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Abiotic Stress Response in *Brachypodium*

Mhemmed Gandour

Abstract

Understanding the mechanisms of physiological response in plants is crucial to building sustainable agriculture, especially under the current worldwide climate and environmental crises. Thus, plants that successfully acclimate to stress can decrease growth under stressful conditions. *Brachypodium*, an undomesticated grass species with close evolutionary relationships to wheat and barley, is a promising model organism of crop research. It can grow under various conditions and possess specific adaptations or tolerance mechanisms. Hence, it promises to greatly accelerate the process of gene discovery in the grasses and to serve as bridges in the exploration of panicoid and pooid grasses, arguably two of the most important clades of plants from a food security perspective. *Brachypodium* could hence efficaciously acclimate to the drought, salinity, cold, heat, and nutrient stress variations by reversible hypo (hyper)-activation of specific genes or sustaining transcription states as well as by reducing growth and osmotic adjustment. Nonetheless, *B. stacei* and *B. hybridum* have more plasticity and more adaptiveness than *B. distachyon* to abiotic stress. This review will describe advancements in knowledge of the physiological and metabolic adjustments that are needed for abiotic stress tolerance.

Keywords: model plant, *Brachypodium*, abiotic stress, physiological response, gene expression

1. Introduction

Throughout the last fifty years, the global climate is changing at an exceptional rate. Simultaneously, the world population has known a significant increase (about twice) accompanied by a considerable increase (3 times) in cereal production, reaching 2.5 billion tn [1]. This population will certainly continue to grow to reach 9.7 billion inhabitants in 2050 [2], and the problem is that we will have to double or even triple agricultural production. This poses a serious problem for food security which, according to the FAO [3], is based not only on a sufficient supply of quantity but also, healthful and active life for humans. Consequently, ensure an increase in this production at the rate of the growth of the population remains an important challenge to which researchers must act, especially since we are aware that the known solutions to increase the productivity of agriculture in the 20th century, including the intensive use of fertilizers, are currently showing their limits.

Cereals are by far the most important food resource in the world, either for human consumption or for animal feed. At the start of the 21st century, they still provide almost half of humanity's food calories and will undoubtedly be brought to play a fundamental role in the face of the demographic and environmental challenges of the century. Average cereal yields thus fell from 1.3 to 3.5 t ha⁻¹ at the global level between 1969 and 2009 [4].

Understanding the mechanisms of physiological response in plants is crucial to building sustainable agriculture, especially under the current worldwide climate and environmental crises. Thus, plants that effectively acclimate to stress can summarize growth under stressful conditions. *Brachypodium*, an undomesticated grass species with close evolutionary relationships to wheat and barley, is a promising model organism of crop research. It can grow under various conditions and possess specific adaptations or tolerance mechanisms. Hence, it promises to greatly accelerate the process of gene discovery in the grasses and to serve as bridges in the exploration of panicoid and pooid grasses, arguably two of the most important clades of plants from a food security perspective. In this review, the diverse physiologic and metabolic responses identified in *Brachypodium* so far are discussed. We also describe and discuss the current and future development of computational tools with a focus on abiotic stress-tolerance trait interactions.

2. Drought stress

Plants respond to drought stress through various crosstalk pathways. In *Brachypodium*, Verelst showed that drought stress mainly affects the final cell size, not the cell number (6% of reduction of the cell number vs. 35% of the decrease in the cell size). Thus, cell extension is affected by drought, while cell proliferation is not, which is in sharp disparity to previous annotations made in other plant species such as barley, maize, rice, wheat, and *Arabidopsis* suggesting that *Brachypodium* possesses mechanisms to defend its dividing cells against the negative impact of drought stress [5]. In addition, the natural genetic variation revealed that *Brachypodium* deals with drought stress through the combination of natural selection on standing intra-population genetic variation and phenotypic plasticity [6]. The strong natural variation in drought resistance was subsequently used to reveal physiological and metabolic mechanisms of *Brachypodium* response to drought stress. In fact, the drought responses in *Brachypodium* were characterized by changes in amino acids, boosting the glutamine that could be functioning as a stress signal. There were also variations in sugars that were appropriate to be an osmotic counter to drought, and changes in bioenergetic metabolism [7]. As well, the drought response is greatly dependent on the developmental stage. Moreover, molecular studies have identified that gene expression is modulated in the proliferation zone and is differentially expressed in the cell expansion and mature zones. In fact, the effect of severe drought on gene expression was most pronounced in the mature leaf zone, where it has been detected significant up-or down-regulation transcripts.

3. Cold

B. distachyon can serve as an attractive model for specific molecular mechanisms implicated in low-temperature responses in core Pooideae species. It encompasses

cold-responsive IRIP genes which have evolved through *Brachypodium* specific gene family expansions [8]. In fact, a large cold-responsive CBF3 subfamily was identified in *B. distachyon*, whereas CBF4 homologs are absent from the genome. In addition, growing under cold conditions lead to the acquisition of novel and targeted cold-induced transcriptional responses by inducing transcriptional responses typical of cold acclimation, including the activation of the transcription factors, C-repeat binding factors (CBFs), and structural genes IRI, COR410, and COR413 [9]. *B. distachyon* could hence efficaciously acclimate to the cold treatment and displays reversible hypoactivation of cold-regulated genes as well as it can entirely acclimate by resuming growth under diurnal-freezing conditions [9, 10]. In fact, by regulating transcriptional adaptation, transcription memory provides plasticity to *B. distachyon*'s stress responses, to develop a freezing tolerant morphology during cold acclimation.

4. Heat

The allopolyploid grass *Brachypodium hybridum* and its progenitor *Brachypodium stacei* exhibit long-term heat stress tolerance, unlike its other ancestor, *Brachypodium distachyon* [11]. Hence, these differences were explained by the fact that *B. hybridum* and *B. stacei* sustained transcriptional states under enduring stress at a similar amplitude than those under normal environments but significantly altered their transcriptome in response to heat after short-term stress whereas *B. distachyon* showed similar expression patterns between normal and heat stress conditions in both short and long-terms treatments [11]. Overall, it has been suggested that after branching out from the common ancestor and during the adaptation process, the heat acclimatization function in *B. distachyon* might have been lost. Thus, the heat-adaptive attribute in the *B. stacei* genome may perhaps influence the subsistence of both individual plants and hybrid progeny under heat stress environments.

5. Salinity

Among the various abiotic strains, salinity causes major limitations for food production, since it presents a multifold challenge to all organisms in terms of osmotic imbalance, ionic disequilibria, and generation of toxic metabolites. It limits crop yield and reduces the use of cultivated land. Plants respond to salt stress through the transcription and translation of response-associated genes, which is a complex mechanism that implicates various crosstalk pathways. In addition, post-translational phosphorylation modification can control protein functions to respond to abiotic stress [12]. In *Brachypodium* and at the protein expression level, most of the differentially expressed proteins (DEPs) were down-regulated under stress conditions. Nonetheless, it principally acted as functional proteins, however, most of the phosphoproteins were categorized as regulatory proteins, suggesting that *Brachypodium* can react and defend against salt strain by two methods: (1) through phosphorylation variation changes, mainly involving signal transduction, transcription/translation, and transport; and (2) via protein expression changes, which mainly happen in photosynthesis and energy production [13]. Furthermore, 101 NAC genes have been identified in *B. distachyon*, among which BdNAC003 and BdNAC044 are stimulated by high salt stress [14]. Wang et al. [15] have characterized 44 BdSnRKs in *B. distachyon*, and the overexpression of BdSnRK2.9 in tobacco enhanced its tolerance to drought

and salt stresses. At the expressions of transcription factor (TF) level, family members such as MYB, bHLH, and AP2/ERF were increased under salt stress, regulating the response of *Brachypodium distachyon* to salt stress. In addition, under 200 mM NaCl stress, the soluble sugar and proline content of *Brachypodium distachyon* increased significantly [16] suggesting that the osmotic adjustment is an imperative mechanism to avoid salt stress. Consequently, it completes osmotic adjustment to reduce salt damage by selectively captivating inorganic ions and accumulating organic solutes that are non-toxic to cells. One of the physiological responses regulated by ABA is associated with stomatal closure, which can avoid excessive transpiration and reduce water loss [17]. In fact, preserving water stability in plant cells is a vital strategy for plants to shield against salt stress, just as most halophytes have the characteristics of succulents [18]. For non-succulent glycophytes, it is also an imperative method to alleviate plant ion toxicity and osmotic shock by controlling the stomatal opening and wax metabolism of epidermal cells in plant leaves to reduce water loss [15, 19].

6. Nutrient availability

Nutrient stress (deficiency or excess) seriously affects plant growth, yield, and quality. *Brachypodium distachyon* (*Brachypodium*) has been proposed as a good model to enhance this knowledge in C3 temperate cereals [20]. Thus, it interacts with increased nutrient concentration by increasing biomass [21]. In fact, P and N supply had great effects on the root system of *B. distachyon*. The most noticeable effect of both N and P scarcity on *B. distachyon* was that only Leaf Node Root was significantly reduced by minor nutrient supply [21] which suggests that *B. distachyon* cannot be considered “low-P-N adapted”. Comparable observations have been made in wheat in which seminal roots were much less sensitive to N, P, and K deficiencies than nodal root growth and emergence [22]. By comparing plant growth at diverse concentrations of P and N, it appeared that *Brachypodium* required approximately three to four times more N than P for the same biomass production. Overall, *Brachypodium* showed plasticity in its biomass allocation pattern in response to variable P and N conditions, specifically by prioritizing root expansion overshoot productivity under poorly soluble P or N conditions (shoot productivity was depressed in *Brachypodium distachyon* while the root system development was sustained) [23]. *B. distachyon* was revealed as a good model to study ammonium nutrition since it responded likewise to other monocot crops, but with less complexity. The plants increased the storage of NH_4^+ in roots, as well as the synthesis of amino acids and proteins. Indeed, it seemed to be moderately tolerant to ammonium. Notably, 1 mM was considered an N-sufficient condition, since expanding NO_3^- supply to 2.5 mM did not further increase plant biomass. Nevertheless, when NH_4^+ was elevated to 2.5 mM plants showed moderate indicators of ammonium toxicity in terms of leisurely growth. In addition, the root system is shown as a physiological barrier acting as a reservoir for free NH_4^+ and increasing NH_4^+ assimilation to amides.

At the molecular level, an extensive BLAST search was carried to identify putative orthologues of the *Arabidopsis* *NRT2* genes in the wholly sequenced *Brachypodium* genome. Seven genes encoding putative high-affinity nitrate transporters (*BdNRT2*) were identified. Only *BdNRT2.1* and *BdNRT2.2* were highly expressed in the root and classified as inducible genes, suggesting they are likely the main contributors to root nitrate uptake. *BdNRT2.5* has shown to be stifled by nitrate resupply however further

members were constitutively expressed in the root. Conspicuously, great ammonium concentrations also induced analogous gene expression regulation, suggesting *BdNRT2* gene expression was also governed by inside nitrogen status, not just outside nitrate concentrations [24]. Additionally, *BdNRT2.1* was also strongly expressed in the stem, indicating that it has useful roles other than nitrate uptake.

Concerning zinc, *Brachypodium* exhibited the typical performance of a zinc-sensitive, excluder plant [25]. It prioritized shoot zinc accumulation upon deficiency and majorly retaining zinc in roots upon excess, in both cases to preserve the photosynthetic function in leaves. In addition, clear repression of vegetative growth was accompanied by increased leaf number suggesting that in order to optimize nutrient use efficiency in shoot and maintain photosynthesis, plants have adjusted leaf area partitioning [26]. Deficiency and excess treatments increased lateral root number and length relative to the primary root, and nodal roots, post-embryonic shoot-born roots emerging from successive shoot nodes and a unique feature of monocots, were strongly affected. At the molecular level, The *Brachypodium* homolog of *AtbZIP19* (in *Arabidopsis*), *Bradi1g30140* was previously suggested to be involved in a zinc deficiency-induced oxidative stress response [27, 28]. However, it was slightly more expressed in zinc-deficient shoots compared to control plants and displayed a very flattened V-shape dynamics upon zinc resupply. *AtbZIP19* and *AtbZIP23* are proposed to be specialized in either roots or shoots, respectively [29, 30]. In *Brachypodium*, *BdbZIP9* was more expressed in shoots than roots. Interestingly, another *bZIP* gene, *Bradi1g29920*, was majorly expressed in roots. Moreover, 113 TFs from diverse families such as *bZIP* (9 genes), *bHLH* (11 genes), *MYB* (22 genes), *AP2* (24 genes), and *WRKY* (25 genes), were known DEG. But no one of them are homologs of identified zinc regulatory genes and formed potential candidates for a role in zinc homeostasis regulation in grasses [31].

7. Conclusions and future perspectives

Engineered plants will cover the way for future strategies to adapt them for higher biomass production to meet the demands of a growing population in a changing climate scenario. Similarly, understanding the mechanisms of physiological and molecular response in plants will uncover the complexity of the dynamic changes during cell wall development and abiotic stress response. In parallel, phenomics can help in identifying the key factors affecting plant growth and health, and subsequently plant productivity, since this technology allows the non-destructive screening of hundreds of plants in a very short time. Thus, employing the developing omics approaches especially the signaling cascades in response to abiotic stresses in tolerant plants will help to manipulate susceptible crop plants and increase agricultural productivity in the near future. Moreover, GWAS will contribute to better understanding the abiotic stress response.

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