penetrate more deeply into the soil than those of lowland cultivars [14]. Root distribution has also been quantitatively characterized by using several traits, including root length, volume, and density in the soil at different depths, and these characteristics differed among cultivars [92, 138–140].

3. Future prospects of rice root study

Understanding and improvement of root system and its genetics plays a pivotal role to become self-sufficient and to achieve sustainability in rice production. Actually more yields from the limited input rely on our capability to unambiguously manipulate the plants. And exploring the diversity of root architecture both in genetic and phenotypic basis will directly connect to this concern. Although great strides have been made to understand the root morphology but in future, more intense investigations to elucidate the functional implication of root morphological variation may aid in selection of root system with anticipated characteristics.

Future exploration of stress responses regulated by roots at cellular or tissue level will open the door of further breeding research. Besides the modern gene pools, exploration of genes and alleles in wild relatives and landraces will also provide interesting features that will be easier to transfer to cultivated rice. Further it is important to have a better understanding on the epigenetic regulation of roots and root development under stressful conditions. There will be a need for high throughput phenotyping systems coupled with automated data analysis for accelerating the development. Endorsement of approaches including both root ideotype-based screening and selection for grain yield may establish a fruitful screening system. Alongside designing new genetic screening methods based on a better knowledge of the integrated stress responses will be also appreciated. Dynamic root/soil interaction modeling will aid in integrating different functional parameters (e.g. water uptake per length of root) under a variety of environmental conditions. Overall the root system being less accessible and more complex than other agronomic traits, achieving the ambitious goal of future rice root research, coordinated effort and joint resources are required. The sensible and appropriate efforts will have a crucial role to play in future crop production in vulnerable climate and resource scarcity prioritizing the objective of serving food to 9 billion world populations by the year 2050.

Conflict of interest

“The authors declare no conflict of interest.”

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