The physiology of plant responses to drought

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Drought alone causes more annual loss in crop yield than all pathogens combined. To adapt to moisture gradients in soil, plants alter their physiology, modify root growth and architecture, and close stomata on their aboveground segments. These tissue-specific responses modify the flux of cellular signals, resulting in early flowering or stunted growth and, often, reduced yield. Physiological and molecular analyses of the model plant Arabidopsis thaliana have identified phytohormone signaling as key for regulating the response to drought or water insufficiency. Here we discuss how engineering hormone signaling in specific cells and cellular domains can facilitate improved plant responses to drought. We explore current knowledge and future questions central to the quest to produce high-yield, drought-resistant crops.

Drought is a misfortune for agriculture, humanity, and livestock alike (1). Climate change is leading us toward a hotter, more parched world (2). There is an urgent need to produce high-yielding plants that use water more efficiently than their present-day counterparts (Fig. 1A). In the past decade, global losses in crop production due to drought totaled ~$30 billion. Global population rose from 5 billion inhabitants in 1990 to more than 7.5 billion presently and is predicted to rise to 9.7 billion to 10 billion by 2050 (3), at which time 5 billion people are projected to be living in water-scarce regions (Fig. 1B) (4). Despite the moderate increase in global arable land, an additional 1 million ha will be needed to ensure food security (Fig. 1C) (5). In addition, water demand for agriculture could double by 2050, whereas the availability of fresh water is predicted to drop by 50%, owing to climate change (Fig. 1D) (6). Certainly, plant biotechnology holds one of the promises to meet the societal demand for increased global crop production.

Water is crucial for plant survival, and water deficits limit plant growth. However, plants have strategies to prevent water loss, balance optimal water supply to vital organs, maintain cellular water content, and persevere through periods of drought. The ability of a plant to sense the water-deficiency signal and initiate coping strategies in response is defined as drought resistance. Drought resistance is a complex trait that proceeds through several mechanisms: (i) escape (acceleration of plant reproductive phase before stress that could hinder its survival), (ii) avoidance (endurance with increased internal water content and prevention of tissue damage), and (iii) tolerance (endurance with low internal water content while sustaining growth over the drought period) (7). After a period of drought, the percentage of viable plants upon rewetting is referred to as the drought survival rate. From the perspective of molecular biology, cellular water loss marks the first event of drought stress. At the cellular level, drought signals promote production of stress-protectant metabolites such as proline and trehalose, trigger the antioxidant system to maintain redox homeostasis, and deploy peroxidase enzymes to prevent acute cellular damage and membrane integrity. Factors such as the extent of water stress and the plant organ in which the stress is sensed also trigger specific signaling responses, including but not limited to abscisic acid, brassinosteroids, and ethylene phytohormone pathways (8–11).

Drought’s impact on agriculture depends on the degree and duration of the reduced precipitation and soil water gradients, as well as on plant species and developmental stages (8). In most instances, crops experience moderate droughts caused by prolonged precipitation deficits, reduced groundwater levels, and/or limited access to water supplies, leading to substantial losses in overall yield. Therefore, investigating the mechanisms of how a plant sustains its growth during moderate drought and devising strategies to improve plant health during such periods can provide solutions for future food security. Understanding the response of cellular signaling to water shortage is key for shedding light on these modern agricultural problems (12). Here we explore how water availability cues cell and tissue growth patterns and how these patterns are coordinated in the whole plant to improve drought resistance without loss of yield. Overexpression of drought-responsive genes often results in growth deficits and yield loss. Tissue- or time-specific expression of drought-response traits may improve drought response without depressing yield. A combination of strategies may boost agricultural yields despite increased water insecurity.

**Traits for improving drought resistance**

During drought spells, plant systems actively maintain physiological water balance by (i) increasing root water uptake from the soil, (ii) reducing water loss by closing stomata, and (iii) adjusting osmotic processes within tissues (13). Activated stress response pathways include phytohormone signaling as well as antioxidant and metabolite production and mobilization (11).
Roots respond to changes in soil moisture at the cellular scale and with the entire root system architecture. The root stem cell niche, meristem, and vasculature each coordinate responses to drought (Fig. 2, A and B). During periods of water scarcity, the root system architecture undergoes morphological changes to enhance its ability to absorb water and nutrients (9, 10). These modifications can be traced to coordinated cell division, elongation, and differentiation events in the root apex. In the pursuit of moisture, root systems grow differentially and adapt their architecture to be either deep or shallow (Fig. 2C). Longer and deeper roots with reduced branching angles can efficiently capture water from soil that is dry at the surface but retains moisture in deep layers. By contrast, shallower root architectures are more beneficial for maximizing water capture from the soil surface in regions of low precipitation (9). Roots that encounter a soil environment with nonhomogeneous water distribution display hydropatterning by favoring lateral root emergence toward soil patches with higher water content, a process that is also mediated by auxin signaling (9, 14). Another adaptive response to nonhomogeneous distribution of moisture through soil is hydrotropism (Fig. 2D), in which root tips grow toward zones with higher water content to optimize the root system architecture for water acquisition (15).

Stomatal closure is a more rapid defense against dehydration (Fig. 2, D and E). Stomatal pores on leaf surfaces open or close according to the turgidity of the surrounding guard cells. The turgor-driven shape changes of guard cells are affected by the cell wall structure, plasma membrane, tonoplast properties, and cytoskeletal dynamics (16). Plant vascular tissues, the xylem and phloem, transmit water availability signals from roots to shoots and transmit photoassimilates from shoots to roots, respectively (17). Development of these inner vasculature tissues also affects drought resistance. Crop yield becomes most vulnerable if the drought occurs during a plant’s reproductive phase. In Arabidopsis thaliana, early flowering associated with drought escape is linked to phloem loading and transport of the photoperiod-dependent protein FLOWERING LOCUS T (FT) from leaves to the shoot apical meristem (18).

Phytohormones to combat drought

The hormone abscisic acid (ABA) regulates plant responses to dehydration and optimizes water use. Dehydration signals stimulate local production of ABA in different plant organs. However, ABA production is more efficient in the leaf mesophyll cells than in the root tissues (19). The accumulated ABA then activates downstream signaling components (20). ABA executes its function during stress by mediating signal cross-talk with other pathways (Fig. 3) (21). Many existing schemes to improve water use efficiency and drought resistance engage the ABA pathway.

Genetic engineering to improve the function of PYR/PYL/RCAR (Pyrabactin Resistance 1/ PYR1-Like/Regulatory Component of ABA Receptors) and SnRK2 (SNF1-related protein kinase 2) and repress the negative regulator PP2C (clade A type 2C protein phosphatase) has resulted in improved water use efficiency in plants such as A. thaliana and wheat under controlled laboratory growth conditions and greenhouses (22–25). A regulatory network of ABA pathway genes, a hierarchy of ABA-related transcription factors, and signaling feedback were identified among ABA-mediated stress responses to drought (26). Engineering the ABA receptor PYR1 for heightened sensitivity toward the preexisting agrochemical mandipropamid resulted in improved drought resistance in A. thaliana and tomato (22). Virtual screening for ABA receptor agonists led to the identification of a bioactive ABA mimic called opabactin. This small molecule can enhance ABA receptor activation and downstream signaling to improve water use efficiency and drought resistance in A. thaliana, tomato, and wheat (27). Thus, computational design combined with experimental biology led to identification of a small molecule that can mitigate the effects of drought on crop yields.

Brassinosteroid hormones also regulate drought response through signaling components linked to the ABA response pathway (Fig. 3) (28, 29). Brassinosteroid signaling negative regulator BRASSINOSTEROID-INSENSITIVE 2 (BIN2) is dephosphorylated by ABA INSENSITIVE1 (ABI1) and ABI2. ABA activates BIN2 by inhibiting the activity of ABI1 and ABI2 (30). BIN2 phosphorylates SnRK2s and activates the downstream pathway (31). ABA signals can also converge with the brassinosteroid pathway at the level of downstream transcription factors (Fig. 3). BRI1-EMS-SUPPRESSOR 1 (BES1) inhibited ABA induction of a drought-related transcription factor RESPONSIVE TO DESECCATION 26 (RD26) (32). RD26 shows reciprocal antagonism with brassinosteroid by modulating BES1-regulated transcription and inhibiting brassinosteroid-regulated growth (33). WRKY46,
-54, and -70 belong to another class of transcription factors that interact with BES1 to promote plant growth while repressing drought responses (34). BIN2 can phosphorylate and destabilize WRKY54 to negatively regulate its effect on the BES1-mediated brassinosteroid response (35). BIN2 phosphorylates and activates the ubiquitin receptor protein DSK2, which leads to BES1 degradation via autophagy and coordinates plant growth and survival under drought conditions (36). An AP2/ERF transcription factor called TINY is another candidate that balances brassinosteroid-mediated stress adaptation with growth. TINY interacts with BES1 and antagonizes brassinosteroid-regulated growth. BIN2, on the other hand, phosphorylates and stabilizes TINY to promote ABA-induced stomatal closure and drought resistance (37). Thus, brassinosteroids as well as ABA aid drought resistance.

**Tissue-specific responses for drought resistance**

Stomatal closure preserves water in the plant. ABA content in leaves regulates stomatal movement in response to water availability (25) (Fig. 3). Because stomatal movements control CO₂ influx and transpiration, efforts to reduce water loss via stomatal closure occur at the cost of photosynthesis, growth, and yield (13). Therefore, most strategies to improve water efficiency and drought resistance in plants focus on fine-tuning stomatal conductance and manipulating ABA signaling via stomata-specific promoters (38). With optogenetics, scientists have improved the responsiveness of the stomata and overcome the coupling of CO₂ uptake with water vapor loss. Upon introducing BLINK1 (a light-activated synthetic K⁺ channel) into guard cells, storing BLINK1 (a light-activated synthetic water vapor loss. Upon introduction of the exocytosis system, is expressed in root tips. EXO70A3 regulates local auxin transport by affecting the homeostasis of the auxin efflux carrier PIN-FORMED 4 in root columella cells (Fig. 3). Natural variation in EXO70A3 was correlated with seasonal precipitation and conferred different adaptive root system architecture configurations under different rainfall patterns. In areas with high temperatures and irrigated soils, deeper root architectures proved better for drought adaptation. In rice, the auxin-inducible gene DEEPER ROOTING1 provides drought resistance by promoting a more vertical and deeper root system architecture (47). Although auxin modulates root architecture under stress (40, 41), hydrotropic root responses function relatively independent of auxin and involve ABA signaling in root elongation zones. Coordinated activity of ABA-inducible MIZU-KUSSEI1 (MIZ1) and SNF1-RELATED KINASE 2 (SnRK2:2) in root elongation zone cortical cells interprets water potential gradients in soil environments (15, 42).

Brassinosteroid receptors regulate root hydrotropic responses (Fig. 3). Overexpression of the vascular-enriched brassinosteroid receptor BRI1–Like3 (BRL3) promotes root hydrotropic bending. The brl1brl3bak1 triple mutant of the BRL3 signalosome shows a reduced hydrotropic response, suggesting a role for the vascular BRL3 receptor complex in regulating hydrotropic responses (43) (Fig. 3). Activation of the BRL3 pathway in vasculature triggers accumulation of osmoprotectant metabolites such as proline, trehalose, and raffinose family oligosaccharides in plant roots in response to water withdrawal, which improves drought resistance without penalizing growth (43) (Fig. 3). Phloem-specific localization of BRL3 is likely to be the determining factor for promoting drought resistance without impairing yield (29, 43).

In drought conditions, roots sense water scarcity from soil. The above-ground segments of plants respond by closing stomata in leaves, implicating a systemic communication system. In times of drought, the CLE25 peptide is produced in the roots and moves through the vasculature to plant leaves to drive ABA production by activating the biosynthetic enzyme NCED3. This burst of ABA synthesis leads to stomatal closure and improved water balance, thereby promoting drought survival (44) (Fig. 3). This insight into small-peptide signaling in *A. thaliana* may help with identification of similar mechanisms in crop plants for root-to-shoot mobilization of stress signals.

**A view to the future**

Genetic traits that sustain crop plant growth under moderate drought may come from multiple sources, including natural genetic variation in wild relatives or bioengineering. Traditional breeding has been the main strategy for exploiting the genetic diversity of adaptive traits in natural alleles. The advent of genomic

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*Fig. 3. Hormone signaling events underpinning drought.* Schematic representation of hormone signaling modules that control drought adaptation. Plants work against dehydration in organs such as leaves, vasculature, and roots. ABA, through SnRK2, activates a variety of genes that trigger stomata closure and improve water balance. When roots sense drought, the CLE25 peptide moves through the vasculature to the leaves, where it locally controls ABA biosynthesis and stomata closure. brassinosteroids also play roles in regulating plant drought response. Brassinosteroid pathways converge with ABA by activating SnRK2 through downstream pathway component BIN2 and vice versa. Independently of ABA, brassinosteroid receptors (BRI1, BRL1, and BRL3) modulate hydrotropic responses in the roots. The vascular BRL3 receptor coordinates plant growth and survival under drought stress by promoting the accumulation of osmoprotectant metabolites in the root tissues. Furthermore, noncanonical auxin responses via EXO70A3 and PIN4 can modulate root architecture patterning and depth to boost water absorption from the soil, thereby improving drought tolerance.
technologies and gene mapping tools such as genome-wide association study (GWAS) and precision genome editing with the CRISPR-Cas9 system has been instrumental for the generation of alleles that can improve plant yield and performance under various stresses. Molecular studies that use tissue- or cell-specific promoters coupled with live microscopy techniques for real-time visualization of cellular processes are paving the way for analysis of drought response networks that can be targeted by various approaches (Fig. 4). Small molecules such as peptides or hormone agonists may be useful for fine-tuning drought response pathways while preserving yield in agriculture. Together, research efforts aimed at uncovering the physiology of plant responses to drought in model systems and translating these findings to crops will deliver new strategies to combat water scarcity. Discovering ways to ameliorate agriculture’s “thirst” will ease competition for freshwater resources, even as the world’s population grows.

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Fig. 4. The promise of overcoming drought in agriculture. Genetic strategies provide solutions to counteract drought and can be used to develop drought-smart crops. Traditional breeding approaches have selected drought characteristics to obtain more-resistant crops. Advancements in gene mapping tools such as GWAS can explore the genetic diversity of drought resistance traits in natural alleles with nucleotide-level precision. Genetic engineering of drought response markers at the spatiotemporal scale and precise genome editing with tools such as CRISPR-Cas9 have opened new horizons for developing crops with improved drought resistance, without sacrificing yield. Emerging techniques such as optogenetics allow fine manipulation of cell- and tissue-specific responses to signaling and therefore increase growth and plant resistance to drought. Small peptides, hormone mimics, and receptor agonists can be used to design better agrochemicals and fine-tune drought resistance while preserving yield.

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