Trends in Plant Science

CellPress

Opinion

To Grow or not to Grow?

George W. Bassel[1,*]

The seed to seedling transition in plants is initiated following the termination of seed dormancy. Here, I present a simplified developmental framework describing the events underlying this transition. I discuss putative mechanisms of signal integration and their relation to a global developmental fate switch in seeds within this framework. I delineate the events that occur before and after the flipping of this switch, marking an important distinction between these different developmental states. To end, I propose that the final fate switch resides within the embryo, and is informed by the endosperm in arabidopsis (*Arabidopsis thaliana*). This framework can serve as a template to focus future research in seed science.

Trends

Environmental signal integration in seeds is mediated by the relative abundance of the hormones abscisic acid (ABA) and gibberellins (GA). The dynamic regulation of hormone synthesis and degradation is regulated by exogenous cues.

An irreversible developmental fate switch underlies the commitment to make the transition from seed to seedling. Both hormone and protein thresholds likely represent components of this switch.

Events downstream of the flipping of the switch include the transcriptional induction of GA synthesis and cell wall-modifying gene expression. These act as downstream molecular markers indicating the developmental fate switch has been previously flipped.

Current evidence suggests that the final switch resides within the embryo, where the decision to germinate is ultimately reached.

Seed Dormancy

Seed dormancy is classically defined as an intrinsic block to the germination of seeds under otherwise optimal conditions (adequate moisture, temperature, etc.) [1]. Dormancy in seeds is an adaptive trait that enables plants to move through time and space [2,3], while defining their entry into ecosystems. Dormancy control also has a central role in plant agriculture with regards to crop establishment and weed management strategies [4]. Dormant seeds maintain an embryonic cell identity [5] and desiccation tolerance [3]. The termination of dormancy and induction of the germination program are both cellular phase transitions from the embryonic to vegetative state and the discrete induction of plant growth.

Research into the molecular mechanisms of both seed dormancy and germination is an active and rapidly advancing field [6]. Here, I present a simplified developmental framework, outlining the events underlying the transition from dormancy to growth in seeds. Recent developments in the field are integrated within this framework to conceptually delineate the different stages of this transition. I focus on arabidopsis seed research, because most molecular studies have been performed using this species.

A Simplified Developmental Framework

Following the completion of seed development, seeds receive a continuous stream of information from the environment, which is used to time their decision to terminate dormancy and commence germination (Figure 1). Following the perception of these signals, downstream signalling events integrate these multiple inputs, a process that concludes with a single output: the flipping of a developmental fate switch initiating the embryonic to vegetative cellular phase transition. Only following the flipping of this deterministic and irreversible switch are the cellular differentiation and expansion events initiated that drive the seed to seedling transition.

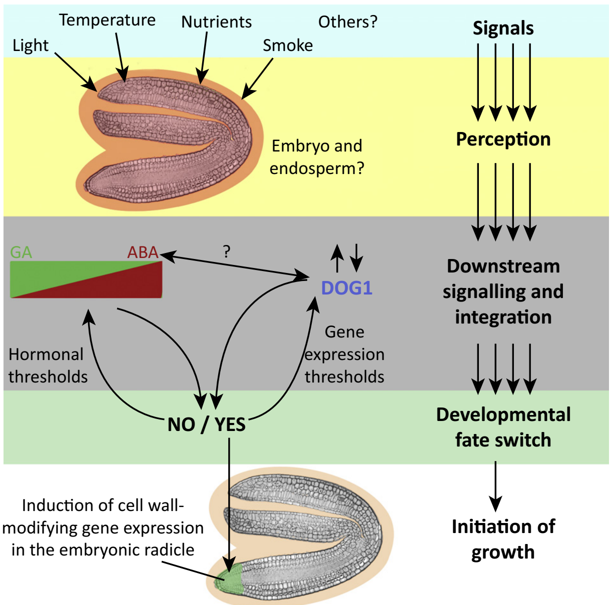
Perception

Seeds use multiple cues from the environment to terminate dormancy and decide where and when to establish a new plant. Primary signals used by arabidopsis seeds to guide their timing to germinate include light [7], temperature [8–11], nutrients [12], smoke [13], and likely other signals, to provide positional and seasonal information. The perception of light in arabidopsis [14,15] is a necessary requirement for the completion of germination in nondormant seeds, and

[1]School of Biosciences, University of Birmingham, Birmingham, B15 2TT, UK

*Correspondence: g.w.bassel@bham.ac.uk (G.W. Bassel).

 http://dx.doi.org/10.1016/j.tplants.2016.02.001



Trends in Plant Science

Figure 1. Simplified Developmental Framework of the Seed to Seedling Transition. From the top down, multiple signals from the environment are perceived, initiating the process of downstream signalling and signal integration using both hormonal [abscisic acid/gibberellins (ABA/GA) balance] and gene expression (*DOG1*) thresholds. This integration process collectively acts upon a final irreversible developmental fate switch that, when flipped, initiates the process of embryo growth and growth-promoting gene expression principally within the embryo radicle.

likely not a primary signal in the breaking of primary dormancy [16]. These signals are perceived through diverse receptors and sensory mechanisms.

Downstream Signalling and Signal Integration

Proteins associated with the primary receptors and sensors of the environment transduce perceived external information into signals within plant cells. A range of genetic loci and diverse biochemical pathways [17] has been reported to be involved in these downstream signalling processes, and have been reviewed previously [3,18].

Central to the integration of environmental signals in seeds are the endogenous signalling molecules abscisic acid (ABA) and gibberellins (GA), which promote dormancy and germination, respectively [2]. The hormone balance theory [19] postulates that the mutual inhibition between the activities of these hormones mediates the decision whether to germinate. The relative abundance of these hormones appears to be more important than their absolute levels, and their synthesis and degradation are tightly controlled in response to the environment [20]. There exists extensive evidence for crosstalk between ABA signalling and other hormone signalling pathways, including ethylene [21], nitric oxide [22], and reactive oxygen species [17], each of which can attenuate the activity of this central inhibitory factor. Therefore, the downstream signalling and integration network in seeds comprises, at least partially, ABA and GA, and their associated signal transduction pathways. These hormones bind their receptors (GID1 for GA [23] and PYL/PYR/RCAR for ABA [24]), and their respective signal transduction pathways in turn feed back to hormone synthesis and degradation gene expression [25]. Further control of the balance between these hormones is mediated by complex feedback and feedforward mechanisms [26].

Hormonal interactions in the integration of environmental signals controlling other aspects of plant development, including shoot branching [27], have been proposed previously. This integration process occurs through a summation of information over time via accumulated inputs [28], and terminates when a decision has been reached [9], leading to a developmental phase transition.