

A New Order through Disorder: Intrinsically Disordered Proteins Reshape the Cytoskeleton under Drought Stress

Many proteins have a clearly defined structure-function relationship: specific three-dimensional folds can be linked to specific protein functions. We do, however, know that many proteins, referred to as intrinsically disordered proteins (IDPs), lack rigid three-dimensional organization. In recent years, IDPs have been recognized as key components of many signaling networks. In plants, they are linked particularly to stress responses, during which they perform important functions to elicit appropriate physiological and developmental changes that are needed for environmental acclimation and survival (Covarrubias et al., 2017). Intrinsic disorder allows these proteins to interact with multiple partners but also to form highly complementary binding interfaces that ensure high binding specificity. Moreover, while many proteins tend to aggregate under adverse conditions, such as heat or water shortage, their flexible structure renders IDPs generally less prone to aggregation. Taken together, these features make them excellent candidates for signaling hubs under stress conditions (Sun et al., 2013; Liu and Huang, 2014). While many IDPs are associated with plant stress responses, our understanding of the underlying signaling mechanisms is still fairly limited. In this issue of *Plant Physiology*, Hsiao et al. (2020) reveal how a group of rice (*Oryza sativa*) IDPs contributes to changes in root architecture under drought stress.

Upon perception of water shortage, plants trigger an array of responses to ensure survival, ranging from short-term physiological acclimation such as stomatal closure to long-term alterations in their development. Growth usually slows down when water is scarce, and

although root growth is usually less inhibited than shoot growth, prolonged water shortage does eventually cause progressive inhibition of root elongation (Sharp et al., 2004). Both root growth maintenance and growth arrest are regulated by the phytohormone abscisic acid (ABA; Sharp et al., 2004; Sun et al., 2018). Accumulation of ABA is a widespread response to drought and in turn triggers the expression of many stress-associated genes. In rice, expression of the *REPETITIVE PROLINE-RICH PROTEIN* (*OsRePRP*) gene family is strongly up-regulated in the root elongation zone upon water stress and ABA treatment, and the respective proteins are required to restrict root elongation growth under severe drought stress (Tseng et al., 2013).

OsRePRPs are predicted to be intrinsically disordered, with a Pro content of up to 40% (Tseng et al., 2013), and these Pro-rich domains bear resemblance to actin-binding proteins in animals. This observation prompted Hsiao et al. (2020) to investigate whether *OsRePRPs* interact with actin as well as tubulin, the other main component of the plant cytoskeleton. They indeed observed interaction of *OsRePRP1* and *OsRePRP2* with both actin and tubulin in vitro and in vivo and found *OsRePRPs* to colocalize with cytoskeleton markers in planta. Taken together, these observations imply a functional link between *OsRePRPs* and the plant cytoskeleton. While the cytoskeleton takes on manifold functions, in plant cells it is particularly important for cell wall structure and composition: actin filaments provide roads for vesicle trafficking to and from the plasma membrane, while microtubules

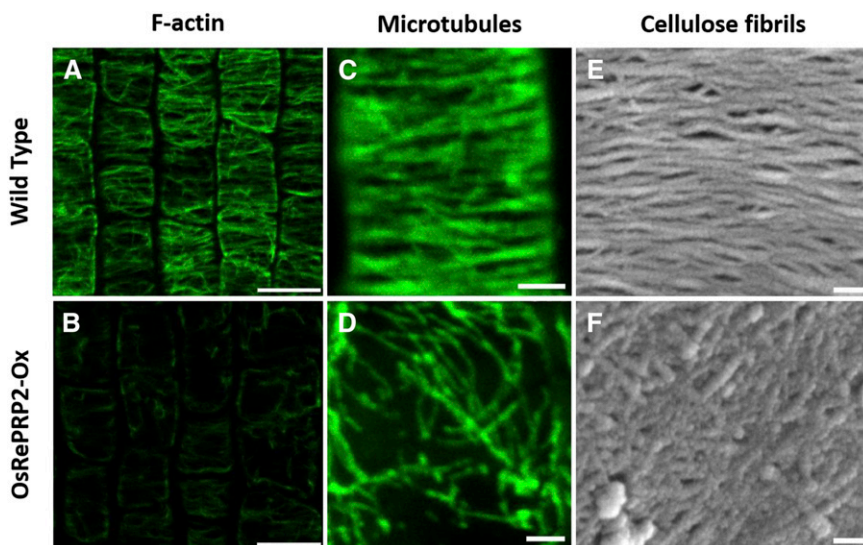


Figure 1. *OsRePRPs* affect plant cytoskeleton organization. Micrographs show actin filaments (A and B) and microtubules (C and D) detected with fluorescent markers and cellulose fibrils (E and F) observed by scanning electron microscopy. Phenotypes were analyzed in roots of wild-type and *OsRePRP2* overexpressor (*OsRePRP2-Ox*) plants. Bars = 10 μm (A and B), 2 μm (C and D), and 100 nm (E and F). Reproduced from Hsiao et al. (2020), figures 4, 5, and 6.

guide cellulose synthase complexes and thereby determine the orientation of cellulose fibrils within the cell wall. Do OsRePRPs affect these processes? To answer this question, the authors analyzed multiple molecular and cellular phenotypes in *OsRePRP2* overexpressor and *OsRePRP1/2* RNA interference knockdown lines. Their analyses revealed that OsRePRPs reduce the abundance of actin filaments (Fig. 1, A and B), causing reduced transport of noncellulosic polysaccharides to the plasma membrane. In parallel, OsRePRPs trigger reorientation of microtubules, which translates into a disorganized network of cellulose microfibrils in the cell wall (Fig. 1, C–F). Together, these effects hamper cell expansion and thereby restrict elongation growth in roots.

Notably, Hsiao et al. (2020) find that severe water shortage and *OsRePRP* overexpression make roots not only shorter but also heavier: OsRePRPs boost starch accumulation, which is potentially linked to increased Suc synthase activity, and thereby cause roots to gain weight. Therefore, it seems that, under severe drought stress, rice roots switch from source to sink mode: they arrest growth and become a dormant storage organ. Entering a quiescent state is also observed under what could be considered the opposite condition, namely prolonged submergence. The molecular response to flooding is quite distinct from the drought response and involves accumulation of the plant hormone ethylene (Loreti et al., 2016). While the signaling cascades leading to it differ considerably under different circumstances, quiescence may represent a general strategy of certain rice cultivars to overcome unfavorable environmental conditions and ensure plant survival.

In conclusion, the study by Hsiao et al. (2020) uncovers a molecular role for IDPs of the OsRePRP family, which can reorganize the highly ordered structure of a cell's cytoskeleton to alter root growth and physiology

to promote stress tolerance. Especially the fact that they can interact with both major types of plant cytoskeleton filaments is quite remarkable and certainly warrants further investigation. It remains to be seen how exactly the OsRePRPs establish these interactions and thereby trigger cytoskeletal reorganization; a combination of cell biological, biophysical, and biochemical approaches will be required to fully understand the underlying mode of action of these proteins.

Martin Balcerowicz^{1,2}

ORCID ID: 0000-0001-9462-4436

Assistant Features Editor

**Sainsbury Laboratory, University of Cambridge,
Cambridge CB2 1LR, United Kingdom**

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¹Author for contact: martin.balcerowicz@slcu.cam.ac.uk.

²Senior author.

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