Multifunctionality of the LEC1 transcription factor during plant development

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LEC1 acts as a key regulator of embryogenesis in Arabidopsis thaliana, but is involved in a wide range of functions, all the way from embryo morphogenesis to seed maturation. New data show that LEC1, partially in conjunction with abscisic acid, affects auxin synthesis, and both brassinosteroid and light signaling. The phenotype of LEC1 overexpressors confirms LEC1’s known participation in the regulation of somatic embryogenesis, but also indicates additional roles in embryonic and extra-embryonic cell elongation. Here we present an integrated model of LEC1 function and suggest potential directions to be taken in future research in this important area of plant science.

The regulation of transcription by transcription factors (TFs) relies on their specific interaction with sequence motifs in their target gene promoter, a process which triggers the downstream transcriptional machinery. Many TFs have been shown to be involved in multiple developmental events and/or responses to environmental cues, through the variability of their spatio-temporal expression and their interaction with other TFs. LEC1 and Embryogenesis

LEC1 transcript abundance peaks at the globular-to-heart stage transition and then declines steadily toward early seed maturation10 (Fig. 1A, B). During embryo morphogenesis, the most prominent function of LEC1 is the specification of cotyledon identity. The lec1 mutant produces leafy cotyledons, whereas the ectopic expression of LEC1 results in the formation of cotyledonary leaves9 (Fig. 1C). During seed maturation, LEC1 expression is required for the synthesis of storage compounds, including components of lipid synthesis and storage (such as oleosins).9,12 As part of the NF-YC2 complex, the LEC1 product activates the promoter of certain storage protein encoding genes.13

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maturation-related functions are dependent on the presence of abscisic acid (ABA) (Fig. 1D). Since the relevant ABA responsive elements (ABREs) are over-represented in LEC1-regulated target promoters, it is conceivable that LEC1 probably confers ABA inducibility to its target genes by the recruitment of additional ABRE binding transcription factors such as bZIP. An example of this type of interaction is represented by the substitutability of bZIP67 for ABA, as a cofactor of LEC1 in the regulation of a specific storage protein encoding gene. A comprehensive genome-wide analysis of the LEC1 interactome would therefore be useful to allow the identification of further co-operating factors.

LEC1 and Etiolation

The expression of LEC1 has also been detected in etiolated seedlings, an observation fully consistent with the de-etiolated, short hypocotyl phenotype of dark-grown lec1 seedlings (Fig. 1B, C) and the mimicking of etiolation (including hypocotyl elongation and hook formation) shown by LEC1 overexpressing seedlings. Given that LEC1 activity regulates genes implicated with auxin, brassinosteroid (BR) and light, the hypothesis has been mooted that both hypocotyl elongation and hook formation may be integrated by LEC1. Hypocotyl elongation as well as certain other processes appear to be enhanced via a positive synergy between BR and auxin. Light signaling factors which form part of the photomorphogenic response have also been implicated with hypocotyl elongation in dark-grown plants, a process which is additionally influenced by the fatty acid reserve of the endosperm. These observations are suggestive of a connection between the seed maturation- and seedling elongation-related functions of LEC1. While the global role of ABA in the elongation process is only poorly understood, it has been established that ABA inhibits both BR signaling and embryonic stem elongation. This elongation-inhibiting role of ABA led us to assume that LEC1 during etiolation may act independent of ABA (Fig. 1D). Discriminating between the
The formation by the vegetative seedling of cotyledonary leaves and *pickle*-like root tips able to accumulate storage compounds can be induced by the ectopic expression of *LEC1* and the provision of exogenous ABA. The supply of auxin induces the initiation of somatic embryogenesis from competent tissues, a phenomenon consistent with the activation of transcription of the auxin synthesis gene *YUCCA10* when *LEC1* is expressed in the presence of ABA. The seed-specific expression of *YUCCA10* may affect the elongation of the embryo downstream of the activity of *LEC1*, and opposing phenotypes due to varying auxin concentrations have been described. Enhanced auxin signaling is known to inhibit the elongation of the embryonic axis during germination and auxin synthesis suppresses hypocotyl growth post germination. However, some elongation-promoting effects of auxin have also been described.

The *LEC1* induced and auxin-mediated embryonic differentiation of structures associated with the shoot (cotyledonary leaves) and root (pickle roots) raises the question of their cellular origin. Currently it is unclear whether these structures are either derived from relit undifferentiated stem cells or whether a process of trans-differentiation (possibly via a de-differentiated state) is required. The analysis of stem cell marker expression in a system of controlled activation of *LEC1* expression will help to answer this question.

Conclusions

Recent insights into the function of *LEC1* have revealed the complexity of downstream regulatory interactions involving this TF, acting at various stages of plant development. *LEC1* appears to be an integrator of a number of regulatory events, including the action of heterologous TFs as well as both light and hormone signaling. At present it is only possible to investigate a minor part of the full combinatorial potential associated with this TF, which only emphasizes the need for developing more holistic analytical approaches to better understand plant differentiation and development.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.