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Energy as a seasonal signal for growth and reproduction

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Abstract

Plants measure photoperiod as a predictable signal for seasonal change. Recently, new connections between photoperiod measuring systems and metabolism in plants have been revealed. These studies explore historical observations of metabolism and photoperiod with modern tools and approaches, suggesting there is much more to learn about photoperiodism in plants.

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Plants, Photperiod, Metabolism, Circadian clock, Flowering.

Introduction

Planetary obliquity causes predictable changes in the durations of night and day during the year. This results in seasonal changes in the environment for most places on Earth. Many organisms have biological measuring systems to calculate day or night length and coordinate developmental, cellular, and biochemical functions with the proper season. The so-called “true” photoperiod measuring mechanisms allow organisms to calculate the number of hours of light or dark irrespective of the intensity of light within a range [1]. These mechanisms control incredible and orchestrated seasonal phenomena, such as butterfly migration and autumn leaf fall, but also lie at the heart of human disease syndromes such as seasonal affective disorder [2,3].

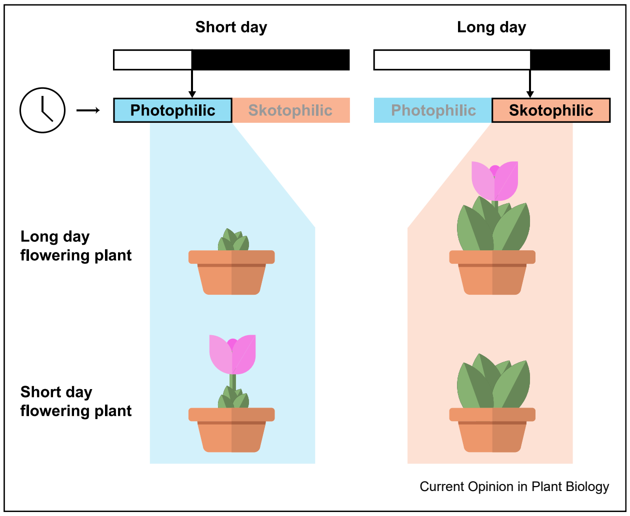
Plants are a vanguard model system for photoperiodism research due to the stunning, and easily observable, phenomenon of photoperiod-controlled flowering. The arrival of ‘electrohorticulture’ in the late 1800s, prompted by the invention of incandescent lamps, allowed scientists to control day length and directly test the effects on flowering time in the absence of other seasonal changes. Of important note are Garner and Allard, early pioneers in photoperiod research credited with formalizing the study of biological responses to day length and who coined the terms ‘photoperiod’ and ‘photoperiodism’ while grouping plants into the photoperiodic classifications for flowering time that we recognize today.

Over the last century, studies of photoperiodic flowering inspired hypotheses for how an organism can count day or night lengths and helped establish a set of ‘guidelines’ for what constitutes a photoperiod measuring system. One particularly important researcher, Erwin Bünning, used studies of flowering time to develop the idea that plants can count day or night length with a simple coincidence detection system (Figure 1) [4–6]. He theorized that the plant would exist in one of two biological ‘states’ in a 24-h day, naming these photophilic (light loving) and skotophilic (dark loving) states. In the first part of the day, the plant is in the photophilic state, and in the second half of the day the plant is in the skotophilic state. Bünning postulated that the photophilic and skotophilic states were controlled by the circadian clock, although hourglass-like timers have also been implicated in photoperiod measuring systems in plants and animals. Depending on the season, dusk either falls in the photophilic or skotophilic state, giving rise to two different developmental outcomes (i.e. long day plants flower when dusk falls in the latter half of the day, or skotophilic state). Combined, the system was termed ‘external coincidence’ because it incorporates an environmental rhythm (photoperiod) with an endogenous rhythm (a circadian clock controlled process).

The advent of molecular genetics in Arabidopsis crystallized the external coincidence model when it was discovered that the CONSTANS/FLOWERING LOCUS T (CO/FT) module is critical for photoperiodic measurement in plant seasonal flowering [7,8]. Briefly, in Arabidopsis accumulation of *CO* mRNA is controlled by the circadian clock and phased to the latter half of a 24-h day. This defines the photophilic (*CO* mRNA is low) and skotophilic (*CO* mRNA is high) states. Light acts to stabilize the CO protein, thus when dusk occurs in the skotophilic state when *CO* mRNA is high, the CO protein accumulates and triggers the expression of *FT*, the tissue-mobile florigen (Figure 2). Subsequently, many labs have expanded on the components that make up this system, as can be found in recent reviews on the subject [9,10].

In addition to flowering, researchers have identified additional processes that are controlled by photoperiod. Some of these include specialized metabolite production, growth, hypocotyl elongation, seed germination, sexual dimorphism, asexual reproduction, leaf fall, tuberization, bud formation, and a host of other physiological and developmental phenomena. Interestingly, these photoperiod-regulated processes can be induced independently of photoperiodic flowering, suggesting, and in some cases showing, that other photoperiod measuring or sensing systems exist in plants [11,12]. Recently, advances in our understanding of the connection between photoperiod and plant metabolism has put intense focus on the role of starch in daily allocation of nutrients and how photoperiod affects these allocations to maintain photostasis across the year.

Figure 1



Current Opinion in Plant Biology

Photoperiod measuring in plants. The circadian clock acts to divide the 24-h day into two different response states. The first half of the day is called the photophilic state and the second half of the day is called the skotophilic state. If dusk occurs in the photophilic state, as what would occur in a short winter-like day (left side), one developmental outcome occurs. While if dusk occurs in the skotophilic state, similar to a long summer-like day, a different developmental outcome would occur. For long-day plants, short days result in slow growth and prevention of flowering, while long days result in rapid growth and rapid flowering. For short-day plants, growth is also slow in short days but flowering is fast, while growth is fast in long days but flowering is slow.

Photoperiodic regulation of starch and metabolism

The production of photoassimilates requires light to drive photosynthesis, but the storage, distribution, and interconversion of photoassimilates is tightly regulated by signaling pathways that accurately measure features of light such as duration, intensity, or color. One of the most critical photoassimilates for photostasis in changing light environments is the storage polysaccharide, starch [13]. Starch can be stored for future use in times when light levels drop below the compensation point (point at which photosynthetic rate matches respiration, resulting in zero net fixation of carbon), for instance at night. More than 40 years ago it was recognized that starch allocation is sensitive to photoperiod in soybean and that a higher percentage of photoassimilate is committed to starch when days are short [14]. This was subsequently affirmed and expanded on in other plant species [15,16]. A remarkable feature of plant metabolism was discovered when it was shown that Arabidopsis plants could predict night length under a variety of photoperiods and alter starch degradation rates to utilize starch reserves nearly completely by dawn of the next day [17,18]. This process requires a properly timed circadian clock which allows the plant to accurately calculate when dawn will occur and photosynthesis can begin again. The physiological importance of such a system is evident in starch synthesis and breakdown mutants that enter into a metabolic ‘free-run’ state in which nutrient levels oscillate with the diurnal cycle, rising to high levels in the light but then being exhausted soon after dusk [19–21]. This results in the mutant plant entering a starvation state in any daily light cycle that contains a dark period, with accentuated defects in physiology when nights are long [15]. These pioneering experiments demonstrated that daily and seasonal information is integrated into plant metabolism through the control of starch synthesis and turnover and helps maintain photostasis.

It can be difficult to tease apart the roles of light duration and light intensity in plant metabolic processes, but this was recently tackled by a carefully constructed study that demonstrated that the percentage of photoassimilate dedicated to starch was determined by the photoperiod, independent of the light intensity (within a range of intensities) [22]. Light intensity does control the total level of photoassimilate, but photoperiod controlled the percentage that was converted to starch or other metabolites. Again, short photoperiods were shown to dedicate a higher percentage of photoassimilate to starch than long photoperiods.

As noted previously, the circadian clock is a central component in photoperiod measuring systems and starch metabolism, and recently a host of clock mutants were shown to have effects on starch synthesis and breakdown [23–25]. These mutants exhaust starch reserves before dawn or are unable to fully capitalize on accumulated starch by inappropriately keeping starch in reserve at the end of the night. One critical metabolic function of the circadian clock is to coordinate the daily onset of starch turnover, and this function could be important for understanding the photoperiodic regulation of nutrient production. In a series of elegantly designed pulse-chase experiments, it was shown that in the light period of a short day, starch is exclusively being synthesized and not being turned over [26]. But, when the light period is longer than approximately 14 h, starch turnover begins to occur simultaneously with starch synthesis (Figure 3). As expected this results in increased cellular concentrations of glucose and sucrose that can be utilized for physiological processes. Thus when the photoperiod extends past 14 h of light, Arabidopsis receives a 'burst' of nutrients each day that can go on to promote growth and reproduction. Furthermore, it is now well established that sugars also play roles in setting the pacing of the circadian clock suggesting that the regulation of daily metabolism by the clock is reciprocal [25,27–32].

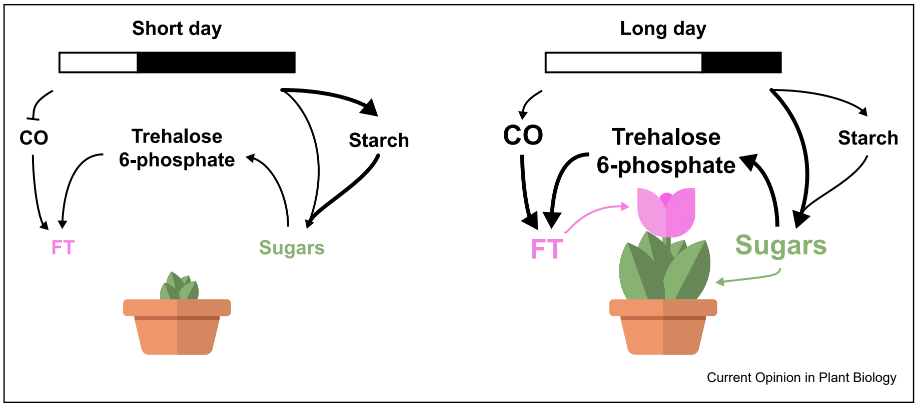
Metabolic control of photoperiodic flowering

Flowering and metabolism are both regulated by photoperiod, and in turn there is a long history investigating the role of metabolism in flowering. Plants, and other photoautotrophic organisms, rely on light for the production of energy, making it imperative that they are exquisitely tuned to the intensity, color, and duration of light. In addition to flowering, growth and vegetative health are also responsive to photoperiod, with longer photoperiods triggering growth due to increased photosynthetic capacity. Initially, it was difficult to disentangle the role of photosynthesis in photoperiodic flowering because plants that flower in long days also have greater photosynthetic capacity and growth. This was addressed when an early photoperiod researcher, Julien Tournois, observed that short-day flowering plants could induce flowering even when growth is restricted (Figure 1) [33]. This critical observation was one of the first to begin the process of disentangling photosynthetic energy capture from the photoperiodic control of flowering time, and strongly suggested that the driver for photoperiodic flowering was in fact day length rather than the daily light integral (number of photosynthetically active photons per day).

Despite the work of Tournois suggesting that photosynthesis may be distinct from flowering, the role of photoassimilates in flowering has been an area of intense study. Contrary to the idea that photosynthesis and flowering time are totally separable, sugar supplementation, especially supplementation with sucrose, promotes flowering in a host of plants [34]. Sucrose even seems to have an important role in flowering in short-day flowering plants. For instance, when some short-day flowering plants are transferred from photosynthetically advantageous long days to photosynthetically disadvantaged short days there are pulses of sucrose exported to the meristem that accompany the transition to flowering [35]. This indicates that flowering under any photoperiod may require, or be enhanced by, the presence of photoassimilates which need to be transported with the florigen to promote flowering.

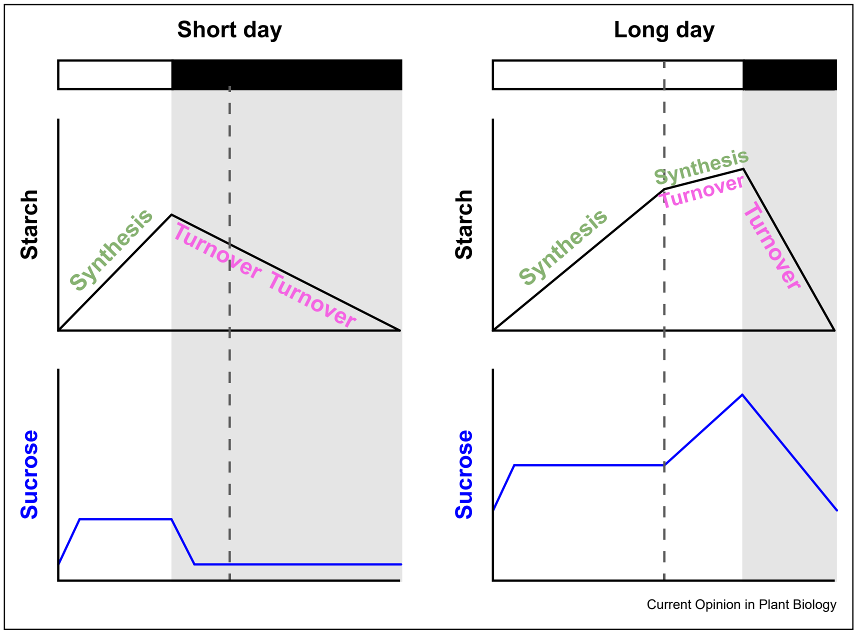
Sucrose can play a variety of roles in plants including serving as a signaling molecule, being converted to glucose and fructose for consumption, and even acting as a cryoprotectant. The role of sucrose in flowering time was further elucidated when it was discovered that the disaccharide signaling sugar, trehalose 6-phosphate, is

Figure 2



Photoperiod control of flowering and metabolism in long-day plants. Flowering and metabolism are controlled by photoperiod. In short days, CO activity is blocked preventing activation of *FT*. At the same time, the plant is dedicating much of its photoassimilate production to starch in order to maintain sugar levels throughout the long night. In long days, CO becomes active and activates *FT* expression. Concurrently, the plant is dedicating a higher percentage of photoassimilate to sugars which fuel production of trehalose 6-phosphate, also activating *FT* expression.

Figure3



Current Opinion in Plant Biology

Photoperiod control of photoassimilate partitioning. Adapted from Ref. [26]. In short days, a large percentage of photoassimilate is dedicated to starch synthesis during the day and starch turnover rates are adjusted to maintain levels until dawn. At the same time, sucrose levels rise sharply after dusk but quickly drop to low levels after dark. In days longer than 14 h starch is synthesized starting after dawn, but at 14 h after dawn (dotted line) starch is both synthesized and turned over in the light. After dusk, starch is turned over at a high rate. At the same time, sucrose is synthesized after dawn but reaches a plateau. Then after 14 h post-dusk, when starch synthesis and turnover happen concurrently, sucrose levels rise above the plateau and then drop again at night, but remain relatively high until dawn.

required for proper flowering time in Arabidopsis [36–38]. Trehalose 6-phosphate levels strongly correlate with cellular levels of sucrose in plants, and when TREHALOSE 6-PHOSPHATE SYNTHASE 1 (TPS1), a critical enzyme for the production of trehalose 6-phosphate is mutated, Arabidopsis flowering is delayed. This delay is caused by a decrease in the expression of *FT*, with little effect on CO, suggesting that the presence of sugars is a critical priming step preempting the canonical photoperiod measuring system for flowering (Figure 2). One way that trehalose 6-phosphate can function is through the direct binding and inactivation of Snf1-related protein kinases (SnRKs) [39]. Constitutive expression of a regulatory subunit of SnRK1, called KIN10, causes delayed flowering in concordance with the idea that trehalose 6-phosphate controls flowering through its signaling function [38,40].

Roles of energy in winter photoperiodism

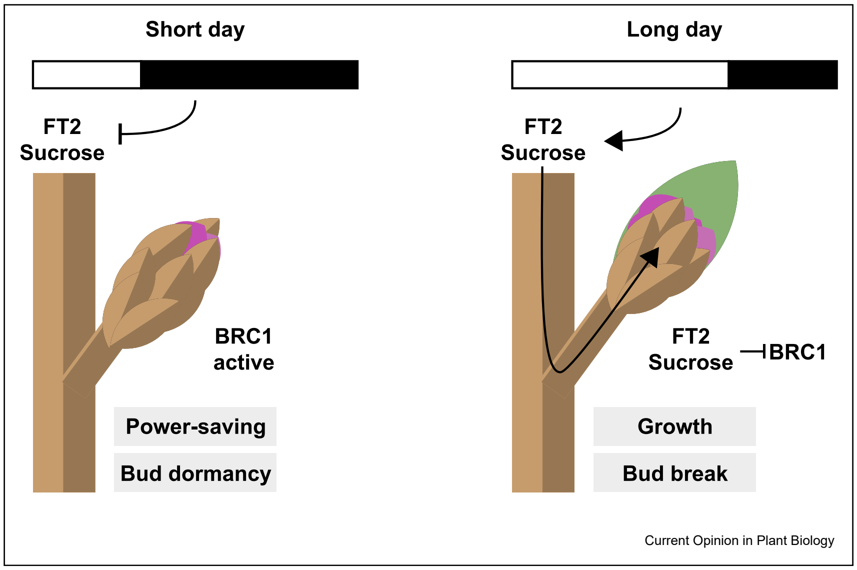
The role of starch in regulating physiology in different photoperiods is clear from a long history of genetic and metabolic studies, but recently its role in controlling photoperiodic gene expression has been explored in greater detail. Initially, microarrary studies of plants that are unable to generate starch, such as the *phosphoglucomutase 1* mutant (*pgm*), show large defects in diurnal gene expression profiles [21]. Coming from a different angle, our lab recently showed that starch mutants, such as *pgm*, prevent the plant from accurately inducing photoperiodic gene expression in short winter-like days [41]. A bioinformatics search for photoperiod-regulated genes resulted in the identification of a group of short-day-induced genes that are critical for winter-photoperiod fitness and are controlled independent of the canonical CO/FT module. A real-time photoperiod reporter system was developed to track the expression of these genes under a variety of photoperiods and growth conditions and showed that the circadian clock, photosynthesis, and starch production are necessary for proper winter-photoperiod gene expression. This coincided well with other genome-wide photoperiod expression studies and suggests the presence of a core gene regulatory network that functions in winter physiology [21,40,42].

Tree species are appealing study systems for cellular and developmental changes associated with short photoperiods. This is because growth cessation and onset of dormancy are critical for survival through wintertime conditions in boreal and temperate regions, and in tree species these processes are tightly linked to photoperiod and easy to observe [43–45]. Recent advances in genomic technologies and techniques of genetic manipulation have further propelled trees, such as hybrid aspen, as models for photoperiodism. From these studies have emerged a clear delineation of the steps in photoperiod-controlled growth cessation and dormancy: upon transfer to inductive short photoperiods the meristematic cells enter an energy-saving program where cell cycle is minimized; plasmodesmatal transport of compounds that promote growth is blocked; buds (development of protective scales around more sensitive tissues) begin to form; and eventually dormancy is established.

Akin to classic studies of photoperiodic flowering, a short night break can prevent photoperiod-controlled entry into growth cessation and dormancy developmental programs in *Populus*, suggesting that analogous mechanisms may be at play [46]. Extensive work on the genetic and molecular components of this process have revealed that a modified CO/FT module controls the ability of the plant to enter and exit these states at the appropriate time of year. Briefly, shortening photoperiods result in the repression of an ortholog of the Arabidopsis *FT* called *FT2*. One of *FT2*'s functions is to activate the gene *LIKE-AP1* (*LAP1*) which in turn represses the critical branching and dormancy regulator *BRANCHED1* (*BRC1*). When *BRC1* is active it can feedback to further inhibit *FT2* function and maintain growth cessation (Figure 4) [47–50].

Interestingly, recent reports have suggested that metabolic mechanisms also converge on the regulation of *BRC1* [51–54]. One such study challenged the long-standing hypothesis that auxin is the initial signaling molecule controlling maintenance of apical dominance [55]. Using time lapse photography to accurately measure bud growth, the authors show that photoassimilate accumulation precedes the arrival of auxin by nearly 24 h in buds that have broken dormancy and begun to grow. They then link this effect back to the suppression of *BRC1* by sugars, which, as mentioned previously, plays a critical role in maintenance of bud dormancy in short photoperiods (Figure 4). In addition to molecular genetic studies, genome-wide expression studies, and a meta-analysis of those studies, have revealed that an evolutionarily conserved energy conservation program accompanies dormancy in a variety of species [56,57]. Critically, a genome-wide transcriptional program, resembling that seen in carbon starvation, is triggered by various stimuli, including shortening of the photoperiod, and across a range of plant species. The core set of genes and biological processes that are induced by bud dormancy point toward energy recycling, catabolism, and hormone regulation as important cellular processes associated with bud dormancy. Interestingly, these processes are the same that are induced in Arabidopsis vegetative tissues by shortening photoperiods [21,41,42,58], suggesting that conserved gene regulatory networks may serve a variety of photoperiodic functions in plants. In the coming years, the relationships between the CO/FT module and metabolism in the control of growth cessation and dormancy in tree species should reveal novel insights into how winter metabolism controls important annual developmental programs. One additional area that should be further explored is the role of temperature in these processes.

Figure 4



Photoperiod regulation of buds. In shortening days (left), CO function is decreased and FT2 levels drop. This allows for the activation of *BRC1*, but is also accompanied by a change in gene regulatory networks putting the bud into a low energy power saving state. As days lengthen (right) sucrose levels rise and CO becomes active to promote *FT2* expression. Both of these signals converge to suppress *BRC1* allowing the bud to utilize sugars in order to break dormancy and resume growth.

Cold temperatures can signal the conversion of starch into sucrose, and temperature plays important roles in bud set and bud emergence [59,60]. Starch and other metabolites may a play a central role in the integration of a variety of seasonal signals to optimize plant development across the year.

Concluding remarks

Progress in the study of photoperiodism has been driven by research in plant systems. Plants are a desirable system to study photoperiodism due to their propensity to flower in a particular season, but their photoautotrophic nature complicates understanding of the role of light in controlling development. What has become clear over centuries of research is that photoperiod impacts plant development from germination to senescence and that photoperiodic regulation of metabolism plays a key role in vegetative health and reproduction. Recent work opens the door to the discovery of the genes, proteins, and signaling networks controlled by photoperiod-regulated metabolism to provide a more comprehensive view about how plants measure and respond to day length. This has become an issue of critical importance as the climate crisis continues to rapidly dissociate predictive day length from the other environmental signals that the plant is attempting to preempt, such as temperature, water availability, and predation [61,62]. We must continue to understand these systems to ensure robustness and optimal photostasis in our plants in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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** of outstanding interest

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