

Response of Plant Roots to Drought Stress

Atsushi Kato, Saki Hoshiyasu, Akiho Yokota and Kinya Akashi*

Graduate School of Biologiccal Sciences, Nara Institute of Science and Technology
*Corresponding author: Graduate School of Biologiccal Sciences, Nara Institute of Science and Technology,
8916-5 Takayama, Ikoma, Nara, 630-0192 Japan
Tel.: +81 743 72 5561; fax: +81 743 72 5569.
akashi@bs.naist.jp

Abstract

Around the world, terrestrial plants are strongly affected by abiotic stresses such as drought, high or low temperatures, high light and salt stress. Among them, drought is one of the major factors limiting distribution and productivity of plants. Understanding the mechanisms for drought resistance in plants is important for breeding new crop varieties which can grow under water deficit conditions. In particular, plant root plays pivotal roles in water uptake and maintenance of water status of plants, thus is an important research target for plant physiologists and molecular biologists. Responses of plant roots to drought have been extensively investigated in model plants such as *Arabidopsis*, which have offered basic knowledge on the molecular mechanisms underlying the multilateral physiological responses in the roots. Moreover, recent physiological and molecular studies on drought-resistant plants have shed lights on how these 'xerophytes' cope with severe water deficit conditions by developing unique survival strategies.

Keywords: root development, drought stress, abscisic acid, xerophyte, wild watermelon

Morphological changes of roots in response to drought stress

Drought stress severely inhibits plant growth (Larcher, 1995). However, development of root is usually less affected than that of shoot under drought. In maize, it is reported that root growth is maintained at lower water potentials, while shoot growth is completely inhibited (Sharp *et al.*, 2004). This report also showed that elongation activity is highly retained in root tip regions under water deficits. On the other hand, in the case of *Brassicaceae* species including *Arabidopsis*, inhibition of primary root elongation under drought is accompanied with morphogenetic differentiation process in the lateral roots. In this process, lateral roots remain short, hairless and often take a tuberized shape with concomitant accumulation of starch and proline (Vartanian *et al.*, 1994; Xiong *et al.*, 2006). This so-called 'short-roots' then switch to a dormant mode under prolonged drought periods, until the resume of growth upon rehydration conditions (Wasilewska *et al.*, 2008). These observations therefore offer an illustrative example on the flexibility of root system architecture in plants under fluctuating water availability in the soils.

Abscisic acid (ABA) signaling and root morphogenesis

ABA is one of the major plant hormones which mediate adaptation of plants to environmental stresses. Many plants synthesize a large quantity of ABA in every tissue under stress (Shinozaki *et al.*, 2003). In the leaves, ABA is well known to stimulate stomatal closure and thus reduce transpirational loss of water under drought. In the roots, on the other hand, ABA inhibits elongation of primary roots (Leung *et al.*, 1997; Bai *et al.*, 2009) and decreases a number of lateral roots (Xiong *et al.*, 2006). Moreover, ABA is shown to be implicated in the development of the 'short-roots' (Schnall and Quatrano, 1994). Furthermore, analysis of *Arabidopsis* mutants revealed that ABA-deficiency inhibits morphological changes of roots in response to the stress, which impaired stress resistance in these mutants. It is suggested that ABA and ABA signaling elements

are important factors for regulating morphological changes of the roots under drought stress (Wasilewska *et al.*, 2008).

Compatible solutes in the roots

In many plant species, responses to drought stress involve changes in the fluxes of specific metabolic pathways, which lead to the accumulation of compatible solutes such as sugar derivatives and amino acids. Previous studies suggested that proline accumulation in the roots contributes to the osmotic adjustment and fortification of water uptake (Sharp *et al.*, 1990; Voetberg and Sharp, 1991). In a recent study using *Arabidopsis* mutants impaired in proline metabolism, it is demonstrated that proline biosynthesis, transport and degradation are regulated in tissue- and stage-specific manners during drought (Sharma *et al.*, 2011). Under drought condition, proline is mainly synthesized in photosynthetic tissue, and a part of the proline is transported to root meristems, which is further catabolized to various metabolites to support continued growth at low water potential. *Arabidopsis* mutants deficient in ABA biosynthesis show impaired proline metabolism and root growth elongation under water deficits, which is reversed by exogenous ABA (Sharma *et al.*, 2011). These observations suggested that proline metabolism is partly regulated by ABA signaling pathway under drought, and these molecular networks coordinately contribute to the adaptation response of plants under stress conditions.

Root tropism under drought

In response to environmental signals, plants exhibit tropism to control the direction of their growth. Root system development is largely directed by the interaction of gravitropism and hydrotropism, which are the responses to gravity and moisture gradient, respectively (Gilroy and Masson, 2008). Gravitropism is dominantly orientated on primary roots, which is mediated by sedimentation of starch anchors in the amyloplasts of columella cells. The lateral gradient of auxin in the root cap is also known to be implicated in the root gravitropism. In water-stressed roots, hydrotropism is accompanied by the rapid degradation of amyloplasts in columella cells, which reduces responsiveness to gravity (Takahashi *et al.*, 2003; Eapen *et al.*, 2005). Recent genetic analysis in *Arabidopsis* revealed that hydrotropism is mediated by novel factors such as MIZ1 and GNOM, the latter encoding guanine-nucleotide exchange factor for ADP-ribosylation factor-type G protein (Kobayashi *et al.*, 2007; Miyazawa *et al.*, 2009), suggesting that GNOM-mediated vesicular trafficking plays a pivotal role in hydrotropism.

Root development in xerophytes

Plants which survive in water-deficit environments are called xerophytes, which develop unique drought resistance mechanisms (Wickens, 1998; Graham and Nobel, 1999; Akashi *et al.*, 2008). Most xerophytes are characterized by their deep root system architecture. A global-scale investigation of 253 woody and herbaceous plant species reported that plants in the arid and semi-arid regions have more developed roots, with an average of 9.5 ± 2.4 m for desert, and 15.0 ± 5.4 m for tropical grassland/savanna, which are deeper than those for more humid regions such as temperate deciduous forest (2.9 ± 0.2 m), temperate grassland (2.6 ± 0.2 m) and tundra (0.5 ± 0.1 m) (Canadell *et al.*, 1996). Notably, maximum rooting depth was found to be 68 m for *Boscia albitrunca* in the central Kalahari Desert. These results illustrated that development of deep root system is advantageous for reaching to the deep water table in the soils, thereby enabling the survival in the water-limiting environments.

Interestingly, some xerophytes are characterized by their very shallow root system architecture (Graham and Nobel, 1999). For example, African baobab (*Adansonia digitata*) reaches to a height of 25 m with a trunk of up to 10 m diameter; nevertheless, roots of mature trees are

significantly shallow and rarely elongate beyond 2 m (Sidibe and Williams, 2002). Similarly, cactus (*Opuntia ficus-indica*) and agaves (*Agave deserti*) develop shallow and broad root system in which lateral roots are extensively produced. It has been discussed that these shallow roots are advantageous for capturing water derived from light rains, which are notorious for their infrequency in arid regions. These observations therefore suggest that contrasting strategies are employed by various xerophytes, to survive in the competitive environments for water resources.

Wild watermelon as a xerophyte model to study root response under drought

Deep root system observed in xerophytes is a favorable trait for future molecular breeding program towards water-saving agriculture. However, molecular mechanisms underlying this trait have not been fully elucidated. Wild watermelon is a xerophyte inhabiting the Kalahari Desert in Botswana, despite carrying out C₃-type photosynthesis (Kawasaki *et al.*, 2000; Miyake and Yokota, 2000), therefore offers an interesting model for how C₃ plants can cope with severe drought conditions. Previous physiological and molecular analyses demonstrated that root development of wild watermelon is significantly enhanced at the early stage of drought stress, which is accompanied with a dynamic change in the root proteome in this plant (Yoshimura *et al.*, 2008). Drought-induced proteins include those for root morphogenesis such as actin and α -tubulin. Various enzymes for carbon/nitrogen metabolisms such as triosephosphate isomerase, malate dehydrogenase and methionine synthase are also induced under the stress, suggesting a global change in the cellular metabolism in the roots to support root growth at the early stage of drought stress. Interestingly, further changes in root proteome are observed at the later stage of drought stress, where factors for stress tolerance such as lignin synthesis-related proteins and molecular chaperones are preferentially induced at this stage. These results, therefore, suggested the presence of complex molecular networks for regulating abundance of respective proteins in this plant, in a temporally-programmed manner.

Towards understanding the molecular mechanisms for developing deep root system, experimental systems for exploring genetic resources in a given xerophyte should offer great opportunities to characterize genes involved in their root growth. A system for genetic engineering has been recently established in wild watermelon, where hairy root transformation technique enables to integrate a given foreign gene construct to both wild and domesticated varieties of watermelon (Kajikawa *et al.*, 2010). Moreover, generation of a large-scale EST database, as well as transcriptome analysis are ongoing for wild watermelon, which should offer valuable platforms for screening and mining useful genes in this xerophyte. It is anticipated that these approaches would unravel the molecular mechanisms of root vigor in this xerophyte under drought.

References

- Akashi K, Yoshimura K, Nanasato Y, Takahara K, Munekage Y and Yokota A. 2008. Wild plant resources for studying molecular mechanisms of drought/strong light stress tolerance. *Plant Biotechnol.* 25: 257-263.
- Bai L, Zhang G, Zhou Y, Zhang Z, Wang W, Du Y, Wu Z and Song CP. 2009. Plasma membrane-associated proline-rich extensin-like receptor kinase 4, a novel regulator of Ca signalling, is required for abscisic acid responses in *Arabidopsis thaliana*. *Plant J.* 60: 314-327.
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE and Schulze ED. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108: 583-595.
- Eapen D, Barroso ML, Ponce G, Campos ME and Cassab GI. 2005. Hydrotropism: Root growth responses to water. *Trends Plant Sci.* 10 :44–50.
- Gilroy S and Masson PH. 2008. Plant tropisms. Blackwell Publishing. Iowa. USA. Pp123-129.
- Graham EA, Nobel PS.1999. Root water uptake, leaf water storage and gas exchange of a desert succulent: implications for root system redundancy. *Ann. Bot.* 84: 213–223.

- Kajikawa M, Morikawa K, Abe Y, Yokota A and Akashi K. 2010. Establishment of a transgenic hairy root system in wild and domesticated watermelon (*Citrullus lanatus*) for studying root vigor under drought. *Plant Cell Rep.* 29: 771-778.
- Kawasaki S, Miyake C, Kohchi T, Fujii S, Uchida M and Yokota A. 2000. Responses of wild watermelon to drought stress: accumulation of an ArgE homologue and citrulline in leaves during water deficit. *Plant Cell Physiol.* 41: 864–873.
- Kobayashi A, Takahashi A, Kakimoto Y, Miyazawa Y, Fujii N, Higashitani A and Takahashi H. 2007. A gene essential for hydrotropism in roots. *Proc. Natl. Acad. Sci. USA.* 104: 4724-4729.
- Larcher W. 1995. Physiological plant ecology. Springer-Verlag, Berlin, Heidelberg, New York. Pp 277.
- Leung J, Merlot S and Giraudat J. 1997. The *Arabidopsis* ABSCISIC ACID-INSENSITIVE2 (ABI2) and ABI1 genes encode homologous protein phosphatases 2C involved in abscisic acid signal transduction. *Plant Cell* 9: 759–771.
- Miyake C and Yokota A. 2000. Determination of the rate of photoreduction of O₂ in the water-water cycle in watermelon leaves and enhancement of the rate by limitation of photosynthesis. *Plant Cell Physiol.* 41: 335–343.
- Miyazawa Y, Takahashi A, Kobayashi A, Kaneyasu T, Fujii N and Takahashi H. 2009. GNOM-mediated vesicular trafficking plays an essential role in hydrotropism of *Arabidopsis* roots. *Plant Physiol.* 149: 835-840.
- Schnall JA, Quatrano RS. 1992. Abscisic acid elicits the water-stress response in root hairs of *Arabidopsis thaliana*. *Plant Physiol.* 100: 216–218.
- Sharma S, Villamor JG and Verslues PE. 2011. Essential role of tissue-specific proline synthesis and catabolism in growth and redox balance at low water potential. *Plant Physiol.* 157: 292-304.
- Sharp RE, Hsiao TC and Silk WC. 1990. Growth of the maize primary root at low potentials. 2. Role of growth and deposition of hexose and potassium in osmotic adjustment. *Plant Physiol.* 93: 1337-1346.
- Sharp RE, Poroyko V, Hejlek LG, Spollen WG, Springer GK, Bohnert HJ and Nguyen HT. 2004. Root growth maintenance during water deficits: physiology to functional genomics. *J. Exp. Bot.* 55: 2343–2351.
- Shinozaki K, Yamaguchi-Shinozaki K and Seki M. 2003 Regulatory network of gene expression in the drought and cold stress responses. *Curr. Opin. Plant Biol.* 6: 410–417.
- Sidibe M and Williams JT. 2002. Baobab, *Adansonia digitata* L. Fruits for the future 4. International centre for underutilised crops. Chichester. England. Pp 15.
- Takahashi N, Yamazaki Y, Kobayashi A, Higashitani A and Takahashi H. 2003. Hydrotropism interacts with gravitropism by degrading amyloplasts in seedling roots of *Arabidopsis* and radish. *Plant Physiol.* 132, 805–810.
- Vartanian N, Marcotte L and Giraudat J. 1994. Drought rhizogenesis in *Arabidopsis thaliana*, differential responses of hormonal mutants. *Plant Physiol.* 104: 761–767.
- Voetberg GS, and Sharp RE. 1991. Growth of the maize primary root at low water potentials 3. Role of increased proline deposition in osmotic adjustment. *Plant Physiol.* 96: 1125-1130.
- Wasilewska A, Vlad F, Sirichandra C, Redko Y, Jammes F, Valon C, Frey N and Leung J. 2008. An update on abscisic acid signaling in plants and more. *Mol. Plant* 1:198–217.
- Wickens GE. 1998. Ecophysiology of economic plants in arid and semi-arid lands. Springer, Berlin, Germany.
- Xiong L, Wang R, Mao G and Koczan JM. 2006. Identification of drought tolerance determinants by genetic analysis of root response to drought stress and abscisic acid. *Plant Physiol.* 142: 1065-1074.
- Yoshimura K, Masuda A, Kuwano M, Yokota A and Akashi K. 2008. Programmed proteome response for drought avoidance/tolerance in the root of a C₃ xerophyte (wild watermelon) under water deficits. *Plant Cell Physiol.* 49: 226–241.

-- back to Table of Content --