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1 **MANUSCRIPT TYPE:** Review article

2 **TITLE:** The Physiology of Plant Responses to Drought

3

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8

9 **KEYWORDS**

10 Drought, abiotic stress, signaling, root, hydrotropism, stomata, water use efficiency, climate  
11 change, food security, Arabidopsis, cereals, sorghum, crops.

12

13 **ABSTRACT**

14 Drought alone causes more yield loss annually than all pathogens combined (1). To adapt to  
15 moisture gradients in soil, plants alter their physiology, modify root growth and architecture, and  
16 close stomata on the above-ground plant. These tissue-specific responses modify the flux of signals  
17 along the plant, resulting in early flowering or stunted plant growth that often reduce yield.  
18 Physiological and molecular analyses of the model plant *Arabidopsis thaliana* (Arabidopsis) have  
19 identified phytohormone signaling as key for regulating response to drought or water insufficiency.  
20 Here, we discuss how engineering hormone signaling in specific cells and cellular domains  
21 promises to improve plant responses to drought. We explore current knowledge and future  
22 questions in the quest to produce high-yield, drought-resistant crops.

23

24

## 25 INTRODUCTION

26 Drought is a misfortune for agriculture, humanity and livestock alike. Climate change is leading  
27 us towards a hotter, more parched world (2). There is an urgent need to produce high-yielding  
28 plants that are more efficient at using water (Fig. 1a). In the last decade, global losses in crop  
29 production due to drought estimated around 30 billion dollars. Global population raised from 5  
30 billion inhabitants in the 1990 to over 7.5 billion presently and is predicted to raise to 9.7-10 billion  
31 by 2050 (3), half of which (i.e. 5 billion people) is estimated to be living in water-scarce areas of  
32 the planet (Fig. 1b) (4). Despite the moderate increase in global arable land, an additional 1 million  
33 Ha will be needed to ensure food security (Fig. 1c) (5). In addition, water demand for agriculture  
34 need to duplicate by 2050, whereas the fresh water availability is predicted to drop by half cause  
35 of climate change (Fig. 1d) (6). Certainly, plant biotechnology holds one of the promises to meet  
36 the societal demand to duplicate crop production in the planet.

37

38 Water is crucial for plant survival and water deficit limits plant growth. However, plants have  
39 strategies to prevent water loss, to balance optimal water supply to all vital organs, to maintain the  
40 cellular water content, and to persevere through periods of drought. The ability of a plant to sense  
41 the water deficiency signal and initiate the coping strategies in response to drought signal is defined  
42 as drought resistance. Drought resistance is a complex trait that impinges on several mechanisms  
43 referred as: i) escape (acceleration of plant reproductive phase before stress that could hinder its  
44 survival), ii) avoidance (endurance with increased internal water content and preventing tissue  
45 damage), and iii) tolerance (endurance with low internal water content, whereas sustaining growth  
46 over the drought period (7). The percentage of viable plants after a period of drought upon re-  
47 watering is referred as drought survival. From molecular biology perspective, cellular water loss

48 marks the first event of drought stress. At the cellular level, drought signals promote production  
49 of stress-protectant metabolites such as proline and trehalose; trigger antioxidant system to  
50 maintain redox homeostasis and prevent acute cellular damage and membrane integrity by  
51 peroxidase enzymes. Factors such as extent of water stress and the plant organ in which the stress  
52 is sensed also trigger specific signaling responses, including but not limited to; abscisic acid,  
53 brassinosteroids, and ethylene phytohormone pathways (8-11).

54  
55 The impact that drought has on agriculture depends on the degree and duration of the reduced  
56 precipitation and soil water gradients as well as on the species and developmental stage of the  
57 plants (8). However, for most instances, crops experience moderate droughts caused by prolonged  
58 precipitation deficits, reduced ground water levels, and/or limitation in accessing water supplies  
59 leading to substantial losses in overall yield. Therefore, investigating the mechanisms of how a  
60 plant sustains its growth during moderate drought and devising new strategies to improve plant  
61 health during such moderate drought periods can provide us solution for future food security.  
62 Understanding the response of cellular signaling to water shortage is a priority to answer the above-  
63 mentioned questions for modern agriculture (12). Here we explore how water availability cues cell  
64 and tissue growth patterns and how these growth patterns are coordinated in the whole plant to  
65 improve drought resistance without loss of yield. Overexpression of drought-responsive genes  
66 often results in growth deficits and yield loss. Tissue- or time-specific expression of drought-  
67 response traits may improve drought response without depressing yield. A combination of  
68 strategies may improve agricultural yields despite increased water insecurity.

69

70 ***Traits for improving drought resistance***

71 During drought spells, plant systems work actively to maintain the physiological water balance.  
72 This is achieved by: i) increased root water uptake from the soil, ii) reduced water loss by closing  
73 stomata, and iii) osmotic adjustment within plant tissues (13). Activated stress response pathways  
74 include phytohormone signaling, antioxidant and metabolite production and mobilization (11).

75

76 Roots respond to changes in soil moisture both at the cellular scale and at the entire root system  
77 architecture. The root stem cell niche, meristem, and vasculature each coordinate responses for  
78 drought (Fig. 2a, b). During water scarcity, the root system architecture undergoes morphological  
79 changes to enhance its ability to absorb both water and nutrients (9,10). These modifications can  
80 be traced to coordinated cell division, elongation and differentiation events in the root apex. Root  
81 systems grow differentially to adapt their architecture to be either deep or shallow, in search of  
82 moisture (Fig. 2c). Longer and deeper roots with reduced branching angles can efficiently capture  
83 water from soil that may be dry at the surface but have deep layers retaining moisture. In contrast,  
84 shallower root architectures are more beneficial in regions of low precipitations to maximize water  
85 capture from the soil surface (9). Roots that encounter a soil environment with non-homogeneous  
86 water distribution display hydro-patterning by favoring lateral root emergence towards soil patches  
87 with higher water content, a process that is also mediated by auxin signaling (9, 14). Another  
88 adaptive response to non-homogeneous distribution of moisture through soil is hydrotropism (Fig.  
89 2d), where root tips grow towards zones with higher water content to optimize the root system  
90 architecture for water acquisition (15).

91

92 Stomatal closure is a more rapid defense against dehydration (Fig. 2d, e). Stomatal pores, on leaf  
93 surfaces, open or close according to turgidity of the surrounding guard cells. The turgor-driven

94 shape changes of guard cells are affected by cell wall structure, the plasma membrane, the  
95 tonoplast properties, and cytoskeletal dynamics (16). Plant vascular tissues, xylem and phloem,  
96 transmit water availability signals from roots to shoots and transmit photoassimilates from shoots  
97 to roots respectively (17). Development of these inner vasculature tissues also affects drought  
98 resistance. Crop yield becomes most vulnerable if the drought occurs during reproductive phase  
99 of plant. In Arabidopsis, early flowering associated to drought escape is linked with the phloem  
100 loading and transport of photoperiod-dependent protein FLOWERING LOCUS T (FT) from  
101 leaves to the shoot apical meristem. (18)

102

### 103 ***Phytohormones to combat drought***

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

110

111 Genetic engineering to improve Pyrabactin Resistance 1/PYR1-Like/Regulatory Component of  
112 ABA Receptors (PYR/PYL/RCAR) and SnRK2s functions and repress the negative regulators  
113 clade A type 2C protein phosphatases (PP2Cs) have resulted in improved water use efficiency in  
114 plants such as Arabidopsis and wheat under controlled laboratory growth conditions and  
115 glasshouses (22-25). A regulatory network of ABA pathway genes, a hierarchy of ABA-related  
116 transcription factors, and signaling feedback were identified among ABA-mediated stress

117 responses to drought (26). Engineering the ABA receptor PYR1 for heightened sensitivity towards  
118 the pre-existing agrochemical mandipropamid resulted in improved drought resistance in  
119 Arabidopsis and tomato (22). Virtual screening for ABA receptor agonists led to the identification  
120 of a bioactive ABA mimic called opabactin. This small molecule can enhance ABA receptor  
121 activation and downstream signaling to improve water use efficiency and drought resistance in  
122 Arabidopsis, tomato and wheat (27). Thus computational design combined with experimental  
123 biology led to identify a small molecule that can mitigate the effects of drought on crop yields.

124

125 Brassinosteroid hormones also regulate drought response through signaling components linked to  
126 the ABA response pathway (Fig. 3) (28, 29). Brassinosteroid signaling negative regulator  
127 BRASSINOSTEROID-INSENSITIVE 2 (BIN2) is dephosphorylated by ABA INSENSITIVE1  
128 (ABI1) and ABI2. ABA activates BIN2 by inhibiting ABI1/ABI2 activity (30). BIN2  
129 phosphorylates SnRK2s and activates the downstream pathway (31). ABA signals can also  
130 converge with the brassinosteroid pathway at the level of downstream transcription factors (Fig.  
131 3). BRI1-EMS-SUPPRESSOR 1 (BES1) inhibited ABA induction of a drought-related  
132 transcription factor RESPONSIVE TO DESICCATION 26 (RD26) (32). RD26 shows reciprocal  
133 antagonism with brassinosteroid by modulating BES1-regulated transcription and inhibiting  
134 brassinosteroid -regulated growth (33). WRKY46, 54, and 70 belong to another class of  
135 transcription factors that interact with BES1 to promote plant growth while repressing drought  
136 responses (34). BIN2 can phosphorylate and destabilize WRKY54 to negatively regulate its effect  
137 on the BES1-mediated brassinosteroid response (35). BIN2 phosphorylates and activates the  
138 ubiquitin receptor protein DSK2, which leads to BES1 degradation via autophagy and coordinates  
139 plant growth and survival under drought conditions. (36). An AP2/ERF transcription factor called

140 TINY is another candidate that balances brassinosteroid-mediated stress adaptation with growth.  
141 TINY interacts with BES1 and antagonizes brassinosteroid-regulated growth. BIN2 on the other  
142 hand phosphorylates and stabilizes TINY to promote ABA-induced stomatal closure and drought  
143 resistance (37). Thus, brassinosteroid as well as ABA aids drought resistance.

144

#### 145 *Tissue-specific responses for drought resistance*

146 Stomatal closure preserves water in the plant. ABA content in leaves regulates stomatal movement  
147 in response to water availability (25) (Fig. 3). Since stomatal movements control CO<sub>2</sub> influx and  
148 transpiration, efforts to reduce water loss via stomatal closure occur at the cost of photosynthesis,  
149 growth, and yield (13). Therefore, most strategies to improve water efficiency and drought  
150 resistance in plants focus on fine-tuning stomatal conductance and manipulating ABA signaling  
151 via stomata-specific promoters (38). With optogenetics, scientists have improved the  
152 responsiveness of the stomata and overcome the coupling of CO<sub>2</sub> uptake with water vapor loss.  
153 Upon introducing BLINK1, a light-activated synthetic K<sup>+</sup> ion channel, into guard cells, stomata  
154 became more synchronized with fluctuating light conditions (39). This manipulation improved the  
155 performance of the stomata and, as a consequence, growth and productivity of the plant. Thus,  
156 water use efficiency was improved by engineering stomata to maximize the amount of carbon  
157 fixed per unit of water lost.

158

159 Improving water acquisition by roots can also improve plant performance upon drought. In  
160 Arabidopsis, an auxin pathway modulator EXOCYST SUBUNIT EXO70 FAMILY PROTEIN A3  
161 (EXO70A3) that regulates depth of the root system was identified using a genome-wide  
162 association (GWA) mapping (40). EXO70A3, a component of the exocytosis system, is expressed



163 in root tips. EXO70A3 regulates local auxin transport by affecting the homeostasis of auxin efflux  
164 carrier PIN-FORMED 4 in root columella cells (Fig. 3). Natural variation in EXO70A3 was  
165 correlated with seasonal precipitation and conferred different adaptive root system architecture  
166 configurations under different rainfall patterns. In areas with high temperatures and irrigated soils,  
167 deeper root architectures proved better for drought adaptation. In rice, an auxin inducible gene  
168 *DEEPER ROOTING1* provides drought resistance by promoting a more vertical and deeper root  
169 system architecture (41). Although auxin modulates root architecture under stress (40, 41),  
170 hydrotropic root responses are fairly auxin-independent and involve ABA signaling in root  
171 elongation zones. Coordinated activity of the ABA inducible MIZU-KUSSEI1 (MIZ1) and SNF1-  
172 RELATED KINASE 2 (SnRK2.2), in root elongation zone cortical cells interprets water potential  
173 gradients in soil environments (15, 42).

174  
175 Brassinosteroid receptors regulate root hydrotropic responses (Fig. 3). Overexpression of a  
176 vascular-enriched brassinosteroid receptor BRI1-Like3 (BRL3) promoted root hydrotropic  
177 bending. The *brl1brl3bak1* triple mutant of BRL3 signalosome showed reduced hydrotropic  
178 response, suggesting a role for the vascular BRL3 receptor complex in regulating hydrotropic  
179 responses (43) (Fig. 3). Activation of the BRL3 pathway in vasculature triggered accumulation of  
180 osmoprotectant metabolites such as proline, trehalose, and raffinose family oligosaccharides in  
181 plant roots in response to water withdrawal, which improved drought resistance without penalizing  
182 growth (43) (Fig. 3). Phloem-specific localization of BRL3 is likely to be the determining factor  
183 for promoting drought resistance without impairing yield (29, 43).

184

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

192

### 193 *A view to the future*

194 Genetic traits that sustain crop plant growth under moderate drought may come from multiple  
195 sources, including natural genetic variation in wild relatives or bioengineering. Traditional  
196 breeding has been the main strategy for exploiting the genetic diversity of adaptive traits in natural  
197 alleles. The advent of genomic technologies and gene mapping tools such as GWAS and precision  
198 genome editing with the CRISPR/Cas9 system became instrumental for the generation of new  
199 alleles that can improve plant yield and performance under various stresses Molecular studies  
200 using tissue/cell-specific promoters coupled with live microscopy techniques for real-time  
201 visualization of cellular processes pave the way for analysis of drought responses network that can  
202 be used as targets for various biotechnological approaches (Fig. 4) . Small molecules, such as  
203 peptides or hormone agonists, may be useful for fine-tuning drought-response pathways while  
204 preserving yield in agriculture (. Together, uncovering the physiology of plant responses to drought  
205 in model system and translating that to crops will deliver new strategies to combat water scarcity.  
206 Agriculture is a thirsty enterprise. Discovering ways to ameliorate agriculture's thirst will ease  
207 competition for freshwater resources from increasing population growth.

208

209 **FIGURE LEGENDS**

210 **Figure 1: The power of biotechnology to solve the problem of drought-induced food**  
211 **insecurity.**

212 a) Most scenarios predict that the scarcity of water will increase in years to come. With the world's  
213 population continuously raising, crop production must be duplicated to fulfill civilization's basic  
214 needs. For this purpose, the efficiency of water usage in plants will need to be improved. b)  
215 Estimated world population for the 1990-2050-time period. Arrow indicates estimated number of  
216 people potentially living in water-scarce areas of the planet. c) Global arable land for agriculture  
217 for the 1990-2050-time period. Arrow indicate predicted demand of arable land to assure food  
218 security, given current rates of crop production per hectare. d) Global fresh water demand for  
219 agriculture for the 1990-2050-time period. Arrow indicates predicted decline in fresh water  
220 availability for agriculture in the current tendency of climate change and precipitations.

221

222 **Figure 2: Root and shoot traits that account for drought resistance.**

223 a-b) Plants first sense drought through their roots, where particular cell types such as stem cells,  
224 cells in the cortex and vasculature mediate adaptive responses towards water limitations. Roots  
225 can modulate their system architecture to c) maximize access to superficial humidity or delve into  
226 deep humid soil layers, and d) bend towards more humid soil zones (hydrotropism). e-f) In  
227 aboveground plant organs such as leaves and stem stomata work actively against dehydration. In  
228 water limiting conditions, stomata remain closed to reduce water loss.

229

230 **Figure 3: Hormone signaling events underpinning drought.**

231 Schematic representation of hormone signaling modules controlling drought adaptation. Plants  
232 work against dehydration in all their organs such as leaves, vasculature and roots ABA, through  
233 SnRK2, activates a variety of genes that cause stomata closure and improve water balance. When  
234 drought is sensed in the roots, CLE25 peptide moves through the vasculature to leaves where  
235 locally controls ABA biosynthesis and stomata closure. Brassinosteroids also play roles in  
236 regulating plant drought response. Brassinosteroid pathway converge with ABA by activating  
237 SnRK2 through downstream pathway component, BIN2 and *vice versa*. Independently of ABA,  
238 brassinosteroid receptors (BRI1, BRL1, BRL3) modulate hydrotropic responses in the roots.  
239 Vascular BRL3 receptor coordinates plant growth and survival under drought stress by promoting  
240 the accumulation of osmoprotectant metabolites in the root tissues. Furthermore, non-canonical  
241 auxin responses via EXO70A3 and PIN4 can modulate root architecture patterning and depth, to  
242 improve water absorption from the soil improving drought tolerance.

243

244 **Figure 4: The promise of overcoming drought in agriculture.**

245 Various strategies can provide solutions to counteract drought and can be used to develop drought-  
246 smart crops. Natural allelic variations found in plants can be selected to improve drought resistance  
247 and yield. Traditional plant breeding approaches have successfully employed such useful traits to  
248 obtain more resistant crop varieties in fields. Advancements in gene mapping tools such as GWAS  
249 can explore the genetic diversity of drought resistance traits in natural alleles with nucleotide-level  
250 precision. Genetic engineering of drought response markers at spatio-temporal scale and precise  
251 genome editing with tools such as the CRISPR/Cas9 have opened new horizons to develop crops  
252 with improved drought resistance without impairing yield. New techniques such as optogenetics  
253 allow fine manipulation of cell/tissue specific responses to signaling and therefore increase growth

254 and plant resistance to drought. Bio-stimulants such as small peptides, hormone mimics and  
255 receptor agonists can be used to designing better agrochemicals and fine-tune drought resistance  
256 while preserving yield.

257

258

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428 A.G. and A.I.C.-D wrote the manuscript. A.G. and A.R.-M. designed the figures. All authors  
429 reviewed the manuscript.

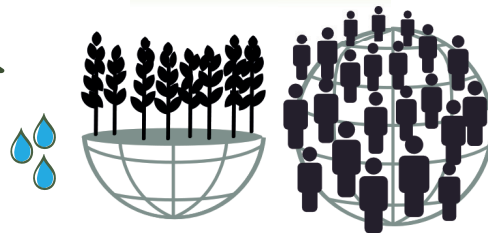
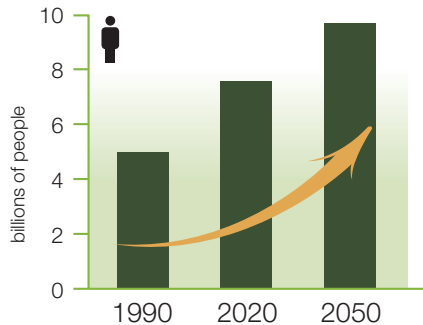
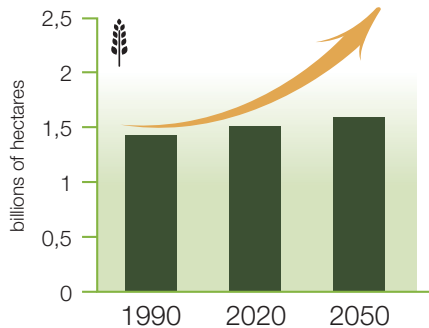
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432 The authors declare no competing or financial interests.

**a****Year 2020**

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