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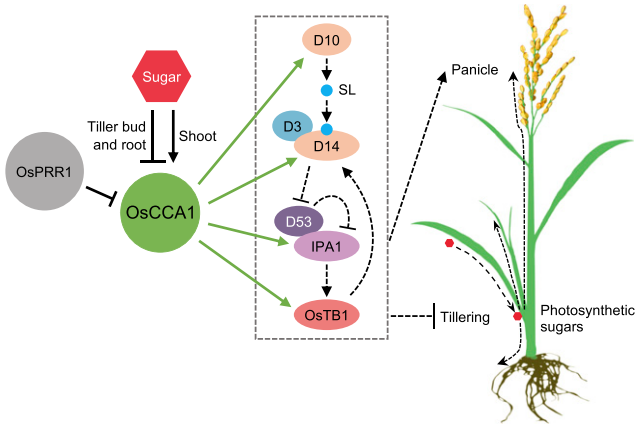
IN BRIEF

Sugars Inform the Circadian Clock How to Shape Rice Shoots via the Strigolactone Pathway[OPEN]

Circadian clocks act as universal timekeepers to harmonize internal processes with external day/night rhythms. Genetic feedback loops gear these inner clocks by approximating time in response to dawn/dusk cycles. In plants, development, growth, hormone action, metabolism, and other downstream events are crucially synchronized with the clock (Greenham and McClung, 2015). How the clock shapes plant architecture and yield remain key questions. In this issue of *The Plant Cell*, in an illuminating report, **Wang and colleagues (2020)** uncover genetic mechanisms in rice (*Oryza sativa*) by which the circadian clock integrates photosynthetic sugars to regulate the phytohormone strigolactone (SL) pathway, axillary bud potential (i.e., tiller outgrowth), panicle architecture, and yield.

The rice clock is composed of the hub transcription factor CIRCADIAN CLOCK ASSOCIATED1 (OsCCA1) and its antagonist factor PSUEDORESPONSE REGULATOR1 (OsPRR1) that are homologous to Arabidopsis (*Arabidopsis thaliana*) clock regulators (Murakami et al., 2007). To explore whether tinkering with the clock affects shoot architecture and yield traits, the authors leveraged a series of transgenic experiments (overexpression, gene silencing, and CRISPR/Cas9 gene editing) that tested *OsCCA1* and *OsPRR1* function. Interestingly, tiller bud outgrowth increased or decreased when *OsCCA1* was either downregulated or upregulated, respectively; altering *OsPRR1* levels produced opposite effects. SL is a known inhibitor of rice tillering (Wang et al., 2018). To connect tiller outgrowth with *OsCCA1* function, the authors mined published chromatin immunoprecipitation sequencing data for Arabidopsis CCA1 and panned for genes in the SL pathway. Among the putative AtCCA1-SL pathway targets were rice homologs of *TEOSINTE BRANCHED1* (*OsTB1*), *DWARF10* (*D10*), *D14*, and *IDEAL PLANT ARCHITECTURE1* (*IPA1*), all of which house CCA1 binding sites in their respective promoters.



Sugar Sensing by *OsCCA1* Regulates SL and Rice Shoot Architecture.

Photosynthetic sugar controls *OsCCA1* levels that act as a key integrator of circadian rhythms, the SL pathway, tiller outgrowth, panicle architecture, and yield in rice.
(*Adapted from Wang et al. [2020], Figure 8.*)

OsTB1 is a known repressor of tiller outgrowth (Wang et al., 2018). An elegant series of in vitro and in vivo experiments demonstrated that *OsTB1* is a direct target of OsCCA1. As an added brake on tiller outgrowth, the SL biosynthesis gene *D10* was also shown to be a direct target of OsCCA1. Genetic interaction and overexpression analyses placed *OsTB1*, *D10*, and SL signal-encoding genes *D14* and *D53* downstream of *OsCCA1*. The authors then probed for factor(s) operating upstream of *OsCCA1*.

Sugars promote axillary bud outgrowth in pea (*Pisum sativum*; Wang et al., 2018) and influence *CCA1* levels through *PRR7* in Arabidopsis (Haydon et al., 2013). The authors hypothesized that sugar regulates *OsCCA1* levels, which would in turn impact tillering. To test this hypothesis, a series of sugar induction experiments were conducted in rice shoots that utilized endosperm removal and exogenous sugar supplementation, panicle removal, and chemical inhibition of photosynthesis. *OsCCA1* and *OsTB1* expression were consistently downregulated in tiller buds, and subsequently, tiller outgrowth increased, supporting the idea that sugar, in part, governs the clock to regulate tiller bud dormancy release.

Among the putative OsCCA1 targets was *IPA1*, an integral regulator of inflorescence architecture and yield in rice. The authors found that panicle size increased in *OsCCA1* overexpression lines and conversely was decreased by *OsCCA1* silencing. Altering *OsPRR1* levels yielded opposite effects on panicle architecture. Through a strong series of in vitro and in vivo experiments, along with generating a novel knockout allele of *IPA1* by CRISPR/Cas9 and performing genetic interaction and overexpression studies, *IPA1* function was placed downstream of *OsCCA1* and shown to be a direct target of OsCCA1.

Wang and et al. (2020) summarize their in-depth study with a model (see figure)

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and leave some questions to be further explored. For example, how does the clock integrate multiple factors to balance tillering and panicle development? Does IPA1 converge on similar target genes in the shoot apex and panicle? How does sugar regulate *OsCCA1* expression positively in shoots but negatively in roots? Open and compelling questions raised by this important work provide several avenues for future studies on this exciting topic.

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