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Circadian Regulation of Horticultural Traits: Integration of Environmental Signals

Marcos Egea-Cortines, Fabiola Ruiz-Ramon, and Julia Weiss
Genetics, Institute of Plant Biotechnology
Department of Agricultural Science and Technology
Escuela Técnica Superior de Ingeniería Agronómica
Technical University of Cartagena
30203 Cartagena, Spain

ABSTRACT

Plants, animals, and fungi have evolved to contain an internal physiological clock that responds to external stimulus such as the light/dark cycles created by the rotation of the Earth. This pacer is known as the circadian clock. It is composed of a complex set of genes that is conserved in higher plants. Originally thought to be a mere coordinator of basic processes, research has shown that the clock plays a key role in aspects as important as flowering time, productivity, tuberization, and dormancy. Its functions are all related to the seasonal development in many crops. But the circadian clock intimately controls other biological processes such as adaptation to cold, pathogen resistance, stomatal movement, and scent production. Most of the knowledge about the plant circadian clock has been established by research on *Arabidopsis* but the apparent conservation of the circadian clock components in cereals, trees, and floriculture crops means that the circadian clock may influence many agriculturally relevant traits such as flowering, dormancy, productivity, or fruit and flower aromas.

KEYWORDS: cold acclimatization; dormancy; flowering time; gibberellins; plant growth; productivity; scent production; tuberization

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I. INTRODUCTION

Plants are sessile organisms that have to cope with environmental fluctuations such as sharp changes in light and temperature on a daily basis. As a result, developmental programs in plants are partly controlled by environmental cues. How the main environmental signals are integrated into a default program of growth and development has been elucidated in many plants by a mixture of field experiments, breeding, genetics, and physiological studies. Today important evidence suggests that most if not all responses of phytoplankton (Prezelin 1992), cyanobacteria (Sandh et al. 2009), mosses (Imaizumi et al. 2002), and higher plants (Koornneef and Peeters 1997) to the environment are somewhat controlled by the circadian clock (de Montaigu et al. 2010). The circadian clock is formed by a set of genes whose main function appears to be the coordination of environmental cues and physiological responses (see below). Initial observations of rhythms in plants started with the rhythmic movement of leaves, reported already in 1726 (see McClung 2006 for a historical perspective of research on circadian rhythms in plants). Although early molecular experiments were performed in pea and wheat (Kloppstech 1985; Nagy et al. 1988), much of our knowledge has been accumulated in the plant model *Arabidopsis thaliana*. Given the importance of the circadian clock as a general controller of plant growth, development, and response to stress, we expect to see an increase of knowledge transferred to horticultural crops. *Arabidopsis* might be used further to identify clock genes and how they function, but proof/application of the concept requires the identification of genes from the circadian clock causing modifications in horticultural traits such as flowering time, abiotic stress resistance, productivity, or volatile production. Furthermore, differences with *Arabidopsis* might explain crop singularities helping to improve cultural practices and breeding.

Circadian regulation is often considered plant specific, but rhythmic regulation of biological processes also occurs in cyanobacteria, fungi, and animals. It is extensively studied in the field of chronobiology. Two extensive reviews on the historical perspective of the circadian clock in plants have been published recently (McClung 2006, 2011). Harmer (2009) reviewed clock structure in *Arabidopsis*, while Yakir et al. (2007) and de Montaigu et al. (2010) reviewed the current view on circadian outputs controlling plant growth, flowering time, and cold response. The object of the current review is to provide an overview of the clock structure. We cover with some detail the environmental inputs that set the clock, a process called entrainment. We include examples of the knowledge of clock and related topics in plants of horticultural interest.

As many biological processes show rhythmic patterns, a detailed terminology describing a rhythm and its changes has developed over the years, which helps to identify changes in this phenomenon. An important component of the language used in chronobiology and data analysis tools originated in the field of signal processing in electrical engineering where wave-like signals are analyzed. Thus, it has remained a common language to a large extent, and new concepts related to biological aspects have enriched it, making it quite elaborate. Although not all the terminology has been used in the current review, we have compiled a table with a comprehensive list of terms used in chronobiology, for educational purposes and to ease reading further literature (Table 1.1). It is just good practice that data gathering, terminology, and measurements are standard as it allows proper data analysis, sharing of data, and classification of the different responses. Fig. 1.1 presents examples that indicate how changes in circadian regulation are observed.

II. GENERAL STRUCTURE OF THE PLANT CIRCADIAN CLOCK

A. *Arabidopsis*

Two physical signals, light and temperature, are constantly changing as a result of Earth axial rotation providing night and day as well as the

Table 1.1. Terminology used in chronobiology.

Term	Definition and/or description
Acclimation	Physiological changes occurring within the lifetime of an organism that reduce the strain caused by experimentally induced changes in particular climatic factors such as ambient temperature and/or photoperiod. The acclimation period is critical to obtaining reliable experimental data.
Acrophase	Peak of a mathematical curve fit to data. Refers to the time when a process has its maximum, starting from a point defined by the scientist, for example, dawn. It may be expressed in (negative) degrees as the lag from the acrophase reference (360°C = 1 period) or in calendar time units (hours, minutes, etc.).
Aliasing	Detection of a false period that is longer than the underlying true period as a result of sampling taken wide apart.
Amplitude	Distance from rhythmic mean to the peak or to the trough of a mathematical model (e.g., cosine) used to approximate a rhythm. A process without rhythm will have amplitude of zero.
CC	Constant environmental conditions. In chronobiology, CC indicates lack of environmental synchronizers, that is, constant light, constant temperature.
Circadian	Roughly 24 h, describing rhythms with about a 24 h cycle length whether they are synchronized with a 24 h periodic surrounding or not.
Circadian time	Time that spans the circadian period in relation to the light/dark regimen under synchronized conditions.
Circannual	A rhythm with a period of about 1 year (±2 months), synchronized with or desynchronized from the calendar year.
Circaseptan	A rhythm with a period of about 7 (±3) days, which may or may not be synchronized with the calendar week.
Circatrigintan	A rhythm with a period of about 30 (±5) days.
Cosinor procedure	A mathematical–statistical method of describing a rhythm by determining by least squares technique the cosine curve best fitting to the data and exploring the presence of a rhythm by examining the null hypothesis for amplitude in an *F*-test. If a rhythm can be described by this procedure, the cosinor yields a rhythm-adjusted mean (MESOR), an amplitude as measure of the extent of the rhythm, and an acrophase as indication of its timing with variance estimates for each of the three parameters.
Damping	Decrease in amplitude of a rhythm over time.
DD	Continuous dark conditions.
Endogenous rhythm	A biological rhythm that persists in the absence of external cues and is probably genetic.
Entrainment	Coupling of the period and phase of a biological rhythm (e.g., circadian) with another cycle (e.g., 24 h solar day). Entrainment signals (synchronizers) are light and temperature. Probably other components such as sugars play a role.
Free-running	Desynchronization of the period of a biological rhythm from the period of a known environmental synchronizer. Status of a rhythm under constant conditions (absence of synchronizers).

Table 1.1. (*Continued*)

Term	Definition and/or description
Frequency	Number of cycles for a given amount of time. It is the reciprocal of the period.
Gating	Pacing, or limiting a biological event to a certain period.
LD	Light period followed by dark period. Thus, 16 h light:8 h dark. LD might not always be 24 h periods as some experiments test effect of shorter or longer LDs.
Lighting regime	The light–dark cycle (LD), or constant light (LL), or constant dark (DD) conditions used for chronobiologic studies.
LL	Continuous illumination.
Masking	Change of rhythm characteristics (acrophase, amplitude, or Mesor) as a result of changes in environmental conditions.
Mesor	Midline estimating statistic of rhythm. The value midway between the highest and the lowest values of the (cosine) function best fitting to the data. The "M" is equal to the arithmetic mean only for equidistant data covering an integral number of cycles.
Pacemaker	A functional entity capable of self-sustaining oscillations that synchronize other rhythms. It is an internal component or set of components, not an external synchronizer.
Period (t)	Duration of one complete cycle in a rhythmic variation.
Photoperiod	In a light/dark regimen the duration of the light span (e.g., in light/dark = LD 12:12 h, the photoperiod L = 12 h).
Scotoperiod	In a light/dark regimen the duration of the dark span (e.g., light/dark = LD 12:12 h, the scotoperiod D = 12 h).
Synchronizer	Environmental signal or input that entrains a biological rhythm. In the literature several synonyms are used such as entraining agent, time giver, or Zeitgeber.
Trough	The lowest point in a series of measurements obtained as a function of time.
Ultradian rhythm	Peak of a mathematical curve fit to data. Refers to the time when a process has its maximum, starting from a point defined by the scientist, for example, dawn. It may be expressed in (negative) degrees as the lag from the acrophase reference (360° period) or in calendar time units (hours, minutes, etc.).
Zeitgeber	Time giver (German), it does not give time, but is a synchronizer.
Zeitnehmer	Time receiver (German); a molecule or mechanism that serves as input of environmental signals to the clock.

revolution of the tilted Earth around the sun that provides seasonal effects. It is a challenge for organisms to maintain a stable program of morphogenesis when important parameters regularly vary. The current hypothesis is that the circadian clock has evolved as a gene network that has a robust behavior, allowing daily adjustments to environmental changes such as photosynthetic apparatus maintenance or emission of

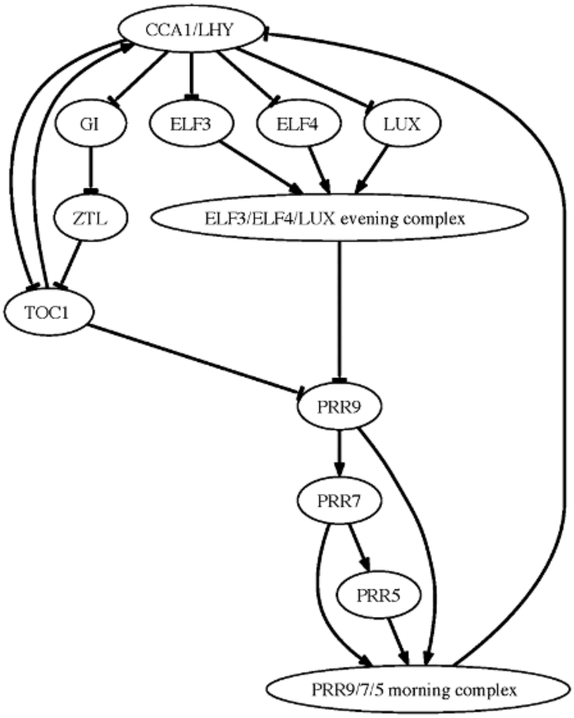

Fig. 1.1. A simplified structure of the current model of the circadian clock in *Arabidopsis*. The current model of the circadian clock comprises three groups of genes that are classified as the morning, midday, and evening loop. The morning loop is formed by three members of the same gene family *PRR9*, *PRR7*, and *PRR5*. These proteins form a complex that inhibits the midday loop formed by the genes *CCA1* and *LHY*. The evening loop is formed by *GI* and *ZTL*, two proteins that inhibit *TOC1* (another member of the *PRR* family), and a complex formed by *ELF3*, *ELF4*, and *LUX*. This evening complex inhibits the morning complex, thus closing the daily circle.

scent matching the time of pollinator activities (Locke et al. 2006; Akman et al. 2010; Thommen et al. 2010). A second task would be to consider long-term morphogenetic changes such as flowering, winter dormancy, and adaptation to cold or heat during the seasons. An endogenous clock should help maintain a constant flux of processes yet must be robust enough—for example, to prevent a short-day plant, would flower after being exposed to random shading on a dark day.

The current proposed structure of the plant circadian clock consists of three interrelated loops of genes that act by mutual activation and repression (Pokhilko et al. 2012) (Fig. 1.2). These feedback loops form an

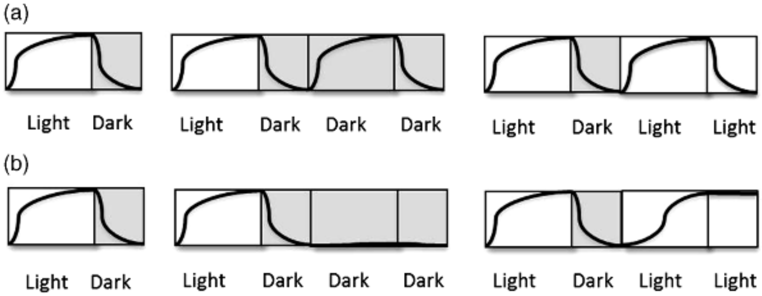

Fig. 1.2. Experimental design to identify processes that are circadian regulated in plants. As circadian experiments are timed usually, time zero is when light are turned on for a period and then off. This gives a pattern of light/dark, in most cases represented as LD. It follows that after a period of LD, the system is challenged with either a continuous light LL or an extended night (continuous dark) or DD. (a) Processes that are circadian regulated will maintain a rhythmic function in continuous dark (DD) and continuous light (LL). (b) A process that is light dependent will typically show a downregulation in continuous dark (DD) and constant high level in continuous light (LL).

oscillator that effectively cycles every day at a certain pace or amplitude (Table 1.1). As in many other biological regulatory processes, at least two levels of interaction occur inside the clock. One is at the transcriptional level, where activation and repression of gene expression play the main role. The second level of interaction is posttranslational changes where proteins form complexes and are selectively degraded or modified by phosphorylation. But the clock in plants also has an additional degree of complexity as several genes involved in clock function code for a photoreceptor that changes conformation and activity as a result of the light input (Jarillo and Pineiro 2006).

There are five *PSEUDORESPONSE REGULATOR* genes in the *Arabidopsis* genome, *PRR9*, *PRR7*, *PRR5*, *PRR3*, and *PRR1*, the latter known as *TIMING OF CAB EXPRESSION 1* (*TOC1*) (Uemura et al. 2010). All of them are components of the plant circadian clock. Assuming the morning as the beginning of a daily cycle, the first genes that show activity in the circadian clock are *PRR5*, *PRR7*, and *PRR9*. These genes act repressing the next loop of the clock in such a way that it causes a delay in its activation (Nakamichi et al. 2010). Two MYB transcription factor paralogs *LATE ELONGATED HYPOCOTYL* (*LHY*) and *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*) form the middle loop, as they are expressed during the early part of the day. *CCA1* and *LHY* expression is repressed by *PRR5*, *PRR7*, and *PRR9*, from morning till midnight (Nakamichi et al. 2010), but *CCA1* and *LHY* activate *PRR5*, *PRR7*, and *PRR9*. This interplay of repressing a function that then activates backwards creates a temporal pacer. A second component of the middle loop is *TOC1*. Recent work has shown that *TOC1* and the rest of the *PRR* family members are DNA-binding proteins (Gendron et al. 2012), indicating that their function in transcriptional control occurs via direct binding to regulatory sequences of target genes. The gene *REVEILLE8/ LIKE CCA1 LHY 5* is a MYB transcription factor found recently to activate the *TOC1* gene, thus creating an additional connection between the morning and evening loops (Farinas and Mas 2011). The REV8 protein physically interacts with regulatory region of *TOC1* activating histone hyperacetylation. This causes a local loosening of the chromatin increasing the accessibility to the transcriptional machinery.

The evening loop comprises the genes *EARLY FLOWERING 3* and *4* (*ELF3* and *ELF4*), *LUX ARRHYTHMO* (*LUX*), *GIGANTEA* (*GI*), and the protein with photoreceptor capacity *ZEITLUPE* (*ZTL*). A recent work has shown that the ELF3, ELF4, and LUX proteins form a protein complex called the evening complex (Nusinow et al. 2011). The evening complex can bind DNA via LUX (Helfer et al. 2011), and represses its own expression and that of the morning gene *PRR9* (Dixon et al. 2011). This repression of the morning loop by the night loop closes the circle. Two recent papers have shown that *TOC1* is a general transcriptional repressor of the evening genes, that is, during the night, many genes have low transcriptional activity because of *TOC1* (Huang et al. 2012; Pokhilko et al. 2012). Again this mutual activation and repression of the clock genes creates waves of activation and repression that effectively pace the plant cell. The evening part of the clock is not completely understood. A number of components are missing and the way known components interact with each other remains incompletely defined. As a summary, the plant circadian clock has the architecture of several negative feedback loops interconnected with each other. These loops have been defined as morning, midday, and evening loop based on the time of the day when these genes display a maximum peak of expression.

B. Clock Genes in Crops

If we consider circadian regulation, we identify three layers where evolution might show conservation and divergence. One is the presence of conserved genes, orthologous to those found in *Arabidopsis* and other plants. A second more subtle but in this case as important is the conservation of the gene interactions found in other clocks, that is, the network motifs (Alon 2007). Yet a third level is the conservation of input signals and output reactions. We will cover the conservation of these three levels, considering the fact that our depth of knowledge varies greatly for each of the layers depending on the trait described.

The actual knowledge of both the structure of the circadian clock and its functions is in its infancy in plants beyond *Arabidopsis*. The first layer of comparison, that is, identification of orthologs and paralogs, is the stage where most of our knowledge in crops is right now. Orthologs of *CCA1* or *LHY* are not always found as gene pairs in plants with complete genome sequence, which would allow comprehensive identification of coding sequences without missing one of the genes. Indeed, in the monocots, rice, and sorghum, there is a single-copy gene with higher homology to *CCA1*. Genes in core eudicots (Bremer et al. 1998) such as *Mesembryanthemum crystallinum* and the cactus pear (*Opuntia ficus-indica*) show higher degree of phylogenetic similarity to *CCA1* (Takata et al. 2009; Mallona et al. 2011), whereas in eudicots such as *Poplar*, *Castanea*, *Vitis*, or *Phaseolus*, the genes found tend to be *LHY*-like genes either as single or as double copies (Takata et al. 2009). The synteny analysis suggests *LHY* might be ancestral (Lou et al. 2012). Experiments in soybean show that there are *LHY* and *CCA1* orthologs in this crop with circadian expression patterns resembling *Arabidopsis* in the leaf tissues (Hudson 2010). In *Poplar*, two *LHY* paralogs, *LHY1* and *LHY2*, show differing expression patterns, indicating that they might have divergent functions (Takata et al. 2009). It remains to be determined whether the function of *CCA1* and *LHY* is conserved in other plants or if there are functional differences.

The five *PRR* genes in *Arabidopsis* are conserved in rice (Murakami et al. 2003). Sequencing of other eudicots has shown that there are 5 *PRR* genes in papaya (*Carica papaya*) (Ming et al. 2008; Uemura et al. 2010) while *Populus* has 11 *PRR* genes (Ramirez-Carvajal et al. 2008). *Brassica* comprises a large number of crops including Chinese cabbage, bok choy, turnip, broccoletto, or rapeseed. Recent work has shown that in the rapeseed (*Brassica rapa*), an amphidiploid, there are at least eight *PRR* genes and they show differences at the gene structure level indicating possible divergence in function with *Arabidopsis* (Kim et al. 2012). This emerging hypothesis awaits support of functional studies in this important group of plants.

There is a single copy of *GIGANTEA* in the *Arabidopsis* genome. The structure of the *GIGANTEA* locus has been studied in the yellow poplar (*Liriodendron tulipifera*). The *GI* locus is conserved in eudicots but is more divergent from rice or sorghum, indicating a possible departure at the genome level (Liang et al. 2010). A recent analysis of the only *GI* ortholog found in the rice genome, Os-*GI*, has shown a somewhat different picture of what one would predict from the *Arabidopsis* data (Izawa et al. 2011). Rice plants carrying a null allele of Os-*GI* do not show extreme flowering time phenotypes or yield changes. Furthermore, although 75% of the 27,201 genes analyzed by microarray were significantly affected in the loss of function allele Os-*GI*, only the phenylpropanoid pathway showed changes at the metabolic level, indicating an extreme robustness of the clock under field conditions. These experiments also suggest that the two additional layers of conservation, that is, gene networks and clock input and outputs, might be different for *GI* between rice and *Arabidopsis*.

Based on studies in several plants, the genetic functions of many of these genes seem to be highly conserved. The gene *ELF3* seems to be conserved in most plants. Work performed in rice and barley shows that it plays a crucial role in adaptation to different environments (see below on flowering time). A recent genomic comparison between *B. rapa* and *Arabidopsis* has shown that except for *ZTL*, circadian clock genes tend to maintain gene copy number after genome-wide duplication events, indicating that there is selection against losing one gene out of a complex network (Kim et al. 2012).

Overall circadian clock genes are extremely well conserved, not only in terms of specific genes but also in terms of the number of genes present in the genome. This indicates that orthologs and paralogs of the core clock genes are probably found in all higher plants. However, detailed work is required to understand the structure of the clock in crops, and maybe more important is to test their effect in controlling certain important traits for horticulture. The knowledge about outputs is expanding rapidly and it shows great promise in this group of genes (see below).

III. ENVIRONMENTAL INPUTS

A. Light

Light plays two distinct roles for plants: one is the source of energy for photosynthesis and the second is as a signal for development. Most plant processes are controlled by light, and comprehensive reviews on photoperiod, photoreceptors, and plant development in all its aspects have been published in recent years (Fankhauser and Staiger 2002; Jarillo and Pineiro 2006; Jiao et al. 2007; Franklin and Quail 2010). Like in other parts of this review, most of our detailed molecular knowledge on light has been obtained in *Arabidopsis* and only recently has this knowledge spread into other plants of horticultural importance.

Light is perceived in plants by at least four types of receptors: phototropins, phytochromes, cryptochromes, and members of the *ZTL/LOV KELCH PROTEIN 2* (*LKP2*)/*FLAVIN-BINDING KELCH REPEAT F-BOX 1* (*FKF1*) gene family (Fankhauser and Staiger 2002). Some of the clock proteins (ZTL and FKF1) are photoreceptors, and others, such as ELF3, can form complexes with ZTL. The distinction between light signaling and circadian clock is not always possible and could be somewhat artificial. First, red light activates the transcription of the morning loop genes *CCA1* and *LHY* (Alabadi et al. 2001) but this activation requires, to some extent, the proper function of the evening loop gene *TOC1* (Mas et al. 2003a). *CCA1* activated by light signals directly binds to promoters of *CHLOROPHYLL A/B BINDING PROTEIN* (*CAB*) genes, thus anticipating the morning (Wang et al. 1997).

The first gene found to act as a zeitnehmer or time taker (Table 1.1) is *ELF3* (McWatters et al. 2000). Indeed *elf3* mutants do not have detectable circadian rhythms in continuous light, but display circadian rhythms in the dark (Hicks et al. 1996). The protein ELF3 interacts with PHYTOCHROME B protein (Liu et al. 2001) and apparently gates red and blue light receptor signals (Covington et al. 2001). The null allele *elf3-1* displays gating defects in repressing light-dependent gene expression during the dark. For example, *CAB* is activated by light during the subjective night in *elf3* but not in wild-type plants (McWatters et al. 2000; Covington et al. 2001). The important concept is that light-induced genes and the corresponding processes do not maintain similar levels throughout the day and night because there is a rhythmic repression of the light-signaling pathway during dark periods, partly controlled by *ELF3*.

Two proteins, ZTL and LKP2, regulate TOC1 via degradation (Mas et al. 2003b). As the protein LKP2 has light sensing properties (Imaizumi et al. 2003), the complex picture becomes somewhat easier to interpret. Light entrains the clock by activation and degradation of several components, thus achieving a sort of rhythmic input partly caused by the fact that the morning and evening components are differentially affected, that is, morning elements *CCA1* and *LHY* mRNA synthesis is activated by light, whereas the evening element TOC1 protein is targeted for degradation.

It turns out that ZTL itself is a blue light receptor as the LOV (light, oxygen, voltage) domain present in the ZTL protein is a flavin-binding domain. When light is present, the ZTL protein binds to GI and is stabilized, but is selectively degraded in the dark. Mutations in the LOV domain result in poor binding of ZTL to GI (Kim et al. 2007). The stability of ZTL is important as ZTL directly controls the protein levels of TOC1 (Fujiwara et al. 2008).

The conclusions are that there are at least three places where the clock directly interacts with the light signaling, one via CCA1/PHYB interaction, the second one also dependent of PHYB, that is, ELF3/PHYB, and the third one via ZTL and FKF1 as photoreceptors and clock genes. Morning light signals enhance transcription of other genes, whereas evening light is interpreted in terms of protein degradation of clock components.

B. Temperature

As plants cannot actively control the temperature of their organs, changes in environmental temperature have several parallel effects on plants. First, many biochemical reactions have a linear dependency on temperature. The so-called Q10 or temperature coefficient measures the rate of change in chemical reactions as a result of increasing the temperature by 10°C. Indeed biochemical reactions have certain temperature optima, that area seldom maintained for long periods in plants, as day temperature fluctuates, and on a given day, temperatures will not stay the same for more than 3 or 4 h. Second, extreme temperatures cause damages, and adaptation to cold and hot weathers involves genetic activation of the so-called acclimation processes (Browse and Xin 2001). Finally, temperature plays a role as a signal for important developmental processes that include seed germination (Bewley 1997), growth, winter dormancy, and flowering (Henderson et al. 2003). Thus, the three aspects described could be seen as short-term (hours), middle-term (days to weeks), and long-term (weeks to season) responses elicited by temperature.

Studies performed in *Drosophila* and *Neurospora*, two organisms that, like plants, are poikilothermic, that is, they do not control body temperature, indicate that an intrinsic aspect of biological circadian clocks is the temperature compensation that allows biological processes to maintain a rhythm as autonomous as possible (Hogenesch and Ueda 2011). The identification of temperature compensation mutants in *Arabidopsis* was performed by analysis of accession-specific variations in the pattern of temperature compensation for rhythms of leaf movement between the ecotypes Columbia (Col) and Landsberg erecta (Ler) and between Ler and Cape Verde Islands (Cvi). This experimental approach identified several quantitative trait loci

(QTL) and some of them corresponded to known clock genes (Edwards et al. 2005). One QTL matched to the gene Flowering Locus C (FLC) (Edwards et al. 2006). Indeed at 27°C, a fairly high temperature for *Arabidopsis*, *FLC* lengthens the circadian period, thus compensating for otherwise excessive speed of metabolic processes. In contrast, the gene *GIGANTEA* is required to maintain rhythmicity at 12 and 27°C (Gould et al. 2006), indicating that several genes in the clock are involved in temperature compensation. The genes *PRR3*, *PRR5*, and *PRR9* form the morning loop, and PRR7 and PRR9 are involved in compensation at high temperatures, as the double mutant *prr7,prr9* overcompensates at 30°C, indicating that they are involved in repression of an otherwise fast-paced clock under these conditions (Salome et al. 2010).

One molecular mechanism of part of the temperature compensation was recently found for *CCA1*, which tends to bind to its target genes with higher affinity at higher temperatures. This increased affinity is counterbalanced by a protein kinase 2 (CK2) that phosphorylates CCA1 at higher temperatures, lowering its DNA-binding affinity. This effectively compensates the tendency of part of the clock reactions, like any other reaction in the cell, to run faster as temperature increases (Portoles and Mas 2010).

In conclusion, temperature changes have a lower effect on plant basic processes in plants because the circadian clock compensates daily differences. Nevertheless, temperature entrains the system in a way that is not fully understood. Adaptation to temperatures and their effect on development are discussed below.

IV. CONTROL OF PLANT GROWTH AND MORPHOGENESIS

Plant growth and morphogenesis is a complex process comprising shoot and root apical meristem maintenance, lateral organ formation, flowering, tuber formation, or seed development. Some of these processes are controlled in a number of plants by environmental cues. As a result, evidence has accumulated that some of the major decisions during plant morphogenesis are somehow related to clock function. There is clear evidence about the effect of plant growth regulators on morphogenesis, and there is very strong evidence showing that at least gibberellins (GAs) are directly under the control of the clock. We present an overview of what is known about plant hormones and several developmental processes found to be directly controlled by the clock machinery.

A. Plant Hormones and Circadian Clock

Endogenous plant hormones regulate an extensive array of physiological processes over the whole plant life cycle from seed germination to flowering. The phytohormones include cytokinin, auxin, brassinosteroid (BR), abscisic acid (ABA), GA, ethylene, and salicylic acid (SA). They function like partially interacting mediators allowing plants to sense their exogenous and endogenous conditions in order to assure maximal fitness under the varying environment (Hanano et al. 2006).

Among the exogenous growth conditions that affect the endogenous plant hormones are light, temperature, abiotic stress, and disease. But the biological oscillations in the form of the circadian rhythm also affect phytohormones. Comprehensive transcriptome data set analysis clearly demonstrated a circadian periodicity in genes responsible for synthesis of plant hormones and responses (Covington and Harmer 2007; Covington et al. 2008; Mizuno and Yamashino 2008; Maloof et al. 2011) and transgenic plants carrying promoter-luciferase reporter gene fusions (Bancos et al. 2006; Hanano et al. 2006) further confirmed that the circadian system modulates plant responses to most hormones.

The phytohormone GA controls important aspects of plant growth such as seed germination, elongation growth, and flowering. A key role in GA signaling lies in its interaction with the DELLA repressor protein in a GA-dependent manner. DELLA proteins restrain GA-dependent growth responses, and their repressor activity is relieved by their GA-dependent degradation (Schwechheimer and Willige 2009). Several pathways have been shown to cross talk with GA signaling, including the circadian clock, and it was proposed that GA pathways contribute to the diurnal growth pattern (Maloof et al. 2011). Rhythmic plant growth, characterized by maximum rates during the second half of the night, is controlled by a concerted action of both the light signaling, which represses growth during the day, and the circadian clock that gates growth toward the end of the night. The transcription factors *PHYTOCHROME-INTERACTING FACTOR4* (*PIF4*) and *PIF5* are key elements in the hormone gating through the circadian clock (Nozue et al. 2007). The PIF proteins physically interact with members of the phytochrome family and transduce environmental light signals to responsive nuclear genes (Quail 2000). According to a model proposed by Nozue et al. (2007), during the day, light inactivation of PIF as well as an inhibitory interaction between DELLA and PIF proteins prevents growth (Nozue et al. 2007). DELLA interacts with PIF4/5 and inhibits their DNA-binding abilities. Early during the night, circadian clock genes prevent PIF transcription, leaving growth-promoting PIF action to a short period before dawn, when DELLA protein levels are reduced (Alabadi 2009; Yamashino et al. 2010). Suppression of growth during light periods might be further related to maximum expression of genes for GA catabolic enzymes, as observed in *Arabidopsis* (Zhao 2007).

Auxin is an additional phytohormone whose action is found to be circadian clock gated as auxin-related genes, including production and response, show clock-regulated expression (Covington and Harmer 2007; Thines and Harmon 2011). Auxin is a central controller of plant growth, development, and cellular physiology including embryogenesis, vascular patterning, formation of lateral and adventitious roots, control of apical dominance, phototropism, gravitropism, cell turgor, elongation, division, and cell differentiation. The subset of auxin-related transcripts in *Arabidopsis* exhibiting circadian cycling includes those of *de novo* auxin biosynthesis genes, auxin responsive genes, genes involved in auxin signaling, and negative regulators of auxin responses (Thines and Harmon 2011). The above-mentioned *PIF4* and *PIF5*, which integrate light and circadian clock signaling to generate rhythmic plant growth, were proposed to directly modulate auxin pathway and response genes (Kunihiro et al. 2011; Maloof et al. 2011). PIFs therefore play a fundamental role in the circadian clock gating of both GA and auxin responses. Still, other PIF-independent pathways might also contribute to the circadian regulation of growth via auxin gating, such as the transcription factor *REVEILLE1* (*RVE1*) from *Arabidopsis*, homologous to the central clock genes *CCA1* and *LHY*. *RVE1* controls free auxin levels by positively regulating the expression of the auxin biosynthetic gene *YUCCA8* (*YUC8*) during the day (Rawat et al. 2009).

A third group of phytohormones regulated by the circadian clock includes BRs, one of the most recently characterized groups of plant hormones. BRs are involved in seed germination, stem and root elongation, vascular differentiation, leaf expansion, and apical dominance, responses that are also controlled by auxins (Halliday 2004). It was shown that brassinosteroid and auxin signaling pathways converge at the level of the transcriptional regulation of common target genes (Nemhauser et al. 2004). In *Arabidopsis*, two BR-biosynthetic genes, *CPD* and *CYP85A2*, are under diurnal regulation (Bancos et al. 2006), and similar to the circadian regulation of auxin action, light regulation of *CPD* is primarily mediated by phytochrome signaling (Bancos et al. 2006). Interestingly, under light, but not in the dark, transcriptional control is independent of hormonal BR feedback regulation, showing that rhythmicity also involves changes in plant sensitivity to a hormone via feedback loops.

Circadian regulation has also been described for genes contributing to the signaling of ABA. The core clock protein TOC1 is linked to ABA signaling-related growth processes by a feedback loop. TOC1 binds to the promoter of the ABA-receptor ABAR/CHLH/GUN5 (Legnaioli et al. 2009), repressing *ABAR* expression, and *TOC1* is in turn induced by ABA. The reciprocal regulation allows fine-tuning of circadian responses to ABA (Thines and Harmon 2011). ABA plays a major role in seed maturation and germination, as well as in adaptation to abiotic environmental stresses. It further promotes stomatal closure by rapidly altering ion fluxes in guard cells (Leung and Giraudat 1998). It was proposed that some aspects of plant stress responses are mediated by ABA through the circadian clock. Thus, plants prepare properly for action against common ambient stresses that keep changing in response to the light/dark and hot/cold daily cycling by anticipating the diurnal day/night cycle (Mizuno and Yamashino 2008; Legnaioli et al. 2009).

In summary, phytohormonal control of processes that fluctuate on a daily basis, such as plant growth or stress due to hot/cold cycling, is gated by the circadian clock, allowing anticipation of the diurnal day/night period and a fine-tuning of daily plant responses. The largest body of evidence has been found so far for the GA signaling involved in germination, growth, and flowering. But other plant hormones such as BR and ABA are also circadian regulated.

B. Seed Development and Germination

From a horticultural perspective seeds are important both as plant material for propagation and as a product. The involvement of circadian regulation on seed development before maturation is not understood with detail. Evidence comes from the fact that transient starch synthesis is circadian regulated and sugars are used in developing seeds as sources to accumulate important metabolites, that is, carbohydrates, fats, and proteins. Recent work has shown that in soybean there is a circadian regulation of genes involved in carbohydrate metabolism related to photosynthesis and lipid synthesis, whereas carbohydrate metabolism unrelated to photosynthesis did not follow a circadian trend (Hudson 2010). The flag leaf of rice is thought to be the source of carbohydrates for rice grain formation, and a strong diurnal cycling was found in this leaf and seedling leaf whereas additional genes showed a diurnal pattern only in flag leaves, suggesting their importance in the grain filling process (Xu et al. 2011). These data indicate a role for circadian regulation on grain productivity (see below).

Seed germination is an important aspect in the plant nursery, and proper expertise and practices make a difference in terms of percentages of germination and seedling quality. Plants assess the environmental situation to avoid germination when environmental conditions are not conducive to seedling establishment. Studies in different plants have shown that seeds have some degree of dormancy. In principle, seed dormancy is not a wanted horticultural trait as high-speed germination and growth are an asset in most crops. However, a complete lack of dormancy may cause the so-called preharvest sprouting, an unwanted trait selected against in cereals such as rice, sorghum, and wheat (Iusem et al. 2001; Humphreys et al. 2009; Sugimoto et al. 2010). Thus, a balance between both processes is required. Indeed seed dormancy and germination are thought to be one and the same process where levels of abscisic acid and gibberellins counteract each other in equilibrium (Bewley 1997). Recent reviews cover this issue in depth (Finch-Savage and Leubner-Metzger 2006; Penfield and King 2009). But the involvement of the circadian clock on seed germination and dormancy is a relatively new concept. Light plays a role in seed germination and hundreds of experiments have shown the importance of light of different qualities to promote germination in uncountable species. As these three parameters, that is, light, ABA, and GAs, are known to be entraining signals and output pathways of the clock, it was not surprising that a direct link was found.

Under natural conditions, once seed development occurs, seed dormancy is established, and a period called afterripening takes place where time and environment determine germination potential of dry seeds (Carrera et al. 2008; Holdsworth et al. 2008). The clock genes *CCA1* and *LHY* show partially redundant function in germination. The *cca1,lhy* double mutants show enhanced germination under continuous cold treatment (Penfield and Hall 2009). Both *lhy* and *cca1,lhy* double mutants show better germination than wild types under cycling temperature regimes (27°C at day and 17°C at night), indicating that clock genes play a direct role in the control of seed dormancy and signaling to germinate, in this case by temperature. The mutant *gi* has opposite effects to those observed in *cca1,lhy* double mutants, as it displays poor germination after storage. This means that the GI protein is required for afterripening, an important process in cereals and any seed that will be maintained for more than just a few days before germination.

C. Flowering Time

Flowering time in plants is among the most important traits in horticulture. Work in *Arabidopsis* showed that several pathways can promote flowering including gibberellins, photoperiod, temperature, or even vegetative growth (Simpson et al. 1999). As a result, today flowering time is dissected into the so-called GA-dependent, light-dependent, temperature-dependent, and autonomous pathway. One current hypothesis is that differences between plants relate to the degree of importance of these pathways involved in flowering time. This hypothesis is supported by studies in several crops such as tomato, a neutral-day plant that follows the autonomous pathway (Lifschitz and Eshed 2006; Lifschitz et al. 2006). Rice, on the contrary, is a short-day plant and it flowers in a manner opposite to *Arabidopsis* (Tsuji et al. 2011).

As some of the *Arabidopsis* mutants affected in the photoperiodic flowering pathway turned out to be clock genes, it became clear that at least this pathway is circadian regulated (Hayama and Coupland 2003). Among the clock genes that show a flowering time phenotype in *Arabidopsis* are *ELF3*, *ELF4*, *CCA1*, *LHY*, and *GI*. Strong evidence of a role of clock genes in flowering in crops has started to accumulate. The identification of *PDD-H1*, the ortholog of *PRR7* from barley, as major determinant of flowering, and partly responsible for the winter or summer genotypes, indicated that the clock genes play a role in flowering in monocots. Variations in orthologs of *GIGANTEA* from the evening loop with a function in flowering have been found in pea and soybean (Hecht et al. 2007; Watanabe et al. 2011), indicating that this part of the loop might have conserved functions in flowering time in *Arabidopsis* and legumes. The evening loop gene *ELF3* also shows conserved functions in *Arabidopsis*, barley, and rice where it shares a function on responses to photoperiod (Fu et al. 2009; Saito et al. 2012). Finally, *GHD7*, a gene with sequence homology to the PRR family, has been found in rice that increases yield and has additional heading phenotypes (Xue et al. 2008). The data show that a number of clock genes play a role in flowering time, and in some cases, they also have additional functions in growth and productivity. A list of genes with phenotypes relevant to flowering in *Arabidopsis*, which show modified phenotypes in other plants, can be seen in Table 1.2.

One of the clock outputs that is better understood is the activation of flowering through the gene *CONSTANS* (*CO*). During the evening of long days, there is an increase in the level of mRNA of *CO* resulting from the inhibition of *CYCLING DOF FACTOR* by *GIGANTEA*. This allows the formation of CO protein that activates the gene *FLOWERING TIME* (*FT*).

The *CO* gene activates the transcription of *FT*, currently thought to be the flowering signal (Samach et al. 2000; Suarez-Lopez et al. 2001). The

Table 1.2. Flowering and growth-related phenotypes of clock genes in *Arabidopsis* and in crop plants.

Clock position	Species	Gene	Phenotype
Morning loop	*Arabidopsis*	*PRR7*	Light insensitive (Kaczorowski and Quail 2003)
	Barley	*Pdd-H1* ortholog of *PRR7*	Major determinant of photoperiod (winter vs. spring) (Turner et al. 2005)
Midday loop	*Arabidopsis*	*cca*,*lhy* double mutant	Semidwarf, early flowering in short days, pale green in short days, accelerated germination (Mizoguchi et al. 2002; Penfield and Hall 2009)
		cca1 loss of function	Early flowering in short days (Mizoguchi et al. 2002)
		lhy loss of function	Delayed flowering and elongated hypocotyls (Schaffer et al. 1998)
Evening loop	*Arabidopsis*	*Early flowering 3*, *ELF3*	Early flowering, photoperiod independent (Zagotta et al. 1992) Defective inhibition of hypocotyl elongation (Zagotta et al. 1996)
		Gigantea; *gi*	Late flowering (Araki and Komeda 1993)
	Barley	HV Elf3; *Praematurum a* (*mat-a*); *early maturity 8*, *eam8*	Adaptation of barley to lower latitudes, early flowering irrespective of photoperiod (Faure et al. 2012; Zakhrabekova et al. 2012)
	Pea	*PsELF4/DNE*	Early flowering (Liew et al. 2009)
		PsGi/Latebloomer1	Allele specific response to photoperiod. Late flowering (Hecht et al. 2007; Liew et al. 2009)
	Rice	*OsELF3*	Later flowering irrespective of photoperiod (Fu et al. 2009; Saito et al. 2012)
		OsGi overexpression	Photoperiod-independent late flowering (Hayama et al. 2003)
	Soybean	*GmGia*	Early flowering (Watanabe et al. 2011)
Unknown	Rice	*Ghd7*	Increased yield and delayed heading time under long days (Xue et al. 2008)

gene *FT* from *Arabidopsis* is expressed in the vascular tissue but the protein is exported to and travels to the SAM where it activates the flowering program. This has been empirically demonstrated as FT signal can be transmitted from stock to scion in tomato, a neutral-day plant (Lifschitz et al. 2006), and in *Arabidopsis*, a long-day plant (Corbesier et al. 2007). Although rice is a short-day plant, FT is the conserved flowering signal (Tamaki et al. 2007). Furthermore, overexpression of the FT (*MdFT1*) in *Poplar* and apple causes extreme early flowering, as apples flower directly in *in vitro* culture (Trankner et al. 2010). The FT protein activates among other genes the gene *SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS* (*SOC1*) that is involved together with other genes in triggering the flowering process (Samach et al. 2000; Lee and Lee 2010).

Experiments around this process are bringing mechanistic ways to understand some phenomena such as alternate bearing in fruit trees (Monselise and Goldschmidt 1982). Recent work performed in mandarins with the alternate bearing variety ‘Moncada’ has shown that both timing of fruit harvest and load directly affect expression of *SOC1* (Munoz-Fambuena et al. 2011). This gives for the first time a mechanistic explanation to this important fruit tree behavior opening a new approach to improve and homogenize yields. The accumulated evidence for a key role of circadian regulators on flowering and related processes in crops, especially in trees, has significant horticultural implications.

The effect of gain and loss of function of core clock genes and their orthologs on flowering time in plants of agricultural importance is emerging at high speed in cereals, legumes, and trees. Clearly, there is a huge gap between what we know in *Arabidopsis* and what is known in other plants, but the evidence of a role of the clock in flowering time seems to be universal.

D. Winter Dormancy

Woody plants go through the so-called dormancy period. The process of dormancy in plants refers to the cessation of growth and development during its life cycle. Temperate woody plants show a dormancy period in the winter and some tropical trees go dormant during the dry season. It is considered an adaptive trait of woody plants that allows survival during especially hard periods. Dormancy is induced by environmental cues. Indeed, in most woody plants, short days lead to growth cessation. Additional dormancy features include leaf fall and cold tolerance (Allona et al. 2008). When spring conditions appear and dormancy is broken, growth rates increase, and floral buds appear. Thus, it is important to consider that during the juvenile period, dormancy leads to seasonal growth cessation during winter period, followed by growth periods. Only when the juvenile period is over, dormancy break is accompanied by seasonal flowering (Egea-Cortines and Weiss 2001). The juvenile period can last several years in many trees, for instance oranges (Peña et al. 2001). Breakthrough experiments performed in hybrid aspen showed that the constitutive expression of the *FT* gene from poplar induces flowering within 4 weeks compared to the 8–20 years required for wild-type trees (Bohlenius et al. 2006). This indicates that FT or downstream genes can overcome the juvenile phase. Short-day-induced growth cessation is also disrupted in these plants, indicating that flowering and dormancy are part of the same process. Furthermore, natural variation in day length for growth cessation of accessions of European aspen (*Populus tremula*) ranging between 51° and 63° latitude can be explained by changes in the *PtCO* gene, indicating that the time to flower and seasonal growth cessation are controlled by a common mechanism.

Work performed in dormant chestnut (*Castanea sativa*) showed that winter dormancy disrupts cycling of *CsTOC1* and *CsLHY* (Ramos et al. 2005). Further work has shown that *CsPRR5*, *CsPRR7*, and *CsPRR9* are also disrupted in their expression pattern during the winter (Ibañez et al. 2008). This disturbance in cycling was also achieved by cold temperatures of 4°C. Artificial transfer of plants that have not fulfilled the chilling requirements during the winter, to temperatures of 22°C, causes a reactivation of the endogenous clock (Ramos et al. 2005; Ibañez et al. 2008). Studies in hybrid aspen have also shown that downregulation of *PttLHY1* and *PttLHY2* using RNA-i interference caused a delay in bud burst (Ibañez et al. 2010), indicating again that dormancy in trees is under direct control of the circadian clock.

Altogether, it is clear that juvenility and winter dormancy are processes related to flowering time and as such, the circadian clock probably plays a role. The data obtained in hybrid aspen indeed indicate that future studies could find additional connections in trees, not only helping to solve growth and seasonality problems but also increasing the efficiency of fruit tree breeding programs.

E. Tuberization

The process of tuberization in potato is controlled by day length as commercial cultivars undergo tuber formation under short days (Rodriguez-Falcon et al. 2006). Although flowering time and tuberization are affected by day length, genetic experiments show that flowering time in *S. tuberosum* ssp. *andigena* is not responsive to photoperiod whereas tuberization remains short-day dependent (Gonzalez-Schain and Suarez-Lopez 2008). It has long been known that application of GA3 inhibits this process (Rodriguez-Falcon et al. 2006). This indicates that two independent pathways can promote tuberization, one dependent on GA signals and the second dependent on short days.

The day-length-dependent pathway involved in flowering in *Arabidopsis* has as a major output the activation of *CO* (see above). The first evidence of a role of *CO* in tuberization was obtained in transgenic potatoes expressing the *AtCO* gene. These plants are smaller than control plants and tuberization is inhibited under short-day conditions (Martinez-Garcia et al. 2002). These results demonstrate a negative effect of *CO* on the photoperiodic control on tuberization. The activation of the gene *FT* by *CO* in tomato, rice, and *Arabidopsis* indicates that *FT* is the active signal that causes flowering (Suarez-Lopez et al. 2001; Yanovsky and Kay 2002; Hayama et al. 2003; Lifschitz et al. 2006). A recent study has shown that expression of the *Hd3a* gene from rice, ortholog of *FT*, can induce strict short-day tubering types to tuberize under long-day conditions (Navarro et al. 2011). As the *FT* signal is graft transmissible, the authors demonstrated that the *Hd3a* signal could travel from stock to scion. Furthermore, it appears that in potato two *FT* paralogs, *StSP3D* and *StSP6A*, respond to independent environmental cues. The gene *StSP3D* seems to be involved in flowering, whereas *StSP6A* is responsible for tuberization (Navarro et al. 2011).

F. Productivity

Productivity, understood as the amount of useful yield of a crop, is a loose term, as it might refer to fruits, grain, leaves, or number of flowers. However, all of these horticultural products are the result of plant growth. As the circadian clock controls growth, we present the evidence of direct relations between clock genes and this important trait.

One large family of genes in plants is the *CYCLING DNA BINDING WITH ONE FINGER FACTORS* (*CDF*). One of them, *CDF*, represses *CO* involved in flowering (Fornara et al. 2009). However, there are *CO* genes in nonflowering single cell algae such as *Chlamydomonas reinhardtii*. In this unicellular alga, *CrCO* plays a completely different role: it controls starch accumulation and the circadian control of cell cycle progression (Serrano et al. 2009). There are at least 30 *CDF* genes in rice and 36 in *Arabidopsis* (Lijavetzky et al. 2003). Recent work found that in rice, reduced expression of *RICE DOF DAILY FLUCTUATION 1* (*RDD1*) by means of antisense RNA caused significant decrease in plant size, late flowering, and significant reduction in grain yield (Iwamoto et al. 2009). As *RDD1* maintains circadian gene expression under continuous light and continuous dark conditions, the authors concluded that *RDD1* is circadian regulated and plays a role in rice productivity by a mechanism that is not determined.

Recent work has shown that expression of the gene *BBX32* from *Arabidopsis* in soybean increases yield in grain in a multiyear in experiments performed in the United States and Argentina (Preuss et al. 2012). This gene was found to increase the period of pod and seed development while inhibiting leaf senescence. As *GmBBX32* shows circadian expression and its overexpression affects *GmTOC1* and *GmCCA1* expression, the authors conclude that genes related to the circadian clock are of major importance for productivity.

It remains to be determined the extent and tightness of the connection. Independent works linking GA to heterosis in cereals (Auger et al. 2005; Su et al. 2005; Zhang et al. 2007; Wang et al. 2009) might increase this emerging evidence.

G. Primary Metabolism

Primary metabolism comprises synthesis and degradation of macromolecules including RNA, protein, and carbohydrates. Early experiments using large-scale transcriptomics showed that the number of total genes from the *Arabidopsis* genome that showed daily cyclic expression was much larger than expected. Indeed, two independent experiments showed that between 6% and 8% of all the open reading frames could be circadian regulated (Harmer et al. 2000; Schaffer et al. 2001). These experiments were later replicated in other plants and the hypothesis does hold tight. Circadian regulation under light cycling involves 23% of the annotated genes in maize (Hayes et al. 2010), and 30–40% in rice and poplar (Filichkin et al. 2011). Experiments in *Arabidopsis* with a golden-standard annotated genome have shown that from 20,000 transcripts, 89% cycle and show a peak level at a certain time of the day when tested for photocycle, thermocycle, or circadian cycle. From these genes, 34–53% are diurnally regulated, and 6–31% are circadian regulated (Michael et al. 2008). Furthermore, thermocycles can drive half of the transcripts. Genes involved in large-scale processes show distinct patterns of phasing. For instance, expression of genes involved in DNA processing, energy metabolism, cell cycle, and protein synthesis is phased between midnight and dawn under the thermocycle conditions. In contrast, the expression of those related to the energy metabolism is phased after dawn under photocycle conditions (Michael et al. 2008).

Rhythmic changes in mRNA do not always translate into circadian enzymatic activities as different isoforms can mask each other's activities when measured in bulk. Furthermore, accurate determination of individual protein levels is technically challenging compared to transcriptomic analyses. Work performed in rice has shown that proteins involved in carbohydrate metabolism, redox regulation, protein binding and folding, nitrogen and protein metabolism, energy conversion, and secondary metabolism display a light/dark cycling (Wang and Wang 2011).

At the metabolic level a number of works show effects of circadian clock mutants. The coordination of several apparently independent metabolic pathways has been found as a result of metabolomic characterization of *prr9,prr7,prr5* triple mutants that show regulation of chlorophyll, carotenoid, ABA, and alfa tocopherol synthesis modifications (Fukushima et al. 2009). The circadian clock seems to control nitrogen assimilation rates and free amino acid levels. The enzymes nitrate reductase, glutamine synthase, and glutamine dehydrogenase show circadian oscillation (Lillo and Meyer 2001; Lillo et al. 2001). Although the enzyme activities may fluctuate as a result of circadian clock control, only few amino acids show quantitative changes in constant light (Fukushima et al. 2009), indicating that nitrogen levels might be more stable than carbohydrate levels.

Altogether primary metabolism seems to be extensively controlled by the circadian clock (Farre 2012). The best evidence is at the large-scale transcriptional level. Changes in protein levels or in certain metabolic pathways seem to be a case-by-case situation. As carbohydrate metabolism plays such an important role in plants and it has been studied with more detail, we have reviewed it separately.

H. Starch Metabolism

Plant productivity is not a simple equation of carbon uptake. Plant photosynthate is converted into raw biomass for growth, stored, or lost as a result of photorespiration, emission of volatiles, or root exudates. Partitioning of photosynthate between storage (starch, fructan, and lipids) or growth is currently not understood. The so-called transient starch that is produced during the light period of the day, and consumed during the night to foster growth and inner metabolism, is the key to plant productivity (Smith and Stitt 2007; Sulpice et al. 2009). A series of *Arabidopsis* mutants that cannot degrade starch at the proper speed or cannot accumulate starch show decreased growth rates (Graf and Smith 2011).

Starch granules are in equilibrium of synthesis during the day and degradation during the night. In snapdragon, the *GRANULE BOUND STARCH SYNTHASE*, an ortholog of the *waxy* gene in maize, is circadian regulated (Merida et al. 1999). Further work in *Arabidopsis* has shown that *GBSS1* oscillation is abolished by overexpression of *CCA1* (Tenorio et al. 2003). This indicates that starch granule synthesis is directly controlled by the circadian clock.

Plants can measure day and night length with a great deal of accuracy, and starch degradation is adjusted to night length, thus ensuring a proper carbohydrate balance until dawn. This balance or speed of degradation becomes adjusted every day by the circadian clock. Elegant experiments performed in *Arabidopsis* have shown that when plants are grown for a period of time at a certain light regime such as 12 h light/12 h dark, a single elongated night causes a situation of carbon starvation during the period of the first extended night. This is immediately corrected to accommodate a new speed of starch degradation according to the new expected night lengths (Graf et al. 2010). Giving an early night, that is, starting the dark period before the schedule, causes an immediate rearrangement of starch metabolism to decrease degradation speed and maintain levels until dawn.

Studies performed in maize, a C4 plant, show that key enzymes involved in starch synthesis display circadian regulation. Expression of *AGPL*, a subunit of AGPase that is the major regulatory enzyme in starch biosynthesis, converting glucose 6-phosphate to ADP-glucose, the substrate for starch synthase, peaks at dawn. Two STARCH SYNTHASE transcripts peak early in the morning (Khan et al. 2010), showing that, like in *Arabidopsis*, maize anticipates carbon requirements and launches the starch synthesis machinery to be ready for action when photosynthesis starts.

I. Photosynthesis

The light-harvesting CHLOROPHYLL a/b protein, small subunit of RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, and early light-induced protein were the first genes found to cycle in a circadian fashion in peas (Kloppstech 1985). The expression of the photosynthesis apparatus genes shows daily maxima at the end of the night. In contrast, those with tasks in electron transport photosystems show their maximum transcriptional activity during the day. This is true in maize (Khan et al. 2010), rice, poplar (Filichkin et al. 2011), or *Arabidopsis* (Harmer et al. 2000).

Circadian assimilation of CO_2 has been demonstrated in *Phaseolus* leaves (Hennessey and Field 1991). Circadian regulation of stomatal opening, electron transport, and light-induced electron flow also occurs in legumes (Fredeen et al. 1991; Hennessey et al. 1993), indicating that the photosynthetic process as a whole is strictly coordinated. Studies using *Arabidopsis* mutants have shown that photosynthesis is affected in clock mutants causing reduced growth and fitness (Dodd et al. 2005). In spite of a cause–effect of circadian regulation on photosynthesis, our mechanistic understanding of how it happens is shallow, suggesting that new discoveries in this field could uncover important advances in terms of productivity.

Plants with CAM photosynthesis behave opposite to C3 and C4 metabolic-based plants as they absorb CO_2 during the night (Mizrahi et al. 1997). Studies performed in cactus pear, an obligate CAM, show that the circadian clock oscillator is different from that in *Arabidopsis* (Mallona et al. 2011). Two clock genes *OfiPRR9* and *OfiCCA1* display two significant expression peaks, one in the morning, and the second in the evening. This would indicate that the evolution of photosynthesis could be the result of changes in a few circadian clock genes that control it, rather than the modification of hundreds of genes at their regulatory regions.

J. Scent Production

Plant scent production is among the most complex and least well-understood traits. Although a great deal of information is available about the biochemical pathways of volatile biosynthesis, there are gaps in our understanding on how these pathways are controlled during development and modulated by the environment. It is known, however, that fragrance is involved in pest repellence, and pollinator and seed-dispersing animal attraction. From an economic perspective, scent is probably one of the most important traits as it is directly responsible of the flavor and aroma of edible crops and their products. Furthermore, changes in composition of plant volatiles can give resistance to pests (Gatehouse 2002; Kessler and Baldwin 2002). Most flowers emit scent during certain day periods in order to attract specific pollinators. Rhythmic emission of floral scent has been found in many plants including rose (Helsper et al. 1998), orchids (*Odontoglossum constrictum*), citron (*Citrus medica*), *Hoya carnosa*, and *Stephanotis floribunda* (Matile and Altenburger 1988). Circadian regulation of these rhythmic emissions was demonstrated using extended periods of light and dark. Snapdragon and petunia show opposite volatile emission patterns. Snapdragon produces volatiles in the morning, whereas petunia does it in the evening, but both emit in a rhythmic fashion (Kolosova et al. 2001).

Volatile compounds identified in plants include fatty acid derivatives, benzenoids, phenylpropanoids, isoprenoids, and nitrogen- and sulfur-containing compounds with over 1,700 independent compounds identified in different plants (Knudsen et al. 1993). Many of these are produced in vegetative parts as a result of response to insect attacks but the biochemical pathways and many of the genes involved in their synthesis are either the same or paralogs with a specific function in floral scent production (Dudareva et al. 2004; Pichersky et al. 2006).

Methyl benzoate is one of the major volatile compounds produced from the phenylpropanoid pathway. This compound is produced by methylation of benzoic acid in a reaction catalyzed by benzoic acid carboxyl methyltransferase (BAMT) and follows a rhythmic oscillation. Analysis of BAMT activity in snapdragon petals shows slight variations in enzyme activity during day/night cycles, following a rhythmic pattern. The coincidence of high levels of BAMT enzymatic activity with low levels of methyl benzoate emission during the night period, as well as during continuous night conditions, suggests that BAMT activity is not the factor controlling oscillations. Therefore, it is thought that the amount of benzoic acid available in petal cells is the limiting/driving factor (Kolosova 2001). Indeed, measuring endogenous benzoic acid at different times of day/night cycle in snapdragon demonstrated that BA follows a circadian rhythm, reaching maximum levels during the day and minimum levels during the night. Moreover, the rhythmic fluctuation of benzoic acid levels may be caused by the rhythmic regulation of phenylalanine ammonia-lyase (PAL) and/or other enzymes upstream in the biosynthesis pathway. Analysis of PAL activity shows a difference in oscillations by almost 12 h, compared to BAMT activity, at the transcriptional level (Kolosova et al. 2001). The mRNA levels are constant under constant night conditions, a result consistent with the theory that light signalling regulates the amounts of BAMTand PAL mRNA (Fig. 1.2).

Methyl benzoate is also one of the major volatile compounds emitted by *Nicotiana silvestris*, *Nicotiana. suaveolens* (Loughrin et al. 1991), and Petunia (Kolosova et al. 2001). Unlike snapdragon, these plants reach maximum levels of emission during the night, indicating that it is not the biochemical pathway but rather the regulation of emission the one important factor in terms of harvesting tissue for extraction of chemicals. Additionally, other phenylpropanoids, such as phenethyl alcohol and phenethyl acetate, have been found in the floret tissue of *Trifolium repens*. These compounds are released from their glucoside conjugates by a β-glucosidase. Analysis in *T. repens* shows that the concentration of volatiles is highest both in the tissue and in the headspace just prior to flowering (Jakobsen and Christensen 2002). As the relationship between volatiles in the tissue and emitted volatiles is not linear, the authors interpret that a second factor is responsible for the rhythmic emission, a hypothesis formulated earlier as a result of similar data observed in other plants (Altenburger and Matile 1990).

Terpenoids are derived from two different pathways, the methylerythritol phosphate (MEP) pathway that provides isopentenyl diphosphate IPP and dimethylallyl diphosphate for hemiterpene, monoterpene, and diterpene biosynthesis, and the mevalonate pathway that takes part in sesquiterpene biosynthesis. Nevertheless, floral volatile terpenes are only derived from the MEP pathway (Dudareva et al. 2005). Experiments about volatile composition in *Antirrhinum* confirm that the mayor terpenoids emitted are three monoterpenes, myrcene, (*E*)-β-ocimene and linalool, and the sesquiterpene nerolidol (Dudareva et al. 2003). Furthermore, all of these compounds are mainly emitted during the day following a rhythmic pattern that coincides with MEP activity. This oscillation is strongly correlated with the pattern of 1-desoxy-D-xylulose phosphate synthase (DXPS) gene expression, which is one of the first steps of the MEB pathway (Dudareva et al. 2003). This information, together with data that confirm that during DD continuous dark periods oscillations of myrcene and nerolidol continue under free-running conditions, indicates that circadian clock is responsible for volatile terpene rhythmic emission.

Another example of terpenoids rhythmic emission is found in rose flowers. The main terpenes emitted are germacrene D and geranyl acetate. Both compounds oscillate in the same way during the daily cycle with a peak early in the light period. However, expressions of their biosynthetic genes are dramatically different. On the one hand, ALCOHOL ACETYL TRANSFERASE (*RhAAT*), the geranyl acetate biosynthetic gene, maintains rhythmic expression under continuous illumination and/or continuous darkness and the endogenous level of this compound also cycles. This information indicates that the circadian clock regulates geranyl acetate emission. On the other hand, the endogenous level of germacrene D and the expression of its biosynthetic gene, *GERMACRENE D SYNTHASE* (*RhGDS*), are constant throughout the day and oscillations of germacrene D emission stop under LL. This suggests that the mechanism of germacrene D production is light dependent (Hendel-Rahmanim et al. 2007).

Some terpenoids are produced from carotenoid degradation. These compounds are important in floral scent and fruit aroma (Simkin et al. 2004a). Indeed, they are correlated with taste ratings (Vogel et al. 2010). The volatiles, β-ionone, pseudoionone, and geranylacetone, are produced by the *CAROTENOID CLEAVAGE DIOXIGENASE 1* (*CCD1*) in tomato (Simkin et al. 2004a) as well as in Petunia (Simkin et al. 2004b). In Petunia, this gene shows oscillations in normal conditions of day/night cycle. Under DD and LL conditions, transcript levels maintain this rhythm but the decrease in transcript levels and the residual oscillations observed in constant darkness suggest that *PhCCD1* is regulated by both light and circadian mechanisms (Simkin et al. 2004a).

Osmanthus fragrans var. *aurantiacus* is one of the plants emitting the highest diversity of carotenoid-derived scent compounds. In this plant, carotenoid content, volatile emissions, and *Of*CCD1 transcript levels are subjected to rhythmic changes increasing during daylight hours. The two primary carotene products of *Osmanthus* flowers are α- and β-ionone. As in petunia, the β-ionone emission is still increasing when transcript levels begin decreasing during the afternoon. It suggests that there may be some limitation due to the substrate availability. In addition, analysis in *Osmanthus* suggests that volatile emission is light inducible and is controlled by the circadian clock (Baldermann et al. 2010).

Altogether, scent production is controlled in one way or another by the circadian clock. This is true for scent compounds produced from the phenylpropanoid pathway, the nonmevalonate pathway, terpenoids produced from both synthesis and fatty acid degradation. The complexity of scent and the possible points of control at the RNA, protein, and metabolite level make it a challenge worth taking for future studies.

V. ADAPTATION TO BIOTIC AND ABIOTIC STRESS

In spite of our improvements in cultural practices and breeding material, abiotic and biotic stresses represent the major challenge for productivity and in postharvest loss of crops. These two types of stresses have been linked to circadian regulation at different paces and for different reasons. While the evidence of circadian clock relations to pathogen resistance is only recent and is the result of transcriptomic studies, the connection with abiotic stress has been known for a longer period of time and some details are known about how they connect. We describe the work in *Arabidopsis* that has as special feature its natural resistance to cold compared to many horticultural crops such as tomato, cucumber, or cut flowers, just to name a few. Current evidence in horticultural crops is lacking and this is probably one of the fields of work where more profit could be obtained, as some of the pathways are understood with good detail.

A. Pathogen Resistance

Pathogen resistance was thought to be a process dependent on resistance genes but evidence has shown that time of the day and environmental signals also play a role in the way plants react to pathogens. First evidence about a connection between circadian clock and pathogen resistance was obtained in *Arabidopsis* exposed to *Pseudomonas syringae*. These plants showed an upregulation of a transcript, *PCC1*, that displayed a circadian expression pattern in plants treated with $MgCl_2$, suggesting that the upregulation was not totally related to the presence of the bacteria (Sauerbrunn and Schlaich 2004). Furthermore, plants overexpressing *PCC1* are resistant to virulent oomycetes, indicating a potential circadian component in pathogen resistance. A phosphate transporter *PHT4* has been shown to be important for the defense against *P. syringae*, and again this gene is circadian regulated indicating that at least part of the components involved in plant defense are under control of the circadian clock (Wang et al. 2011a).

Among the day signals involved in plant defense light stands as an important cue. Experiments performed in *Arabidopsis* have shown that launching of systemic acquired resistance requires signal transduction of PHYA and PHYB (Griebel and Zeier 2008). Biotrophic pathogens depend, to a large extent, on the plant metabolic status. The main defense strategy against biotrophic pathogens is based on resistance genes or R genes that launch programmed cell death (PCD). Recent analysis of 22 new mutants compromised in resistance against *Hyaloperonospora arabidopsidis* (*Hpa*), an obligate biotrophic oomycete pathogen that causes downy mildew disease, was carried out in *Arabidopsis* (Wang et al. 2011b). Bioinformatic analysis showed that the regulatory region of 14 genes had an enrichment of night elements or CCA1/binding sites, and showed circadian gene expression. This led to the direct testing of resistance in circadian clock gene mutants. Mutants in *CCA1* and *ZTL* had compromised resistance to pathogens whereas overexpressors of *CCA1* showed increased resistance. These results suggest that the circadian clock launches a preventive basal resistance in the absence of pathogens, "anticipating" attack according to a circadian schedule.

Recent work in wheat has shown that effector-triggered susceptibility to necrotic pathogens is under control of a gene *TSN1* with features typical of plant resistance genes (Faris et al. 2010). Attempts to identify changes in gene expression levels failed to give a clear pattern, leading the authors to perform samplings with 3 h intervals. This allowed uncovering a circadian regulation of *TSN1*, indicating that circadian control of at least part of the pathogenesis response is a common feature to higher plants.

The accumulation of evidence suggesting a role of the circadian clock apparatus in controlling plant pathogen resistance data supports a connection between both processes. As a result, experiments in growth chambers should take into account time of the day, light, and temperature as variables that profoundly affect experimental outcomes. Experiments done in naturally illuminated greenhouses or in the field will be under truly natural conditions but timing of infections might also play a role.

The circadian behavior of insects seems to be matched by plants. Recent work has shown that cabbage loopers (*Trichoplusia ni*) have a circadian feeding behavior. When plants are entrained with the rhythm of the insects, they suffer moderate leaf loss compared to those entrained out of phase (Goodspeed et al. 2012). The accumulation of jasmonic acid and salicilate that act in opposite ways also shows opposite phase accumulations, indicating that these two compounds are under circadian regulation. A proper circadian clock seems to be required to launch a proper defense against insect attacks.

B. Cold Sensing and Cold Tolerance

Adaptation of plants to cold or cold acclimation occurs when plants gain tolerance to cold while exposed to chilling (nonfreezing temperatures) for a short period of time. Cold acclimation is thought to occur via orchestrated activation of several parallel transcriptional pathways (Chinnusamy et al. 2006). Although low-temperature receptors are not well understood in plants, there is ample evidence that cold causes changes in gene expression that results in increased cold tolerance.

One conserved mode of cold response is via the activation of the C-*REPEAT BINDING FACTOR* genes or CBFs, also known as *DEHYDRATION* RESPONSIVE ELEMENT *BINDING PROTEINS* or DREBs. The CBF/DREB family of transcription factors contains AP2 DNA-binding domains, a protein domain specific to plants (Okamuro et al. 1997;

Gilmour et al. 1998). Misexpression of *CBFs* in different plants, such as tomato (Hsieh et al. 2004), *Arabidopsis* (Jaglo-Ottosen et al. 1998; Gilmour et al. 2000), *Brassica* (Savitch et al. 2005), tobacco (Gutha and Reddy 2008), grapevine (Tillett et al. 2011), or apples (Wisniewski et al. 2011), causes important increases in cold resistance. Pleiotropic effects accompany this increased resistance, and in the case of apples, it causes modification of flowering time. The decreased growth observed under cold conditions can be mechanistically explained, at least in part, because *CBF* activates GA2 oxidase synthesis that causes a decrease in the levels of active GAs (Achard et al. 2008). The data available show that the CBF transcription factors can activate a cold response in different plants improving cold tolerance.

Daily fluctuations in temperature can be larger than 20°C in many climates and pioneering work showed that activation of cold adaptation occurs when plants sense low temperatures during day but not during the night. The interpretation is that decreases in day temperatures are indicative of seasonal changes, whereas low night temperatures may not. Several independent experiments have shown that the circadian clock gates activation of the CBF pathway. Expression of *CBF* genes is increased if the cold treatment occurs 4 h after dawn compared to 4 h after dusk (Fowler et al. 2005). Experiments performed in *cca1 lhy* double mutants show that *CBF1*, *CBF2*, and *CBF3* are not properly activated by cold, demonstrating a connection of the circadian clock machinery with cold response. Importantly CCA1 and LHY bind directly to the *CBF* locus that comprises three genes, the aforementioned *CBF1*, *CBF2*, and *CBF3*, thus showing that the control is direct (Dong et al. 2011). Thus, the circadian clock would be involved in activation of the CBF regulon. Notably, *cca1,lhy* double mutants are compromised in cold acclimation and show higher death rates than wild type when temperatures drop (Dong et al. 2011).

Expression of *CBF* without activation by cold has been reported also in triple mutants for the morning loop genes *PRR9*, *PRR7*, and *PRR5* (Nakamichi et al. 2009). This line called *d975* (Nakamichi et al. 2005) by the authors displays an extreme late flowering phenotype and can survive at −5°C whereas wild-type plants display complete mortality under the experimental setup of the authors (Nakamichi et al. 2009). The *d975* line displays constitutive expression of *CBF1*, *CBF2*, and *CBF3*, thus explaining the observed resistance to cold, and also to other abiotic stresses including drought and salinity. The interaction between salinity, cold, and drought stress is a general response as abiotic stresses share some components in the signaling process (Seki et al. 2002), and CBF1/DREB1 is one of them (Kasuga et al. 1999).

From a practical perspective, the importance of the current data on circadian regulation stems from two aspects. First, identification of cold resistance cultivars could be the result of loss of function alleles that show recessive or additive segregation. But perhaps, more relevant is the way experiments are performed, for example, in growth chambers rather than in the field. Indeed, the number of genes found to change by cold varied depending on when the cold treatment was given to the plants, showing a higher level when cold was applied during the day (Bieniawska et al. 2008). The fact that cold temperature disrupts the clock in *Arabidopsis* and chestnut (Ramos et al. 2005; Bieniawska et al. 2008; Ibañez et al. 2008) underscores the point and understanding of clock outputs could help us improve crops for this difficult trait.

Although the *CBF/DREB* pathway is understood to some extent, other pathways are responsible for cold acclimation. It was found that mutations in *GI* cause hypersensitivity to cold (Cao et al. 2005), but this resistance did not cause increased levels of *CBF/DREB* expression. This suggests that the circadian clock machinery has several points of interaction with the cold response.

Postharvest management of fruits, vegetables, and flowers is performed under conditions matching the industrial chain (Fernandez-Trujillo et al. 1998; Malacrida et al. 2006; Gomez di Marco et al. 2009). In most cases, fresh fruits, vegetables, and flowers are stored in cold chambers in the dark with temperatures ranging between 2 and 10°C, depending on the availability of the facility. It is interesting to note that experiments performed mimicking industrial conditions failed to find *CBF* activation by cold in tomato fruits (Weiss and Egea-Cortines 2009). These results suggest that under certain circumstances experimental designs geared toward established industrial processes might hamper identification of circadian processes.

VI. SUMMARY AND CONCLUSIONS

The involvement of the circadian clock in so many traits that span development, productivity, and resistance to both biotic and abiotic stresses indicates that it should be taken into account when scientists design experiments. Physiological parameters and genetic studies should be carefully controlled with the following aspects in mind:

1. In terms of horticultural research, proper experimental design should take into account the circadian clock scheme if any of the traits being studied are known to be circadian clock regulated.

Many studies take into account the time of the day during sampling, although, in most cases, the sampling times are too far apart to detect a circadian effect due to the aliasing problem (Table 1.1).

2. We have not covered the mathematical analysis of circadian clock data to be able to uncover differences between samples. This is by no means a trivial aspect that would require a complete review about the topic. Mathematical methods include fast Fourier-transform analysis (Bitter et al. 1973), hierarchical segmentation (Fushing et al. 2009), maximum entropy (Langmead et al. 2002), or nonparametric methods (Hughes et al. 2010); see Refinetti et al. (2007) for a review on procedures. Data handling can become cumbersome if we take samples every 2 h as compared to a sample per day, making imperative an experimental design tailored to pattern identification based on time series analysis.
3. The number of candidate genes influencing a trait should include clock or related genes. This is especially true for flowering time where most natural variation found in trees and cereals seems to fall in this group and not into pure flowering time genes. However, in those cases where candidate gene approaches are carried out, clock genes should be included as part of the analysis.

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