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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

80 reciprocal regulation between the circadian oscillator and energy metabolism exists across

81 several Kingdoms of life. For example, in mammals there are circadian rhythms of NAD^+ and

82 ATP synthesis and feeding can reset the circadian oscillator, and in both plants and

83 cyanobacteria, the availability of energy can regulate circadian rhythms (Rust *et al.*, 2011;

84 Bass, 2012; Haydon *et al.*, 2013). Therefore, the long circadian period caused by AKIN10

85 overexpression (Shin et al. 2017) could point to a role for AKIN10 in interfacing the circadian

86 oscillator with both metabolism and environment, given the extensive influence of

87 environmental conditions upon the metabolic state of plants. In future, it will be informative to

88 determine the function and position of SnRK1 within the circadian system, to understand

89 how a sensor of cellular energy status contributes to the responses of plants to the daily

90 changes that occur in the environment.

91

92 **Figure legend**

93 **Figure 1.** Reciprocal regulation between the environment, metabolism and circadian

94 rhythms in *Arabidopsis thaliana*. SnRK1 is thought to regulate metabolic enzyme activity and

95 transcription in response to energy availability. In this issue, Shin et al. (2017) have identified

96 a new role for the SnRK1 catalytic subunit AKIN10 in regulating circadian period (shown in
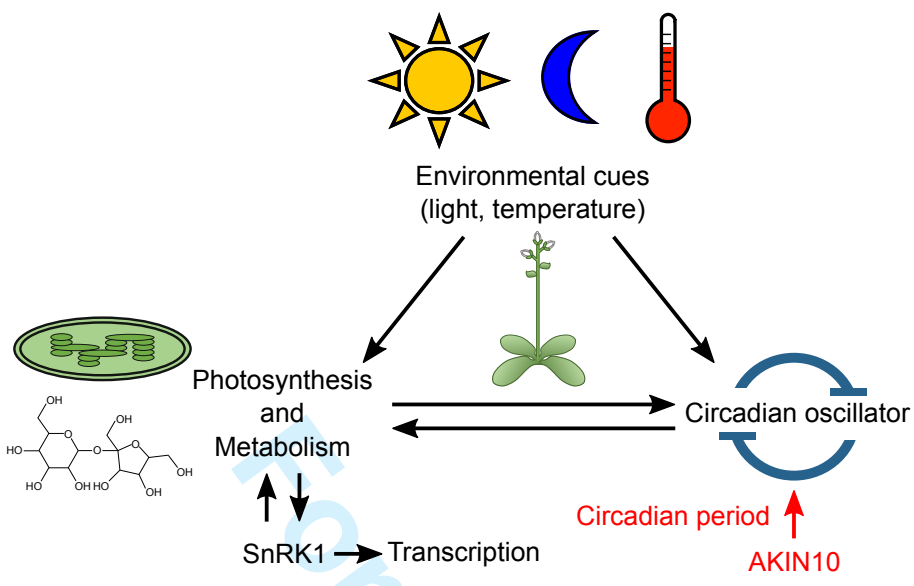
97 red).

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