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1 **A new link between plant metabolism and circadian rhythms?**

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9 The rotation of the Earth around its axis generates 24 h cycles of environmental change,
10 such as daily rhythms of light and temperature. Circadian clocks, cellular biological
11 oscillators that generate 24-hour rhythms of gene expression and metabolism, are thought to
12 synchronize the functioning of organisms with these daily environmental changes. Circadian
13 regulation enables organisms to anticipate environmental changes such as dawn and dusk,
14 and co-ordinate their metabolism, physiology and behaviour with daily changes in the
15 environment. This is particularly important for plants, which cannot move to escape
16 environmental challenges.

17 In the experimental model *Arabidopsis thaliana* (Arabidopsis), correct circadian regulation
18 increases photosynthesis, biomass accumulation, survival, seed number and viability (Green
19 *et al.*, 2002; Dodd *et al.*, 2005). It is estimated that almost 90% of Arabidopsis transcripts
20 can oscillate in abundance over the 24 h cycle, with about 30% of transcripts being
21 circadian-regulated (Michael *et al.*, 2008). This multitude of genes under circadian control
22 highlights the pervasiveness of circadian regulation in co-ordinating the functioning of plants
23 with their rhythmic environment. Because photosynthetic light harvesting can only occur
24 during the day, and stored carbohydrate reserves require mobilization at night to supply
25 respiration and growth, plant metabolism is intimately associated with cycles of day and

26 night. Building upon extensive underpinning research into the molecular genetics of
27 circadian oscillators, the interactions between metabolism, signalling and circadian
28 regulation have become an important growth area in plant circadian biology. For example,
29 breakthroughs have demonstrated that the rate of nocturnal starch breakdown is intricately
30 timed so that plants do not starve at night (Graf *et al.*, 2010), sugars produced by
31 photosynthesis can entrain the circadian clock (Haydon *et al.*, 2013), and the concentrations
32 of ions such as Ca^{2+} and Mg^{2+} are regulated by, and can regulate, the circadian oscillator
33 (Dodd *et al.*, 2007; Feeney *et al.*, 2016).

34 In this issue of *Plant, Cell and Environment*, Shin *et al.*, 2017 identified another potential
35 connection between metabolism and circadian regulation. The authors established that an
36 energy-sensing protein complex can influence circadian rhythms. AKIN10 (known also as
37 KIN10 or SnRK1.1) is a catalytic α -subunit of Snf1 (sucrose non-fermenting1)-related kinase
38 1 (SnRK1), which is an evolutionarily conserved energy sensor. SnRK1 controls metabolic
39 enzymes through protein phosphorylation (Sugden *et al.*, 1999), and also regulates > 1000
40 transcripts in response to starvation by controlling transcription factor activity (Baena-
41 González *et al.*, 2007; Mair *et al.*, 2015). SnRK1 plays such a fundamental role in energy
42 metabolism that AKIN10 knockouts are lethal (Baena-González *et al.*, 2007). By
43 overexpressing AKIN10 with a chemically-inducible promoter, the authors explored the role
44 of AKIN10 in circadian regulation. They found that inducing very high levels of AKIN10
45 expression caused the circadian clock to assume a long period, of up to 5 h longer than
46 controls, when plants were under conditions of continuous light. Interestingly, the long
47 circadian period caused by AKIN10 overexpression disappeared in experiments performed
48 under continuous darkness, such that AKIN10 overexpressing plants had the same circadian
49 period as the controls. When AKIN10 overexpressors were in constant darkness,
50 supplementing the growth media with sugars did not restore the long circadian period that
51 occurred in the light. The authors interpret this to indicate that starvation does not cause the
52 insensitivity of circadian period to AKIN10 overexpression in darkness. Instead, Shin *et al.*

53 (2017) propose that the influence of AKIN10 upon circadian period forms a response to the
54 light environment.

55 The study also found that under both light/dark cycles and constant light, AKIN10
56 overexpression caused a delay in the peak of expression of transcripts encoding the
57 evening-expressed circadian oscillator component GIGANTEA (GI). This is interesting
58 because *gi-11* mutants are insensitive to a long-term effect of sucrose upon the circadian
59 oscillator (Dalchau *et al.*, 2011). Additionally, the authors found that the period of plants
60 harbouring the *tic-2* mutation in the circadian oscillator gene *TIME FOR COFFEE (TIC)* had
61 reduced sensitivity to the effects of AKIN10 overexpression, suggesting a role for TIC in the
62 regulation of circadian period by AKIN10.

63 It is intriguing that AKIN10, a key player in the regulation of energy metabolism of
64 Arabidopsis, can influence circadian rhythms. The work of Shin *et al.* (2017) builds on
65 studies demonstrating bidirectional regulatory interactions between circadian regulation and
66 metabolism (Fig. 1). For example, the environmental cycles of day and night dictate when
67 photosynthesis can occur, and photosynthesis is also regulated extensively by the circadian
68 oscillator (Dodd *et al.*, 2014). Importantly, the products of photosynthesis can, in turn, entrain
69 the circadian oscillator (Haydon *et al.*, 2013). Each morning, the upregulation of
70 photosynthesis causes an accumulation of sugars, which alters circadian oscillator gene
71 expression and can adjust the circadian phase (Haydon *et al.*, 2013). Similarly, the circadian
72 oscillator controls the rate of nocturnal starch consumption (Graf *et al.*, 2010), with one
73 mathematical model for the regulation of nocturnal starch degradation assuming the
74 presence of a sugar sensing mechanism (Feugier & Satake, 2013). In this way, the
75 environment affects metabolism, metabolism regulates the circadian oscillator, and the
76 circadian oscillator regulates metabolism (Fig. 1).

77 By demonstrating that a subunit of the central energy sensor SnRK1 affects the functioning
78 of the circadian oscillator, Shin *et al.* (2017) have identified a mechanism that has the
79 potential to couple metabolism with circadian regulation. This adds to the evidence that

reciprocal regulation between the circadian oscillator and energy metabolism exists across several Kingdoms of life. For example, in mammals there are circadian rhythms of NAD⁺ and ATP synthesis and feeding can reset the circadian oscillator, and in both plants and cyanobacteria, the availability of energy can regulate circadian rhythms (Rust *et al.*, 2011; Bass, 2012; Haydon *et al.*, 2013). Therefore, the long circadian period caused by AKIN10 overexpression (Shin *et al.* 2017) could point to a role for AKIN10 in interfacing the circadian oscillator with both metabolism and environment, given the extensive influence of environmental conditions upon the metabolic state of plants. In future, it will be informative to determine the function and position of SnRK1 within the circadian system, to understand how a sensor of cellular energy status contributes to the responses of plants to the daily changes that occur in the environment.

Figure legend

Figure 1. Reciprocal regulation between the environment, metabolism and circadian rhythms in *Arabidopsis thaliana*. SnRK1 is thought to regulate metabolic enzyme activity and transcription in response to energy availability. In this issue, Shin *et al.* (2017) have identified a new role for the SnRK1 catalytic subunit AKIN10 in regulating circadian period (shown in red).

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