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SHORT COMMUNICATION

Rice *OsERF71*-mediated root modification affects shoot drought tolerance

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ABSTRACT

Drought is the most serious problem that impedes crop development and productivity worldwide. Although several studies have documented the root architecture adaption for drought tolerance, little is known about the underlying molecular mechanisms. Our latest study demonstrated that overexpression of the *OsERF71* in rice roots under drought conditions modifies root structure including larger aerenchyma and radial root growth, and thereby, protects the rice plants from drought stresses. The *OsERF71*-mediated root modifications are caused by combinatory overexpression of general stress-inducible, cell wall-associated and lignin biosynthesis genes that contribute to drought tolerance. Here we addressed that the *OsERF71*-mediated root modifications alter physiological capacity in shoots without evidence of developmental changes for drought tolerance. Thus, the *OsERF71*-mediated root modifications provide novel molecular insights into drought tolerance mechanisms.

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Plants have evolved adaptive strategies to cope with the drought stress. Particularly, root architecture modification provides an informative example for plant response to drought stress. Plant roots are capable of detecting soil information such as water contents. Upon drought perception, plants give rise to root structural modification including length, number and radial expansion.[1-8] Alternatively or simultaneously, plant roots release uncharacterized drought-inducible signals that move to the aerial parts of the plants and confer drought tolerance to the shoot.[9-14] Although several studies have documented the root adaption for drought tolerance, little is known about the underlying molecular mechanisms not only that give rise to root morphological modification but also by which the root morphological adaptation affects plant capacity to drought stresses. Our latest study in Plant Physiology investigated drought-inducible rice OsERF71 transcription factor and explored the molecular mechanisms for drought-related root morphological adaptation that enhance plant capacity against drought stresses.[15]

OsERF71-*mediated root modification for drought tolerance*

Expression of OsERF71, a gene for an AP2/ERF transcription factor, is drought-inducible in an ABA independent mechanism. Overexpression of OsERF71 under the control of two different promoters, driving expression either in whole plant body (GOS2 promoter), or specifically in root (RCc3 promoter), results in drought-tolerant phenotypes at the vegetative growth stage. In addition, the transgenic rice plants with root-specific OsERF71 expression show the enhanced grain yield under drought stress in rice paddy field. These data indicate that the OsERF71 overexpression in roots is sufficient to confer drought tolerance. The OsERF71-mediated drought tolerance is connected to a root structure adaptation. The OsERF71 overexpression in roots alters radial root growth including larger aerenchyma and more cell layers between metaxylem cells. The larger aerenchyma are a root modification commonly found in drought tolerant rice plants, such that overexpression of OsNAC5, OsNAC9 and OsNAC10 activates radial root growth that enhances tolerance to drought stress.[4,6,7] Maize roots with large cortical aerenchyma also promote drought tolerance since it reduces the metabolic cost of soil exploration under water stress, permitting greater root growth and water acquisition from drying soil.[16] In addition to radial root growth, root elongation and high number of roots are associated with root structural adaptation to drought stresses.[3,5,8] For example, rice inbred lines (IR20 × MGL-2) with long and thick roots exhibit enhanced drought tolerance.[1] What is more, overexpression of TaNAC2 and HRD (HARDY) in A. thaliana or rice promotes primary and lateral root growth, increases root numbers and thereby enhances drought tolerance.[3,5] In this way, the drought-inducible OsERF71 that over-produced in rice roots under drought conditions, modifies root structure including larger aerenchyma and radial root growth, and thereby, protects the rice plants from drought stresses.

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Molecular mechanisms of the OsERF71-mediated drought tolerance

In our latest study of Plant Physiology, genome-wide analysis was performed to identify numerous downstream genes that are upregulated by OsERF71 transcription factor in the transgenic rice roots. They are divided into three categories: general stress-inducible genes, cell wall-associated genes, and lignin biosynthesis genes. Cell wall-associated proteins such as EXPANSIN, CHITINASE, and PECTINESTERASE are thought to be important for plant adaptation to drought stress by modifying root structure such as larger aerenchyma.[17-19] Additionally, OsERF71 controls lignin biosynthesis genes in roots by directly regulating the expression of CINNAMOYL-CoA REDUCTASE 1 (OsCCR1), a key gene in lignin biosynthesis. Since lignin is a key component of cell wall, OsERF71-mediated lignification contributes to cell shape and physiological modification together with other upregulated cell wall-associated genes and thereby, induces radial root growth. Furthermore, root lignification is known to be triggered by drought stress,[20-22] suggesting that the hydrophobic lignin property prevents water transpiration from plant tissues under drought conditions. Consequently, the OsERF71-mediated cell wall modifications such as lignification and cell wall loosening provide molecular insights into drought tolerance mechanisms via root structural adaptations.

Can the OsERF71-mediated root modification enhance shoot drought tolerance?

OsERF71 overexpression in rice roots induces drought tolerance in whole rice plants. To understand whether the OsERF71-induced root modification affects shoot capacity against drought stress, the photochemical efficiency of photosystem II that is determined by F_v/F_m measurements and that is reduced by drought stress, was analyzed with detached leaf discs from transgenic leaves. We treated leaf discs with drought stress for 1 h, because NT (non-transgenic) leaves exhibit a rapid decrease in F_v/F_m values as early as 1 h after the onset of the drought treatment. Under non-drought conditions, the F_v/F_m values were approximately 0.8 in leaf discs from two-week-old transgenic and NT rice plants (Fig. 1); however, under drought conditions, OsERF71 overexpression lines showed 20–35% higher F_v/F_m values than those of the NT controls (Fig. 1). These data suggest that OsERF71 overexpression in rice root is sufficient to enhance drought tolerance in rice shoots.

How does the OsERF71-mediated root modification affect shoot drought capacity against drought stress? The OsERF71-mediated root modification may affect developmental changes of shoots. For example, drought treatment to roots causes leaf growth inhibition and stomatal behavior modification together with leaf cell-wall-hardening via osmotically generated hydraulic signals and ABA.[13,23-25] Inhibition of leaf growth is often a primary plant response to moderate water stress.[23,26] However, since we found no developmental abnormality in shoots of OsERF71 overexpression rice plants, it is not persuasive. Alternatively, plant shoots get drought tolerant capacity based on physiological modification without developmental changes.

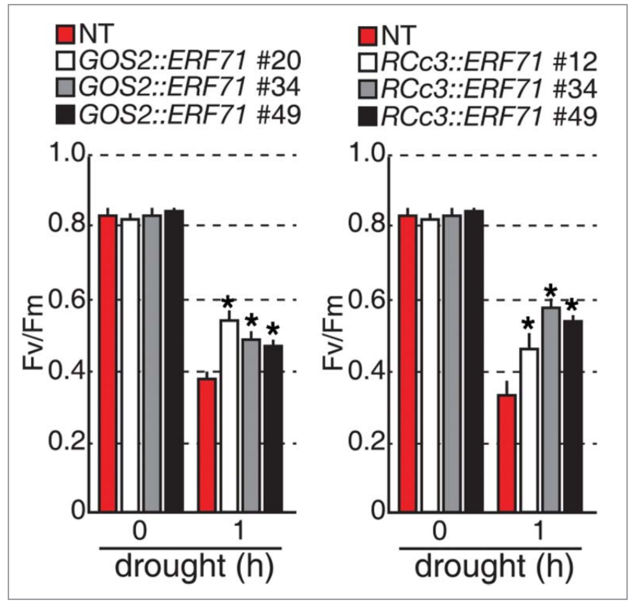

Figure 1. Photochemical efficiency (F_v/F_m) of *GOS2::OsERF71* and *RCc3::OsERF71* transgenic rice plants. Three independent homozygous *GOS2::OsERF71* and *RCc3::OsERF71* transgenic lines and NT controls were grown in soil for 2 weeks and detached leaf discs were exposed to a drought stress. F_v/F_m values were measured using a pulse modulation fluorometer. Data are shown as the mean + SD (n = 30). Asterisks indicate significant differences compared with NT control plants (*$P < 0.05$* by Student's t-test).

The OsERF71 overexpression rice leaves may have high water content due to reduction of water loss in roots by OsERF71-mediated root lignification. For example, transcription levels of two maize lignin biosynthesis CCR1 and CCR2 genes are increased after only 1 hr of drought stress treatment in the root elongation zone.[20] Accumulation of lignin in the root is involved in water loss prevention and, therefore can supply water to the aerial part of plants.[27] Thus, the OsERF71-mediated root lignification modifies physiological capacity in shoots for drought tolerance.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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