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REVIEW PAPER

Diel patterns of leaf and root growth: endogenous rhythmicity or environmental response?

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Abstract

Plants are sessile organisms forced to adjust to their surrounding environment. In a single plant the photoautotrophic shoot is exposed to pronounced environmental variations recurring in a day–night 24 h (diel) cycle, whereas the heterotrophic root grows in a temporally less fluctuating environment. The contrasting habitats of shoots and roots are reflected in different diel growth patterns and their responsiveness to environmental stimuli. Differences between diel leaf growth patterns of mono- and dicotyledonous plants correspond to their different organization and placement of growth zones. In monocots, heterotrophic growth zones are organized linearly and protected from the environment by sheaths of older leaves. In contrast, photosynthetically active growth zones of dicot leaves are exposed directly to the environment and show characteristic, species-specific diel growth patterns. It is hypothesized that the different exposure to environmental constraints and simultaneously the sink/source status of the growing organs may have induced distinct endogenous control of diel growth patterns in roots and leaves of monocot and dicot plants. Confronted by strong temporal fluctuations in environment, the circadian clock may facilitate robust intrinsic control of leaf growth in dicot plants.

Key words: Carbohydrate, circadian, dicot, diurnal, environment, growth, leaf, monocot, regulation, root.

Introduction

The question of how leaf and root growth are controlled forms the basis of many attempts to generate more successful plants for various purposes and under a range of boundary conditions. In order to achieve this goal, it is crucial to understand the control mechanisms of short-term growth responses on a scale that is relevant to important and/or recurring environmental variations. Furthermore, functional plant modelling, vegetation analysis in the context of global climate change, and modern plant breeding also require an improved understanding of dynamic growth processes, including those observed under day–night 24 h (diel) fluctuations of the environment.

Plant growth is a result of the interplay between environment and physiological processes controlled by endogenous regulatory mechanisms. The environment provides conditions and resources for growth, while the internal regulatory machinery integrates and translates the information coming from various environmental cues and orchestrates the output processes in the form of growth, defence, and reproduction to optimize resource acquisition and utilization, which eventually enhances fitness of the plant (Dodd *et al.*, 2005; Graf *et al.*, 2010; Kerwin *et al.*, 2011). Like most other organisms on Earth, plants use the circadian clock to anticipate daily and seasonal fluctuations in their environments [higher plants (Harmer, 2009), mammalia (Ukai and Ueda, 2010), and algae (Matsuo and Ishiura, 2010)].

Leaves and roots, though part of the same organism, are exposed to completely different environments; the atmosphere and the pedosphere, respectively. These environments

Abbreviations: ABA, abscisic acid; CAB2, CHLOROPHYLL A/B-BINDING PROTEIN 2; CAT3, CATALASE 3; CCA1, CIRACADIAN CLOCK ASSOCIATED 1; CRY, cryptochrome; ELF, early flowering; FKF1, FLAVIN BINDING KELCH F-BOX 1; GI, GIGANTEA; LER, leaf elongation rate; LHY, LATE ELONGATED HYPOCOTYL; LIP1, LIGHT INSENSITIVE PERIOD 1; LKP2, LOV KELCH PROTEIN2; LOV, light, oxygen and voltage; LWD, LIGHT-REGULATED WD; MYB, myeloblast; PHY, phytochrome; PIF, phytochrome-interacting factor; PRR, PSEUDO-RESPONSE REGULATOR; SRR, sensitivity to red light reduced; TCA, tricarboxylic acid; TOC1, TIMING OF CAB 1; XCT, XAP5 CIRCADIAN TIMEKEEPER; ZTL, ZEITLUPE.

differ from each other in chemical composition and physical properties, and have distinct spatial and temporal heterogeneities. The atmosphere is characterized by strong and often predictable diel and seasonal variations in temperature, light intensity, and daylength. Other environmental factors such as wind or air humidity can also affect plant growth (de Langre, 2008), yet these changes are less predictable and do not follow regular cycles. In contrast to the atmosphere, the pedosphere is mainly characterized by spatial heterogeneity. The physicochemical properties of the soil substrate determine the soil capacity for water and mineral retention. Furthermore, soil compactness restrains root expansion (Bengough *et al.*, 2006). Temporal changes in temperature do occur in the pedosphere as well, but they are delayed and dampened in amplitude compared with those in the atmosphere. For example, in a typical diel temperature cycle the atmospheric temperature varies by 16 °C and reaches a maximum at ~14:00 h, whereas soil temperature at 10 cm depth varies by merely 3 °C and reaches a maximum 2 h later at 16:00 h (Walter *et al.*, 2009).

The anatomical differences between leaves of mono- and dicotyledonous plants, especially the position of the growth zone in which cell division and elongation take place, predispose their leaf growth to distinct perception and sensitivity to atmospheric environments (Fig. 1). In dicots the leaf growth zone is more directly exposed to environmental changes, whereas that of monocots is in a more protected microclimate shielded by sheaths of older leaves (Davidson and Milthorpe, 1966). In addition, growing leaf tissue is already engaged in photosynthesis in many dicot species, while growth zones of monocot leaves remain heterotrophic for longer. In 1987, Rozema *et al.* already suggested that differences in diel leaf elongation of halophytic monocotyledonous and dicotyledonous plants are due to differences in the spatial arrangement of tissues and in hydraulic control mechanisms (Rozema *et al.*, 1987). Similar to the monocot leaf, root growth occurs unidirectionally and in root-defined, linearly organized growth zones. Unlike the monocot leaf, however, the root growth zones are exposed more directly to the rhizosphere or pedosphere environment.

In this review, an overview of leaf and root growth patterns in monocot and dicot plants on a diel scale is first given. Then the control of diel growth is discussed, focusing on the effects of external cycles of environmental stimuli (e.g. light and temperature) and the role of the endogenous circadian clock and carbohydrate metabolism.

Diel fluctuations of root growth

The first diel measurements of root elongation rate date back to 1965 (Head, 1965). Time-lapse movies with an interval of 4 h were made for several days to study cherry (*Prunus avium*) root growth. The author reported a diel root elongation rate pattern with the highest growth rate at night and the lowest growth rate during the day. Unfortunately, no comments were made on the environmental conditions of the experiment (daylength, temperature, soil properties, or water availability), making it difficult to interpret these diel root growth patterns.

More recent studies with higher temporal resolutions (minutes instead of hours) revealed that root growth is highly responsive to temporal changes in environmental conditions. Root growth of *Zea mays* and *Nicotiana tabacum* quickly adjusted to new temperature regimes within a few minutes (Walter *et al.*, 2002). In particular, root elongation growth seems to follow alterations in temperature almost linearly within a physiological temperature range between 20 °C and 30 °C (Fig. 1E) (Walter *et al.*, 2002; Hummel *et al.*, 2007). The root elongation rate is also sensitive to changes in nutrient availability (Walter *et al.*, 2003), soil water potential (Sharp *et al.*, 1988), and mechanical impedance of the soil (Bengough *et al.*, 2006) (for a review, see Bengough *et al.*, 2011).

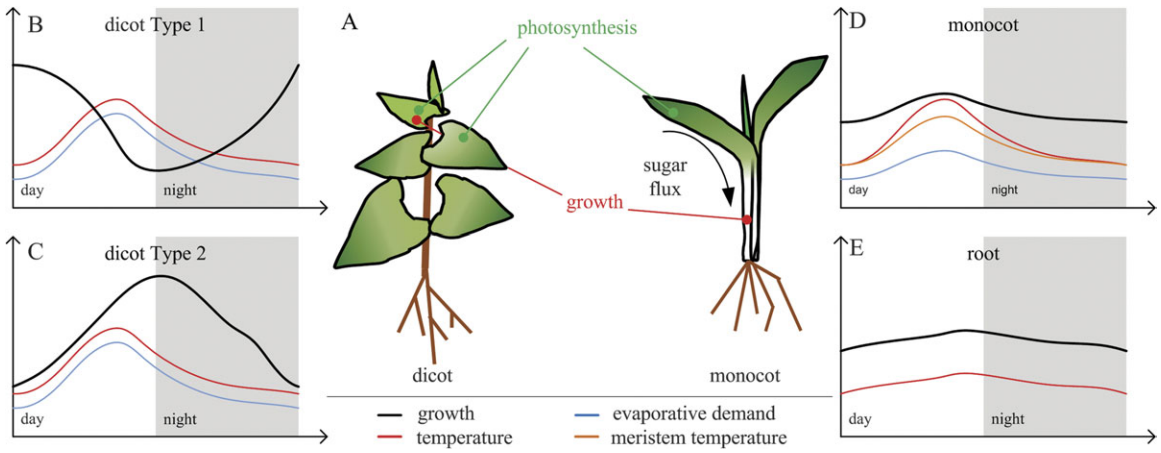

Fig. 1. Plant architecture, prevailing diel variations of environmental factors, and predominant diel leaf growth patterns. Schematic drawings for a characteristic monocot and dicot with the growth zone (red) and photosynthesis zone (green) marked (A). Schematic diel pattern of dicot Type 1 leaf growth (B), dicot Type 2 leaf growth (C), monocot leaf growth (D), and root growth (E) under changing temperature and evaporative demand.

When environmental conditions were kept constant, no change in diel root growth pattern was found in a number of species such as *Arabidopsis thaliana* (Chavarría-Krauser *et al.*, 2008), *Oryza sativa* (Iijima *et al.*, 1998), *Sorghum bicolor* (Iijima *et al.*, 1998), *Z. mays* (Walter *et al.*, 2002, 2003), and *N. tabacum* (Walter and Schurr, 2005; Nagel *et al.*, 2006). These results are consistent with the strong effects of environment on root growth demonstrated under changing conditions as summarized above. Interestingly, marked diel oscillations of root tip growth have been reported recently in *A. thaliana* under constant conditions (Yazdanbakhsh and Fisahn, 2010); a growth maximum was recorded 1 h after dawn, followed by a steep decrease to reach a minimum at dusk and recuperation during the night.

An important difference between the experimental conditions of Yazdanbakhsh and Fisahn (2010) and those of Walter *et al.* (2002, 2005) or Iijima *et al.* (1998) is direct exposure of the entire root system, including the growing root tips, to light–dark cycles in the study by the former. As light is known to inhibit root growth (Pilet and Ney, 1978), the observed oscillation patterns in *Arabidopsis* root growth may be influenced by the inhibitory effect of root illumination (Schmidt and Walter, 2009). Also, complete enclosure of seedlings in a Petri dish—a widely used condition for root growth analysis—can affect growth processes through ethylene emission by leaves (Eliasson and Bollmark, 1988; Hummel *et al.*, 2009).

Diel fluctuations of monocot leaf growth

Leaf elongation in monocots occurs in a defined growth zone at the basal part (Fig. 1A). The pattern of leaf elongation rates follows three phases: (i) exponential elongation rates before leaf appearance; (ii) stable elongation rates; and (iii) progressive decrease of elongation rates until the leaf reaches its final size (Parent *et al.*, 2009). Leaf elongation rates (LERs) in several monocots, such as *Hordeum vulgare*, *Z. mays* and *S. bicolor*, have been shown to be stable and constant for a relatively long period (5–7 d) after the initial exponential growth (Bernstein *et al.*, 1993; Munns *et al.*, 2000; Sadok *et al.*, 2007); one of the reasons for this is the spatial invariance of their elongation zone during this period (Muller *et al.*, 2001). In *O. sativa*, on the other hand, this stable elongation period is very short, if it exists at all, and is followed by a long period of gradual elongation decrease (Parent *et al.*, 2009).

Close analysis of diel growth patterns in monocot leaves has revealed either constant elongation or a slow decrease independent of time of day (Munns *et al.*, 2000; Parent *et al.*, 2009; Poiré *et al.*, 2010*b*). Increasing evidence indicates that there is a strong correlation between the short-term changes of monocot LER and changes in temperature or water potential (Ben-Haj-Salah and Tardieu, 1995; Munns *et al.*, 2000; Sadok *et al.*, 2007; Poiré *et al.*, 2010*b*). Below, the effects of temperature and water relations on LER in monocot plants are highlighted.

Temperature

Nocturnal LER in monocots (*Triticum aestivum*, *Z. mays*, and *O. sativa*) has been shown to follow temperature alterations linearly in a range between 10 °C and 30 °C (Ben-Haj-Salah and Tardieu, 1995; Pietruszka and Lewicka, 2007; Poiré *et al.*, 2010*b*). Variations of LER and temperature coincide almost perfectly throughout the diel cycle when evaporative demand is low (Poiré *et al.*, 2010*b*). Thus, meristem temperature seems to be the dominant factor in controlling the rate of leaf elongation in monocots (Ben-Haj-Salah and Tardieu, 1995) even though plant-internal water relations, evapotranspiration, and alterations of environmental factors can modulate the diel leaf growth cycle. At constant temperature and low evaporative demand, no diel pattern of LER is observed (Parent *et al.*, 2010; Poiré *et al.*, 2010*b*) although transient effects of light–dark transitions may appear (Sadok *et al.*, 2007).

Given the strong correlation with temperature, nocturnal (or diel) monocot LER (at low evaporative demand) can be described on the basis of thermal time (Fig. 1D) (Sadok *et al.*, 2007). The classical concept of 'thermal time' is based on the linearity between the elongation rate and temperature:

$$R = a(T - T_0) \quad (1)$$

where R is the LER over a given time t, T is the temperature, T_0 is the threshold temperature below which the elongation rate is considered to be zero, and a is a constant (Granier and Tardieu, 1998; Bonhomme, 2000). In non-steady state, the formula is:

$$R = a\int_0^t (T - T_0)\mathrm{d}t \quad (2)$$

In other words, the LER is a linear function of the thermal input the leaf receives over a certain time. It is important to notice that this formula can be used only when the relationship between elongation rate and temperature is linear, which holds true within a certain, species-specific temperature range (Bonhomme, 2000). For calculation of development rates in a temperature range extending to extremes, a recent formula (Parent *et al.*, 2010) based on a combination of molecular reaction rates and the reversible inhibition of enzymes (Eyring, 1935; Johnson *et al.*, 1942; Parent *et al.*, 2010) with temperature changes can be considered. Finally, it should also be noted that care has to be taken when applying the thermal time concept for modelling diel leaf expansion rates in dicots as they are correlated with temperature changes to a much smaller extent (Poiré *et al.*, 2010*b*).

Evaporative demand and water deficit

During the day period, evaporation and transpiration of leaf water can also affect LER. The LER has been shown to decrease with increasing evaporative demand (Munns *et al.*, 2000; Reymond *et al.*, 2003). Moreover, diurnal changes in LER are closely related to the transpiration rate and proportional to changes in evaporative demand even in the

absence of a soil water deficit (Acevedo *et al.*, 1979; Ben-Haj-Salah and Tardieu, 1996, 1997; Sadok *et al.*, 2007). Hence, LER can be described as by Sadok *et al.* (2007):

$$\mathrm{LER} = e\,(1 - \mathrm{d}J_{\mathrm{w}}) \quad (3)$$

where J_{w} is the transpiration rate per unit leaf area and e is the slope of the relationship between LER and temperature.

Likewise, decreased water potential in the growing tissue due to diminished root water conductivity and the resulting increase in xylem tension can reduce LER during the afternoon (Tang and Boyer, 2008). The effects of soil water deficit on LER (in the absence of evaporative demand) have been shown to be proportional to pre-dawn water potential (Chenu *et al.*, 2008).

The plant hormone abscisic acid (ABA) plays an important role in plant responses to water deficit (Bray, 1997). It has been proposed that ABA has three main effects on growth: (i) increasing the water conductance in the plant; (ii) buffering the negative effect of evaporative demand and related day–night alteration of LER; and (iii) a modest influence on non-hydraulic effects (Tardieu *et al.*, 2010).

Diel dicot leaf growth patterns

In many dicot species, expanding cells of growing leaves are photosynthetically active (Stessman *et al.*, 2002). Because gas exchange and growth processes take place in one and the same tissue, pronounced diel fluctuations of carbohydrate and water availability accompany growth processes of dicot leaves. Leaf veins of dicot plants are often arranged in a net-like structure, and leaf lamina expand in both width and length with specific genetic control (Tsukaya, 2006). Moreover, considerable cell division still occurs in elongating parts (Beemster *et al.*, 2005). All of these make the situation more complex for dicot leaves than for monocot leaves.

A base–tip gradient in growth is often observed, with a maximum relative expansion rate at the base and a minimum at the tip region of the growing leaf (Schnyder and Nelson, 1988; Durand *et al.*, 1995; Tardieu *et al.*, 2000). This gradient is coordinated by earlier maturation of the tip part of the lamina compared with the basal part, and it decreases with time (Schmundt *et al.*, 1998; Donnelly *et al.*, 1999; Walter and Schurr, 2005). In *N. tabacum*, for example, there is an ~4 d delay in maturation over the gradient (Walter and Schurr, 1999). However, this base–tip growth gradient is not a general feature of all dicot species. Species such as *Glycine max*, *Populus deltoids*, and *Theobroma cacao* show a homogenous growth distribution over the entire leaf (Ainsworth *et al.*, 2005; Walter and Schurr, 2005; Matsubara *et al.*, 2006; Czech *et al.*, 2009).

On a diel time scale, the rates of leaf expansion in dicot plants do not follow temperature and other environmental variations in the same way as observed in leaves of monocot plants. In *Helianthus annuus* (Boyer, 1968) and *Acer pseudoplatanus* (Taylor and Davies, 1985), maximal leaf growth rates were reported at night, in *Phaseolus vulgaris* (Davies and Van Volkenburgh, 1983) and *Vitis vinifera* (Shackel *et al.*, 1987) maximal growth was reported during the day, and in *Solanum lycopersicum* the highest growth rates were found at the day–night transition (Price *et al.*, 2001). Nevertheless, as the leaf expands, temperature, evaporative demand, and water deficit are factors that can influence the amplitude of the observed pattern, but the pattern itself remains stable (Poiré *et al.*, 2010*a*; Pantin *et al.*, 2011).

In previous studies, dicot leaf growth was mostly analysed by using linear variable displacement transducers that measure leaf elongation along the midvein, not taking expansion in width into account. Moreover, many earlier studies distinguished only between diurnal and nocturnal leaf growth by recording leaf dimensions at the beginning of the day and night, respectively. Time-lapse imaging-based methods became available about a decade ago to enable analysis of two-dimensional expansion dynamics in different dicot plants under a range of environmental conditions (Schmundt *et al.*, 1998). For all species investigated so far, growing leaves exhibit repetitive diel leaf growth patterns without clear correlation to the diel atmospheric temperature regime (for a review of these analyses, see Walter *et al.*, 2009). The observed diel leaf growth patterns can be categorized into two main types called Type 1 and Type 2 (Fig. 1B, C) (Walter *et al.*, 2009). External environmental parameters, such as temperature and light intensity, can influence the amplitude but not the basic character of the observed pattern (Poiré *et al.*, 2010*b*). Type 1 plants, such as *N. tabacum* (Walter and Schurr, 2005) and *A. thaliana* (Wiese *et al.*, 2007), show a sinusoidal growth pattern with maximal growth rates around dawn and directly after onset of light (Wiese *et al.*, 2007). The diel growth pattern of Type 2 plants, such as *G. max* (Ainsworth *et al.*, 2005), *P. deltoides* (Matsubara *et al.*, 2006), and *T. cacao* (Czech *et al.*, 2009), is also sinusoidal but has a maximum at the end of the day. These three Type 2 plants have a homogenous growth distribution over the entire leaf. However, *Populus trichocarpa*, another Type 2 plant, shows a base–tip growth gradient across the lamina (SM, unpublished data), indicating that the formation of spatial and temporal (diel) growth patterns is not necessarily coupled. The contribution of different growth processes (cell division and expansion) cannot explain variations in diel leaf growth patterns either; the specific diel growth patterns, albeit with decreasing amplitude, are maintained over the base–tip gradient of *Arabidopsis* leaves (Wiese *et al.*, 2007) and during transition from the predominantly cell division to cell expansion phase in growing leaves of *T. cacao* (Czech *et al.*, 2009).

The origin of the different diel growth strategies of dicot plants is yet to be elucidated. Nevertheless, a study comparing the behaviour of several dicot and monocot species on transfer from day–night conditions to continuous light conditions has indicated that the circadian clock is an important driver of the observed, repetitive diel growth patterns in leaves of dicot species (Poiré *et al.*, 2010*b*). Whereas an ~24 h leaf growth rhythm continued in dicot plants after transfer to constant light and temperature regimes, the same treatment caused diel leaf growth variations to vanish in monocot species. In addition to these findings,

the presence of the Type 1 growth pattern in isolated leaf discs floating on nutrient solution without any contact with the sink–source system of the intact plant (Biskup *et al.*, 2009) clearly indicates that the circadian clock within the growing leaf itself plays an important role in regulation of the diel dicot leaf growth pattern. For *A. thaliana*, the diel pattern of hypocotyl elongation growth is also controlled by the circadian clock (Nozue *et al.*, 2007); there, the observed Type 1-like growth pattern depends on the diel cycling of phytochrome-interacting factor 4 (PIF4) and PIF5.

Diel control of growth

The Earth's rotation brings all organisms into changing but reccurring environmental conditions. Therefore, living organisms adjust their physiology and behaviour with the help of internal oscillators called the 'circadian clock' to anticipate these recurring events. For autotrophic plants, there is the need to fine-tune their photosynthesis, carbohydrate metabolism, and carbohydrate storage during the entire diel cycle (Lu *et al.*, 2005; Gibon *et al.*, 2009; Graf *et al.*, 2010). As described above, leaf growth of monocot and dicot plants as well as growth of other plant organs follows different diel rhythms requiring an adapted rhythmic control. Diel gene expression of *Arabidopsis* is largely controlled by the circadian clock as well as by the diel changes in carbohydrates (Bläsing *et al.*, 2005). The effects of light, nitrogen, and leaf water deficit show a smaller impact on the diel expression of genes in *Arabidopsis* rosettes (Bläsing *et al.*, 2005). The diel control by the circadian clock, carbohydrates, and their impact on growth will be discussed in the following sections.

Components and function of the circadian clock

The vast majority of recent molecular findings on the function of the circadian clock in plants have involved analyses of *Arabidopsis* shoots (James *et al.*, 2008). The dicot leaf rosette of *Arabidopsis* needs to regulate the complexity of its metabolic constraints and environmental cues by tightly controlling the timing of many processes (Green *et al.*, 2002; Dodd *et al.*, 2005; Covington and Harmer, 2007). Hence, it is no surprise that leaf growth of dicot plants, the result of the integration of many metabolic pathways, is controlled to a strong extent by the circadian clock (Fig. 2). The clock is involved in many physiological events such as flowering time (Yanovsky and Kay, 2003; Imaizumi and Kay, 2006), elongation growth of the hypocotyl (Dowson-Day and Millar, 1999; Nozue *et al.*, 2007) and stomatal responses (Gorton *et al.*, 1993), auxin signalling and responses (Covington and Harmer, 2007), and starch degradation during the night (Graf *et al.*, 2010), and it also plays a role in plant defence (Kerwin *et al.*, 2011). A matching of the oscillation period of the circadian clock with daily rhythms in environmental changes is therefore essential and gives a fitness advantage to the plant (Green *et al.*, 2002; Michael *et al.*, 2003*b*; Dodd *et al.*, 2005; Yerushalmi *et al.*, 2011). In future studies, it will be important to reveal the temporal dynamics of how different elements of the circadian clock are controlling certain phases of the diel leaf growth cycle.

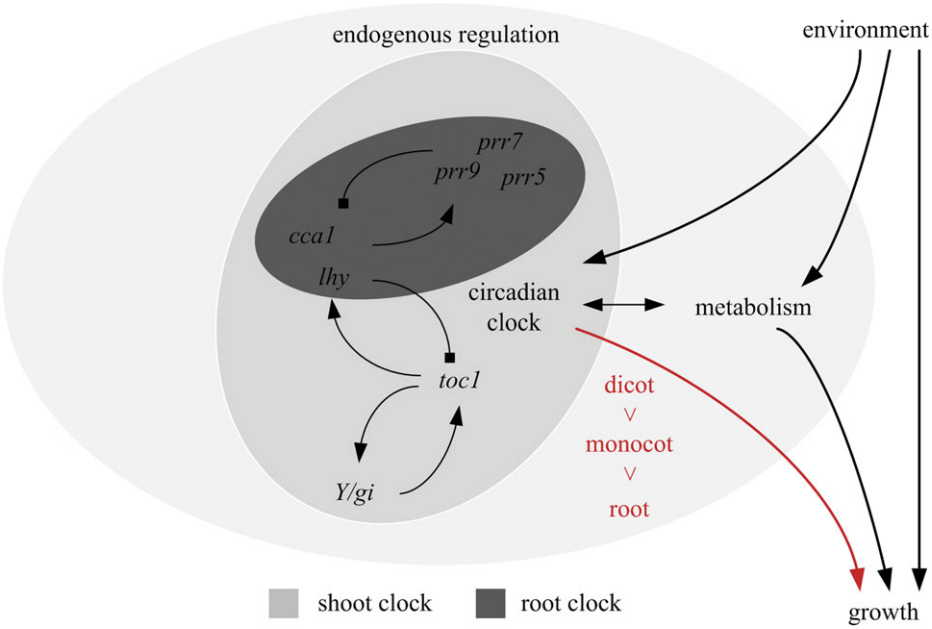

Fig. 2. Schematic drawing of endogenous regulation and environmental control of diel leaf and root growth patterns, interacting with the circadian clock and plant metabolism. The circadian clock comprises three feedback loops. The core oscillator consists of early morning genes, *CCA1* and *LHY*, which inhibit expression of *TOC1*, an evening gene. *TOC1* expression will lead to up-regulated *CCA1* and *LHY* gene expression by the early morning. In the 'morning' loop, the *PRR* genes and *CCA1/LHY* form a negative feedback loop. The 'evening' loop consists of *TOC1* and an unknown component *Y* which reciprocally regulate each other. The root clock consists only of one actively oscillating morning loop. Clock oscillation influences growth to a greater extent in the dicot leaf than in the monocot leaf and in roots.

The circadian clock runs with a period close to 24 h even in the absence of environmental triggers, can be reset by environmental cues (e.g. light or temperature), and is temperature compensated. The oscillator is truly endogenous as rhythmicity is observed in etiolated seedlings that have never been exposed to changing environmental conditions (Salomé *et al.*, 2008). The circadian clock is an endogenous control network consisting of transcriptional–translational feedback loops (Fig. 2). The core of the central loop consists of three components: CCA1 (CIRCADIAN CLOCK ASSOCIATED 1), LHY (LATE ELONGATED HYPOCOTYL), and TOC1 (TIMING OF CAB EXPRESSION1) (Wang and Tobin, 1998; Alabadí *et al.*, 2001). *CCA1* and *LHY* are dawn-phased genes that inhibit the expression of the evening-phased gene *TOC1* by binding directly to the *TOC1* promoter (Alabadí *et al.*, 2001; Mizoguchi *et al.*, 2002). *TOC1*, in turn, reciprocally regulates the expression of *CCA1* and *LHY* transcripts to form a feedback loop (Alabadí *et al.*, 2001; Makino *et al.*, 2002). The 'morning' loop is formed by the repressor activity of the PSEUDO-RESPONSE REGULATOR 9 (PRR), PRR7, and PRR5 on promoters of their activators *CCA1* and *LHY* (Farré *et al.*, 2005; Nakamichi *et al.*, 2010). Lastly the 'evening' loop consists of *TOC1* and an unknown component *Y* which reciprocally regulate each other (Locke *et al.*, 2005; Zeilinger *et al.*, 2006).

The components of the circadian oscillator are tissue specific (Thain *et al.*, 2002; James *et al.*, 2008). Roots, for instance, have a simplified version of the circadian clock consisting solely of a functional morning loop (James *et al.*, 2008). The evening genes, although expressed, do not oscillate and—in general—a smaller number of genes shows diel gene expression in the root compared with genes expressed in the shoot (James *et al.*, 2008). Also in shielded developing maize ears, diel gene expression is strongly reduced compared with the photosynthetically active leaf, where the expression of oscillator genes of all loops shows strongly reduced amplitudes (Hayes *et al.*, 2010). Homologues for most of the genes of the central oscillator are found in other species, both monocot (*Lemna gibba*, *Lemna paucicostata*, *O. sativa*, and *Z. mays*) and dicot (*G. max*, *Ipomoea nil*, and *S. lycopersicum*) (Izawa *et al.*, 2003; Miwa *et al.*, 2006; Hayama *et al.*, 2007; Murakami *et al.*, 2007; Facella *et al.*, 2008; Serikawa *et al.*, 2008; Hayes *et al.*, 2010; Hudson, 2010). This suggests that the fundamental elements of the circadian clock seem to be conserved in monocots and dicots. However, differences in amplitude, phase, and contribution to oscillation were found between species (Miwa *et al.*, 2006; Hayama *et al.*, 2007; Serikawa *et al.*, 2008; Hayes *et al.*, 2010), and it is unclear which clock elements are active in which tissues of the shoot systems. These results suggest that the precise role for some clock genes has diverged in angiosperm evolution (for detailed reviews on the circadian clock, see Harmer, 2009; McClung and Gutierrez, 2010; Pruneda-Paz and Kay, 2010).

Entrainment by the environment: light and temperature

Plants synchronize their clock by signal inputs from the environmental cycles in light and temperature. The red and blue light photoreceptors, phytochromes (PHYs) and cryptochromes (CRYs), respectively, mediate parts of the light signal input into the clock (Somers *et al.*, 1998). The interactions between the PHY/CRY signalling pathways are synergistic and depend on light quality as well as fluence rate (Casal and Mazzella, 1998). Even though light signalling via PHYs and CRYs is important for normal clock function, these pathways are not essential for clock function and can be compensated by other input signals (Yanovsky *et al.*, 2000).

ZEITLUPE (ZTL) and two ZTL homologues, FLAVIN BINDING KELCH F-BOX 1 (FKF1) and LOV KELCH PROTEIN2 (LKP2), act as photoreceptors by a photochemically active LOV domain to regulate *TOC1* expression in the evening part of the oscillator (Mas *et al.*, 2003; Kim *et al.*, 2007; Sawa *et al.*, 2007). Furthermore, *LWD1/2* (Wu *et al.*, 2008), *SRR1* (Staiger *et al.*, 2003), *LIP1* (Kevei *et al.*, 2007), *XCT* (Martin-Tryon and Harmer, 2008), *ELF3* (McWatters *et al.*, 2000), and *ELF4* (Kikis *et al.*, 2005) all affect light input into the oscillator, suggesting a complex regulation of input signalling by light.

The circadian clock is temperature compensated; this compensation is established by a dynamic balancing of morning components (*LHY*/*CCA1*) versus evening components (*TOC1*/*GI*) (Gould *et al.*, 2006; Portoles and Mas, 2010). Nonetheless, temperature cycles are sufficient to keep the oscillator running (Salomé and McClung, 2005; Thines and Harmon, 2010). Moreover, temperature cycles alone can drive at least half of all transcripts critical for synchronizing internal processes, such as cell cycle and protein synthesis (Michael *et al.*, 2008). The genes involved in temperature compensation, together with the other clock genes *ELF3*, *PRR9*, and *PRR7*, are known components of temperature input into the oscillator (Salomé and McClung, 2005; Thines and Harmon, 2010). Different loops of the oscillator appear to have different temperature sensitivity, as two output signals, CAT3 and CAB2 expression, have differential temperature sensitivity (Michael *et al.*, 2003*a*).

The circadian oscillator takes inputs at several time points during the diel cycle to assess the environment and to regulate output accordingly (Sawa *et al.*, 2007). The importance of light and temperature signalling integrated into the clock, in contrast to their direct effect on growth, depends on the dominance of the circadian clock on the organ and plant species. Hence, to derive the exact connection between circadian clock elements and the timing of leaf growth processes, a precise understanding of the role of the above-mentioned elements will be required. This may eventually contribute to clarification of differences between Type 1 and Type 2 species as well as to understanding the variable fine-tuning of diel leaf growth patterns in different species in response to environmental variations.

Clock-induced growth regulation

So far, the regulation of growth by the circadian clock has been best investigated for *Arabidopsis* hypocotyl elongation growth (Dowson-Day and Millar, 1999; Nozue *et al.*, 2007). In short-day conditions, hypocotyl elongation rates were found to be rhythmic and to peak shortly after dawn (Nozue *et al.*, 2007). However, in continuous light, the maximum elongation rate was shifted to the subjective night (Dowson-Day and Millar, 1999; Nozue *et al.*, 2007). Normal expression of the diel hypocotyl growth pattern seems to require light input and circadian regulation, which serves to time the transcript and protein abundance of two positive hypocotyl growth regulators, PIF4 and PIF5, at the end of the night (Nozue *et al.*, 2007). Recently the molecular basis of the circadian gating in hypocotyl growth has been unravelled. The circadian evening component ELF3 forms a complex with ELF4 and LUX (LUX ARRHYTHMO), two other clock components; then LUX targets the entire complex to the PIF4 and PIF5 promoter by directly binding to it (Nusinow *et al.*, 2011). All three components have been shown to be required for the proper expression of PIF4 and PIF5 (Nusinow *et al.*, 2011). Since dicot leaf growth in continuous light shows rhythmicity as the hypocotyl does (Poiré *et al.*, 2010*b*), a similar control pattern of growth timing can be hypothesized.

The special role of carbohydrates in growth control

Carbohydrates are required for growth as building blocks to produce, for example, cell wall polymers, and as energy carriers to drive growth activities. To control the availability and quality of carbohydrates, plants and other organisms evolved a complex signalling system that allows the integration of carbohydrates as signalling molecules into the control of gene expression, metabolism, growth, and development (Rolland *et al.*, 2006; Smeekens *et al.*, 2010). Carbohydrates are the product of photosynthesis during the day, and a defined fraction of them is stored as starch. This fraction provides a nocturnal supply to source and sink cells, and its degradation is adjusted to the expected night period (Gibon *et al.*, 2004; Lu *et al.*, 2005; Graf *et al.*, 2010). The availability and efficient degradation of this starch reservoir is required for nocturnal growth, as can be concluded from the negative correlation of biomass and the remaining starch reservoir at dawn (Cross *et al.*, 2006). Diurnal growth on the other hand is limited by carbohydrate storage during photosynthesis, as suggested by the negative correlation of shoot biomass to starch content at dusk (Sulpice *et al.*, 2009; Graf and Smith, 2011). Also, starch degradation, but not starch synthesis, was shown to correlate strongly and positively with the relative growth rate of *Arabidopsis* in varying daylengths (Gibon *et al.*, 2009). Therefore, carbohydrate metabolism plays a very important role in the control of leaf growth. In later stages of leaf development, leaf growth is not only restricted by the metabolic component. The hydraulic status of the leaf then becomes an even more limiting factor (Pantin *et al.*, 2011). It would exceed the scope of this review to elaborate putative control mechanisms of the hydraulic status of leaf growth such as the interaction of turgor with yielding of the expanding cell wall, stiffening of cell walls by components such as lignin, the activity of transmembrane proteins such as aquaporins, the generation of reactive oxygen species, or the generation of hydraulic gradients within the leaf by varying xylem element sizes. All of these dynamically altering regulatory mechanisms could potentially interact with the circadian clock. As one example of dynamic metabolic input into growth, carbohydrate metabolism is highlighted here.

Leaves of intact plants, excised leaf discs, and roots of *Arabidopsis* starch deficiency mutants do not grow or grow very slowly during the night due to a lack of available carbohydrates (Gibon *et al.*, 2004; Wiese *et al.*, 2007; Biskup *et al.*, 2009; Yazdanbakhsh *et al.*, 2011). Instead, in such mutants, a leaf growth increase at the end of the day correlates with an excess of soluble carbohydrates. The carbohydrate status apparently has a direct impact on the amplitude of the observed pattern, while still retaining the general phasing of the leaf growth cycle comparable with that of wild-type plants (Wiese *et al.*, 2007). Overall the starch metabolism acts as an integrator of the metabolic response in a regulatory network that balances growth with the carbon supply (Sulpice *et al.*, 2009; Graf *et al.*, 2010; Graf and Smith, 2011). Furthermore, many sugar-responsive genes show marked diel expression changes and sugar levels have a profound impact on diel gene regulation (Bläsing *et al.*, 2005).

The diel carbohydrate status of the dicot plant has a huge effect on the observed growth pattern of leaves and roots (Gibon *et al.*, 2004; Nagel *et al.*, 2006; Wiese *et al.*, 2007; Yazdanbakhsh *et al.*, 2011). Similarly, carbohydrate availability is an important driving force in the basal zone of monocot leaf growth (Davidson and Milthorpe, 1966; Schnyder and Nelson, 1987). The completely shielded growth zone of the monocot leaf is heterotrophic and provided with photosynthates from the already fully differentiated tip part of the leaf (Allard and Nelson, 1991), and is also supported by surrounding fully expanded leaves (Brégard and Allard, 1999). Thus, in monocot leaves, photosynthesis is spatially clearly separated from the growth zone (Fig. 1), comparable with the situation in roots. The diel export of carbohydrates from the distal, source part of a young maize leaf correlates positively with LER (Kalt-Torres and Huber, 1987). Yet the diversity in monocot carbohydrate storage forms (fructans, sucrose, and starch) and cellular compartmentalization of storage carbohydrates leads to a very complex situation there that is far from being elucidated.

In roots, carbohydrate availability strongly regulates dynamic growth activity (Aguirrezabal *et al.*, 1994; Freixes *et al.*, 2002). Even a change of light intensity—an environmental parameter to which the shoot is exposed—affects root growth via carbohydrate availability within <1 h (Nagel *et al.*, 2006), demonstrating the important role of carbohydrates in short-term whole-plant growth control.

Interaction of carbohydrates and the clock—a link between resource utilization and integration of environmental changes

In *Z. mays*, 10% of the transcriptome is under direct circadian regulation, and in *A. thaliana* this number even reaches ~30% (Covington *et al.*, 2008; Khan *et al.*, 2010). When different conditions are taken into account, the total sum of transcripts that can show diel rhythmicity is estimated to be close to 90% (Michael *et al.*, 2008). Many clock-controlled genes are modulated in a diurnal/nocturnal regime concomitant with the changing carbohydrate metabolism (Bläsing *et al.*, 2005), and sucrose modulates the clock oscillation in amplitude and phase in *Arabidopsis* shoot and root tissue (Dalchau *et al.*, 2011). The observed difference of clock oscillation or clock output in developing ears of *Z. mays* and also in seeds of *G. max* (Hudson, 2010) compared with leaves might be caused by the sugar-importing sink status of these organs (Hayes *et al.*, 2010). A significant proportion of genes under circadian regulation are involved in metabolism or hormone signalling in plants (Michael *et al.*, 2008; Khan *et al.*, 2010). The circadian clock influences plant metabolism and hormone signalling including auxin gating, the tricarboxylic acid (TCA) cycle, and carbohydrate metabolism and storage (Lu *et al.*, 2005; Covington and Harmer, 2007; Fukushima *et al.*, 2009; Graf *et al.*, 2010). Increased starch accumulation has been shown for mono- and dicotyledonous plants lacking the oscillator gene *GI* (Eimert *et al.*, 1995; Izawa *et al.*, 2011).

The circadian clock ensures carbohydrate availability throughout the night (Graf *et al.*, 2010), exerting an indirect control of the nocturnal growth potential (Graf and Smith, 2011). Therefore, carbohydrate flux to or accumulation in sink organs is a crucial mediator and modulator of clock oscillations and might be key to the mechanistic understanding of the interaction between the circadian clock and growth processes.

Interaction of root and shoot growth

Roots and leaves live in completely different settings and have adapted to these in unique ways. Diel growth patterns often differ between above- and belowground organs. However these organs are integral parts of a single plant system and they are highly dependent on each other for growth and survival. Optimal resource use efficiency demands highly coordinated fluxes of carbohydrates, water, and mineral nutrients that are acquired by one organ and delivered to the other. Hence, organ growth patterns that have evolved under certain environmental constraints can be considered to reflect the optimal reaction pattern with which an organ can grow in its environmental context. How this optimized resource use efficiency is realized with respect to shoot–root signalling is outside the scope of this review. Clearly the signalling between shoot and root growth is modulated by phytohormones (Sharp and LeNoble, 2002; Ghanem *et al.*, 2011). In addition, carbohydrate- and water-related effects of dynamic organ growth control are known to be linked to shoot–root signalling (Nagel *et al.*, 2006). The diminished transport of water by cooled roots, for example, has been shown to diminish diurnal but not nocturnal leaf growth (Poiré *et al.*, 2010*a*). A photosynthesis signal, possibly sucrose or a derivative, is proposed to synchronize the circadian oscillators of shoot and root (James *et al.*, 2008). Furthermore, expression of genes coding for transport of water, ions, metabolic solutes such as sucrose, micronutrients, and signalling molecules, including Ca^{2+}, shows diel rhythmicity and might contribute to the control of fluxes between root and shoot, optimizing the overall plant performance (Haydon *et al.*, 2011).

Conclusions

Monocots and dicots, as well as different plant organs, cope in different ways with their surrounding environment, and this is reflected in the growth patterns (Fig. 1). Differing organ and plant architectures conceivably contribute to the evolution of differing growth strategies. Through the course of evolution, the leaves of dicots started adjusting their growth to a greater extent to the circadian clock to avoid growth at unfavourable times during the diel cycle as the growth zone is vulnerably exposed to strong fluctuations in the environment. In contrast, the monocot leaf growth zone and root growth zones are less exposed to environmental fluctuations in the diel cycle and probably therefore do not require such a stringent diel control by the circadian clock. Thereby they invested more in the optimization of their growth performance to direct environmental conditions (Fig. 2).

Interestingly, the growing dicot leaf can sustain a lot of its growth activities from its own photosynthesis, whereas the heterotrophic monocot growth zone and the root growth zones are true sink tissues. The intensity of the sink strength of these organs might be another reason as to why monocot leaf growth and root growth are less responsive to the circadian clock: Circadian gene expression might simply be overridden by the high flux of imported carbohydrates or by more intense metabolic feedback loops there.

References

Acevedo E, Fereres E, Hsiao TC, Henderson DW. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. *Plant Physiology* **64,** 476–480.

Aguirrezabal LAN, Deleens E, Tardieu F. 1994. Root elongation rate is accounted for by intercepted PPFD and source–sink relations in field and laboratory-grown sunflower. *Plant, Cell and Environment* **17,** 443–450.

Ainsworth EA, Walter A, Schurr U. 2005. Glycine max leaflets lack a base–tip gradient in growth rate. *Journal of Plant Research* **118,** 343–346.

Alabadí D, Oyama T, Yanovsky MJ, Harmon FG, Más P, Kay SA. 2001. Reciprocal regulation between TOC1 and LHY/CCA1 within the arabidopsis circadian clock. *Science* **293,** 880–883.

Allard G, Nelson CJ. 1991. Photosynthate partitioning in basal zones of tall fescue leaf blades. *Plant Physiology* **95,** 663–668.

Beemster GTS, De Veylder L, Vercruysse S, West G, Rombaut D, Van Hummelen P, Galichet A, Gruissem W, Inze D, Vuylsteke M. 2005. Genome-wide analysis of gene expression profiles associated with cell cycle transitions in growing organs of Arabidopsis. *Plant Physiology* **138,** 734–743.

Ben-Haj-Salah H, Tardieu F. 1995. Temperature affects expansion rate of maize leaves without change in spatial-distribution of cell length. Analysis of the coordination between cell-division and cell expansion. *Plant Physiology* **109,** 861–870.

Ben-Haj-Salah H, Tardieu F. 1996. Quantitative analysis of the combined effects of temperature, evaporative demand and light on leaf elongation rate in well-watered field and laboratory-grown maize plants. *Journal of Experimental Botany* **47,** 1689–1698.

Ben-Haj-Salah H, Tardieu F. 1997. Control of leaf expansion rate of droughted maize plants under fluctuating evaporative demand. A superposition of hydraulic and chemical messages? *Plant Physiology* **114,** 893–900.

Bengough AG, Bransby MF, Hans J, McKenna SJ, Roberts TJ, Valentine TA. 2006. Root responses to soil physical conditions; growth dynamics from field to cell. *Journal of Experimental Botany* **57,** 437–447.

Bengough AG, McKenzie BM, Hallett PD, Valentine TA. 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany* **62,** 59–68.

Bernstein N, Silk WK, Lauchli A. 1993. Growth and development of sorghum leaves under conditions of NaCl stress—spatial and temporal aspects of leaf growth-inhibition. *Planta* **191,** 433–439.

Biskup B, Scharr H, Fischbach A, Wiese-Klinkenberg A, Schurr U, Walter A. 2009. Diel growth cycle of isolated leaf discs analyzed with a novel, high-throughput three-dimensional imaging method is identical to that of intact leaves. *Plant Physiology* **149,** 1452–1461.

Bläsing OE, Gibon Y, Gunther M, Hohne M, Morcuende R, Osuna D, Thimm O, Usadel B, Scheible WR, Stitt M. 2005. Sugars and circadian regulation make major contributions to the global regulation of diurnal gene expression in Arabidopsis. *The Plant Cell* **17,** 3257–3281.

Bonhomme R. 2000. Bases and limits to using 'degree.day' units. *European Journal of Agronomy* **13,** 1–10.

Boyer JS. 1968. Relationship of water potential to growth of leaves. *Plant Physiology* **43,** 1056–1062.

Bray EA. 1997. Plant responses to water deficit. *Trends in Plant Science* **2,** 48–54.

Brégard A, Allard G. 1999. Sink to source transition in developing leaf blades of tall fescue. *New Phytologist* **141,** 45–50.

Casal JJ, Mazzella MA. 1998. Conditional synergism between cryptochrome 1 and phytochrome B is shown by the analysis of phyA, phyB, and hy4 simple, double, and triple mutants in Arabidopsis. *Plant Physiology* **118,** 19–25.

Chavarría-Krauser A, Nagel KA, Palme K, Schurr U, Walter A, Scharr H. 2008. Spatio-temporal quantification of differential growth processes in root growth zones based on a novel combination of image sequence processing and refined concepts describing curvature production. *New Phytologist* **177,** 811–821.

Chenu K, Chapman SC, Hammer GL, Mclean G, Salah HBH, Tardieu F. 2008. Short-term responses of leaf growth rate to water deficit scale up to whole-plant and crop levels: an integrated modelling approach in maize. *Plant, Cell and Environment* **31,** 378–391.

Covington MF, Harmer SL. 2007. The circadian clock regulates auxin signaling and responses in Arabidopsis. *PLoS Biology* **5,** e222.

Covington MF, Maloof JN, Straume M, Kay SA, Harmer SL. 2008. Global transcriptome analysis reveals circadian regulation of key pathways in plant growth and development. *Genome Biology* **9,** R130.

Cross JM, von Korff M, Altmann T, Bartzetko L, Sulpice R, Gibon Y, Palacios N, Stitt M. 2006. Variation of enzyme activities and metabolite levels in 24 arabidopsis accessions growing in carbon-limited conditions. *Plant Physiology* **142,** 1574–1588.

Czech AS, Strzalka K, Schurr U, Matsubara S. 2009. Developmental stages of delayed-greening leaves inferred from measurements of chlorophyll content and leaf growth. *Functional Plant Biology* **36,** 654–664.

Dalchau N, Baek SJ, Briggs HM, *et al*. 2011. The circadian oscillator gene GIGANTEA mediates a long-term response of the Arabidopsis thaliana circadian clock to sucrose. *Proceedings of the National Academy of Sciences, USA* **108,** 5104–5109.

Davidson JL, Milthorpe FL. 1966. Leaf growth in Dactylis glomerata following defoliation. *Annals of Botany* **30,** 173–184.

Davies WJ, Van Volkenburgh E. 1983. The influence of water deficit on the factors controlling the daily pattern of growth of Phaseolus trifoliates. *Journal of Experimental Botany* **34,** 987–999.

de Langre E. 2008. Effects of wind on plants. *Annual Review of Fluid Mechanics* **40,** 141–168.

Dodd AN, Salathia N, Hall A, Kevei E, Toth R, Nagy F, Hibberd JM, Millar AJ, Webb AA. 2005. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Science* **309,** 630–633.

Donnelly PM, Bonetta D, Tsukaya H, Dengler RE, Dengler NG. 1999. Cell cycling and cell enlargement in developing leaves of Arabidopsis. *Developmental Biology* **215,** 407–419.

Dowson-Day MJ, Millar AJ. 1999. Circadian dysfunction causes aberrant hypocotyl elongation patterns in Arabidopsis. *The Plant Journal* **17,** 63–71.

Durand J-L, Onillon B, Schnyder H, Rademacher I. 1995. Drought effects on cellular and spatial parameters of leaf growth in tall fescue. *Journal of Experimental Botany* **46,** 1147–1155.

Eimert K, Wang SM, Lue WI, Chen J. 1995. Monogenic recessive mutations causing both late floral initiation and excess starch accumulation in Arabidopsis. *The Plant Cell* **7,** 1703–1712.

Eliasson L, Bollmark M. 1988. Ethylene as a possible mediator of light-induced inhibition of root growth. *Physiologia Plantarum* **72,** 605–609.

Eyring H. 1935. The activated complex in chemical reactions. *Journal of Chemical Physics* **3,** 107–115.

Facella P, Lopez L, Carbone F, Galbraith DW, Giuliano G, Perrotta G. 2008. Diurnal and circadian rhythms in the tomato transcriptome and their modulation by cryptochrome photoreceptors. *PLoS One* **3,** e2798.

Farré EM, Harmer SL, Harmon FG, Yanovsky MJ, Kay SA. 2005. Overlapping and distinct roles of PRR7 and PRR9 in the Arabidopsis circadian clock. *Current Biology* **15,** 47–54.

Freixes S, Thibaud MC, Tardieu F, Muller B. 2002. Root elongation and branching is related to local hexose concentration in Arabidopsis thaliana seedlings. *Plant, Cell and Environment* **25,** 1357–1366.

Fukushima A, Kusano M, Nakamichi N, Kobayashi M, Hayashi N, Sakakibara H, Takeshi M, Saito K. 2009. Impact of clock-associated Arabidopsis pseudo-response regulators in metabolic coordination. *Proceedings of the National Academy of Sciences, USA* **106,** 7251–7256.

Ghanem ME, Albacete A, Smigocki AC, *et al*. 2011. Root-synthesized cytokinins improve shoot growth and fruit yield in salinized tomato (Solanum lycopersicum L.) plants. *Journal of Experimental Botany* **62,** 125–140.

Gibon Y, Blasing OE, Palacios-Rojas N, Pankovic D, Hendriks JHM, Fisahn J, Hohne M, Gunther M, Stitt M. 2004. Adjustment of diurnal starch turnover to short days: depletion of sugar during the night leads to a temporary inhibition of carbohydrate utilization, accumulation of sugars and post-translational activation of ADP-glucose pyrophosphorylase in the following light period. *The Plant Journal* **40,** 332–332.

Gibon Y, Pyl ET, Sulpice R, Lunn JE, Hohne M, Gunther M, Stitt M. 2009. Adjustment of growth, starch turnover, protein content and central metabolism to a decrease of the carbon supply when Arabidopsis is grown in very short photoperiods. *Plant, Cell and Environment* **32,** 859–874.

Gorton HL, Williams WE, Assmann SM. 1993. Circadian rhythms in stomatal responsiveness to red and blue light. *Plant Physiology* **103,** 399–406.

Gould PD, Locke JCW, Larue C, *et al*. 2006. The molecular basis of temperature compensation in the Arabidopsis circadian clock. *The Plant Cell* **18,** 1177–1187.

Graf A, Schlereth A, Stitt M, Smith AM. 2010. Circadian control of carbohydrate availability for growth in Arabidopsis plants at night. *Proceedings of the National Academy of Sciences, USA* **107,** 9458–9463.

Graf A, Smith AM. 2011. Starch and the clock: the dark side of plant productivity. *Trends in Plant Science* **16,** 169–175.

Granier C, Tardieu F. 1998. Is thermal time adequate for expressing the effects of temperature on sunflower leaf development? *Plant, Cell and Environment* **21,** 695–703.

Green RM, Tingay S, Wang ZY, Tobin EM. 2002. Circadian rhythms confer a higher level of fitness to Arabidopsis plants. *Plant Physiology* **129,** 576–584.

Harmer SL. 2009. The circadian system in higher plants. *Annual Review of Plant Biology* **60,** 357–377.

Hayama R, Agashe B, Luley E, King R, Coupland G. 2007. A circadian rhythm set by dusk determines the expression of FT homologs and the short-day photoperiodic flowering response in Pharbitis. *The Plant Cell* **19,** 2988–3000.

Haydon MJ, Bell LJ, Webb AAR. 2011. Interactions between plant circadian clocks and solute transport. *Journal of Experimental Botany* **62,** 2333–2348.

Hayes KR, Beatty M, Meng X, Simmons CR, Habben JE, Danilevskaya ON. 2010. Maize global transcriptomics reveals pervasive leaf diurnal rhythms but rhythms in developing ears are largely limited to the core oscillator. *PLoS One* **5,** e12887.

Head GC. 1965. Studies of diurnal changes in cherry root growth and nutational movements of apple root tips by time-lapse cinematography. *Annals of Botany* **29,** 219–224.

Hudson KA. 2010. The circadian clock-controlled transcriptome of developing soybean seeds. *Plant Genome* **3,** 11.

Hummel GM, Naumann M, Schurr U, Walter A. 2007. Root growth dynamics of Nicotiana attenuata seedlings are affected by simulated herbivore attack. *Plant, Cell and Environment* **30,** 1326–1336.

Hummel GM, Schurr U, Baldwin IT, Walter A. 2009. Herbivore-induced jasmonic acid bursts in leaves of Nicotiana attenuata mediate short-term reductions in root growth. *Plant, Cell and Environment* **32,** 134–143.

Iijima M, Oribe Y, Horibe Y, Kono Y. 1998. Time lapse analysis of root elongation rates of rice and sorghum during the day and night. *Annals of Botany* **81,** 603–607.

Imaizumi T, Kay SA. 2006. Photoperiodic control of flowering: not only by coincidence. *Trends in Plant Science* **11,** 550–558.

Izawa T, Mihara M, Suzuki Y, *et al*. 2011. Os-GIGANTEA confers robust diurnal rhythms on the global transcriptome of rice in the field. *The Plant Cell* **5,** 1741–1755.

Izawa T, Takahashi Y, Yano M. 2003. Comparative biology comes into bloom: genomic and genetic comparison of flowering pathways in rice and Arabidopsis. *Current Opinion in Plant Biology* **6,** 113–120.

James AB, Monreal JA, Nimmo GA, Kelly CL, Herzyk P, Jenkins GI, Nimmo HG. 2008. The circadian clock in Arabidopsis roots is a simplified slave version of the clock in shoots. *Science* **322,** 1832–1835.

Johnson FH, Eyring H, Williams RW. 1942. The nature of enzyme inhibitions in bacterial luminescence. Sulfanilamide, urethane, temperature and pressure. *Journal of Cellular and Comparative Physiology* **20,** 247–268.

Kalt-Torres W, Huber SC. 1987. Diurnal changes in maize leaf photosynthesis. 3. Leaf elongation rate in relation to carbohydrates and activities of sucrose metabolizing enzymes in elongating leaf tissue. *Plant Physiology* **83,** 294–298.

Kerwin RE, Jimenez-Gomez JM, Fulop D, Harmer SL, Maloof JN, Kliebenstein DJ. 2011. Network quantitative trait loci mapping of circadian clock outputs identifies metabolic pathway-to-clock linkages in Arabidopsis. *The Plant Cell* **23,** 471–485.

Kevei É, Gyula P, Fehér B, *et al*. 2007. Arabidopsis thaliana circadian clock is regulated by the small GTPase LIP1. *Current Biology* **17,** 1456–1464.

Khan S, Rowe SC, Harmon FG. 2010. Coordination of the maize transcriptome by a conserved circadian clock. *BMC Plant Biology* **10,** 126.

Kikis EA, Khanna R, Quail PH. 2005. ELF4 is a phytochrome-regulated component of a negative feedback loop involving the central oscillator components CCA1 and LHY. *The Plant Journal* **44,** 300–313.

Kim WY, Fujiwara S, Suh SS, Kim J, Kim Y, Han LQ, David K, Putterill J, Nam HG, Somers DE. 2007. ZEITLUPE is a circadian photoreceptor stabilized by GIGANTEA in blue light. *Nature* **449,** 356–360.

Locke JCW, Millar AJ, Turner MS. 2005. Modelling genetic networks with noisy and varied experimental data: the circadian clock in Arabidopsis thaliana. *Journal of Theoretical Biology* **234,** 383–393.

Lu Y, Gehan JP, Sharkey TD. 2005. Daylength and circadian effects on starch degradation and maltose metabolism. *Plant Physiology* **138,** 2280–2291.

Makino S, Matsushika A, Kojima M, Yamashino T, Mizuno T. 2002. The APRR1/TOC1 quintet implicated in circadian rhythms of Arabidopsis thaliana: I. Characterization with APRR1-overexpressing plants. *Plant and Cell Physiology* **43,** 58–69.

Martin-Tryon EL, Harmer SL. 2008. XAP5 CIRCADIAN TIMEKEEPER coordinates light signals for proper timing of photomorphogenesis and the circadian clock in Arabidopsis. *The Plant Cell* **20,** 1244–1259.

Mas P, Kim WY, Somers DE, Kay SA. 2003. Targeted degradation of TOC1 by ZTL modulates circadian function in Arabidopsis thaliana. *Nature* **426,** 567–570.

Matsubara S, Hurry V, Druart N, Benedict C, Janzik I, Chavarria-Krauser A, Walter A, Schurr U. 2006. Nocturnal changes in leaf growth of Populus deltoides are controlled by cytoplasmic growth. *Planta* **223,** 1315–1328.

Matsuo T, Ishiura M. 2010. New insights into the circadian clock in Chlamydomonas. *International Review of Cell and Molecular Biology* **280,** 281–314.

McClung CR, Gutierrez RA. 2010. Network news: prime time for systems biology of the plant circadian clock. *Current Opinion in Genetics and Development* **20,** 588–598.

McWatters HG, Bastow RM, Hall A, Millar AJ. 2000. The ELF3 zeitnehmer regulates light signalling to the circadian clock. *Nature* **408,** 716–720.

Michael TP, Mockler TC, Breton G, *et al*. 2008. Network discovery pipeline elucidates conserved time-of-day-specific cis-regulatory modules. *PLoS Genetics* **4,** e14.

Michael TP, Salomé PA, McClung CR. 2003*a*. Two Arabidopsis circadian oscillators can be distinguished by differential temperature sensitivity. *Proceedings of the National Academy of Sciences, USA* **100,** 6878–6883.

Michael TP, Salomé PA, Yu HJ, Spencer TR, Sharp EL, McPeek MA, Alonso JM, Ecker JR, McClung CR. 2003*b*. Enhanced fitness conferred by naturally occurring variation in the circadian clock. *Science* **302,** 1049–1053.

Miwa K, Serikawa M, Suzuki S, Kondo T, Oyama T. 2006. Conserved expression profiles of circadian clock-related genes in two Lemna species showing long-day and short-day photoperiodic flowering responses. *Plant and Cell Physiology* **47,** 601–612.

Mizoguchi T, Wheatley K, Hanzawa Y, Wright L, Mizoguchi M, Song H-R, Carré IA, Coupland G. 2002. LHY and CCA1 are partially redundant genes required to maintain circadian rhythms in Arabidopsis. *Developmental Cell* **2,** 629–641.

Muller B, Reymond M, Tardieu F. 2001. The elongation rate at the base of a maize leaf shows an invariant pattern during both the steady-state elongation and the establishment of the elongation zone. *Journal of Experimental Botany* **52,** 1259–1268.

Munns R, Passioura JB, Guo JM, Chazen O, Cramer GR. 2000. Water relations and leaf expansion: importance of time scale. *Journal of Experimental Botany* **51,** 1495–1504.

Murakami M, Tago Y, Yamashino T, Mizuno T. 2007. Characterization of the rice circadian clock-associated pseudo-response regulators in Arabidopsis thaliana. *Bioscience, Biotechnology, and Biochemistry* **71,** 1107–1110.

Nagel KA, Schurr U, Walter A. 2006. Dynamics of root growth stimulation in Nicotiana tabacum in increasing light intensity. *Plant, Cell and Environment* **29,** 1936–1945.

Nakamichi N, Kiba T, Henriques R, Mizuno T, Chua NH, Sakakibara H. 2010. PSEUDO-RESPONSE REGULATORS 9, 7, and 5 are transcriptional repressors in the Arabidopsis circadian clock. *The Plant Cell* **22,** 594–605.

Nozue K, Covington MF, Duek PD, Lorrain S, Fankhauser C, Harmer SL, Maloof JN. 2007. Rhythmic growth explained by coincidence between internal and external cues. *Nature* **448,** 358–361.

Nusinow DA, Helfer A, Hamilton EE, King JJ, Imaizumi T, Schultz TF, Farre EM, Kay SA. 2011. The ELF4–ELF3–LUX complex links the circadian clock to diurnal control of hypocotyl growth. *Nature* **475,** 398–402.

Pantin F, Simonneau T, Rolland G, Dauzat M, Muller B. 2011. Control of leaf expansion: a developmental switch from metabolics to hydraulics. *Plant Physiology* **156,** 803–815.

Parent B, Conejero G, Tardieu F. 2009. Spatial and temporal analysis of non-steady elongation of rice leaves. *Plant, Cell and Environment* **32,** 1561–1572.

Parent B, Turc O, Gibon Y, Stitt M, Tardieu F. 2010. Modelling temperature-compensated physiological rates, based on the co-ordination of responses to temperature of developmental processes. *Journal of Experimental Botany* **61,** 2057–2069.

Pietruszka M, Lewicka S. 2007. Effect of temperature on plant elongation and cell wall extensibility. *General Physiology and Biophysics* **26,** 40–47.

Pilet PE, Ney D. 1978. Rapid, localized light effect on root-growth in maize. *Planta* **144,** 109–110.

Poiré R, Schneider H, Thorpe MR, Kuhn AJ, Schurr U, Walter A. 2010*a*. Root cooling strongly affects diel leaf growth dynamics, water and carbohydrate relations in Ricinus communis. *Plant, Cell and Environment* **33,** 408–417.

Poiré R, Wiese-Klinkenberg A, Parent B, Mielewczik M, Schurr U, Tardieu F, Walter A. 2010*b*. Diel time-courses of leaf growth in monocot and dicot species: endogenous rhythms and temperature effects. *Journal of Experimental Botany* **61,** 1751–1759.

Portoles S, Mas P. 2010. The functional interplay between protein kinase CK(2) and CCA1 transcriptional activity is essential for clock

temperature compensation in Arabidopsis. *PLoS Genetics* **6,** e1001201.

Price LE, Bacon MA, Young PC, Davies WJ. 2001. High-resolution analysis of tomato leaf elongation: the application of novel time-series analysis techniques. *Journal of Experimental Botany* **52,** 1925–1932.

Pruneda-Paz JL, Kay SA. 2010. An expanding universe of circadian networks in higher plants. *Trends in Plant Science* **15,** 259–265.

Reymond M, Muller B, Leonardi A, Charcosset A, Tardieu F. 2003. Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit. *Plant Physiology* **131,** 664–675.

Rolland F, Baena-Gonzalez E, Sheen J. 2006. Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annual Review of Plant Biology* **57,** 675–709.

Rozema J, Arp W, Diggelen JV, Kok E, Letschert J. 1987. An ecophysiological comparison of measurements of the diurnal rhythm of the leaf elongation and changes of the leaf thickness of salt-resistant Dicotyledonae and Monocotyledonae. *Journal of Experimental Botany* **38,** 442–453.

Sadok W, Naudin P, Boussuge B, Muller B, Welcker C, Tardieu F. 2007. Leaf growth rate per unit thermal time follows QTL-dependent daily patterns in hundreds of maize lines under naturally fluctuating conditions. *Plant, Cell and Environment* **30,** 135–146.

Salomé PA, McClung CR. 2005. PSEUDO-RESPONSE REGULATOR 7 and 9 are partially redundant genes essential for the temperature responsiveness of the Arabidopsis circadian clock. *The Plant Cell* **17,** 791–803.

Salomé PA, Xie Q, McClung CR. 2008. Circadian timekeeping during early Arabidopsis development. *Plant Physiology* **147,** 1110–1125.

Sawa M, Nusinow DA, Kay SA, Imaizumi T. 2007. FKF1 and GIGANTEA complex formation is required for day-length measurement in Arabidopsis. *Science* **318,** 261–265.

Schmidt M, Walter A. 2009. Root growth is affected differently by mechanical wounding in seedlings of the ecological model species Nicotiana attenuata and the molecular model species Arabidopsis thaliana. *Plant Signaling and Behavior* **5,** 290–292.

Schmundt D, Stitt M, Jahne B, Schurr U. 1998. Quantitative analysis of the local rates of growth of dicot leaves at a high temporal and spatial resolution, using image sequence analysis. *The Plant Journal* **16,** 505–514.

Schnyder H, Nelson CJ. 1987. Growth-rates and carbohydrate fluxes within the elongation zone of tall fescue leaf blades. *Plant Physiology* **85,** 548–553.

Schnyder H, Nelson CJ. 1988. Diurnal growth of tall fescue leaf blades: I. Spatial distribution of growth, deposition of water, and assimilate import in the elongation zone. *Plant Physiology* **86,** 1070–1076.

Serikawa M, Miwa K, Kondo T, Oyama T. 2008. Functional conservation of clock-related genes in flowering plants: overexpression and RNA interference analyses of the circadian rhythm in the monocotyledon Lemna gibba. *Plant Physiology* **146,** 1952–1963.

Shackel KA, Matthews MA, Morrison JC. 1987. Dynamic relation between expansion and cellular turgor in growing grape (Vitis vinifera L.) leaves. *Plant Physiology* **84,** 1166–1171.

Sharp RE, LeNoble ME. 2002. ABA, ethylene and the control of shoot and root growth under water stress. *Journal of Experimental Botany* **53,** 33–37.

Sharp RE, Silk WK, Hsiao TC. 1988. Growth of the maize primary root at low water potentials. 1. Spatial-distribution of expansive growth. *Plant Physiology* **87,** 50–57.

Smeekens S, Ma JK, Hanson J, Rolland F. 2010. Sugar signals and molecular networks controlling plant growth. *Current Opinion in Plant Biology* **13,** 274–279.

Somers DE, Devlin PF, Kay SA. 1998. Phytochromes and cryptochromes in the entrainment of the Arabidopsis circadian clock. *Science* **282,** 1488–1490.

Staiger D, Allenbach L, Salathia N, Fiechter V, Davis SJ, Millar AJ, Chory J, Fankhauser C. 2003. The Arabidopsis SRR1 gene mediates phyB signaling and is required for normal circadian clock function. *Genes and Development* **17,** 256–268.

Stessman D, Miller A, Spalding M, Rodermel S. 2002. Regulation of photosynthesis during Arabidopsis leaf development in continuous light. *Photosynthesis Research* **72,** 27–37.

Sulpice R, Pyl ET, Ishihara H, *et al*. 2009. Starch as a major integrator in the regulation of plant growth. *Proceedings of the National Academy of Sciences, USA* **106,** 10348–10353.

Tang AC, Boyer JS. 2008. Xylem tension affects growth-induced water potential and daily elongation of maize leaves. *Journal of Experimental Botany* **59,** 753–764.

Tardieu F, Parent B, Simonneau T. 2010. Control of leaf growth by abscisic acid: hydraulic or non-hydraulic processes? *Plant, Cell and Environment* **33,** 636–647.

Tardieu F, Reymond M, Hamard P, Granier C, Muller B. 2000. Spatial distributions of expansion rate, cell division rate and cell size in maize leaves: a synthesis of the effects of soil water status, evaporative demand and temperature. *Journal of Experimental Botany* **51,** 1505–1514.

Taylor G, Davies WJ. 1985. The control of leaf growth of Betula and Acer by photoenvironment. *New Phytologist* **101,** 259–268.

Thain SC, Murtas G, Lynn JR, McGrath RB, Millar AJ. 2002. The circadian clock that controls gene expression in Arabidopsis is tissue specific. *Plant Physiology* **130,** 102–110.

Thines B, Harmon FG. 2010. Ambient temperature response establishes ELF3 as a required component of the core Arabidopsis circadian clock. *Proceedings of the National Academy of Sciences, USA* **107,** 3257–3262.

Tsukaya H. 2006. Mechanism of leaf-shape determination. *Annual Review of Plant Biology* **57,** 477–496.

Ukai H, Ueda HR. 2010. Systems biology of mammalian circadian clocks. *Annual Review of Physiology* **72,** 579–603.

Walter A, Feil R, Schurr U. 2003. Expansion dynamics, metabolite composition and substance transfer of the primary root growth zone of Zea mays L. grown in different external nutrient availabilities. *Plant, Cell and Environment* **26,** 1451–1466.

Walter A, Schurr U. 1999. The modular character of growth in Nicotiana tabacum plants under steady-state nutrition. *Journal of Experimental Botany* **50,** 1169–1177.

Walter A, Schurr U. 2005. Dynamics of leaf and root growth: endogenous control versus environmental impact. *Annals of Botany* **95,** 891–900.

Walter A, Silk WK, Schurr U. 2009. Environmental effects on spatial and temporal patterns of leaf and root growth. *Annual Review of Plant Biology* **60,** 279–304.

Walter A, Spies H, Terjung S, Kusters R, Kirchgessner N, Schurr U. 2002. Spatio-temporal dynamics of expansion growth in roots: automatic quantification of diurnal course and temperature response by digital image sequence processing. *Journal of Experimental Botany* **53,** 689–698.

Wang Z-Y, Tobin EM. 1998. Constitutive expression of the CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) gene disrupts circadian rhythms and suppresses its own expression. *Cell* **93,** 1207–1217.

Wiese A, Christ MM, Virnich O, Schurr U, Walter A. 2007. Spatio-temporal leaf growth patterns of Arabidopsis thaliana and evidence for sugar control of the diel leaf growth cycle. *New Phytologist* **174,** 752–761.

Wu SH, Wu JF, Wang Y. 2008. Two new clock proteins, LWD1 and LWD2, regulate Arabidopsis photoperiodic flowering. *Plant Physiology* **148,** 948–959.

Yanovsky MJ, Kay SA. 2003. Living by the calendar: how plants know when to flower. *Nature Reviews Molecular Cell Biology* **4,** 265–276.

Yanovsky MJ, Mazzella MA, Casal JJ. 2000. A quadruple photoreceptor mutant still keeps track of time. *Current Biology* **10,** 1013–1015.

Yazdanbakhsh N, Fisahn J. 2010. Analysis of Arabidopsis thaliana root growth kinetics with high temporal and spatial resolution. *Annals of Botany* **105,** 783–791.

Yazdanbakhsh N, Sulpice R, Graf A, Stitt M, Fisahn J. 2011. Circadian control of root elongation and C partitioning in Arabidopsis thaliana. *Plant, Cell and Environment* **34,** 877–894.

Yerushalmi S, Yakir E, Green RM. 2011. Circadian clocks and adaptation in Arabidopsis. *Molecular Ecology* **20,** 1155–1165.

Zeilinger MN, Farré EM, Taylor SR, Kay SA, Doyle FJ. 2006. A novel computational model of the circadian clock in Arabidopsis that incorporates PRR7 and PRR9. *Molecular Systems Biology* **2,** 58.