Invited Review

Morpho-physiological and molecular mechanisms of phenotypic root plasticity for rice adaptation to water stress conditions

Nonawin Lucob-Agustin†1,3), Tsubasa Kawai†1), Mana Kano-Nakata2), Roel R. Suralta3), Jonathan M. Niones3), Tomomi Hasegawa1), Mayuko Inari-Ikeda3), Akira Yamauchi1) and Yoshiaki Inukai*2)

1) Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya, Aichi 464-8601, Japan
2) International Center for Research and Education in Agriculture, Nagoya University, Nagoya, Aichi 464-8601, Japan
3) Philippine Rice Research Institute, Central Experiment Station, Science City of Muñoz, Nueva Ecija, 3119, Philippines

Different types of water stress severely affect crop production, and the plant root system plays a critical role in stress avoidance. In the case of rice, a cereal crop cultivated under the widest range of soil hydrologic conditions, from irrigated anaerobic conditions to rainfed conditions, phenotypic root plasticity is of particular relevance. Recently, important plastic root traits under different water stress conditions, and their physiological and molecular mechanisms have been gradually understood. In this review, we summarize these plastic root traits and their contributions to dry matter production through enhancement of water uptake under different water stress conditions. We also discuss the physiological and molecular mechanisms regulating the phenotypic plasticity of root systems.

Key Words: root system formation, phenotypic plasticity, stress avoidance, drought, soil water fluctuations.

1. Introduction

Phenotypic plasticity is generally defined as the ability of an organism, with a given genotype, to change its phenotypes with changes in environmental conditions (O’Toole and Bland 1987). In particular, phenotypic root plasticity is highly relevant in rice, given that the plant is cultivated under the widest range of soil hydrologic conditions of any cereal crop, from irrigated anaerobic to rainfed conditions. In rice, the plastic root system confers improved performance and sustained productivity in stressful environments, such as water-limited and nutrient-poor soils, but especially in rainfed systems (Sandhu et al. 2016, Suralta et al. 2018a). Rice genotypes that are tolerant to drought stress exhibit highly developed root systems, compared to drought-sensitive genotypes (Henry et al. 2011, Kano et al. 2011, Niones et al. 2012, Owusu-Nketia et al. 2018a, Siopongco et al. 2006, Suralta 2008a, 2012, Yamauchi et al. 1996). However, given the complexities of rainfed (upland or lowland) environments, diverse and functional root plasticity traits contributing to root system development are manifested depending on the characteristics of the rainfed environment (Kameoka et al. 2015, Menge et al. 2016). Here, we have summarized the important plastic root traits and their contributions to dry matter production through enhancement of water uptake under different water stress conditions. We have also discussed the physiological and molecular mechanisms regulating the phenotypic plasticity of root systems.

2. Phenotypic root plasticity under different water stress conditions

2.1. Functional root phenotypic plasticity traits in cereal crops under rainfed upland conditions

In rainfed upland conditions, a deep root system is a desirable trait for drought resistance (Kato et al. 2007, Uga et al. 2011). Uga et al. (2013) cloned the DEEPER ROOTING1 (DRO1) gene controlling root growth angle, which constitutively increases rooting depth; the effectiveness of this deep rooting trait has been shown to increase the yield under upland drought conditions, using near-isogenic lines. Studies in maize have indicated that plasticity in greater rooting depth, responds to drought stress, resulting in reduced adventitious (also called shoot-borne, crown, or nodal) roots and greater crown root elongation, which contribute to greater water acquisition from the drying soil (Fig. 1A, Lynch 2018, Sebastian et al. 2016). Additionally, plastic response in the form of reduced lateral root branching density has been shown to improve the drought tolerance of maize plants under greenhouse and field conditions (Fig. 1A, Lynch 2018, Zhan et al. 2015). Lynch (2013,
Zhan et al. (2015) proposed that fewer crown roots and reduced lateral root production and branching would reduce counterproductive internal plant resource (primarily carbohydrates) competition and thus permit further rapid elongation of the remaining crown root axes into deeper soil layers, which would, in turn, contribute to improved water and nitrogen capture, plant growth, and yield of the plant during drought stress (Fig. 1A). In contrast, plasticity in the deep root system, as well as enhanced lateral root branching have been observed in rice, under progressive drought conditions. Kameoka et al. (2015) and Menge et al. (2016) reported that a variety with the ability to increase root length density in a deeper soil layer under progressive drought stress was more tolerant to stress than a variety that did not have this ability. This plasticity trait is either a result of the promotion of crown root elongation or a decrease in vertical root angle, as well as plasticity in lateral root development. Lateral roots have been categorized into distinct types that substantially vary in length, diameter, and histological structures, in rice (Kono et al. 1972). The S-type lateral roots are short, unbranched, and have a thin diameter and simple vasculature, whereas the L-type lateral roots are generally long and highly branched, with a thick diameter and a well-developed vasculature (Kawai et al. 2017, Yamauchi et al. 1996). Therefore, L-type lateral roots play an important role in increasing lateral root distribution vertically and horizontally, and therefore, rice plants produce these root types under drought stress conditions (Fig. 1B, Kameoka et al. 2015, Menge et al. 2016). Similarly, rice and other cereal crops seem to have different phenotypic responses; the former promotes lateral root formation, while the latter reduce them. This may be attributed to the different intensities of drought stress. Generally, rice is more susceptible to drought stress than other cereal crops; thus, rice crops cannot survive under severe stress conditions. Under such severe conditions, rapid elongation of the crown roots by reduced lateral roots may be the most important trait in other cereal crops.

2.2. Functional root phenotypic plasticity traits in rice under rainfed lowland conditions

2.2.1. Functional root phenotypic plasticity traits under progressive drought conditions

In contrast to rainfed uplands, rainfed lowland rice fields contain a hardpan at approximately 20 cm beneath the soil surface, which restricts rice roots from growing into the deep soil layer (Samson et al. 2002, Yano et al. 2006). Thus, rice roots are almost entirely limited to the water and nutrients found above the hardpan. Under such conditions, phenotypic root plasticity traits have been precisely quantified using genetically related lines, such as chromosome segment substitution lines (CSSLs), to curb the effects of genetic confounding. The CSSLs, a genetic construction containing the major genetic background of the original parent, Nipponbare, with overlapping chromosome segments of the donor parent, Kasalath, were grown under soil moisture gradients with a line source sprinkler system.
It was revealed that the shoot growth of Nipponbare and susceptible lines sharply decreased as soil moisture content decreased. On the other hand, the shoot growth of tolerant lines was maintained under mild (15%–30% SMC) and severe drought (<15% SMC) conditions to some extent, which was attributed to the increase in total root length through promotion of lateral root branching and elongation, and consequent increases in water uptake. However, the high total root length did not support shoot growth under severe drought stress, indicating that plasticity in lateral root development could maintain shoot growth under mild drought stress, but not under severe water deficit conditions (Kano et al. 2011, Kano-Nakata et al. 2011). Menge et al. (2016) also demonstrated that under a similar line source sprinkler system with a 20-cm soil depth, the plasticity in lateral root development increased total root length under mild drought stress (11%–28% SMC) relative to well-watered conditions, and consequently contributed to the maintenance of dry matter production. Furthermore, this root plasticity expression was enhanced by standard and high nitrogen applications (Menge et al. 2019, Tran et al. 2014, 2019), regardless of nitrogen forms (Fig. 2, Tran et al. 2015), and led to increased shoot growth, thus indicating that root plasticity expression could be induced by controlling the level of nitrogen in soils.

### 2.2.2. Functional root phenotypic plasticity traits under soil moisture fluctuations

Apart from progressive drought, soil moisture fluctuation (SMF; alternate recurrences of waterlogging and water deficit conditions) is recognized as a prevalent stress in rainfed conditions, due to erratic rainfall patterns. Under such conditions, rice plants are exposed to the absence (anaerobic) or presence of oxygen (aerobic) brought about by excess water under waterlogged conditions and limited water availability under drought conditions. Hence, expression of normal root adaptations to prevailing stress conditions, such as aerenchyma formation under waterlogged conditions, is affected by the preceding water stress (e.g., drought) that occurs prior to transient waterlogged conditions and vice versa (Suralta et al. 2008a, 2008b). Based on this knowledge, SMF is perceived to be more stressful to the plant than either constant waterlogging or progressive drought. According to Suralta et al. (2008a, 2008b, 2018a), the key root plasticity traits under SMF increase the formation of aerenchyma when drought-stressed roots are subjected to sudden waterlogged conditions, and promote root elongation and lateral root development when previously stagnant roots are subjected to progressive soil drying conditions. These key root plasticity traits were observed to contribute to better adaptation through enhanced transpiration and photosynthesis, thereby

![Fig. 2. Root plastic response of rice to continuous drought stress under rainfed lowland conditions and its importance for the stress avoidance.](image)
affecting dry matter production and yield, and were expressed uniquely under SMF, but not under continuously waterlogged or progressive drought stress conditions (Fig. 3, Niones et al. 2012, Suralta et al. 2010). Interestingly, a quantitative trait locus (QTL) for aerenchyma formation from the Kasalath allele on chromosome 12 (Niones et al. 2013) was identified and was reported to directly promote lateral root growth, resulting in greater root system development and the maintenance of total dry matter production under SMF stress (Niones et al. 2015, 2019). This further supports the idea that aerenchyma formation is an essential adaptive trait in SMF. Furthermore, QTLs on root plasticity traits are gradually being detected (Niones et al. 2013, 2015, Owusu-Nketia et al. 2018b, Sandhu et al. 2016, Suralta et al. 2015), and the relationship of this plasticity to increased productivity under SMF or stressful conditions has been studied with the goal of genetic improvement (Owusu-Nketia et al. 2018b, Sandhu et al. 2016).

As mentioned above, a typical rainfed lowland has a pronounced hardpan, which has the highest penetration resistance along the soil profile, which hinders the penetration of roots to the deeper soil layer during drought conditions (Cairns et al. 2004, 2011). In situations where the water availability at the shallow layer is more limited than that below the hardpan layer, the capacity of the roots to penetrate the hardpan layer is critical for the establishment of a deep root system. A recent study by Suralta et al. (2018b) reported that, contrary to most of the studies on root growth and penetration ability that focused more on responses to

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Fig. 3. Root plastic responses of rice for moisture fluctuation management. Compared to susceptible lines, tolerant lines could maintain shoot growth under fluctuation stress. Tolerant lines promoted more lateral root development in response to transient waterlogged-drought conditions. Drought reduced the plant’s ability to produce aerenchyma following the sudden O₂ deficiency caused by waterlogging. However, tolerant lines produced highly developed aerenchyma, suggesting that greater shoot dry matter production in tolerant lines is largely due to improved root system development through increased aerenchyma formation under transient drought–waterlogged conditions. CR: crown root, LR: lateral root (From Niones et al. 2012, Suralta et al. 2008a, 2008b, 2010).
drying soil conditions, the development of deep root systems during SMF was due to the plasticity in crown root elongation through the hardpan expressed during re-watering, which softened the hardpan layer, rather than during drought periods. This root plasticity then contributed to greater water use in the deeper soil during the subsequent drought period, and overall shoot dry matter production (Nguyen et al. 2018).

3. Physiological and molecular mechanisms of general root formation and phenotypic root plasticity

3.1. Regulation of general root formation by the plant hormone auxin

It is well-known that the plant hormone auxin positively regulates root formation. In Arabidopsis, auxin signaling is controlled by the interactions between Aux/IAA proteins, repressors of auxin-responsive transcription, ARF proteins, and transcriptional activators or repressors (Fig. 4A, Liscum and Reed 2002). An auxin signal captured by the auxin receptor TIR1/AFB (Tan et al. 2007) promotes the ubiquitination of the Aux/IAA protein through the TIR1/AFBs complex (Gray et al. 2001). The ubiquitinated Aux/IAA proteins are then degraded by the 26S proteasome, thereby allowing auxin-responsive transcriptional regulation by ARF proteins (Gray et al. 2001). The rapid degradation of Aux/IAA proteins requires the core sequence GWPPV in domain II; thus, mutations in the core sequence block the degradation of Aux/IAA and interrupt the transmission of the auxin signaling pathway by suppressing ARF activity (Ramos et al. 2001), resulting in defects in the formation of lateral roots (Fukaki et al. 2002, Hamann et al. 2002, Rogg et al. 2001, Tatematsu et al. 2004, Tian and Reed 1999, Uehara et al. 2008, Yang et al. 2004). In the case of rice, gain-of-function mutants Osiaa11, Osiaa13, and Osiaa23 also result from a stabilizing mutation in their domain II, and the number of lateral roots in these mutants are dramatically decreased (Kitomi et al. 2012, Ni et al. 2011, Zhu et al. 2012).

On the other hand, arf7 arf19 double mutants in Arabidopsis also show a remarkable reduction in lateral root formation (Okushima et al. 2005). However, the targets and molecular mechanisms downstream of AUX/IAA and ARF proteins in root development had not been resolved. In this aspect, both crl1 and crl5 mutants of rice have a defect in the formation of crown roots. The causative genes, CRL1/ARL1 and CRL5, encode a member of the plant-specific ASL/LBD protein family and the large AP2/ERF transcription factor family protein, respectively.

Fig. 4. Molecular mechanisms regulating phenotypic root plasticity: canonical/non-canonical lateral root formation (A), hydropatterning (B), and xerobranching (C). LR: lateral root (From Bao et al. 2014, Ditengou et al. 2008, Laskowski et al. 2008, Orman-Ligeza et al. 2018, Orosa-Puente et al. 2018, Sheng et al. 2017, Xu et al. 2017).
(Inukai et al. 2005, Kitomi et al. 2011, Liu et al. 2005). Exogenous auxin treatment induced both CRL1/ARL1 and CRL5 expression without de novo protein biosynthesis, and this induction required the degradation of OsIAA proteins. Both CRL1/ARL1 and CRL5 contain putative auxin response elements (AuxREs) in their promoter regions. The proximal AuxREs specifically interacted with rice OsARF and acted as cis-motifs for their expression, suggesting that these genes were direct targets of OsARF (Inukai et al. 2005, Kitomi et al. 2011). Okushima et al. (2007) also reported that the SLR/IAA14 and ARF7 and ARF19 modules regulate the expression of LBD16/ASL18 and LBD29/ASL16 in lateral root founder cells, which positively regulates lateral root initiation. As the number of lateral roots in the rice crll mutant was also reduced (Inukai et al. 2005), LBD/ASL proteins were confirmed to be common regulation factors in both crown and lateral root formation.

3.2. Molecular mechanisms regulating phenotypic root plasticity through the canonical pathway

Plants alter their root system architecture in response to the heterogeneous distribution of water in the soil for efficient water acquisition (reviewed by Fromm 2019). Lateral root formation is promoted towards water patches and suppressed in dry patches or in air. These phenomena are termed hydropatterning and xerobranching, respectively (Fig. 4B, 4C, Bao et al. 2014, Orman-Ligeza et al. 2018). When the roots grow along agar, lateral roots are formed more on the side in contact with water (agar) than on the side in contact with air (termed hydropatterning, Bao et al. 2014). The number of pre-branch sites is higher on the side in contact with water than that with air, suggesting that the preferential lateral root formation toward water is determined during lateral root founder cell specification before initiation (Bao et al. 2014). LBD16, a target gene of the ARF7 transcription factor, exhibits an asymmetric expression, with higher expression on the side in contact with water, which is consistent with the lateral root formation pattern (Orosa-Puente et al. 2018). It has been revealed that SUMOylation (small ubiquitin-like modifier conjugation) of ARF7, which is necessary for its interaction with the IAA3 protein that keeps the auxin signal inactive, is specifically disrupted by unidentified factor(s) on the side in contact with water, resulting in preferential LBD16 expression and lateral root formation on the water side (Fig. 4B, Orosa-Puente et al. 2018). These results indicate that the degradation of the IAA protein is not always necessary to regulate lateral root development to show the plastic response in this hydropatterning. LBD16-like genes are also differentially expressed in maize during hydropatterning (Robbins and Dinneny 2018), suggesting that this plastic root response is regulated by common regulation mechanisms in Arabidopsis and cereals. Additionally, suppression of lateral root formation on the roots growing in the soil air space is also observed in cereals (termed xerobranching, Orman-Ligeza et al. 2018). In barley roots, genes involved in plant hormone signaling, including the ABA signaling pathway, were differentially expressed, and ABA content increased after a transient water deficit. In cereals and Arabidopsis, exogenous ABA treatment can mimic xerobranching, and transient ABA treatment decreased the free IAA levels above the root apical meristem, thereby causing the repression of pre-branch site formation (Fig. 4C, Orman-Ligeza et al. 2018).

Auxin transport and distribution are also important for plastic lateral root formation. Treatment with 2,4-D, which is not polarly transported, can disrupt hydropatterning even at low concentrations, although the transportable form of auxin, IAA, did not have a significant effect, suggesting the importance of auxin transport for hydropatterning (Bao et al. 2014). Local ammonium (NH$_4^+$) supply promotes lateral root formation with more developed higher-order branching (Lima et al. 2010). Under such conditions, the protonation of IAA is promoted by apoplastic acidification, which is caused by enhanced proton release via the P-type H$^+$-ATPases following AMT-dependent ammonium uptake (Meier et al. 2020). Protonated IAA (IAAH), which can pass through the cell membranes via diffusion, diffuses from the vasculature to the outer root cells radially overlays the lateral root primordia, so that genes involved in cell wall loosening are upregulated and the mechanical resistance decreases in the outer cells, thereby leading to lateral root emergence (Meier et al. 2020). Our studies have also suggested the importance of auxin diffusion for meristem size regulation of rice lateral roots; 2,4-D treatment induced L-type lateral root formation at lower concentrations compared to that induced by IAA, and co-treatment with naphthylphthalamic acid (NPA), an inhibitor of polar auxin transport, with lower concentrations of IAA, which did not induce L-type lateral root alone, increased lateral root diameter (Kawai et al. unpublished data).

3.3. Molecular mechanisms regulating phenotypic root plasticity through the non-canonical pathway

Non-canonical auxin signaling pathways also regulate plastic lateral root formation in Arabidopsis (Fig. 4A). Here, lateral root formation can be induced by osmotic stress (Sheng et al. 2017) and mechanical forces, including gravitropic curvature and transient bending (Ditengou et al. 2008, Laskowski et al. 2008), and root-tip excision (Xu et al. 2017), with the upregulated auxin signaling occurring at the convex side of the curvature after bending and in the remaining proximal portion after root-tip excision, respectively.

Defective lateral root formation in auxin signaling mutants of Arabidopsis is recovered by transient bending (arf7-1 arf19-1, Ditengou et al. 2008), root-tip excision (e.g., in slr-1/iaa14, msg2-1/iaa19, and arf7-1 arf19-1, Sheng et al. 2017, Xu et al. 2017), and osmotic stress (arf7-1 arf19-1, Sheng et al. 2017). This indicates that the canonical lateral root formation pathway can be bypassed under stressful conditions. Root cutting induced lateral root
formation is disrupted by the inhibition of auxin biosynthesis and transport in msg2-1/iaa19 (Xu et al. 2017), and by removal of the aerial part in arf7-1 arf19-1 (Sheng et al. 2017), with decreased auxin signaling levels in the proximal portions, thereby indicating that auxin remains necessary for the non-canonical lateral root formation pathway. Furthermore, upregulation of auxin signaling by root-tip excision induces expression of the WOXII transcription factor, which directly binds to the LBD16 promoter and upregulates its gene expression, resulting in the recovery of lateral root formation in arf7-1 arf19-1 (Sheng et al. 2017). This non-canonical lateral root formation mediated by WOXII also functions under osmotic stress (Sheng et al. 2017) and root curvature (Baesso et al. 2018). Gravitropic curvature upregulates auxin signaling in rice and induces L-type lateral root formation on the convex side (Lucob-Agustín et al. 2020b). Additionally, wegl mutants that showed wavy parental roots, including in the seminal and crown roots, and exhibited L-type lateral roots arising from the curvatures of the parental roots, revealed that wavy parental roots are important in increasing the frequency of L-type lateral roots through the non-canonical pathway (Lucob-Agustín et al. 2020b).

To further reveal the molecular mechanisms regulating L-type lateral root formation in rice, we conducted several experiments using root-tip excision, which we previously utilized to induce L-type lateral root growth as a compensatory response to cutting in the proximal regions of the main root of rice (Kawai et al. 2017). Based on these findings, analysis of a novel rice mutant exhibiting the L-type specific recovery of lateral root formation after root-tip excision is ongoing, and will provide insight into the molecular mechanisms underlying lateral root phenotypic plasticity in rice.

3.4. Regulation of phenotypic root plasticity via carbohydrate allocation

During drought periods, roots of rice plants grow plastically to search for water and nutrients at certain depths or areas in the soil. Osmotic adjustment (OA), also called osmoregulation, which is the accumulation of solutes in plant cells as a response to different stresses (Serraj and Sinclair 2002), is suggested to sustain root growth to reach deeper soil under water deficit. OA was first shown to maintain turgor and root growth in pea root tips (Greacen excision is ongoing, and will provide insight into the areas in the soil. Osmotic adjustment (OA), also called...

Moreover, Ogawa et al. (2005) suggested that sugar accumulation along the root apical portions (50-mm) of maize roots induced by osmotic stress conditions is associated with the plasticity of lateral root development, and further suggested that sugars contribute to root formation as a compatible solute for cell elongation and lateral root emergence (Ogawa et al. 2009). Based on these reports, a similar mechanism may regulate root plasticity in rice. Our study on a rice pprl mutant, which exhibited increased lateral root development, revealed that reduced basal shoot starch accumulation, due to the repressed expression of starch biosynthesis genes, and subsequent increased transport of root sugars from shoots to roots were important, and had positive effects on L-type lateral root promotion (Lucob-Agustín et al. 2020a, 2020c). Thus, lateral root formation may be induced by carbohydrate allocation, which is supported by the exogenous glucose application that promotes L-type lateral roots (Lucob-Agustín et al. 2020c). Recently, Kikuta et al. (2019) observed that some drought-tolerant rice varieties could use basal shoot starch for root development during the heading period for the maintenance of yield production under water-limited conditions. These studies highlighted a novel physiological action of both the shoot and root in the regulation of root plasticity in rice.

Conclusion and future prospects

It has been suggested that the highest potential of increasing global crop yields lies in marginal lands and developing countries (Tester and Langridge 2010). Moreover, the challenge of maintaining and improving yields with low water supply will be critical, and increased avoidance ability of crops from drought stresses is needed (Tuberosa 2012). Therefore, root traits that improve water acquisition are major targets for genetic manipulation. As mentioned above, the importance of root plastic traits under different water stress conditions, and their molecular mechanisms have been gradually understood. Additionally, next-generation sequencing technology, coupled with the growing number of sequenced genomes, provides the opportunity to redesign genotyping strategies for more effective genetic mapping and genome analysis (Huang et al. 2009). In recent years, genome-wide association studies (GWAS) have been widely used as a powerful tool to identify natural allelic variations in genetic loci controlling the plasticity of crop root system architecture in response to drought (Kadam et al. 2017, Li et al. 2017, Schneider et al. 2020a, 2020b). For example, Li et al. (2017) employed GWAS with 529 rice accessions to determine markers of root traits at the seed maturation stage under normal and drought stress conditions; 225 of the 264 loci identified by GWAS overlapped with reported root-related QTLs. Importantly, these association results can facilitate the efficient identification of causal genes for root traits, as shown in the two case studies of Nal1 and OsJAZ1 (Li et al. 2017), thereby demonstrating the feasibility of mining for candidate
genes by GWAS. The successful identification of these genes and an increased understanding of the molecular mechanisms will be useful in breeding crops, to allow improved drought avoidance with higher root plasticity.

Author Contribution Statement

YI designed the manuscript. All authors have drafted the manuscript. All authors approved the final version of the manuscript.

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