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REVIEW PAPER

Connections between circadian clocks and carbon metabolism reveal species-specific effects on growth control

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Abstract

The plant circadian system exists in a framework of rhythmic metabolism. Much has been learned about the transcriptional machinery that generates the clock rhythm. Interestingly, these components are largely conserved between monocots and dicots, but key differences in physiological and developmental output processes have been found. How the clock coordinates carbon metabolism to drive plant growth performance is described with a focus on starch breakdown in *Arabidopsis*. It is proposed that clock effects on plant growth and fitness are more complex than just matching internal with external rhythms. Interesting recent findings support that the products of photosynthesis, probably sucrose, in turn feeds back to the clock to set its rhythm. In this way, the clock both controls and is controlled by carbon fluxes. This has an interesting connection to stress signalling and water-use efficiency, and it is now known that the clock and abscisic acid pathways are reciprocally coordinated. These processes converge to drive growth in a species-specific context such that predictions from the *Arabidopsis* model to other species can be restricted. This has been seen from phenotypic growth studies that revealed that dicot shoot growth is rhythmic whereas monocot shoot growth is continuous. Taken together, emerging evidence suggests reciprocal interactions between metabolism, the circadian clock, and stress signalling to control growth and fitness in *Arabidopsis*, but transferability to other species is not always possible due to species-specific effects.

Key words: *Arabidopsis*, barley, circadian clock, diurnal, growth control, hormone signalling, sucrose.

Introduction

The rotation of the earth causes repetitive changes between day and night that are reflected in diurnal cycles of temperature and light. Plants have to adapt to these consistent and predictable environmental conditions. The circadian clock, an endogenous timing mechanism with a periodicity of about 24 h, is a key regulator in this adaptive process. It allows measurement of time independently from day–night phases and enables the plant to trigger metabolism and stress responses at particular time points of the day. In this manner, plants can regulate physiology in an anticipatory manner. This exists as a process that is thought to maximize fitness and growth performance, as well as yield and reproductive success. This review discusses the reciprocal regulatory interaction between the circadian clock and carbon metabolism and its impact on stress signalling and water use. This collectively creates plant performance.

The circadian clock of plants

The transcriptional–translational clock of plants is a set of proteins that forms an interconnected feedback system with multiple loops. These provide temporal information

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to organisms to coordinate developmental and metabolic responses in coincidence with the environment (Sanchez *et al.*, 2011; Farre and Weise, 2012; Bujdoso and Davis, 2013; Kinmonth-Schultz *et al.*, 2013; Staiger *et al.*, 2013). In a process called entrainment, external cues like temperature and light are used as inputs to set the circadian clock every morning and create synchrony between internal rhythmicity of the oscillator and external rhythmicity of the environment. Under conditions of continuous light and temperature, such constant environmental inputs reveal the internal rhythmicity of the oscillator. This internal rhythm is subject to extensive natural variation both within and between species, and this is reported to influence fitness and performance of the plant (Dodd *et al.*, 2005; Boikoglou *et al.*, 2011; Edwards *et al.*, 2011, 2012; Izawa *et al.*, 2011; Yerushalmi *et al.*, 2011; Farre, 2012; Farre and Weise, 2012; Faure *et al.*, 2012; Matsubara *et al.*, 2012; Weller *et al.*, 2012; Anwer and Davis, 2013; Habte *et al.*, 2013; Kinmonth-Schultz *et al.*, 2013; Sulpice *et al.*, 2014). As a consequence, the circadian clock is considered a key regulator of plant physiology and adaptation to different geographic environments.

The Arabidopsis *model*

In the dicotyledonous model plant *Arabidopsis thaliana*, the shoot circadian clock consists of multiple, interlocking feedback loops with predominant elements of negative regulation. The central loop consists of two partially redundant MYB transcription factors CCA1 (CIRCADIAN CLOCK ASSOCIATED 1) and LHY (LATE ELONGATED HYPOCOTYL) as well as the PSEUDO RESPONSE REGULATOR PRR1 (also known as TIMING OF CAB EXPRESSION 1, TOC1). The morning-expressed proteins CCA1 and LHY repress TOC1 by direct binding to its promoter, leading to TOC1 accumulation in the evening and, in turn, transcriptional repression of *CCA1*/*LHY* by TOC1 (Pokhilko *et al.*, 2012, 2013). This core clock is considered crucial for rhythmic maintenance as the *cca1*/*lhy*/*toc1* triple mutant is described to be arrhythmic (Ding *et al.*, 2007).

Associated to this central loop, a morning-phased loop is comprised of the dawn-phased pseudo-response regulators (PRRs) PRR7 and PRR9 that repress *CCA1*/*LHY* expression during daylight (Pokhilko *et al.*, 2012; Bujdoso and Davis, 2013). Feedback to the *PRRs* is established by the evening complex, which is composed of EARLY FLOWERING 3 (ELF3) (Dixon *et al.*, 2011; Herrero *et al.*, 2012), a light-signal-mediator required for the oscillator to cycle (McWatters *et al.*, 2000; Kolmos *et al.*, 2011; Herrero and Davis, 2012; Herrero *et al.*, 2012), the ligand ELF4 and the DNA-binding protein LUX ARRYTHMO (Dixon *et al.*, 2011; Helfer *et al.*, 2011; Herrero and Davis, 2012). Together this evening complex represses *PRR9* and *PRR7* to indirectly activate CCA1/LHY (Kolmos and Davis, 2007; Herrero and Davis, 2012; Pokhilko *et al.*, 2012; Bujdoso and Davis, 2013). They are themselves evening expressed because of repression by *CCA1* and *LHY* (Lu *et al.*, 2012). Another associated loop is evening phased; here, TOC1 protein is in autoregulative feedback with GIGANTEA (GI) and ZEITLUPE (ZTL). The manner of this regulation includes post-translational modifications and proteolysis that results in transcriptional regulation within this feedback loop (Pokhilko *et al.*, 2012). The specific details of how GI fits into this regulatory loop are not fully established. Based on this multiple interlocked feedback system, the oscillator generates continuous rhythms even under rapidly fluctuating conditions typical of weather patterns (Troein *et al.*, 2009).

Transcripts and protein products of clock components cycle in repetitive, diurnal patterns. Most clock components are transcription factors that not only regulate each other in an interactive manner but also regulate other genes outside the clock loops themselves. These are called clock-output processes. Output genes often sit at core internodes of physiology and development and regulate biological processes like growth, metabolism, hormone, and stress signalling (Lu *et al.*, 2005; Covington *et al.*, 2008; Hanano *et al.*, 2008; Dalchau *et al.*, 2010; Sanchez *et al.*, 2011; Farre and Weise, 2012; Kinmonth-Schultz *et al.*, 2013; Stitt and Zeeman, 2012; Seaton *et al.*, 2014). It has been estimated that around 30% of the whole *Arabidopsis* transcriptome follows anticipatory rhythms generated by the clock (Covington *et al.*, 2008), which underpins the central importance of the circadian system (Davis and Millar, 2001; Staiger *et al.*, 2013).

Inference from cycling transcripts to diurnal physiological patterns is not necessarily straightforward. For example, the gene encoding glucan water dikinase (GWD, also termed SEX1), a key enzyme regulating nocturnal starch breakdown in leaves, revealed cycling transcription, but constant protein abundance under free-running conditions (Lu *et al.*, 2005). Interestingly, starch breakdown, the physiological trait regulated by GWD, cycled under constant conditions. Thus, post-translational modification of proteins can hamper direct conclusiveness from diurnal transcription patterns to physiological effects.

Orthology of clock components in higher plants

The angiosperm oscillator seems to be largely conserved in higher plants and between eudicot and monocot species. For example, *Arabidopsis* clock homologues with comparable patterns of transcript accumulation, with respect to peaking time and amplitude, were also identified in other eudicot and monocots species (in Song *et al.*, 2010; McClung, 2013). Consequently, ectopic overexpression of rice *OsTOC1* and *OsZTL* in *Arabidopsis* showed clock-related phenotypes comparable to overexpression of their *Arabidopsis* orthologues *AtTOC1* and *AtZTL* (Murakami *et al.*, 2007). Furthermore, *OsTOC1* was able to partly rescue the *Arabidopsis toc1* null mutant (Murakami *et al.*, 2007), implying a level of commonality within the circadian clockwork of higher plants. Work on the barley orthologous set of clock genes came to a similar conclusion (Campoli *et al.*, 2012). It appears that there is significant overlap in the repertoire of clock genes between species (McClung, 2013).

Reports describe a high degree of conserved genomic sequences and functional protein domains in barley and rice in comparison to *Arabidopsis* (Murakami *et al.*, 2007;

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Campoli *et al.*, 2012). In those two monocots, however, *CCA1* constitutes the only orthologue to the *Arabidopsis* paralogues *AtCCA1*/*AtLHY* (Murakami *et al.*, 2007; Campoli *et al.*, 2012). In addition, the gene family of *PRRs* appears to present a paralogous relationship, suggesting independent duplication and evolution of the three ancestral PRRs in dicots and monocots (Takata *et al.*, 2010). For example, *Arabidopsis PRR9* and *PRR5* are phylogenetically separate, and the phylogenetically associated monocot orthologues *PRR95*/*59* do not clade with these dicot counterparts (Murakami *et al.*, 2003; Campoli *et al.*, 2012). The same holds true for *AtPRR7* and *AtPRR3*, where both resemble the monocot genes *PRR73*/*37* (Murakami *et al.*, 2003; Campoli *et al.*, 2012). Further, whereas the *Arabidopsis PRRs* display transcript peaks in temporal order in the sequence *AtPRR9*, *7*, *5*, *3*, and *TOC1* (Matsushika *et al.*, 2000), the *PRR*s of barley and rice display broad peaks over the day in the sequence *PRR37*/*73*, *PRR59*/*95*, and *PRR1* (Murakami *et al.*, 2007; Campoli *et al.*, 2012). This finding raises a complex question; what are the roles of these paralogous genes in the monocotyledonous clock system? In addition, and in contrast to *Arabidopsis*, *GI* and *TOC1* have been hypothesized as being in positive feedback in rice (Izawa *et al.*, 2011). Nevertheless, remarkable similarities in architecture and function of circadian clocks in higher plants exist.

Plant performance at the physiological level

Circadian clock and photosynthesis

Plants benefit from circadian control of photosynthesis and physiology to achieve higher fitness (Dodd *et al.*, 2005). In that work, higher chlorophyll content, higher carbon fixation, and increased water-use efficiency was associated with synchrony between circadian clock period and day length. This correlated with both a doubling of plant biomass and higher survival rates in a competitive environment. Under a T-cycle of 20 h (a fake day a 10/10 light dark cycle), the *toc1* mutant that has a 20-h clock grew with higher performance than the *ztl* mutant having a 28-h period. Conversely, the *ztl* mutant grew better than *toc1* under T-cycles of 28 h. Thus, the authors observed that, under T-cycle conditions, a match between internal and external rhythmicity led to increased plant performance, whereas a rhythmic mismatch reduced growth and survival (Dodd *et al.*, 2005).

The study by Dodd *et al.* (2005) implied that circadian clocks properly timed to day/night cycles can reliably anticipate dusk and dawn to prepare photosynthesis and physiology in an anticipatory manner for the course of the upcoming day. However, more recent findings implicate that these findings are most applicable to unnatural day-length conditions that deviate from 24-h T-cycles (Graf *et al.*, 2010), which confirmed the observations from Dodd *et al.* (2005) under extreme day-length conditions and extended the experiments to differing photoperiods in a normal 24-h T-cycle. There, Graf *et al.*, 2010) found that biomass of *toc1* and *ztl* mutants was highest under 24-h growth conditions with day/night cycles that were in mismatch with the internal periods of the respective clock mutants. Thus it was concluded that a match of internal circadian period with external T-cycles is not sufficient to generally explain clock effects on growth performance and fitness. Instead, the authors suggested that the circadian control of starch degradation must not be overlooked in this context (Graf *et al.*, 2010; Graf and Smith, 2011).

It is plausible that the cooperative circadian control of anabolism and catabolism are decisive for high plant-growth performance. Indeed an extensive transcriptional network was uncovered that linked clock and metabolic intersections in diurnally regulated gene expression that is seen for thousands of genes (Bläsing *et al.*, 2005). Extending this, Ni *et al.* (2009) reported in allopolyploids that photosynthesis and starch metabolism were differentially regulated by the circadian clock, in comparison to their diploid parents. This led to superior growth in allopolyploids. In these allopolyploids, daytime expression of *TOC1*, *GI*, and additional clock-output genes containing *cis*-elements associated to clock regulation were elevated relative to both parental diploids. This led to an alteration in circadian rhythmicity. This could be attributed to a reduction of transcription-activating methylation marks at the *CCA1* and *LHY* promoters of the allopolyploids, leading to lower CCA1/LHY protein levels at noon (Ni *et al.*, 2009). Thus, clock-output genes causative for higher chlorophyll content, as well as for starch metabolism and sugar transport, were expressed higher in the allotetraploids than their diploid parents. This was all associated to higher biomass in the polyploidy lines, which is one form of hybrid vigour (Ni *et al.*, 2009). However, the extent of circadian effects on photosynthesis to drive growth performance has not been clearly resolved. For example, it has been reported that *Arabidopsis* wild-type plants grown under 28-h period cycles with mismatch to the internal clock period fixed more CO_2 as compared to 24-h cycles, but showed reduced biomass.

CO_2 uptake alone does not appear as the single major factor to increase fitness and performance. It has been proposed that alterations of chlorophyll content happen in a scale that might be insignificant for CO_2 uptake (Jenkins *et al.*, 1989; Sperling *et al.*, 1997; Andersson *et al.*, 2003; Graf *et al.*, 2010). Nevertheless, rhythmicity and expression levels of *CCA1*/*LHY* and *PRR7*/*PRR9* are capable of influencing plant growth performance by inducing and entraining primary metabolism (Fukushima *et al.*, 2009; Graf *et al.*, 2010; Lai *et al.*, 2012).

Circadian clock and carbon supply at night

Apart from photosynthesis, mobilization of storage compounds is another important factor known to contribute to plant growth performance (Sulpice *et al.*, 2009). Graf *et al.* (2010) reported that in *Arabidopsis* starch degradation at night is controlled by CCA1/LHY. They concluded that this regulation is necessary to prevent sucrose starvation and growth penalties at night (Graf and Smith, 2011). Specifically, *cca1*/*lhy* double-mutant plants of *Arabidopsis* in 24-h T-cycles and wild-type plants in 28-h T-cycles depleted starch reserves

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prematurely and showed significantly reduced growth. This premature depletion of nocturnal depots led to activation of sucrose starvation-induced genes before dawn. As sucrose addition could complement for the observed biomass reduction in otherwise starving plants, carbon shortage during the night was causative for reduced growth (Graf *et al.*, 2010). Thus, the circadian clock via CCA1/LHY sets a maximum rate of carbon supply during the night that is adjusted in such a way that starch reserves last until the next morning.

It appears that a fixed rate of sucrose supply from starch cannot be overcome by increased demand. Consequently, in well-nourished plants, where carbon supply limits growth, CCA1/LHY directly regulates plant growth at night (Graf *et al.*, 2010; Yazdanbakhsh *et al.*, 2011). Short-period mutant phenotypes do not necessarily impose premature starch-depot depletion. For example, the *Arabidopsis toc1* mutant is, like *cca1/lhy*, a short-period clock mutant, but it was not found to deplete starch reserves prematurely in 24-h T-cycles (Graf *et al.*, 2010). Additionally the *ztl* long-period mutant did not delay starch exhaustion, as would have been predicted by its delayed-periodicity phenotype. This mutant was found to deplete starch levels in a similar manner as the wild type (Graf *et al.*, 2010). Thus, avoidance of premature starch depletion at night appeared as direct effect of CCA1/LHY on respective clock output targets and not to the short-period phenotype itself. This provided further evidence that a match of circadian period with day length is not sufficient to generally explain higher growth performance in plants.

When *Arabidopsis* wild-type plants were measured for starch levels over 24-h T-cycles, it became clear that the linear rate of starch degradation varied dependent on the length of the night. This was true even when an unexpected early or late onset of the dark phase was encountered. Interestingly, in these experiments, depletion of starch depots was always timed to the onset of the next day (Graf *et al.*, 2010). Even under skeleton days and nights, where a normal day or night is interrupted by a short dark/light phase that partly depletes or regenerates starch depots, starch levels were reliably depleted at the next dawn (Graf *et al.*, 2010; Scialdone *et al.*, 2013; Sulpice *et al.*, 2014). This means that the starch-degradation rate, calculated as the negative slope of starch content loss over time, must be tailored to the starch content present at the onset of night. This strongly indicates that both temporal information and information about starch content are integrated to ensure proper regulation (Graf and Smith, 2011). Obviously, the circadian clock could provide temporal estimation to predict the next dawn, but how plants determine starch content is less obvious.

Several recent modelling studies tackled the question how starch content could be integrated over time and how plants might be able to adjust nocturnal starch-degradation rate to fit experimental data of starch depletion under various conditions and treatments (Scialdone *et al.*, 2013; Seaton *et al.*, 2014). Based on chemical kinetic models, Scialdone *et al.* (2013) proposed that phosphoglucan water dikinase (PWD, also called GWD3) is a key player in this process. It is an enzyme that acts as a focal point to modulate flux through the starch-degradation pathway (Scialdone *et al.*, 2013).

PWD and its related enzyme GWD (glucan water dikinase) work as initial enzymes in the pathway to phosphorylate starch molecules in the chloroplastic granule and trigger its degradation (Smith *et al.*, 2005). Phosphorylation on the granule surface is expected to open up the compacted starch molecules for easier access for further hydrolysis by β-amylases and isoamylase 3. Loss of *PWD* function as well as mutations in major genes involved in the starch-degradation pathway such as *lsf1* and *sex4* in *Arabidopsis* led to reduced overall starch-degradation rate and caused these mutant plants to retain higher amounts of starch at the end of the night than wild-type plants (Scialdone *et al.*, 2013). Nevertheless, after a sudden shift from a 12/12 to a 8/16 light/dark cycle to impose and early unexpected night, all tested mutant plants impaired in starch degradation were, with an exception of *pwd*, able to adjust and lower starch-degradation rate to meet conditions of an early onset of night. The *pwd* mutant retained a higher starch-degradation rate indifferent to the entrained 12-h light conditions (Scialdone *et al.*, 2013). Thus, PWD function appears to be required to adapt nocturnal starch-degradation rate to unexpected onset of the night. As PWD is involved in initiating the phosphorylation status of the starch granules to trigger starch degradation, the starch phosphorylation status was considered a promising candidate to store starch-content information (Scialdone *et al.*, 2013). Indeed, an experiment following starch phosphorylation status over the day found diurnally cycling phosphorylation that could follow starch content during the day (Scialdone *et al.*, 2013). Thus, PWD appears as the hub to control starch-content-dependent flux through the starch-degradation pathway (Scialdone *et al.*, 2013).

Entrainment and gating

The interplay between the circadian clock and metabolism is bidirectional. Several indications exist that metabolites feedback to the oscillator to adjust the circadian clock. Based on computational modelling, GIGANTEA (GI) was identified as a mediator of sucrose-dependent changes on rhythmicity of the shoot clock (Dalchau *et al.*, 2011). Further experiments confirmed that sucrose application acted as a *Zeitgeber* (time giver) to generate and set circadian rhythms in continuous darkness. A different study reported that the circadian clock in *Arabidopsis* roots is a slave of the shoot clock and is set by a photosynthesis-related signal from the shoot, which was proposed to be sucrose (James *et al.*, 2008). Consequently, sucrose feeding to the root altered clock rhythmicity in the root. Related to that, Haydon *et al.* (2013a) reported that photosynthesis-derived sucrose entrains the circadian clock of *Arabidopsis* seedlings. Peaking of sucrose levels in the morning defined a 'metabolic dawn', which could be related to decreased *PRR7* expression. Thus, peaking of leaf sucrose in the morning repressed *PRR7* expression, which in turn, repressed *CCA1* transcription to set the clock. As a consequence, expression of the clock component *CCA1* advanced dependently on metabolic status. Taken together, metabolic cues through sucrose direct the resetting of the clock at dawn dependent on metabolic status. This means that sucrose is signal and metabolite at the same time.

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In addition to carbon metabolism, water status is a further determinant for plant growth. The plant hormone abscisic acid (ABA) is involved in responses to water shortage, and the ABA-signalling pathway is controlled by the circadian clock (Hanano *et al.*, 2006; Covington *et al.*, 2008; Sanchez *et al.*, 2011). This causality generates a phenomenon termed gating where physiological responses differ to comparable stimuli during the course of the day. For example, application of ABA in the morning revealed a higher affect on stomatal closure than application in the afternoon (Correia *et al.*, 1995). This indicated that responses to ABA are gated by the circadian clock.

A prominent example of ABA entrainment on the oscillator and gating was given by Legnaioli *et al.* (2009). This study showed that TOC1 can directly bind to the promoter of one putative ABA receptor ABAR/CHL5/GUN5, where TOC1 negatively regulated *ABAR* expression in a periodic manner. Conversely, ABAR was found to positively regulate *TOC1* transcription, linking ABA perception to the circadian clock. Notable here is that hormone synthesis and perception mutants in the ABA pathway have clock periodicity phenotypes (Hanano *et al.*, 2006). Taken together, sensitivity to ABA is described as a clock-gated process, which, in turn, acts to fine tune the speed of the generated oscillations.

Administration of ABA during the day, but not during the night, led to immediate induction of *TOC1* transcription (Legnaioli *et al.*, 2009). In addition, lower levels of *ABAR* transcripts were linked to higher stomatal conductance and water loss via the leaf surface area, indicating that repression of ABAR reduces ABA-mediated stomata closure and savings of water to reduce wilting (Legnaioli *et al.*, 2009). Thus, reciprocal regulation of TOC1 and ABAR might function as a fine-tuned switch to modulate plant sensitivity to ABA, which is likely to affect water-use efficiency and plant performance. Interestingly, a recent study in barley has shown that osmotic stress applied to the roots altered the expression of clock genes in the shoot suggesting that plant water status can feed back into the clock (Habte *et al.*, 2013). In addition, mutations in the barley clock orthologues *Ppd-H1* and *HvELF3* affected the expression of stress-gene expression, demonstrating that the clock also controls stress responses in monocotyledonous plants. Thus, reciprocal feedback between stress signalling and the clock exists both in monocot and eudicot species, which apparently adapts the clock to acute stress to better regulate future physiological responses under stress. This is likely to increase plant fitness.

Circadian control of ecophysiological traits has been shown to impact on plant growth performance. Edwards *et al.* (2011) reported that natural genetic variation in the *Brassica rapa* circadian clock is associated to phenotypic variation in traits related to photosynthesis. Photosynthesis rate, stomatal conductance, and transpiration rate were significantly correlated with circadian period, indicating that the circadian clock might regulate photosynthesis and related traits in a way to increase resource use efficiency of water and light to increase plant performance and fitness. The authors then showed that genetic variation exists for these correlative events (Edwards *et al.*, 2012). Together, one can wonder if the extensive variation seen in circadian periodicity is in part physiologically selected based on water-use traits.

Plant performance at the phenotypic level

Rhythmicity of expansion growth and clock effects on carbon allocation and plant architecture

Even though structure and function of the circadian system might be widely conserved in higher plants, regulation of clock-output traits need not be similarly conserved. For example, the circadian clock has been shown to be one of the major signalling pathways regulating growth rates in plants (Walter *et al.*, 2009). In dicotyledonous species, two different shoot growth types were found and they differ in peaking of growth rate, which is either at dawn or dusk (Walter *et al.*, 2009). Furthermore, shoot growth of several dicot species remained rhythmic under conditions of continuous temperature and light, proving the circadian clock to control growth processes in the dicot shoot (Walter *et al.*, 2009). In contrast, however, examined monocots displayed constant growth rates under continuous temperature and light (Walter *et al.*, 2009; Poire *et al.*, 2010; Fig. 1). These discrepancies between dicot and monocot studies indicate that growth in the monocot shoot is driven by temperature cycles instead of the circadian clock in dicots (Walter *et al.*, 2009). Such a difference in growth control questions if the clock oscillator has the same importance to regulate physiology, metabolism and growth in monocots as it does dicots.

In *Arabidopsis*, shoot growth peaks towards the end of the night in a clock-controlled manner. In other dicot species, shoot growth is also rhythmic, but a second growth type exists where growth peaks at the beginning of the night (Walter *et al.*, 2009). Monocot shoot growth largely follows diurnal temperature cycles over endogenous rhythms (Poire *et al.*, 2010). There is no obvious relationship here when considering root growth. For example, rice roots grew, like *Arabidopsis* roots, rhythmically under constant darkness (Iijima and Matsushita, 2011). Conversely, roots of the dicot plant tobacco grew in a linear pattern under constant light

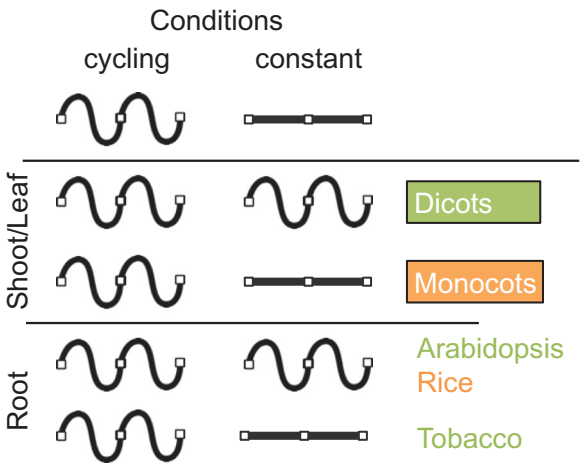

Fig. 1. Species-specific growth control by circadian oscillations. For explanations and references see text. Cycling conditions refer to cycles in temperature and light, constant conditions refers to constant temperature and light. (this figure is available in colour at *JXB* online).

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conditions while the shoot extends rhythmically (Nagel *et al.*, 2006; Poire *et al.*, 2010). As a consequence, growth findings indicate that circadian regulation of growth in the root versus the shoot appears to be species specific.

Differences in morphology between monocot and dicot plants has been hypothesized as one evolutionary reason to explain the basis for such a difference (Walter *et al.*, 2009; Ruts *et al.*, 2012). The monocot shoot meristem is located in the inner bundle sheath and can be more protected from the environment, which in comparison in dicots, the shoot meristem is more exposed around the leaf edge (Ruts *et al.*, 2012). Thus, clock effects on growth physiology might be questionable for knowledge transfer from *Arabidopsis* to other dicot and monocot species. It appears that species-specific investigation has to be undertaken. In addition, differences in root and shoot growth within the same species underline the importance to separately consider organ specific clocks.

Apart from diurnal control of growth rates, the circadian clock has also been implicated to shape plant morphology. Ruts *et al.* (2012) reported that *Arabidopsis* clock mutants reveal aberrant shoot and root phenotypes. Disruption of the clock in the *CCA1*-overexpressor and the *prr5,7,9*-triple mutant significantly reduced rosette leaf size and suppressed lateral root formation. The authors attributed their observation to altered carbon allocation between shoot/root and growth/storage in clock mutants, compared to wild-type plants (Ruts *et al.*, 2012). A similar growth defect is seen in the clock mutant *tic*, which displays numerous carbon-related defects (Sanchez-Villarreal *et al.*, 2013; Shin *et al.*, 2013a).

Circadian clock and direction of growth

Yazdanbakhsh *et al.* (2011) reported that physiological patterns can be shifted from the night into the day when clock genes are mutated. This study analysed rhythmicity of root growth in *Arabidopsis* clock mutants and found that *elf3*, which is arrhythmic and displays an oscillator arrested at dusk (McWatters *et al.*, 2000; Kolmos *et al.*, 2011), lacked the ability to repress root growth during the day nor to promote it at the end of a 24-h cycle (Yazdanbakhsh *et al.*, 2011). This shift of root growth from the night into the day appeared independently of carbohydrate metabolism as it occurred under absence and presence of sucrose fed to the roots. Instead, rhythmic root growth in the *elf3* mutant under light/dark cycles was rapidly lost under constant light conditions (Yazdanbakhsh *et al.*, 2011). These findings are reminiscent to Nozue *et al.* (2007), who reported that functional ELF3 was required to inhibit hypocotyl extension of *Arabidopsis* seedlings during the light and to release it at night. Likewise, ELF3 appears to repress *Arabidopsis* root growth during the day and direct it towards the end of the night. Consequently, light signalling, instead of carbon metabolism, appears to drive ELF3 action in respect to growth regulation in *Arabidopsis* root and shoot (Nozue *et al.*, 2007; Nusinow *et al.*, 2011; Yazdanbakhsh *et al.*, 2011). This is potentially through a cascade of clock regulation on the transcription factors *PIF4* and *PIF5* and the subsequent role of these factors in controlling auxin-driven growth (Nusinow *et al.*, 2011; Hornitschek *et al.*, 2012; Shin *et al.*, 2013b). Such conclusions for ELF3 as a major hub controlling hormone-driven growth are consistent with it acting as a mediator between light signalling and the circadian clock (McWatters *et al.*, 2000; Kolmos *et al.*, 2011).

It appears that regulation of growth acts through at least two different layers, with one comprising carbon metabolism and the other light signalling (Nozue *et al.*, 2007; Yazdanbakhsh *et al.*, 2011). Interestingly here, the clock coordinates both processes. For the first, the clock components CCA1/LHY have been shown to define the rate of starch breakdown to ensure that carbon supply lasts until the end of the night (Graf *et al.*, 2010). This avoids adverse effects on growth by sucrose starvation (Graf and Smith, 2011). For the latter, ELF3, as a clock component mediating rhythmic light signalling, acts to repress growth during light and promote growth at the end of dark (Nozue *et al.*, 2007; Nusinow *et al.*, 2011). This regulatory pattern would be consistent with physiological and ecological benefits of coordinating growth control at several developmental checkpoints.

Repression of growth during the day favours the accumulation of carbohydrate reserves for the night. Direction of growth towards the end of the night would reduce the risk of excessive growth during the first half of the night that would leave the plant without carbon resources before the next sunrise. Furthermore, growth at the end of the night would coincide growth with maximum water availability. Thus, clock regulation of growth appears to coordinate signalling and metabolic pathways to ensure high growth performance during darkness, when the plant has to properly manage metabolic resources, as they cannot be refilled by light-driven carbon fixation until the next morning. However, as two different rhythmic growth types exist in dicot plants and as examined monocot plants do not show rhythms for shoot growth (Walter *et al.*, 2009), one has to be very careful with generalization of the *Arabidopsis* model.

The *Arabidopsis* example shows that the circadian clock is interlinked with both light signalling and carbon metabolism to regulate growth performance. This does not necessarily apply to other species, and might not be general. What is curious here is that mutations in the evening clock components *EAM8* and *EAM10* in barley, which are respective orthologous of *Arabidopsis ELF3* and *LUX* (Faure *et al.*, 2012; Campoli *et al.*, 2013), do not display dramatic growth phenotypes in the shoot. Taken together, it appears that the role of the clock in driving growth depends on the species under consideration. As such, much is to be done to translate *Arabidopsis* circadian findings to improve agricultural gains.

Summary and outlook

The *Arabidopsis* circadian transcriptome displays a particular overrepresentation of genes involved in key physiological pathways of hormone and stress signalling, growth, and development (reviewed in Davis and Millar, 2001; Sanchez-Villarreal *et al.*, 2013; Staiger *et al.*, 2013). Conclusions from

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circadian transcription to metabolic outputs and growth are not generally straightforward due to post-transcriptional and post-translational modifications (Baerenfaller *et al.*, 2012). Additionally species-specific layers of regulation are noted. Related to that, it appears that clock benefits for growth and fitness are more complex than just a simple match between the internal periodicity of a plant with the day/night cycle. It has been suggested that anticipated preparation of photosynthesis is causative for higher growth performance of *Arabidopsis* plants (Dodd *et al.*, 2005), but this was most obvious for unnatural day-length conditions that deviate from a 24-h T-cycle (Graf *et al.*, 2010; Graf and Smith, 2011). It appears likely that the 'dark side' of the day has to be considered to explain differences in plant growth performance between wild-type plants and respective clock mutants (Dodd *et al.*, 2014).

Growth rates in *Arabidopsis* peak at the end of the night when the plants are not photosynthetically capable of capturing photons to fix carbon. Thus, mobilization and allocation of carbohydrate reserves under night must be considered in the explanation if a simple matching of day/night cycles with internal period of the clock mutant is sufficient to explain increased growth performance in *Arabidopsis*. In addition, *elf3* mutant plants that show a severe disruption of clock oscillations of transcription were, in the case of barley, pea, and lentil, kept in breeding. All of these crops were selected and bred as high-yielding cultivars during the migration away from the equator to more northern and temperate latitudes (Faure *et al.*, 2012; Weller *et al.*, 2012). Quantitative variation at *ELF3* has similarly been reported in rice (Matsubara *et al.*, 2012). Understanding the selection pressures that led to clock variation in crops is undoubtedly to include roles for the clock in control of water use, temperature response, and processing stresses to create yield stability.

The circadian clock appears to be both master and a slave in regulation of carbon metabolism. Metabolic status is integrated into the clock during the day, leading to close coherence of oscillations with carbon metabolism. Later at night, this precise entrainment to metabolic status from the day appears beneficial for regulation of carbohydrate catabolism at night, where the plant has to feed from resources gained over the day. As a consequence, the circadian clock is both controlling and being controlled by carbon metabolism (Sanchez *et al.*, 2011; Farre and Weise, 2012; Haydon *et al.*, 2013b). This bimodal interaction leads to the phenomenon of entrainment by and gating of environment-related stimuli. This is likely to ensure coherence between environmental signals and the clock to properly adjust clock output pathways that modulate plant performance.

Clock genes appear to be substantially conserved across species, but their regulatory effects on fitness and growth performance are not as obviously conserved. Dicotyledonous and monocotyledonous species have contradicting patterns in clock control of growth rhythmicity. For example, the circadian clock often controls dicot shoot growth whereas this does not appear to be true in monocots. Secondly, monocots store much of their carbohydrates in soluble forms instead of as starch (Kogel *et al.*, 2010). This difference in nocturnal carbohydrate mobilization is another intrinsic metabolic distinction between species that might explain fundamental differences in regulation of growth performance by the circadian clock between monocot and eudicot species.

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