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Bidirectional regulation between circadian clock and ABA signaling

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ABSTRACT

Circadian clock ensures coordination of rhythmic biological processes with environmental cycles. Correct matching of internal and external rhythmic cycles maximizes plant fitness and environmental adaptation capability and also ensures efficient energy consumption through circadian gating of a variety of physiological processes. Accumulating evidences support that circadian oscillator components extensively participate in circadian gating of output processes. Here, we provide remarkable examples illustrating molecular mechanisms underlying circadian gating of environmental sensitivity. In addition, bidirectional interactions between circadian oscillator and output pathways have been observed in abscisic acid (ABA)-related physiological processes, emphasizing the biological relevance of extensive crosstalk surrounding circadian clock in acute time-of-day responses.

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Circadian clock generates endogenous biological rhythm with a period of approximately 24 hours to coincide with environmental cycles. In *Arabidopsis*, various clock components have been characterized, including CIRCADIAN CLOCK-ASSOCIATED 1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY), TIMING OF CAB EXPRESSION 1 (TOC1), PSEUDO-RESPONSE REGULATOR 5 (PRR5), PRR7, PRR9, EARLY FLOWERING 3 (ELF3), ELF4, and LUX ARRYTHMO (LUX),[1-5] and they establish multiple transcriptional feedback loops, a basic framework of circadian clock, to ensure robust circadian oscillation.[6,7]

Circadian clock regulates over 50% of *Arabidopsis* transcriptome and thus a variety of biological processes, including stomatal opening, gas exchange, and carbon and energy metabolism.[8,9] Consistent with circadian regulation of output pathways, the environmental sensitivity of output pathways depends on the time-of-day: upon the same environmental cue, at some times of day the gate is open and the signal relays, whereas at other times of day the gate is closed to attenuate signal transduction.[10]

Molecular basis of the circadian gating is starting to emerge. A limited number of examples suggest how circadian clock gates output pathways at a relevant time-of-day. The most intuitive mode is direct regulation of core output genes by clock oscillator components, which diurnally oscillate. For instance, cold tolerance is gated around dawn, and consistently, cold induction of *C-REPEAT BINDING FACTOR* (*CBF*) genes is maximized early in the morning.[10] The upstream regulators of *CBF*s, including INDUCER OF CBP EXPRESSION 1 (ICE1) and CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR (CAMTA) proteins, interact with CCA1,[11-13] whose accumulation peaks at dawn.[1] Consequently, the CCA1 protein binds to the *CBF* promoters and acts as a transcriptional activator to gate freezing tolerance at dawn.[14] Additional clock repressors PRRs and Evening Complex (EC) are also involved in shaping *CBF* waveforms (Fig. 1A).

The TOC1-PHYTOCHROME INTERACTING FACTOR 4 (PIF4) complex also gates thermoresponsive growth during the day.[15] The PIF4 transcription factor, a key regulator of thermoresponses, triggers auxin biosynthesis and thus longitudinal growth in response to high ambient temperatures.[16,17] Notably, although *PIF4* is induced at high ambient temperatures throughout the circadian cycle,[18] evening-expressed TOC1 interacts with PIF4 and suppresses its transcriptional activation activity to ensure evening-specific inhibition of thermoresponsive growth.[15] In addition, ELF3, whose expression is high during nighttime, also participates in transcriptional and post-translational regulation of PIF4,[19,20] further providing maximum thermo-responsiveness during the day (Fig. 1B).

Circadian gating of ABA signaling has also been demonstrated. Plants are usually exposed to drought stress during the day, and the water-deficit crisis would be maximum usually at end-of-day.[21] Consistently,

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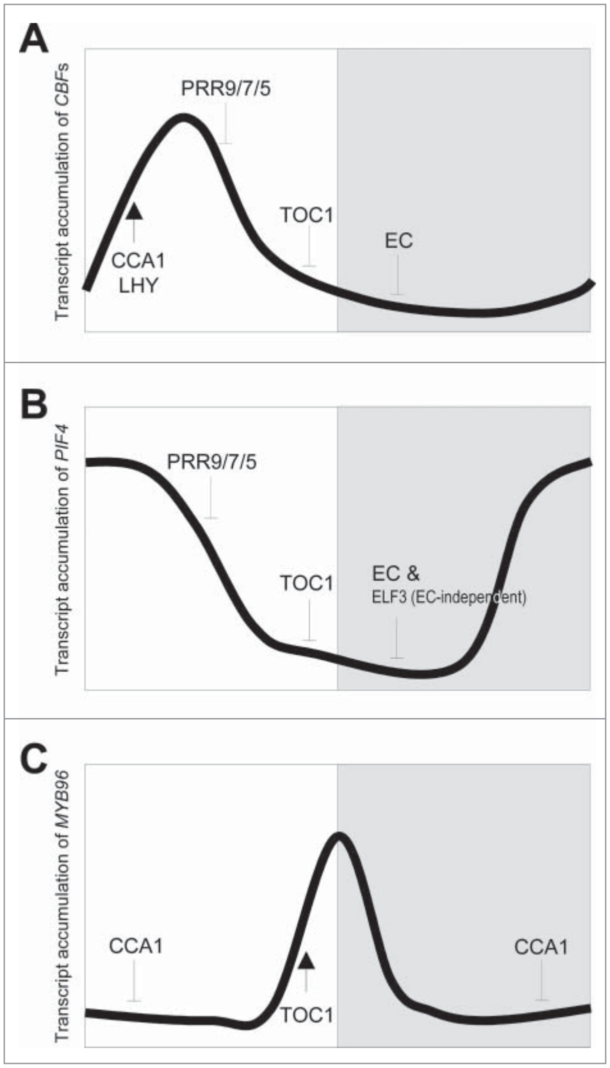

Figure 1. Circadian gating of environmental sensitivity. Core clock components shape rhythmic expression of *CBF*s (A), *PIF4* (B), and *MYB96* (C). The white and gray boxes represent the light condition: white, subjective day; gray, subjective night. Their waveforms reflect induction strength of corresponding genes in response to environmental challenges. EC, evening complex.

ABA-dependent drought responses are gated primarily around dusk.[22] The R2R3-type MYB96 transcription factor is a master regulator of ABA responses and controls various biological processes, including drought tolerance, lateral root development, and cuticular wax accumulation, in response to water-deficit.[23,24] Notably, *MYB96* expression is circadian-regulated and displays a peak at dusk. The CCA1 transcriptional repressor is a putative upstream regulator of *MYB96* and allows its transcript accumulation during the day (Fig. 1C).[25] Collectively, circadian gating optimizes plant fitness and survival but minimizes trade-off, such as growth retardation. Based on evolutionary memories about time-of-day-dependent environmental challenges, nearly all aspects of plant physiological processes anticipate upcoming environmental conditions and are properly gated to ensure biological advantages.

Accumulating evidences have supported the idea that output pathways often feedback circadian oscillator to elaborate output responses.[26,27] Intriguingly, the ABA-inducible MYB96 transcription factor activates *TOC1* expression by binding directly to its gene promoter.[25] MYB96 is included as a circadian component in central loop, which is relevant only in the presence of ABA and influences clock oscillation.[25] In support of this, exogenous ABA treatment shortens circadian period in a MYB96-depedent manner.[25] The reciprocal regulation of circadian oscillator by output pathway would most likely facilitate to delicately readjust circadian oscillation, ensuring near-perfect matching between diurnal physiological process and environmental fluctuation for the best performance of plants in a given condition. This mode of action is not limited for ABA signaling and would underlie wide-ranges of circadian-regulated biological processes. Future studies will shed a light on more general modes of action underlying bidirectional regulation between circadian oscillator and output pathways.

Abbreviations

ABA	abscisic acid
CBF	C-REPEAT BINDING FACTOR
CCA1	CIRCADIAN CLOCK-ASSOCIATED 1
EC	Evening Complex
LHY	LATE ELONGATED HYPOCOTYL
PIF4	PHYTOCHROME INTERACTING FACTOR 4
PRR	PSEUDO-RESPONSE REGULATOR
TOC1	TIMING OF CAB EXPRESSION 1

Disclosure of potential conflicts of interest

No potential conflicts of interests were disclosed.

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