Circadian Rhythms in Plants

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Running Title: Circadian Rhythms in Plants

Abstract

The circadian oscillator is a complex network of interconnected feedback loops that regulates a wide range of physiological processes. Indeed, variation in clock genes has been implicated in an array of plant environmental adaptations, including growth regulation, photoperiodic control of flowering and responses to abiotic and biotic stress. While the clock is buffered against the environment, maintaining roughly 24-hr rhythms across a wide range of conditions, it can also be reset by environmental cues such as acute changes in light or temperature. These competing demands may help explain the complexity of the links between the circadian clock network and environmental response pathways. Here, we discuss our current understanding of the clock and its interactions with light and temperature signalling pathways. We also describe different clock gene alleles that have been implicated in the domestication of important staple crops.

Introduction

Through the day, all organisms are exposed to diel environmental rhythms such as the daily transition from light to dark and the daily fluctuation of temperature. Organisms have evolved light and temperature sensors, which enable them to sense and respond to these changes, maintaining homeostatic balance (Larner et al. 2018). While responding to environmental changes to maintain homeostasis is important, it is also beneficial for organisms to anticipate daily changes and prepare for them beforehand. To this end most organisms, including plants, have developed an internal timing mechanism known as the circadian clock that enables them to anticipate and align internal biological processes with these daily rhythms (reviewed in Harmer 2009; Millar 2016). Circadian clocks are cell autonomous and each cell maintains its own 24-hour rhythm, which allows multicellular organisms to maintain tissue and organ specific-clocks (Endo 2016). The main components of a circadian system are the input signals from the environment that reset the clock, the central oscillator that maintains a roughly 24-hour rhythm even in the absence of input signals, and the output signals that generate daily rhythms in physiology.

In plants, the central oscillator is a complex gene regulatory network of repressors and activators that form multiple interlocking feedback loops (Fig. 1). These clock genes are expressed at specific times of the day and in addition to regulating each other's expression they also influence multiple physiological processes. Clock-regulated pathways may exhibit rhythmicity, with peak activity at distinct times of day, and in addition may be "gated" by the clock such that they are more responsive to environmental stimuli at specific times of day (Greenham and McClung 2015). This mechanism ensures that a plant is most responsive to light during daylight hours, to growth hormones during the night, and to environmental stresses at times when adverse conditions are most likely (Covington and Harmer 2007; Arana et al. 2011; Zhu et al. 2016). In order to appropriately gate plant responses to external factors, the clock is directly linked with the light and temperature signalling pathways, which also ensures synchronicity between the external and internal rhythms (Casal and Qüesta 2017). The cross-talk between these regulatory pathways also provides seasonal information to the plant, allowing for example the determination of day length for the appropriate control of the transition to flowering (Song et al. 2015; Doyle 2018). While the clock can be reset by temperature and light, it would be detrimental to a plant if the clock were sensitive to minor intermittent fluctuations of temperatures throughout the day. To counter this, the clock is not only reset by large temperature changes but is also buffered against ambient changes in a mechanism known as temperature compensation, where the clock maintains an approximately 24-hour period even when temperatures are fluctuating over time (Gil and Park et al. 2018).

Given the central role of the circadian clock in modulating plant responses to environmental cues, it is not surprising that selection of circadian clock variants has been implicated in the adaptation and domestication of many agriculturally important species (Bendix et al. 2015; Blumel et al. 2015). In this review chapter, we discuss our current understanding of the circadian clock network and how environmental cues are integrated into this complex regulatory system. We also discuss the role of the clock in the adaptation of crop species to different latitudes and to distinct biotic and abiotic stresses.

The plant circadian clock

The plant circadian clock is a complex network of intertwined feedback loops comprised of repressor and activator transcription factors (Harmer 2009; Hsu and Harmer 2014; Huang and Nusinow 2016). Levels of these proteins are in constant flux, each peaking at a specific time of day and feeding back to regulate each other's expression. The morning expressed MYB-like transcription factors CCA1 (CIRCADIAN CLOCK ASSOCIATED1) and LHY (LATE ELOGATED HYPOCOTYL) repress the afternoon expressed *PSEUDO-RESPONSE REGULATOR* (*PRR*) genes, including *PRR1/TOC1* (*TIMING OF CAB EXPRESSION1*), *PRR5*, *PRR7* and *PRR9* (Alabadí et al. 2001; Farré et al. 2005; Kamioka et al. 2016). TOC1 along with the other PRR proteins, in turn, repress the expression of *CCA1* and *LHY*, closing this feedback loop (Alabadí et al. 2001; Nakamichi et al.2010). CCA1/LHY are themselves primarily repressors of transcription and bind to a *cis*-motif termed the Evening Element (EE) found in the regulatory regions of many clock genes, including the *PRRs*. Other direct targets of CCA1/LHY activity include genes that encode members of the transcriptional regulatory evening complex, *ELF3* (*EARLY FLOWERING3*), *ELF4* and *LUX* (*LUX ARRHYTHMO*). These three genes are expressed at night, at which time the evening complex feeds back to repress multiple morning- and afternoon-expressed genes to complete another feedback loop in the network (Huang and Nusinow 2016) (Fig. 1).

The circadian regulatory network in plants is not only comprised of negative feedback loops: a second set of midday-expressed MYB-like transcription factors, REVEILLE4 (RVE4), RVE6, and RVE8 has been shown to activate expression of several clock genes including *TOC1*, the *PRRs* and the evening complex genes (Rawat et al. 2011; Farinas and Mas 2011; Hsu et al. 2013). To activate gene expression, RVE8 forms a complex with LNK1 (NIGHT LIGHT-INDUCIBLE AND CLOCK-REGULATED1) and LNK2 and associates with the promoters of *TOC1* and *PRR5* (Xie et al. 2014). The RVE activator proteins are not simply a second layer of regulation on top of the core circadian clock but are connected and embedded into the clock regulatory network (Fig. 1). It has previously been shown that *RVE8* expression is repressed by TOC1 and the PRRs, forming yet another negative feedback loop in this network (Rawat et al. 2011; Hsu et al. 2013). Interestingly, the CCA1 and LHY repressors and the RVE activators both have highly similar DNA-binding domains and can bind the same EE binding site in similar sets of promotors (Harmer and Kay 2005; Rawat et al. 2011). A recent study demonstrated that the balance between the expression levels of the activating and repressing MYB-like factors is more important in regulation of circadian period than the presence or absence of any specific factor (Shalit-Kaneh et al. 2018).

Integrating light and temperature cues into the circadian clock regulatory network

Circadian clocks must be continually adjusted by environmental cues so that the processes they control are appropriately timed even as temperature and daylength change with the seasons. For this reason, the plant clock uses multiple mechanisms to sense and integrate external signals into the feedback loops described above (Fig. 2). The phytochrome signalling pathway is one of the main mechanisms through which plants sense and respond to changes in red light availability and is directly linked to the clock regulatory network (Oakenfull and Davis 2017). Of the phytochrome receptors, phytochrome B (phyB) is the main red-light receptor and its effects on plant growth and development have been extensively studied (Larner et al. 2018). phyB photoconverts from an inactive form (Pr) to an active form (Pfr) upon absorption of red light (Viczian et al. 2017). Pfr interacts with the PHYTOCHROME-INTERACTING FACTORS (PIFs) and targets these transcription factors for degradation during the day to limit cell elongation to the night time hours (Seluzicki et al. 2017). PIF proteins have been established as transcriptional regulators of morning-expressed *LHY* and *CCA1*, directly linking the light and clock regulatory networks (Martínez-García et al. 2000). Recently, PIFs have also been shown to mediate metabolic signals to the circadian oscillator (Shor et al. 2017). Another link between the clock and light signalling pathways occurs via interactions between phyB and the evening complex protein ELF3 (Liu et al. 2001; Huang et al. 2016). ELF3 also binds to PIF4 independently of the other evening complex components to repress PIF4 function, thus regulating a light signalling component controlling hypocotyl elongation (Nieto et al. 2015). Similarly, TOC1 and other PRR proteins have been shown to bind directly to PIF3 and PIF4 and inhibit their ability to activate transcription. Thus, the association of PRR factors with PIFs on the G-box elements of target promoters serves to limit PIF transactivation function to the pre-dawn hours (Soy et al. 2016; Liu et al. 2016; Zhu et al. 2016). The PRRs and the evening complex have also been shown to regulate transcription of *PIF* genes (Nusinow et al. 2011; Nakamichi et al. 2012; Liu et al. 2016). Thus, both ELF3 and the PRR proteins limit the function and expression of the important growth regulatory PIF factors and provide further links between clock and light regulation of growth (Fig. 2a).

The clock protein ZEITLUPE (ZTL) is unique in being both a component of the plant clock and a blue-light photoreceptor. ZTL interacts directly with GIGANTEA (GI), another clock component, and this interaction is stabilized by blue light via the photosensory LOV domain of ZTL. This ZTL-GI complex can maintain circadian rhythms by influencing the stability of both TOC1 and GI proteins (Más et al. 2003; Kim et al. 2007, 2013). GI stability is also affected by a second protein complex consisting of ELF3 and COP1 (CONSTITUTIVE PHOTOMORPHOGENIC1) that acts downstream of the blue light photoreceptor CRY2 (Yu et al. 2008). The ELF3-COP1 complex targets GI for degradation and represents yet another point at which light signals are integrated into the circadian clock network. The LNK2 and RVE8 complex also appears to play a role in the integration of the clock and light signalling pathways (Figure 2a). It is possible that clock entrainment relies on the induction of *LNK* expression by phytochromes in conjunction with the early morning expression of *CCA1* and *LHY* (Rugnone et al. 2013; Kim et al 2003; Wang and Tobin 1998).

Temperature is another external signal that is integrated into the clock network (Fig. 2b). Recent research has revealed that plant photoreceptors can also function as temperature receptors (Delker et al. 2017; Casal and Qüesta 2017). One such receptor is phyB, with the rate of reversion from the active Pfr form to the inactive Pr form increasing at higher temperatures (Jung et al. 2016; Legris et al. 2016). Given the multiple links between phytochrome signalling components and clock proteins described above, temperature regulation of phytochrome function is a likely point of temperature integration into the clock. PIF4 has also been shown to respond to changes in temperature to alter plant development and morphology (Paik et al 2017). Since degradation of PIF4 is promoted by Pfr, the increased rate of Pfr to Pr reversion at higher temperatures may account for the warm temperature-induced post-transcriptional accumulation of PIF4 protein (Zhu et al. 2016; Foreman et al 2011).

Temperature has also been shown to regulate the activity of the evening complex. At higher temperatures, association of ELF3 with target promoters is reduced via an unknown mechanism (Mizuno et al. 2015; Box et al. 2015; Ezer et al. 2017). Thus, in warm conditions, evening-complex mediated repression of targets such as the clock genes *PRR7*, *PRR9*, *GI*, *LUX* and the growth regulating *PIF4* is relieved, leading to elevated levels of these transcripts during warm nights. Integration of cold temperature cues into the clock network can occur via CBF1/DREB1a (COLD-INDUCIBLE C-REPEAT/DROUGHT-RESPONSIVE ELEMENT BINDING FACTOR). *CBF1* expression is highly induced by cold, and this factor has been shown to bind directly to the promoter of the evening complex component *LUX* and promote its high-amplitude rhythmic expression at cold temperatures (Chow et al. 2014). Intriguingly, phyB and PIF proteins have been reported to repress *CBF1* expression (Lee and Tomash 2012; Kidokoro et al. 2009), suggesting links between distinct temperature sensing pathways. Finally, expression of *CBF1* is regulated by a number of clock components including the PRRs, the evening complex, and CCA1/LHY (Kinmonth et al. 2013), providing yet another example of the ubiquitous feedback loops found in the circadian system.

Clock regulation of growth pathways

Plant growth is regulated by both environmental and internal cues, and therefore plant growth pathways are highly interconnected with the circadian clock regulatory network as well as with light and temperature signalling pathways (Nozue and Maloof 2006, Farre´ et al. 2012, Kinmonth-Shultz et al. 2013, Henriques et al. 2018). The best-studied example of plant growth is the elongation of Arabidopsis hypocotyls, which is driven by anisotropic growth of cells formed during embryo development. In short day-conditions, hypocotyl elongation is rhythmic, with peak growth occurring at the end of the night/beginning of dawn. However, in long-day or constant light conditions, the peak phase of growth is shifted to mid-morning or end of the subjective day, respectively. These findings demonstrate that hypocotyl growth is regulated both by light and the circadian clock (Nozue et al. 2007).

The PIF transcriptional activators are key mediators of this and other growth rhythms, and are important integrators of clock, light, and temperature signals (Legris et al. 2017, Paik et al. 2017, Pham et al. 2018). Clock and light regulation of PIF protein levels restricts hypocotyl elongation to the end of the night in short day conditions by the following mechanism. First, *PIF4* and *PIF5* expression is limited to the day and pre-dawn hours due to direct binding of the repressive evening complex to the promoters of these genes (Nusinow et al. 2011). However, during the day, active phyB (Pfr) sequesters PIF proteins and targets them for degradation, preventing PIF protein accumulation and inhibiting cell elongation (Nozue et al. 2007, Park et al. 2012, Soy et al. 2012). During the night, Pfr converts back to Pr and PIF degradation is relieved, allowing PIF protein accumulation and promoting hypocotyl elongation near dawn (Nozue et al. 2007). The circadian clock also regulates hypocotyl elongation via control of PIF transactivation activity though other core clock components. TOC1 and the other repressive PRR proteins physically interact with the transactivating PIF proteins to inhibit the induction of growth promoting genes (Soy et al. 2016, Liu et al. 2016, Zhu et al. 2016, Martín et al. 2018). Thus, the circadian clock and light signalling pathways facilitate late night/early day-phased hypocotyl elongation via multiple mechanisms. Growth in the morning is speculated to ensure that expansion coincides with maximal water availability for increased turgor pressure and higher availability of carbon for cell wall remodelling (Nozue et al. 2007, Robertson et al. 2009).

New findings suggest that the circadian clock can regulate growth not only on a whole plant or organ level but can differentially regulate growth in a subset of cells within a specific organ (Atamian et al. 2016, Endo 2016, Apelt et al. 2017, Ke et al. 2018). The first written record of diel rhythms was the observation in the fourth century BC that a number of plants exhibit daily rhythms in leaf movement (McClung, 2006). Some plants have specialized motor cells, called pulvini, which undergo rapid changes in turgor pressure to facilitate such movements (Whippo and Hangarter 2009). However, most species lack pulvini and leaf movements are thought to rely on differential expansion of cells on the adaxial and abaxial sides of petioles (Polko et al. 2012, Rauf et al. 2013). Recently, this differential growth and leaf movement in Arabidopsis were found to depend upon the *PRR* clock components, with a *prr7prr9* double mutant displaying poor leaf movements compared to wild type plants (Apelt et al. 2017). These results suggest that the circadian clock can regulate the differential expansion of specific cell layers to mediate leaf movement.

A similar growth regulatory mechanism is thought to underlie the daily movement of the stems of juvenile sunflowers. Although their ability to bend from east to west each day to track the apparent movement of the sun is well known, it is less recognized that they bend back from west to east each night in anticipation of the coming dawn. These rhythmic back-and-forth movements persist for several days when plants are moved to constant environmental conditions, suggesting involvement of the circadian clock in heliotropic movements (Atamian et al 2016). This tracking motion in juvenile sunflowers is caused by differential growth on opposite sides of the stem, and indeed signalling genes of the growth hormone auxin are differentially expressed on the east and west sides of solar tracking stems. Disruption of tracking movements causes a reduction in leaf area and biomass, perhaps due to a decrease in leaf photon capture (Atamian et al. 2016). Similarly, a study on diel flower opening in waterlily found that movement was initiated by differential expansion of cells only in a specific region of the petal above its base. This cell expansion and the petal movement was found to be regulated by light signals that are thought to activate downstream auxin signalling and cell wall remodelling pathways (Ke et al. 2018). Taken together these findings suggest that there are further regulatory networks to be explored that limit clock and environmental effects to specific cells which fine-tune plant adaption to environmental challenges.

The role of the plant clock in photoperiodic regulation of flowering

It is important for plants to detect seasonal changes so that biological processes such as flowering, dormancy, and budbreak can be aligned with the appropriate season. Links between the clock and photoperiod-mediated regulation of the transition between vegetative and reproductive growth have been particularly well studied. Integration of information from the light- and thermo-sensory pathways into the photoperiodic flowering time network via the clock helps ensure plants reproduce in the appropriate season, maximizing plant fitness (Song et al. 2015; Blumel et al. 2015; Doyle et al. 2018). Many plant species are photoperiodic, with time to flowering hastened either by long days in the case of long-day plants or by short days in the case of short-day plants. These traits are associated with distinct reproductive strategies; for example, many short-day plants use the shortening days of fall as a cue to produce flowers and seeds before the onset of winter, whereas many long-day plants use the lengthening days of spring as a cue to reproduce before the onset of a hot and dry summer. However, many crop cultivars have been selected for day neutrality, with time to flowering independent of day length. Although many regulators of flowering vary across species, promotion of flowering in response to accumulation of homologs of the FT (FLOWERING LOCUS T) protein in the shoot apex is highly conserved (Andrés and Coupland 2012).

In the long-day plant, *Arabidopsis thaliana*, expression of *FT* is activated in leaf vasculature by the CO (CONSTANS) transcription factor, which increases *FT* expression via a feed forward mechanism (An et al. 2004). *CO* transcript abundance is negatively regulated by the clock-controlled CDF (CYCLING DOF FACTOR) proteins (Fornara et al. 2009). The CDF proteins are degraded by a protein complex comprised of GI and a ZTL-related protein, FKF1 (FLAVIN-BINDING, KELCH REPEAT, F-BOX1). This complex is stabilized by blue light, in a similar manner to the GI-ZTL complex, and degrades the CDF proteins to promote the transition to flowering (Imaizumi et al. 2005; Song et al. 2015). There is also evidence that GI can directly bind to the *FT* promoter to regulate flowering independently of CO, suggesting GI is a central factor regulating flowering time (Sawa and Kay 2011).

In the short-day plant rice, the *CO* and *FT* homologs *Hd1* (*HEADING DATE1*) and *Hd3a* also play key roles in the photoperiodic control of flowering. As is also true in Arabidopsis, the rice homolog of GI promotes expression of the *CO* homolog *Hd1,* and an *ELF3* homolog has also been implicated in photoperiodic control of flowering (Hori et al. 2016). However, while CO promotes flowering in Arabidopsis in long days, the rice CO homolog Hd1 promotes flowering in short days and inhibits it in long days (Izawa 2007). Thus, despite important differences in the molecular circuitry controlling the transition to flowering, clock components play key roles in relaying environmental information to the photoperiodic flowering pathways in both short- and long-day plants.

Selection of clock gene variants for flowering time adaptation

The highly integrated nature of the circadian clock with light and temperature response networks suggest that these genes and pathways play a central role in the ability of plants to adapt to their environment. Indeed, recent studies have found that natural variation in circadian clock genes has facilitated the migration and domestication of many different plant species (Bendix et al. 2015; Blumel et al. 2015). Genetic variation in a number of clock related genes across different crop species have been valuable in expanding their growth range and yield (Bendix et al. 2015; Blumel et al. 2015). Many of these genes result in altered flowering time and photoperiod sensitivity (Table 1). In general, crops that originated in the tropics such as rice, sorghum and maize are short-day plants with flowering inhibited by long days. Many of these crops have been adapted to the long summer days at higher latitudes by breeding for photoperiod insensitive variants that flower earlier under long days than ancestral genotypes (Hung et al. 2012). Soybean is also a short-day plant but was originally adapted to a limited latitudinal range. Expansion of soybean cultivation to higher latitudes has been enabled by selection for varieties that flower early in long days (Weller and Ortega 2015). Conversely, adaptation to more equatorial regions has been achieved by selection for cultivars that are less responsive to inductive short days, allowing more vegetative growth before the transition to flowering and thus increasing biomass and yield (Lu et al 2017b). Many long-day crops such as wheat, barley, pea and lentil are from temperate regions and in the ancestral state flowering is promoted by long days (Weller 2012; Cockram et al 2007). In cereals, like wheat and barley, the long-day growth habit ensures the plants that germinate in the fall will flower in as days lengthen in the spring, allowing for grain filling during the wet season and harvest before the hot dry summers. Selection for short rotation varieties that can be sown in the spring and harvested soon thereafter has enabled production of two successive crops each year, an innovation instrumental in the green revolution (Borlaug 1983; Cockram et al. 2007).

PRR gene variation alters photoperiodic flowering and expands growth range

In the model plant Arabidopsis, mutations in most of the *PRR* genes delay flowering in long days, the inductive photoperiodic condition (Nakamichi et al. 2007). *PRR* genes have been characterized in many monocot crop species (including rice, wheat, barley, sorghum, and maize), however these genes have undergone independent duplications in the cereals leading to ambiguity in the evolutionary relationships between these genes across different species (Li and Xu 2017; Brambilla et al. 2017). To reflect this ambiguity the *PRR* genes in cereals have been named *PRR1*, *PRR37*, *PRR59*, *PRR73* and *PRR95* indicating the closest Arabidopsis relative(s) for each gene (Campoli et al. 2012). Rice *PRR* genes are expressed in a sequential manner throughout the day and function as core components of the rice circadian clock in a similar manner to the *PRR* genes in Arabidopsis (Murakami et al. 2003, 2007).

In rice, analysis of the progeny resulting from a cross between cultivars with different photoperiodic sensitivity led to the identification of several heading date (HD) QTLs (quantitative trait loci). Two of these loci map near *PRR*-like genes (Murakami et al. 2005). One such locus is *Ghd7.1/Hd2*, which corresponds to the *OsPRR37* gene. While a functional version of this gene contributes to delayed flowering in long days, multiple non-functional alleles of this locus are present in Asian and European cultivars and are thought to contribute to adaptation of rice cultivation to higher latitudes (Koo et al. 2013, Yan et al. 2013). A knockout allele, with a T-DNA insertion within the *OsPRR37* locus, causes early flowering due to an increase in *Hd3a* (*FT* homolog) expression in long days (Koo et al. 2013). In barley, ancestrally a long-day plant, delayed flowering in normally inductive photoperiods was associated with genetic variation at the *Ppd-H1* locus (also known as *eam1*) and was shown to be due to a loss-of-function mutation in *HvPRR73* that caused a decrease in *HvFT* expression (Turner et al. 2005), a phenotype similar to that seen in Arabidopsis *prr7* mutants (Yamamoto et al. 2003). Conversely, in wheat, spring varieties have been selected that are photoperiod insensitive due to variation in an allele of *PRR37* (the *Ppd-D1a* locus) that causes an increase in *TaFT* expression and early flowering in short days (Beales et al. 2007). A variant at the sorghum Ma_1 locus, also a *PRR37* homolog, was also found to significantly advance flowering time in normally non-inductive long days (Murphy et al. 2011). How these different *PRR* alleles function on a molecular level in different crops is still under investigation but it is clear that this clock-related gene has played an important role in extending the growth range of several important staple crop species.

The role of the evening complex in modification of photoperiodic flowering requirements

Given the central role of ELF3 and the evening complex in the circadian clock, light signalling, temperature sensing and photoperiodic flowering pathways (Figs. 1 and 2), it is not surprising that evening complex genes have played an important role in the domestication of plants. In Arabidopsis, *elf3* mutants were first identified based on their day-neutral flowering phenotype, flowering significantly earlier than wild type in short days (Zagotta et al. 1996). Later studies provided evidence that mutations in any one of the three evening complex genes not only have major effects on clock function but also result in an early flowering phenotype (Hicks et al. 2001; Doyle et al. 2002; Hazen et al. 2005). Alleles of evening complex genes have been identified as the underlying cause for variation in photoperiod sensitivity and flowering time in multiple crop species (Table 1).

Variation of several genetic loci have been associated with differences in the photoperiodic flowering of barley, with some primarily affecting flowering time in long-day conditions and others primarily affecting flowering time in short-day conditions, such as *eam 7* to *10* and *Ppd-H2* (Boyd et al. 2003). *eam8*, which induces early flowering in short-day conditions, was identified as a homolog of Arabidopsis *ELF3.* Mutations in this gene disrupt clock function and increase *HvFT* expression, resulting in an early flowering phenotype in short days that is advantageous in regions with short growing seasons, such as Scandinavia (Faure et al. 2012; Zakhrabekova et al. 2012). Interestingly, although *HvPRR37/ppd-H1* expression levels are elevated in *eam8* mutants, early flowering is maintained in plants with both the *eam8* and *ppd-H1* alleles (Faure et al. 2012). These data suggest that although *HvELF3* regulates *HvPRR37* expression in barley, there is also an alternate pathway for its regulation of *HvFT* expression and flowering time.

An *ELF3* homolog in pea (*HR* locus) and lentil has also been identified as a genetic factor underlying variation in flowering time (Weller et al. 2015). Similarly, in wheat, one of the genes underlying an *earliness per se* locus that regulates flowering time has been identified as an *ELF3* homolog (Alvarez et al. 2016; Wang et al. 2016[a]). Most of these alleles confer the expected early flowering phenotype, however, the *Eps-A^{m} 1-l* allele appears to confer a late flowering phenotype (Alvarez et al. 2016). The different effects of these alleles appear to be light and temperature sensitive (Lewis et al. 2008), in keeping with the central role of *ELF3* in these signalling pathways as described above. Similarly, in the short-day crop soybean, an *ELF3* homolog has been identified at the *J* locus, an important regulator of flowering time. Loss-of-function alleles of *j* flower late in short days due to loss of inhibition of expression of the legume-specific *E1* gene, which encodes a repressor of *FT* gene expression (Lu et al. 2017a). Importantly, the *j* allele has allowed the expansion of soybean cultivation to equatorial regions by extending the vegetative phase of development in short days. Finally, in rice two orthologs of the Arabidopsis *ELF3* gene have been identified. Mutation in the *OsELF3-1* gene leads to a delay in flowering in both long and short days, while mutations in the duplicate gene have little or no effect on flowering (Zhao et al. 2012; Saito et al. 2012).

Unlike *ELF3*, there are very few *ELF4* homologs characterised in crop species and this gene may not be present in all angiosperms. For example, there does not appear to be an *ELF4* ortholog in rice (Izawa et al. 2003). In maize, a member of the *DUF1313* protein family was found to have sequence similarity to *ELF4* and this gene appeared to be a good marker for days to silking, suggesting it may be involved in photoperiodic flowering (Li et al. 2016). In pea, the *DNE* locus is homologous to Arabidopsis *ELF4* and mutations in this locus result in early flowering in normally noninductive short days (Liew et al. 2009). Interestingly, although the *dne* allele causes early flowering similar to that seen in Arabidopsis *elf4* mutants, clock function appears largely intact in *dne* plants, thus it is not clear if DNE is a core part of the pea circadian clock (Liew et al. 2009).

A few homologs and allelic variants of *LUX*, the final evening complex component, have been identified in barley, wheat and pea (Table 1). Campoli et al. (2013) found that the gene underlying the barley *eam10* locus is a homolog of *LUX* and that this mutation disrupted the expression of core clock genes including the *PRRs* and *CCA1*. The *eam10* region in barley and the *Eps-3A*^{m} locus in spring wheat are syntenic and have been conserved across species (Gawronski et al. 2014). *Eps-3A*^{m} was identified as a causal factor in a very early flowering wheat mutant with disrupted circadian rhythms and high *TaFT* expression. In pea, the *STERILE NODES* (*SN*) locus was identified as a *LUX* homolog and knockdown mutations in this gene produces an early flowering phenotype in short-day conditions (Liew et al. 2014). Genetic interactions between the *SN* (*LUX*), *DNE* (*ELF4*) and *HR* (*ELF3*) loci in pea suggest that the role of the evening complex is well conserved between pea and Arabidopsis (Liew et al. 2014). These findings indicate that alterations in the evening complex of the circadian clock have played a central role in the adaptation of crop species to wide latitudinal distributions.

Other clock gene variants influencing photoperiodic flowering in crop species

Alleles of *GI* have also played an important role in the development of crops that flower in a photoperiod-insensitive manner. Mutations in *GI* result in a delayed flowering phenotype in Arabidopsis under long days but cause no phenotype under short-days (Araki and Komeda 1993). Similarly, in a pea mutant screen under long-day conditions, a delayed flowering allele (*LATE BLOOMER 1*) was identified and associated with a mutation in a pea *GI* homolog. This mutation drastically decreases the expression of the *FT* homolog *PsFTL* and thus delays flowering in a clock and light dependent manner (Hecht et al. 2007). Rice mutant for *GI* also demonstrate a late-flowering phenotype specifically in inductive short-day photoperiods (Izawa et al. 2011). Although maize, like rice, is ancestrally a short-day plant, *GI* mutants in this species display an early flowering phenotype under long days but no phenotype in short days (Bendix et al. 2013). This advance in flowering is due to an early accumulation of *conz1* (the maize *CO* homolog) and increased expression of *zcn8* (a maize *FT* homolog) in these mutants, suggesting that *GI* acts to repress *conz1* under long days (Bendix et al. 2013). A loss-of-function allele in a soybean *GI* homolog was identified as the gene underlying the *e2* QTL that causes early flowering in field-grown plants (Watanabe et al. 2011). Taken together, these results indicate that GI plays an important role in plants ability to distinguish between long and short days and adapt to these growth conditions.

There are fewer reports of allelic variation in other clock genes such as *LHY*, *CCA1*, *TOC1*, *PRR5*, *PRR9*, *RVEs*, and *LNK1* or *LNK2* leading to photoperiod adaptation. In the Chinese cabbage and leafy varieties of *Brassica rapa*, early flowering generally leads to decreased productivity and yield. A recent study found that *B. rapa* cultivars with variable photoperiod sensitivities contained a great deal of sequence variation in the *BrCCA1* homolog and several of these variations could be associated with a delayed flowering phenotype, suggesting that *CCA1* is a good candidate for marker assisted breeding in Brassica (Yi et al. 2017). In tomato, deletion of the *LNK2* homolog likely enabled cultivation of this crop beyond its natural range to higher latitudes, perhaps by lengthening the period of the circadian clock (Müller et al. 2018). It will be interesting to see if other clock genes have also played roles in major crop domestication events or if these genes could be used to drive domestication in the future.

Variation in clock genes enables plant adaptation to stress

Recently, there have been reports of variation in clock genes playing a role in the ability of plants to respond to abiotic stress (Table 1). In natural populations of the annual plant *Mimulus guttatus*, leaf movement rhythms were assessed to monitor clock function and revealed that clock period is correlated with latitude. *Mimulus* populations derived from more northerly latitudes tend to have longer periods than their southern counterparts; these altered rhythms are thought to promote local adaptation to the environment (Greenham et al. 2017). In barley, cultivars with variation in the *HvPRR73* (*Ppd-H1)* and *HvELF3* genes were subjected to osmotic stress. It was found that mutations in *HvELF3* changed the phase and waveform of expression of stress response genes while *HvPRR73* alleles affected the overall levels at which stress response genes were expressed (Habte et al. 2014). A comparison of drought-tolerant and drought-susceptible soybean cultivars under drought conditions revealed differences in *LUX* gene expression. The tolerant cultivar exhibited a significant decrease in *LUX* expression during drought and reverted to normal levels upon watering (Syed et al. 2015). In the same study, the authors found that *TOC1* and *PRR7* homologs were phase shifted under drought and flooding conditions and a *PRR3* homolog underwent significant alternate splicing during these stress events. Freezing tolerance in *Brassica oleracea* was associated with two *BoCCA1* alleles, where *BoCCA1-1* was associated with freezing tolerance and *BoCCA1-2* was linked to freezing susceptibility (Song et al. 2017). In wheat, cultivars from warmer climates have a higher degree of sequence variation within a *LUX* homolog than those from cooler regions, suggesting alterations in this locus may help adapt temperate cereals to warmer climes (Gawronski et al. 2014). Anthocyanins are also well known to play a role in abiotic stress responses, and the circadian clock pathway has long been linked to anthocyanin biosynthesis (Harmer et al. 2000). It has recently been reported that the LNK2 and RVE8 transcriptional regulators directly control expression of anthocyanin biosynthetic genes (Pérez-García et al. 2015). To date, no natural variation in these genes has been associated with anthocyanin biosynthesis and stress response, but this is an interesting area for future research.

In addition to the role of the clock in response to abiotic stress, the circadian system also affects plant-pathogen and plant-pest interactions (Seo and Mas 2015; Lu et al. 2017b). Plant susceptibility to a variety of insects and microbial pathogens is gated by the clock, presumably due at least in part to circadian regulation of the defence hormones salicylic and jasmonic acid (Wang et al 2011; Goodspeed et al. 2012; Korneli et al. 2014; Ingle et al. 2015; Lu et al. 2017b). Genetic analyses have also demonstrated links between clock genes and plant defences, with perturbation of expression of the clock genes *CCA1*, *LHY*, or *ELF3* in Arabidopsis increasing susceptibility to bacterial, fungal and oomycete attack (Bhardwaj et al. 2011; Wang et al 2011; Zhang et al 2013; Lu et al. 2017b) and the silencing of *ZTL* expression rendering wild tobacco more susceptible to a generalist herbivore (Li et al. 2018). Genome-wide association mapping in Arabidopsis identified *LHY* and *LUX* alleles as associated with *Botrytis cinera* infection traits such as lesion eccentricity and size (Corwin et al. 2016; Fordyce et al. 2018). Despite these clear links between the clock and immune responses, whether allelic variation in clock genes of cultivated plants affects biotic stress responses remains to be determined.

Concluding Remarks

This review has touched on several aspects of plant physiology that are known to be circadian regulated, but with a third of all Arabidopsis transcripts being circadian regulated it is likely there are many other ecologically and agronomically important processes regulated by the clock (Covington et al. 2008). It would be interesting to assess crop cultivars with known clock gene variants under different nutrient and environmental stresses to get a fuller picture of the role of the clock in response to different environmental challenges. A relatively unexplored area for future research is how clock-regulated processes in plants affect and are affected by clock-regulated processes in other organisms during plant–pathogen, plant–pollinator and plant–microbiome interactions, and what the implications are for adaptation and domestication (Hevia et al. 2015; Yon et al 2017; Fenske et al. 2018; Hubbard et al. 2018). It is clear that the plant circadian clock has a central role to play in adapting crops to the ever-changing environment, however, there remains a great deal we do not yet know about circadian clocks in different plant species and their roles in distinct environments. Finally, given the central role of the circadian clock in environmental signal perception and response, it is important to understand the trade-offs between different pathways when selecting for or targeting specific clock-related traits.

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Figure Legends

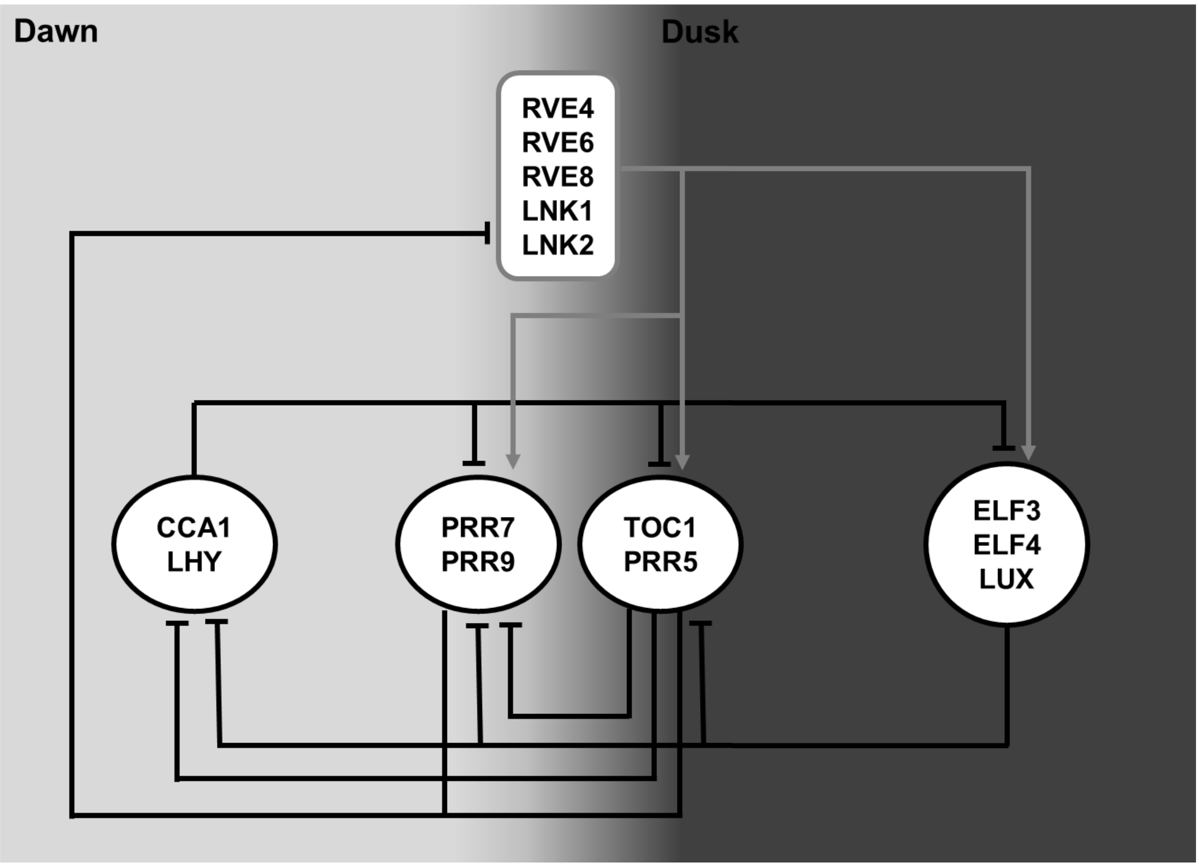

Figure 1. A highly simplified representation of the plant circadian regulatory network. Similar genes operating at similar times during the day in a similar manner are grouped together in white circles. Black lines with blunt ends indicate genes function as repressors in the negative feedback loops. Gray lines and arrows indicate genes acting as activators in the regulatory network.

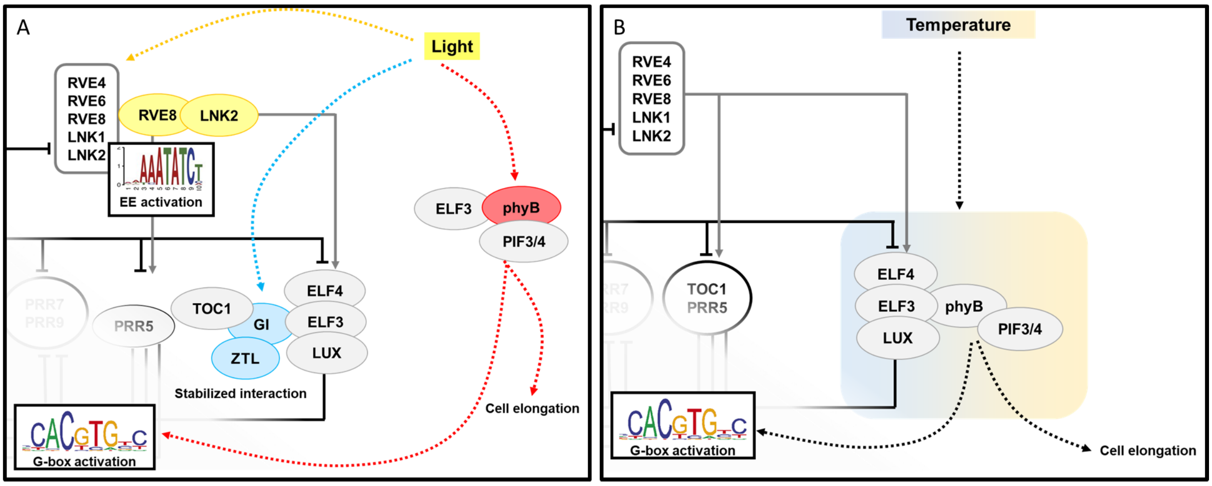

Figure 2. Schematic representation of how light and temperature signalling pathways integrate with the circadian clock regulatory network. The underlying clock network is the same as figure one with either the light signalling pathway (A) or the temperature signalling pathway (B) linking to points in the circadian regulatory network. In (A) the red and blue pathways indicate how these different wavelengths of light are integrated into the clock at different points via independent pathways. In (B) different temperatures influence the same pathway (blue to orange shaded box), with cooler temperatures stabilizing complex formation and warmer temperatures releasing growth factors such and PIFs.

Tables

Table 1. Clock alleles influencing important agronomic traits in different crop species grouped together by phenotype and allele.

Phenotype	Agriculturally important alleles of clock genes	Crop Species	Reference
Early flowering	ELF3-like	*Hordeum vulgare*	(Faure et al. 2012; Zakhrabekova et al. 2012)
		Triticum aestivum	(Wang et al. 2016a; Zikhali et al. 2016)
		Triticum monococcum	(Alvarez et al. 2016)
		Pisum sativum	
		Lens culinaris	(Weller et al. 2012)
	ELF4-like	*Pisum sativum*	(Liew et al. 2009)
		Zea mays	(Li et al. 2016)
	PRR-like	*Sorghum bicolor*	(Murphy et al. 2011)
		Oryza sativa	(Koo et al. 2013)
		Triticum aestivum	(Beales et al. 2007)
	GI-like	*Glycine max*	(Watanabe et al. 2011; Wang et al. 2016b)
		Oryza sativa	(Hayama et al. 2003)
		Zea mays	(Bendix et al. 2013)
	LUX-like	*Hordeum vulgare*	(Campoli et al. 2013)
		Triticum monococcum	(Gawronski et al. 2014; Nishiura et al. 2018)
		Pisum sativum	(Liew et al. 2014)
Delayed flowering	ELF3-like	*Glycine max*	(Lu et al. 2017a)
		Triticum monocuccum	(Alvarez et al. 2016)
		Oryza sativa	(Zhao et al. 2012; Yang et al. 2013; Saito et al. 2012)
	PRR-like	*Oryza sativa*	(Yan et al. 2013) Murakami et al. 2005)
		Hordeum vulgare	(Turner et al. 2005)
	GI-like	*Pisum sativum*	(Hecht et al. 2007)
	CCA1-like	*Brassica rapa*	(Yi et al. 2017)
	LNK2-like	*Solanum lycopersicum*	(Müller et al. 2018)
Water stress	ELF3-like	*Hordeum vulgare*	(Habte et al. 2014)
	PRR-like	*Hordeum vulgare*	(Habte et al. 2014)
		Glycine max	(Syed et al. 2015)
	LUX-like	*Glycine max*	(Syed et al. 2015)
Temperature stress	GI-like	*Brassica rapa*	(Kim et al. 2016; Xie et al. 2015)
	LUX-like	*Triticum monococcum*	(Gawronski et al. 2014)
	CCA1-like	*Brassica oleracea*	(Song et al. 2018)
Biennial growth	PRR-like	*Beta vulgaris*	(Pin et al. 2012)