

Abscisic Acid and WUE

Subjects: Plant Sciences

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ABA controls multiple plant physiological and biochemical processes. Here we have highlighted the role of this hormone in the regulation of plant WUE and reviewed promising biotechnological approaches to confer drought resistance and improve crop WUE.

Keywords: ABA ; drought ; hydraulic conductivity ; WUE ; xylem embolism ; aba receptors

1. Introduction

The phytohormone abscisic acid (ABA) is a fundamental regulator of the morpho-physiological response of plants during drought stress. The central and best-known plant response to ABA during drought is the closure of stomata in seed plants. The effects of ABA on shoot and root growth can be positive or negative depending on its concentration and the plant species [1]. Increased levels of endogenous ABA also play key roles in down-regulating leaf hydraulic conductance (which is proposed to further induce stomatal closure) [1][2][3] and mesophyll conductances [4][5][6], as well as up-regulating the cuticular wax formation (which results in a thicker, less permeable cuticle) [7][8]. Finally, ABA is a critical messenger produced in response to water deficit that promotes a variety of biochemical responses in different plant tissues [9]. Due to the ABA's key roles in the physiology of plants during drought, several promising approaches to manipulate ABA biosynthesis and signaling (i.e., either genetically or through chemical intervention with agonists) have been explored aiming at conferring drought tolerance to major crop species and improving water use efficiency (WUE, i.e., the ratio of photosynthesis to water loss through foliar transpiration). In this review, we cover the progress made in the last decade in our understanding of how ABA signaling regulates plant physiology and biochemistry during drought. Special attention has been paid to (i) the ABA biosynthesis within the plant, (ii) the impacts of ABA on stomatal aperture and xylem embolism, (iii) the regulation of primary and secondary metabolisms by ABA, and (iv) the potential applications of approaches modulating ABA levels and perception to improve WUE and drought tolerance in crop species.

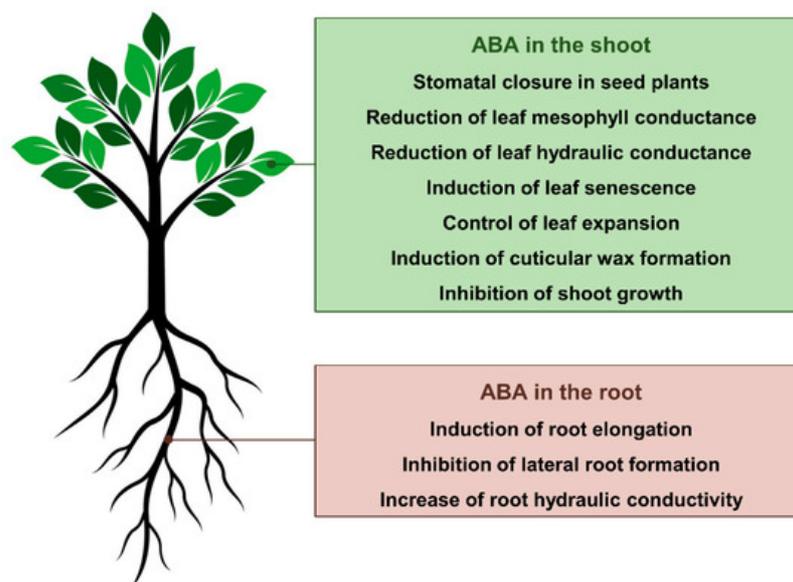


Figure 1. Current understanding of how abscisic acid (ABA) regulates plant form and function during drought.

2. Drought-Induced Biosynthesis of ABA

Given the key role played by ABA in enhancing plant survival during drought, a comprehensive understanding of how the biosynthesis of ABA occurs, how it is regulated within the plant, and where it mostly takes place is of major importance. In recent years, the pathway by which ABA is synthesized in plants has been extensively investigated through the use of

mutants deficient in the synthesis and perception of ABA [10][11][12][13][14]. It has been demonstrated that the biosynthetic pathway for ABA accumulation begins in the chloroplasts with the hydroxylation of β -carotene to zeaxanthin, which is then converted to violaxanthin through the xanthophyll cycle. Next, neoxanthin synthase converts violaxanthin to neoxanthin, which is then isomerized from 9-trans to 9-cis (neoxanthin). The last step of the biosynthetic pathway that occurs in the chloroplasts is the oxidative cleavage of 9-cis-neoxanthin and/or 9-cis-violaxanthin to xanthoxin, which is further catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED). NCED is known to be the key rate-limiting enzyme in the ABA biosynthesis and it is responsible for catalyzing the first non-reversible step in the pathway [15]. The formed xanthoxin then moves from the chloroplasts to the cytosol, where it is converted to abscisic aldehyde, and finally to ABA. ABA accumulation in plants occurs not only through activation of ABA biosynthesis but also by the hydrolysis of its glycosyl ester (i.e., ABA-GE) [16][17], which can be utilized to maintain the high levels of ABA in plants during drought [18][19][20].

Since the first studies linking ABA with stomatal closure under drought, a number of results have led to the critical assumption that the pool of ABA resulting in stomatal closure in leaves is mostly synthesized in the root tips [21][22]. However, this conventional view of root-to-shoot ABA signaling has recently been challenged by studies using a number of experimental approaches, including the reciprocal grafting between ABA biosynthetic mutant and wild-type plants and exogenous labeled ABA [23][24][25][26][27]. In fact, these studies clearly demonstrate that although multiple organs and tissues can accumulate small amounts of ABA, leaves are the predominant site for ABA biosynthesis, and they are even responsible to export ABA to the roots, maintaining normal root levels of ABA levels and determining root architecture and growth [24][26][27]. Inside leaves, phloem companion cells, guard cells, and mesophyll cells have been demonstrated to be capable of synthesizing ABA [28][29][30][31]. In addition, ABA biosynthesis has been recently observed to occur in parenchyma cells around the vascular tissues [32]. Regarding the ABA transport within plants, the recent identification of a number of transmembrane ABA transporters strongly suggests that the movement of this hormone is actively regulated in an intercellular network [9]. However, the fine regulation of ABA biosynthesis and transport among different plant tissues remains a matter of debate [9].

The major production of ABA in leaves, not roots, during drought seems considerably more advantageous for plants to avoid excessive declines in water potential as leaves represent the main organ exchanging (and mostly losing) water with the atmosphere. For instance, a de novo biosynthesis of ABA over an extremely short time-frame following leaf exposure to high vapor pressure deficit (VPD) has been demonstrated to allow an efficient stomatal closure in angiosperm species [33][34]. Declines in leaf water potential to a threshold leaf water potential results in major increases in foliar ABA [35][36] and such threshold water potential strongly coincides with bulk leaf turgor loss point [14][34][37][38]. Although the water potential at turgor loss is broadly accepted as the threshold for the major increment in foliar ABA biosynthesis, it is still uncertain whether changes in turgor itself or changes in cell volume are the main signal up-regulating the enzymes responsible for ABA production [14][39]. In addition, given the lower water potential in the guard cells and the mesophyll cells nearby stomata in transpiring leaves [40], small levels of ABA are expected to be produced in these cells as transpirational demand increases, resulting in stomatal closure even prior to leaf turgor loss point [34].

3. Regulation of ABA Levels and Perception in Crop Species

Ongoing climate change coupled with the projected increase in human population by over 2.4 billion until 2050 [41][42] represents a major challenge for the agricultural sector [43]. Over the next decades, climate change is expected to result in considerable rise in the intensity and frequency of drought events. In this water-limited scenario, achieving 'more crop per drop' (i.e., crop water productivity that is defined as the mass of agricultural produce per unit of water consumed) is a critical target for food production. Especially when considering that 70% of the available fresh water is used for crop production and that drought is expected to cause the largest yield reductions relative to any other abiotic and biotic stresses [44]. Therefore, enhancing crop WUE is still foreseen as a good means for saving water in agriculture [45] and has proven to be an accurate target in both genotype selection [46][47][48] and engineering [49].

The WUE can be determined both at the plant and leaf levels. At the leaf level, the photosynthesis-to-stomatal conductance ratio is defined as the intrinsic water-use efficiency (WUE_i). This parameter is typically determined in studies aimed at improving crop yield while saving soil water and mitigating yield limitations by water deficit [49][50]. In this context, the importance of ABA for WUE_i improvement is well-known due to its central role in regulating plant-water relations, specially by modulating stomatal conductance in several crop species [51][52][53][54]. As outlined above, the direct influence of ABA on WUE_i in angiosperms has already been demonstrated and several studies have concluded that plant responses driven by ABA depend on the severity and the duration of the drought events [55]. Particularly under short-term water deficit, ABA induces stomatal closure through its direct action on guard cells and modulates mesophyll conductance without restraining CO₂ fixation [2][6][32]. During severe and prolonged drought conditions, ABA can trigger further alterations at the transcriptome level, including genes encoding for LEA (late embryogenesis abundant) proteins [56].

Besides, it can alter the levels of osmoprotectants [57] and cause morphological changes in stomatal size and density [58], leaf size, and shoot and root development [1][59]. All these alterations strongly affect plant water balance and WUE in the long-term [60]. In addition, ABA have been observed to regulate WUE through a tissue-specific action on hydraulic conductivity. Particularly in leaves, ABA has been found to decrease the hydraulic conductance by reducing the permeability of bundle sheath aquaporins [2][3][61] and also indirectly controlling mesophyll hydraulic conductances [5][62]. In the roots, ABA has been observed to increase hydraulic conductivity, facilitating water uptake under non-transpiring conditions [1][63]. Therefore, ABA signaling network can be modulated to reduce transpiration and increase crop water productivity under stressful conditions [55][64].

The ABA signal transduction pathway has recently been well documented, consisting of pyrabactin resistance/pyrabactin resistance-like/regulatory component of ABA receptors (PYR/PYL/RCAR), clade A type 2C protein phosphatases (PP2Cs), and SNF1 related protein kinase 2 (SnRK2s) [65][66]. The first attempts to use ABA in large scale agriculture were constrained by the chemical instability of ABA (e.g., under UV-light), its relatively expensive production, and its rapid cellular catabolism [67]. The modulation of ABA signaling, however, can be efficiently achieved through genetically engineered plants with an overexpression of ABA receptors [68][69][49][70] and signal transduction components [71][72], as well as through chemical intervention with ABA agonists [73][74][75][76][77].

Over the last years, studies on ABA overexpression receptors have led to promising results both in the field [78][79] and under controlled conditions [49][70]. The overexpression of PYL/RCAR receptors induces a higher plant sensitivity to ABA, leading to a globally enhanced WUE and drought resistance, as previously demonstrated in rice, poplar, and wheat [69][70][80][81]. The actual challenge, however, is to balance the improvements in WUE against the negative effects on growth due to ABA oversensitivity. Recent studies on plants overexpressing PYL receptors have shown an opposite effect on growth and stress adaptation and this may be due to the specific receptor choice. Indeed, the overexpression of some specific subfamilies result in plants with less transpiration for a similar leaf area and biomass compared to the wild-types, thus leading to an increased WUE [64]. In particular, PYL12/RCAR6 and PYL4/RCAR10 (subfamily I and II) overexpressing lines in Arabidopsis possessed a balance of reduced water use with negligible effects on growth and a “water-saving” phenotype that resulted in a significant improvement in total biomass relative to water use gains [49]. Similar observations have been made in transgenic wheat and in rice, in which the overexpression of specific PYL receptors has led to a reduced transpiration and a concomitant increase in photosynthetic activity compared to the wild-type, improving grain production per liter of water and protecting productivity during water deficit [69][70][79].

A faster and a more manageable alternative to the expression of genes for increasing crop’s WUE and conferring drought resistance is the use of ABA agonists [75][82], which are small synthetic molecules binding ABA receptors and activating ABA signaling pathway [83]. Among the ABA agonists, the first synthesized molecule Pyrabactin has been identified in a chemical genetic screen for seed germination inhibitors and it has been instrumental in showing how ABA binds the PYR/PYL receptor family [66]. The direct application of this molecule is not practical for agricultural purposes since its major effects are in seeds rather than in vegetative tissues. However, the examination of the structure of Pyrobactin and its interaction with ABA receptors has provided a framework for the design of novel ABA agonists [82]. As a consequence, several ABA agonists have been developed during the last ten years, with promising results in increasing crop water productivity [84]. An example is represented by Quinabactin, which appeared to be an overall better ABA agonist than Pyrabactin, inducing ABA responses both in seeds and vegetative tissues. Application of Quinabactin in plants resulted in improved water use upon drought stress [73]. This molecule targets all of the dimeric subfamily III ABA receptors, affecting guard cell closure to prevent water loss from detached leaves and conferring drought tolerance in both Arabidopsis and soybean during drought [73]. In addition, Quinabactin has shown effect in rapeseed and tomato, inhibiting germination and eliciting drought stress responses [85][86][87]. Another example concerns a tetrafluoro derivative of Quinabactin, AMF4, which seems to be more effective than Quinabactin due to its higher stability and bioavailability, even targeting only a subset of ABA receptors [73][88]. Finally, a recent example is represented [73] by the agonist B2, which was shown to improve drought tolerance in wheat by increasing root biomass and preventing leaf dehydration as well as amplifying antioxidant responses and enhancing the photosynthetic performances [77].

A recent innovative approach aims at combining the application of agrochemicals on genetically modified crops such as AMF4 on PYL2 overexpressed plants or mandipropamid on engineered PYR1 receptor (PYR1MANDI) [74]. The mandipropamid-PYR1MANDI system resulted in increased seedling survival during drought and transcriptional responses similar to those induced by ABA. Recently, Cao et al. [88] optimized the synthesis of new molecules based on the Quinabactin backbone and applied them to transgenic Arabidopsis and soybean plants with an abiotic stress-inducible AtPYL2 overexpression. This combined approach dramatically increased drought resistance in these plants, making this system a compelling alternative strategy to manipulate plant water use. Although the utilization of agrochemicals acting as ABA receptor agonists combined with transgenic approaches to increase ABA signaling holds great promise for the

production of plants with enhanced WUE, the translation of these applications at field level into practical improvements in crop yield can be challenging [89][90]. For instance, as previously stated, a recent study conducted on tomato has highlighted a higher vulnerability to embolism of the vascular system of the transgenic line sp12 which overproduces ABA [63]. A reduced hydraulic safety margin can compromise the maintenance of hydraulic conductivity during periods of soil water deficit, with negative consequences not only for photosynthesis and productivity, but also for plant survival [90]. Given the importance of the potential use of plants with increased ABA biosynthesis and signaling to the future of agriculture in a world facing an ongoing climate change, it is of critical importance to confirm whether increased levels of ABA result in more vulnerable xylem and to understand the underlying mechanisms linking ABA signaling and xylem functioning. Important questions remain unanswered, especially those related to the extent of variation in embolism resistance among single crop species and their different varieties [91][92], including the relationship with genotypic variations in endogenous ABA content. Therefore, to optimize WUE strategies in the field, a complete understanding of the changes at the hydraulic and metabolic levels induced by the manipulation of ABA levels is needed. Timely investments in research at different levels will likely allow to improve crop resilience and yields in a water-limited scenario.

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