Auxin Regulates Primary Seed Dormancy

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Phytohormone auxin acts as an outstanding coordinator of plant growth and development. Among other tasks, it has a key role as a signaling molecule that arranges seed life. Recently, auxin has emerged as an essential player that modulates the induction, regulation, and maintenance of primary seed dormancy (PSD). This function was supported by biochemical and genetic evidence. The participation of the transcriptional regulator ABSCISIC ACID (ABA) INSENSITIVE 3 (ABI3) is critical, which demonstrates a cross-talk between auxin and ABA signalings.

Keywords: ABA ; Auxin ; Primary seed dormancy ; ABA insensitive 3 ; primary seed dormancy ; ABA insensitive3 ; YUC ; PIN

1. Introduction

The evolutionary success of higher plants consists of their ability to produce seeds, units responsible for reproduction, dispersal, and survival [1]. Synchronized coordination between hormone signaling networks and environmental cues are being required to control these processes [2]. The viable seed is an entity that originates at the end of the development program progression and it is constituted of three genetically different organs (i.e. endosperm, embryo, and seed-coat) [3][4]. Seed development relies on a strong interdependent control between these three respective organs. Therefore, it is not surprising that all molecular events involved in embryogenesis are tightly coordinated at the genetic and hormonal levels [5][6]. Once all seed tissues are completely differentiated, the embryogenic phase ends and begins the maturation one in which storage compounds accumulate in the endosperm (monocots) or in cotyledons (eudicots). Throughout maturation, desiccation tolerance is acquired, programmed cell death occurs, and PSD is triggered preventing vivipary [7][8][9].

2. Auxin and ABA in seed life

The phytohormone abscisic acid (ABA) is the only hormone known to induce, regulate, and maintain the PSD. Thus, seeds of ABA-deficient mutants germinate faster than the wild-type, and transgenic plants constitutively expressing the ABA biosynthesis gene maintain deep seed dormancy [1][10] . During seed development, ABA is produced in all seed organs, as suggested by the spatiotemporal expression of its biosynthesis genes [11] . ABA synthesized in the endosperm and then transported to the embryo is involved in the induction of seed dormancy [12] . Likewise, ABA shows an accumulation pattern complementary to the gibberellin (GAs), being the main hormone that inhibits all the processes induced by them [13] . On the other hand, auxin represents a key plant hormone that functions as a general coordinator in the execution of multi-functional processes during plant growth and development [14]. A series of evidence clearly relates ABA to the mechanism and mode of action of auxins [15]. Therefore, some evolutionary crosstalk must occur between both plant hormones. However, the study on the participation of auxin in the final part of seed development is not developed enough yet. The auxin is a signaling molecule that is present across all domains of life, including microorganisms [16][17][18] and tryptophan (L-Trp) serves as a common precursor for IAA synthesis in plants and auxin-producing bacteria [14][16]. Regarding the seed, it is now widely accepted that auxin biosynthesis is required for an array of seed developmental processes (e.g., zygotic embryogenesis and endosperm development, among others) [17] . High levels of free-auxins and metabolites found during both early (i.e., cell division and expansion) and last phases of seed development (e.g., endosperm cellularization) suggest that auxin has an essential signaling role [10] . Until now, the role of phytohormones in zygotic embryogenesis mainly refers to the study of eudicots such as Arabidopsis [19][20] . Likewise, the auxin also affects seed germination by altering the ABA/GAs ratio [21] . In order to generate the appropriate response, the auxin polar transport causes its accumulation in specific cellular places, being the embryogenic globular stage the most studied (Figure 1). However, very little is known about auxin biosynthesis and homeostasis, polar auxin transport, and response during early embryogenesis in monocots [22].

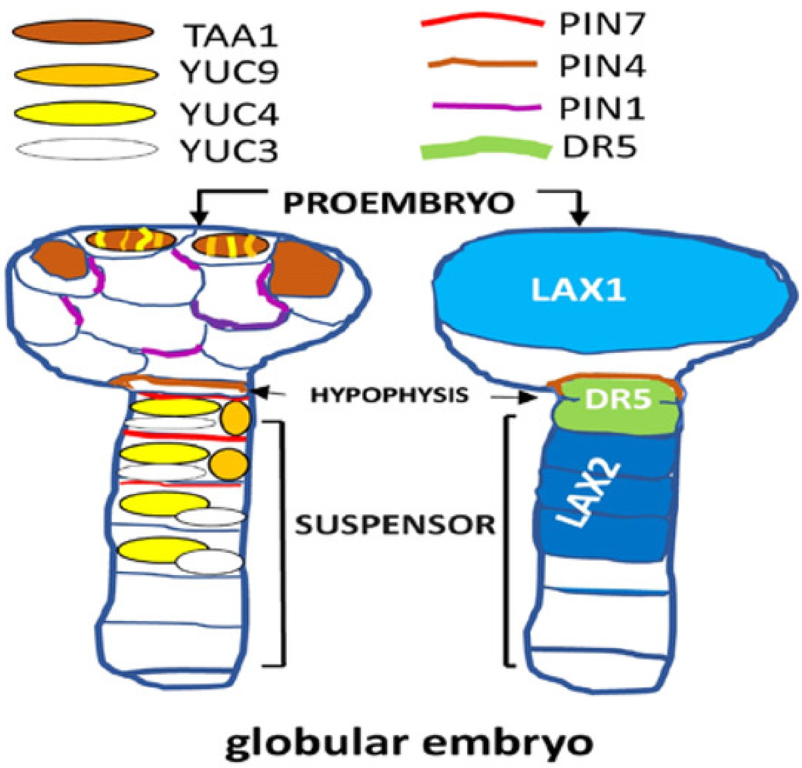

Figure 1. Dynamic of expression and localization (i.e., proembryo, hypophysis, and suspensor) corresponding to several genes for the biosynthesis and transport of auxins in Arabidopsis embryos at the globular stage. LIKE-AUX1/2 (LAX1/2); highly active synthetic auxin response element (AuxRE), is referred to as DR5; auxin efflux carrier PIN-FORMED (PIN); YUCCA (YUC); TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA1).

3. Biochemical and genetic evidence supports the auxin key role

Interestingly, some genetic evidence has suggested the involvement of auxin in the maintenance of PSD in Arabidopsis. During the study of auxin involvement in plant immunity, it was evidenced that auxin protects and strictly regulates PSD through enhancing ABA signal transduction, identifying auxin as a seed dormancy promotor [23][24] . These findings were supported, among other consistent experimental verifications, by the dormancy variation among seeds with altered auxin synthesis genes. Thus, the reduced seed dormancy in taa1 and yuc1yuc6 mutants is linked to decreased ABA sensitivity [23]. However, the mechanism by which auxin controls seed dormancy is a question not yet clearly resolved at the molecular level. Parallel, strong genetic evidence supports a model whereby ABA-mediated inhibition of seed germination requires intact auxin biosynthesis, transport, and signaling. The evidence involves ABI3, a transcription factor induced by auxin [25][26] , and implicated in the initiation and maintenance of the maturation phase and considered to be a major downstream component of ABA signaling. Though genetic and biochemical evidence has been shown that ABI3 is required for auxin-activated PSD [23]. At the evolutionary level, it is interesting to note that the auxin regulatory mechanism evidenced by the He's group [23] was later found and conserved in liverworts [27].

4. Conclusion

A striking aspect of this update lies in the participation of auxin as a key hormone, in conjunction with ABA, in the regulation of specific phases of seed life. That is why this review provides the progress made in recent years on the contribution of auxin in the fertilization process and zygotic and post-zygotic embryogenesis phases. Given the recent demonstration of auxin involvement in the PSD process, this update also considers the events that have led to this outstanding discovery.

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