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Integrating circadian and gibberellin signaling in Arabidopsis

Possible links between the circadian clock and the AtGID1 transcription

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The circadian clock acts as central L coordinator of plant activity, and it regulates key traits for plant fitness such as flowering time, gas exchange, growth and stress responses. In the May issue of the Proceedings of the National Academy of Science we describe the circadian regulation of gibberellin (GA) signaling, through transcriptional control of GA receptor genes (GID1a and GID1b). We show that, in short day photocycles, the expression of GA receptors oscillates in seedlings, yielding a window of strong GA activity at the end of the night that overlaps with the period of maximum growth. This clock-mediated control of GA signaling is not only crucial for the establishment of rhythmic patterns of growth but also affects the expression of many circadian-controlled genes that participate in a wide range of biological processes. Here we propose a possible mechanism that might operate for the transcriptional control of GID1 expression by the circadian clock.

multiple mechanisms to adjust their growth and development in response to environmental cues. These responses require the ability of the organism to rapidly sense and adjust growth under changing conditions in a way that provides developmental robustness and homeostasis. These properties are thought to be inherent to the architecture of a network of interacting signaling pathways,¹ and the circadian clock contributes to them

Plants, as sessile organisms, have evolved

environmental changes under a wide range of conditions.^{2,3} Circadian clocks are endogenous timekeeping mechanisms that generate self-sustained rhythms with an approximately 24-h period and control many aspects of plant biology including flowering, leaf movements, growth and stress responses.⁴⁻⁸ The pervasive role of the circadian clock in plants is reflected by its extensive control on gene expression, since it is estimated that 31 to 41% of the *A. thaliana* genes are under clock control.^{9,10}

Plant growth is among the processes that are restricted to certain times of the day; in this case, maximum growth occurs close to dawn under diurnal conditions. This regulation is achieved by the combined action of light signaling, which represses growth during the light period, and the circadian clock, that represses growth early in the night.11 We have recently shown that the circadian clock gates gibberellin (GA) signaling in A. thaliana through the transcriptional regulation of the GA receptors (GID1a and GID1b).12 Under short day conditions, both GA receptors oscillate in a clock-dependent manner, showing a peak of expression at the end of the light period, resulting in higher stability of DELLA proteins during the day and lower DELLA presence towards the end of the night. This circadian clock-mediated oscillation of GA signaling is critical for the adjustment of seedling growth in daily conditions, since the constitutive expression of GA receptors extended the growth phase well into daytime, almost spanning the whole light period. Consistently, the

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providing the plant with the ability to

anticipate predictable daily and seasonal

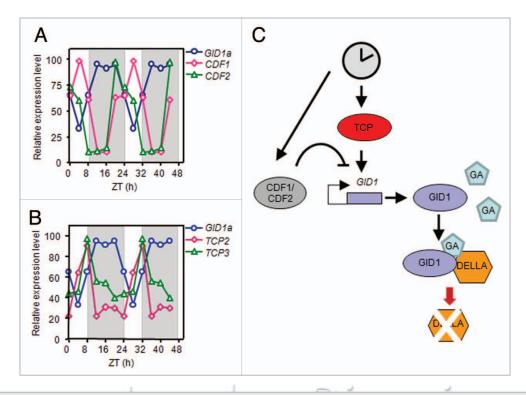


Figure 1. Transcript levels of *CDF1*, *CDF2* and *GID1a* (A), and *TCP2*, *TCP3* and *GID1a* (B) in short-day photocycles (8 h light/16 h darkness), taken from the Diurnal Database. ¹⁴ (C) Proposed model for the clock-mediated control of *GID1* expression in short-day conditions.

pentuple della KO mutant showed a continuous, arrhythmic hypocotyl growth. Moreover, transcriptomic comparison of della KO and wild type plants at different moments of the day showed that the GA pathway mediates the rhythmic expression of many clock regulated genes related to cell wall modification, and to the response to biotic and abiotic stimuli, indicating that, in addition to growth, other clockregulated processes are affected by GA. We therefore propose that the regulation of GA activity by the circadian clock in combination with the GA-mediated control of circadian outputs that are relevant for growth and development, can be critical to adjust the robustness of circadian responses towards unpredicted, above noise changes in the environment.

An intriguing and critical point that still remains to be addressed in this regulation is the link between the circadian clock and the transcriptional regulation of the GA receptors. The in-silico analysis of *GID1a*, *GID1b* and *GID1c* promoters with AthaMap (www.athamap.de/),¹³ indicated an enrichment of binding sites for Dof transcription factors in *GID1a* and *GID1b*. Particularly, the examination

of the diurnal database (diurnal.cgrb.ore-gonstate.edu/)¹⁴ identified two Dof genes *CDFI* and *CDF2*, whose expression oscillate under diurnal conditions (Fig. 1A). CDF1 and CDF2 are known to repress flowering through the inhibition of *CO* transcription, and their diurnal accumulation depends on GI and FKF1.^{15,16} This inhibitory effect on transcription, and the anti-phase cycling of *CDF1* and *CDF2* when compared with *GID1a* and *GID1b* (Fig. 1A), suggests that these two Dof proteins could mediate the regulation of the GA receptors by the circadian clock (Fig. 1C).

In addition to Dof binding sites, both *GID1a* and *GID1b* promoters show cis elements similar to the binding sites for the rice PCF2 transcription factor. In *A. thaliana*, several homologs of PCF2 (e.g., TCP2 and TCP3) are known to interact with components of the central oscillator such as LHY, CCA1 and several APRRs.¹⁷ In this case, the analysis of the Diurnal database indicated that they oscillate in phase with the *GID1s* transcripts (Fig. 1B). It is therefore tempting to speculate that TCPs, in addition to Dof transcription factors, may constitute

the link, or part of it, between the central oscillator and the expression of the GA receptors. Although the observation that *TCP3* overexpression causes a long hypocotyl phenotype¹⁸ is compatible with this model, further molecular and physiological work is needed to test the actual occurrence of such regulation in vivo.

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