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Time to grow: circadian regulation of growth and metabolism in photosynthetic organisms

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Circadian clocks are molecular devices that help adjust organisms to periodic environmental changes. Although formally described as self-sustaining oscillators that are synchronized by external cues and produce defined outputs, it is increasingly clear that physiological processes not only are regulated by, but also regulate the function of the clock. We discuss three recent examples of the intimate relationships between the function of the clock, growth and metabolism in photosynthetic organisms: the daily tracking of sun by sunflowers, the fine computations plants and cyanobacteria perform to manage carbon reserves and prevent starvation, and the changes in clock parameters that went along with domestication of tomato.

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Introduction

The course of Earth around its axis and around the sun exposes the surface of the planet to repetitive changes in light quality and quantity, temperature and water availability. The whole of the biosphere responds with rhythms in biological activity driven, in many organisms, by a molecular pacemaker called the circadian clock. The clock is entrained by environmental signals, yet is able to synchronize physiological and behavioural processes in the absence of external stimuli. Circadian clocks are built upon a group of proteins that are sequentially expressed in response to a setting condition, and mutually control their abundance and activity through transcriptional, translational and post-translational effects generating self-sustained periods of nearly 24 hours. This gear controls the expression of a significant portion of the genomes, allowing organisms to anticipate daily changes and to gauge the agreement between the predicted internal state and the actual environment [1]. Although external cues act as informative inputs, the ability to respond to a same stimulus varies according to the state of the oscillator, a phenomenon called 'gating'; inversely, internal signals reflecting the metabolic or developmental status impinge on the pulse of the oscillators.

In photosynthetic organisms, most physiological and developmental processes are associated with light:dark cycles. An impressive corpus of studies has delineated the plant circadian system as a quite complex genetic regulatory network based fundamentally on sequential, negative feedback loops. We refer to some recent revisions that describe the circuitry of the plant central oscillator [2–4]. Whereas many of the initial findings on clock-related processes stemmed from studies on defective seasonal reckoning in the form of flowering-time mutants, it is increasingly clear that the internal clock controls multitude of developmental processes along the life of plants. We summarize recent findings that exemplify the intimate relationships between the function of the clock, metabolism and growth.

Never doubt that the sun doth move

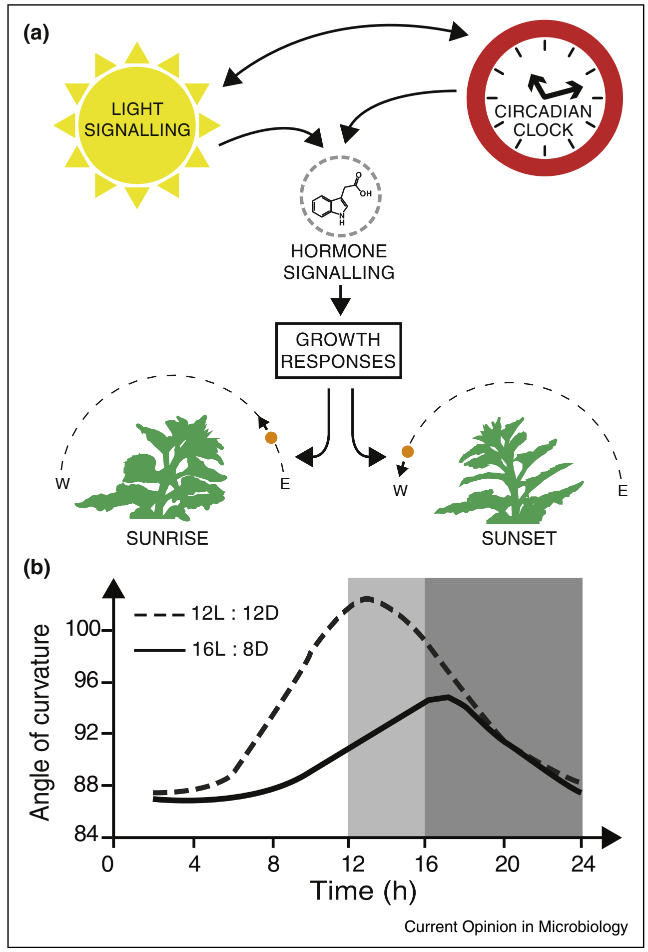
The daily folding of leaflets in legumes was probably the first attested rhythmic process in plants. Theophrastus (IVC BC) refers to the tamarind and its 'sleeping' leaves [5]; more than 2000 years later, Darwin's list of plants with sleep movements included many legumes [6]. However, these movements do not reflect irreversible growth but reversible changes of turgor in specialized cells [7]. In contrast, daily solar tracking (heliotropism) by sunflower (*Helianthus annuus*) apices is intimately associated with unidirectional growth, to the point that tracking movements cease as growth comes to an end when the inflorescences mature. Young sunflower apices point east in the morning, track westward sun movements during the day and regain an eastward orientation during the night. This behaviour depends on a directionally changing light source, but an internal time-keeping mechanism has been long suspected [8,9].

A recent report [10••] convincingly shows that the clock is involved in this behaviour. Solar tracking persists in constant conditions with a period of approximately 24 hours and is severely impaired when plants entrained in 24-hour cycles are transferred to extended day lengths, both hallmarks of clock-driven mechanisms. Heliotropism is caused by alternating growth patterns of both sides of the stems: the eastern side elongates during the day, whereas the western side elongates at night. Stems of sunflower plants under a fixed light source elongate only at night at about the same timing and rate as the western side, suggesting that the diurnal eastern growth is a specialized feature driven by an environmental stimulus but also muted by the clock at night. The expression of clock-related genes is the same in both sides of the stems, but homologs of auxin induced genes involved in phototropic responses in *Arabidopsis thaliana* are differentially expressed; this swaying growth pattern thus depends on an alternating hormonal input or sensitivity, probably driven by the clock (Figure 1a).

Differential growth appears to have several adaptive consequences. Interference with the plant's ability to track the sun leads to lower biomass production [10••], possibly because heliotropism reduces internal shading and may therefore optimize overall photosynthetic efficiency [8]. Also, mature inflorescences facing east heat up more rapidly in the morning, which makes them more appealing for pollinators and probably keeps them drier, preventing the attack of fungi and accelerating the maturation of seeds. However, mature apices are no longer heliotropic. Do young apices track the sun as a precondition to orient mature inflorescences eastwards, instead of using a (clock-gated) phototropic response that makes them face the rising sun?

In field-grown plants under different photoperiods the rate of stem curvature seems to depend on day length (Figure 1b). Given an apparently constant nighttime reorientation rate, this appears to be necessary to return on time to the initial position at dawn. In other words, sunflower apices appear to be able to compute day length and adjust growth rates to precisely reset their orientation according to the presumed time to sunrise. Although seasonal changes in growth patterns may be accounted for by several environmental factors (such as water availability, to which solar tracking in sunflowers is sensitive [8], or differences in light angle and fluence), this behaviour seems to be an aspect of a fundamental property of the clock: to keep track of the length of the day to fine tune the rates of physiological processes. In the next section we discuss two examples of this feature.

Figure 1



Sun tracking by sunflowers as a concerted interplay between the environment and the clock. **(a)** Differential growth of the east and west sides of the stems during the day and night is driven by environmental cues and the clock. **(b)** Daily deflection (in angles) of developing apices in field-grown sunflowers in fall (12 hours light:12 hours darkness, dotted line) and summer (16 hours light:8 hours darkness, full line). In both cases, organ position is precisely reset before dawn. Adapted from data reported by [10••].

Hoy comamos y bebamos … que mañana ayunaremos[2]

Growth of photosynthetic organisms relies ultimately on carbon fixed in the light. Management of reserves is of paramount importance, since short spells of carbon depletion lead to growth inhibition [11,12]. Plants deploy thrifty strategies to prevent starvation during predictable light:dark cycles and when faced to stochastic changes in light supply. Plants linearly accumulate starch during the day and use it up almost completely during the night until dawn. Strikingly, plants are able to immediately reduce the rate of starch degradation when exposed to an early dusk, but exhaust their lot before time in face of a belated dawn [13,14] (Figure 2a). The internal timer thus keeps a record of the expected time until dawn and adjusts metabolic rates accordingly. In fact, mutants with shortened clock periods consume their reserves before dawn when exposed to 24-hour cycles, showing that the internal time, not the external conditions, sets the pace of starch metabolism [14]. Probably as a consequence of this

[2] 'Let's eat and drink today… for tomorrow we shall fast', Juan del Enzina (1468–1529), Cancionero de Palacio.