Nighttime starch degradation, the circadian clock, and plant growth

Journal:	*McGraw-Hill Yearbook of Science & Technology*
Manuscript ID:	YB13-0050
Manuscript Type:	Yearbook Article
Date Submitted by the Author:	07-May-2012
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Keywords:	starch, carbon availability, growth, circadian clock, starvation
Abstract:	

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Manuscripts

Topic one: Plant physiology (571110)

Topic two: Biochemistry and molecular biology (570100)

Nighttime starch degradation, the circadian clock, and plant growth

The steadily rising demand for food and renewable resources has challenged plant breeders and biotechnologists to rapidly increase crop productivity. To realize this goal, a holistic knowledge is required of how plant metabolic pathways are controlled to allow optimal growth. Today, very little is known about the partitioning of photosynthetically assimilated carbon among growth, storage, and respiration. This article describes recent progress in understanding how the model plant *Arabidopsis thaliana* uses its carbon resources to ensure a continuous energy supply for growth during the night.

For Review

Diurnal starch turnover in *Arabidopsis* plants.

During the day, plants assimilate CO_2 to produce sugars (photosynthates) in the process of photosynthesis. Plants use these sugars to fuel their metabolism and growth, producing the primary carbon source for almost all nonphotosynthetic organisms. However, not all photosynthates acquired during the day are used for immediate growth. Plants partition a fraction of the assimilated carbon into storage compounds in leaves to support respiration and continued growth during the night when photosynthesis is not possible.

In many plant species, the main carbon storage compound is starch. The synthesis of starch in leaves during the day and its degradation during the night have been studied intensively in the model plant *A. thaliana*. During a normal day, *Arabidopsis* plants store approximately 50% of the carbon assimilated by photosynthesis as starch granules in the cell plastids

(chloroplasts) of leaves. During the night, starch is degraded with a near-linear rate such that the starch reserves are almost completely utilized by dawn (**Fig. 1***a*).

This match between the length of time taken to degrade the starch reserves and the length of the night is vitally important for normal plant growth. If the night is artificially extended beyond the normal dawn, the growth rate of the plant drops abruptly. Mutant plants that cannot accumulate starch or that degrade it only very slowly have much lower growth rates than wild-type plants and show a severely reduced overall rate of growth. These reductions in growth rate are accompanied by large changes in gene expression indicating carbon starvation.

Considering the importance of a continuous carbon supply during the night for plant growth, it is not surprising that starch turnover is tightly controlled. *Arabidopsis* plants adjust the rates of starch synthesis and degradation to different environmental conditions (for example, temperature, light levels, and day length). The rate of starch synthesis is inversely related to day length: the shorter the day, the greater the proportion of assimilated carbon that is partitioned into starch. The rate of starch degradation is also adjusted such that a linear and almost complete degradation during the night is achieved for day lengths ranging from 18 h to as short as 4 h. Remarkably, the rate of starch degradation in *Arabidopsis* plants can adjust immediately in response to an unexpected early or late onset of night. If plants grown in 12 h of light/12 h of darkness are subjected to darkness after only 8 h of light, the rate of starch degradation is much slower than on previous nights, but remains constant throughout the 16-h night. These observations imply that plants at dusk integrate information about the amount of starch present in leaves and the anticipated length of the night to set the rate of starch degradation. Recent

For Review

investigations have revealed that the timing of starch degradation in *Arabidopsis* plants is linked to the circadian clock.

The circadian clock and starch degradation.

Almost all organisms possess an endogenous oscillating timer called the circadian clock. This timer keeps track of the estimated position of an organism in the 24-h light–dark cycle. The clock controls physiological processes that function at specific, appropriate times of day and supports the anticipation of dusk and dawn. In plants, the circadian clock affects a wide range of physiological and biochemical processes, including expansion growth, flowering time, stomatal aperture, leaf movement, and responses to drought stress and pathogen attack.

An important hallmark of the circadian clock is its free-running 24-h rhythm. Free running refers to the fact that, once entrained by light signals, the circadian clock maintains a 24-h rhythm in continuous light or continuous darkness, anticipating dusk and dawn according to previously encountered conditions. In fact, the property of being a 24-h timer has revealed the involvement of the circadian clock in the control of starch degradation. When plants are grown in light–dark cycles shorter or longer than 24 h, abnormal starch degradation patterns are observed during the night. In 28-h light–dark cycles (14 h of light, 14 h of darkness), starch is degraded extremely fast, so reserves are exhausted before dawn—specifically, at 10 h into the night rather than at the actual dawn after 14 h of night (Fig. 1*b*). Conversely, in 20-h light–dark cycles (10 h of light, 10 h of darkness), starch is degraded too slowly, resulting in the presence of substantial reserves at dawn. If the night is extended beyond dawn, starch is eventually depleted after approximately 14 h of darkness (Fig. 1*c*).

For Review

Measurements of clock-related gene transcription can be used to analyze the timing of the *Arabidopsis* clock. So-called morning-phased clock genes show a sharp expression peak at the anticipated dawn. Quantification of transcription level and starch content during the night has revealed that the anticipation of dawn by the circadian clock coincides with the exhaustion of starch reserves in all light–dark cycles (Fig. 1). These results indicate a link between starch degradation and the timing of the circadian clock in *Arabidopsis*, and they offer an explanation for the abnormal starch degradation pattern in light–dark cycles that are longer or shorter than 24 h. Thus, starch degradation is programmed so that reserves would be exhausted 24 h after the previous dawn, regardless of the timing of the actual dawn experienced by the plant throughout its development.

Work on *Arabidopsis* mutant plants, in which the period of the clock is altered, confirmed these findings. The *Arabidopsis cca1/lhy* mutant lacks two transcription factors that control functioning of the clock. This loss does not eliminate clock function, but causes the clock to run fast. Analogous to wild-type plants in light–dark cycles longer than 24 h, *cca1/lhy* mutants fail to correctly anticipate dawn in a 24-h light–dark cycle (Fig. 1*c*). The expression peak of morning-regulated clock genes, indicating the anticipation of dawn, happens 4 h before the actual dawn. At exactly this time point, *cca1/lhy* mutant plants exhaust their starch reserves. Hence, despite the abnormal behavior of the circadian clock in these mutants, the link between the clock and starch degradation remains intact.

For Review

Because mobilization of starch reserves is linked to the timing of the circadian clock, the normal starch degradation pattern (that is, linear and near-complete degradation of starch over the course of the night period) can only occur if the length of the light–dark cycle matches the clock period (Fig. 1). It might be expected that abnormal rates of starch degradation and hence suboptimal utilization of carbon reserves affect plant productivity. This is indeed the case. Wild-type plants grown in 28-h light–dark cycles (14 h of light, 14 h of darkness) show symptoms of carbon starvation during the night, and plant growth is reduced. Providing sugar in the growth medium prevents carbon starvation during the night and restores normal plant growth. Carbon starvation in 28-h light–dark cycles can also be prevented by genetic modification of plants. *Arabidopsis* starch-excess mutants have defects in starch-related enzymes and show reduced rates of starch degradation. As a consequence, these mutants do not exhaust their starch reserves during the night in either 24-h or 28-h light–dark cycles. Unlike wild-type plants, starch-excess mutants show no symptoms of carbon starvation and no reduction in growth in 28-h light–dark cycles compared to 24-h light–dark cycles. Taken together, these results reveal that mistiming of starch degradation and the resulting carbon starvation during the night have negative effects on plant growth.

The current knowledge of the relationship between circadian timing, starch degradation, and growth can be summarized in a basic model (**Fig. 2**). According to the model, the circadian clock is entrained by light–dark cycles. A functional circadian clock allows the plant to anticipate the length of night, and starch degradation as a clock output is regulated accordingly. The correct timing of starch degradation ensures a continuous supply of carbon from starch throughout the night, thereby maximizing potential productivity.

For Review

Raising questions for the future.

How the circadian clock is linked to starch degradation remains to be established. It is unlikely that control of starch degradation happens on a transcriptional level. Although transcripts for many of the enzymes of starch degradation in *Arabidopsis* show strong diurnal and circadian patterns of abundance, most of these enzymes show little or no change in protein abundance during the light–dark cycle. Thus, at least on a diurnal basis, control of starch degradation probably occurs by posttranslational mechanisms. Regulatory mechanisms such as redox activation, allosteric regulation by metabolites, reversible phosphorylation, and protein–protein interactions have been shown to influence the activity of several starch-related enzymes. However, the significance of these mechanisms for control of flux through starch degradation in vivo remains to be discovered. Elucidation of the signaling pathway that links the clock, located in the nucleus, to the posttranslational control of enzymes in the cell plastids presents an interesting challenge for the future.

In addition, it is still unknown which regulatory mechanisms are used to balance carbon availability and plant growth. When plants are transferred to an unexpected early night, the rate of starch degradation is lower than during the previous night. Thereby, plants ensure a continuous carbon supply from starch throughout the night, despite the lower starch amount at dusk and a longer night. However, because of the lower rate of starch degradation, the carbon availability during the night is reduced, and plant growth needs to be adjusted accordingly. Indeed, measurements of root growth of *Arabidopsis* seedlings grown in 12-h light/12-h dark cycles and shifted to an early night after only 8 h of light show that root growth is adjusted

For Review

immediately. After the transfer to an early night, root growth slows down and continues at a lower level relative to the previous night. How the root perceives signals of lower carbon availability in leaves and how signals are integrated to regulate growth are not known.

Progress made in understanding the timing of starch degradation during the night raises another important question: How do plants measure their starch reserves? To achieve a linear and near-complete utilization of starch during the night, anticipation of the length of the night is not sufficient by itself. Plants also need to sense the amount of starch present in the cell plastids at dusk. The correct rate of starch degradation must be set by a molecular division of the starch amount according to time. How the plant cell achieves this calculation on the molecular level remains elusive.

In summary, consideration of how plants survive the night raises many new and complex questions about the relationship of photosynthesis, carbon storage and utilization, and plant productivity. The research on *Arabidopsis* starch metabolism thus illustrates the importance of considering these questions in attempting to increase crop productivity.

For background information *see* AGRICULTURAL SCIENCE (PLANT); BIOTECHNOLOGY; CARBON; CIRCADIAN CLOCK (PLANTS); PHOTOPERIODISM; PHOTOSYNTHESIS; PLANT DEVELOPMENT; PLANT GROWTH; PLANT METABOLISM; PLANT PHYSIOLOGY; STARCH in the McGraw-Hill Encyclopedia of Science & Technology.

Alexander Graf

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For Review

Key words:

starch; carbon availability; growth; circadian clock; starvation

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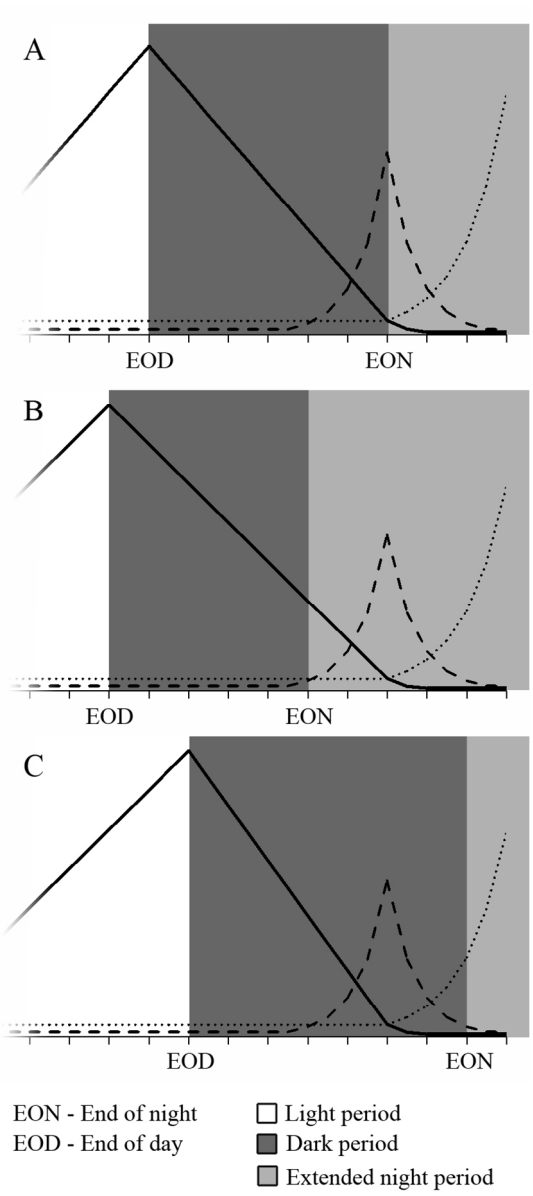
Fig. 1. Starch degradation is timed according to the anticipation of dawn by the circadian clock, regardless of the actual length of the night. The graphs show situations in which the period of the clock matches the length of the light–dark (LD) cycle (*a*), is longer than the LD cycle (*b*), or is shorter than the LD cycle (*c*). Starch (solid line) accumulates in a linear fashion during the light period and is degraded in the dark period. The anticipation of dawn by the circadian clock is revealed by a peak of transcript abundance of morning-phased clock-controlled genes (dashed line). Accumulation of transcripts indicative of starvation (dotted line) occurs only when starch supplies are exhausted. This point is reached early in an artificial extension of the night when the period of the clock matches the length of the LD cycle (*a*), only after several hours of extended night when the period of the clock is longer than the LD cycle (*b*), and well before the end of the

normal night when the period of the clock is shorter than the LD cycle (*c*). EON = end of night; EOD = end of day. (*Based on data from A. Graf et al., Circadian control of carbohydrate availability for growth in Arabidopsis plants at night, Proc. Natl. Acad. Sci. USA, 107:9458–9463, 2010*)

Fig. 2. A proposed relationship between the circadian clock, starch degradation, and growth at night. The circadian clock is entrained by light signals, allowing the anticipation of dusk and dawn, and the length of the night. Information from the circadian clock is transmitted via an unknown signaling pathway to the cell plastid (chloroplast), where it is used to modulate the rate of degradation of the starch granule. Regulation of the starch degradation rate occurs most likely by posttranslational modification of starch-degrading enzymes (schematically represented by E1–E3). The enzyme or enzymes subject to modulation remain to be discovered. Modulation of the rate of starch degradation ensures that substrates for metabolism and growth are available throughout the night.

For Review



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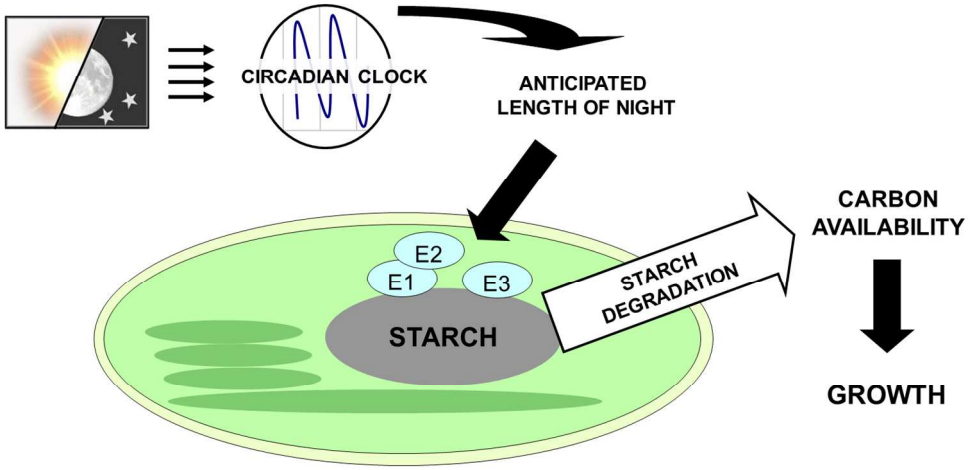

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For Review

Topic one: Plant physiology (571110)

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During the day, plants assimilate CO_2 to produce sugars (photosynthates) in the process of photosynthesis. Plants use these sugars to fuel their metabolism and growth, producing the primary carbon source for almost all nonphotosynthetic organisms. However, not all photosynthates acquired during the day are used for immediate growth. Plants partition a fraction of the assimilated carbon into storage compounds in leaves to support respiration and continued growth during the night when photosynthesis is not possible.

In many plant species, the main carbon storage compound is starch. The synthesis of starch in leaves during the day and its degradation during the night have been studied intensively in the model plant *A. thaliana*. During a normal day, *Arabidopsis* plants store approximately 50% of the carbon assimilated by photosynthesis as starch granules in the cell plastids

For Review

(chloroplasts) of leaves. During the night, starch is degraded with a near-linear rate such that the starch reserves are almost completely utilized by dawn (**Fig. 1***a*).

This match between the length of time taken to degrade the starch reserves and the length of the night is vitally important for normal plant growth. If the night is artificially extended beyond the normal dawn, the growth rate of the plant drops abruptly. Mutant plants that cannot accumulate starch or that degrade it only very slowly have much lower growth rates than wild-type plants and show a severely reduced overall rate of growth. These reductions in growth rate are accompanied by large changes in gene expression indicating carbon starvation.

Considering the importance of a continuous carbon supply during the night for plant growth, it is not surprising that starch turnover is tightly controlled. *Arabidopsis* plants adjust the rates of starch synthesis and degradation to different environmental conditions (for example, temperature, light levels, and day length). The rate of starch synthesis is inversely related to day length: the shorter the day, the greater the proportion of assimilated carbon that is partitioned into starch. The rate of starch degradation is also adjusted such that a linear and almost complete degradation during the night is achieved for day lengths ranging from 18 h to as short as 4 h. Remarkably, the rate of starch degradation in *Arabidopsis* plants can adjust immediately in response to an unexpected early or late onset of night. If plants grown in 12 h of light/12 h of darkness are subjected to darkness after only 8 h of light, the rate of starch degradation is much slower than on previous nights, but remains constant throughout the 16-h night. These observations imply that plants at dusk integrate information about the amount of starch present in leaves and the anticipated length of the night to set the rate of starch degradation. Recent investigations have revealed that the timing of starch degradation in *Arabidopsis* plants is linked to the circadian clock.

For Review

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<sec 2>**The circadian clock and starch degradation.**

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Measurements of clock-related gene transcription can be used to analyze the timing of the *Arabidopsis* clock. So-called morning-phased clock genes show a sharp expression peak at the anticipated dawn. Quantification of transcription level and starch content during the night has revealed that the anticipation of dawn by the circadian clock coincides with the exhaustion of

For Review

starch reserves in all light–dark cycles (Fig. 1). These results indicate a link between starch degradation and the timing of the circadian clock in *Arabidopsis*, and they offer an explanation for the abnormal starch degradation pattern in light–dark cycles that are longer or shorter than 24 h. Thus, starch degradation is programmed so that reserves would be exhausted 24 h after the previous dawn, regardless of the timing of the actual dawn experienced by the plant throughout its development.

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For Review

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For Review

However, the significance of these mechanisms for control of flux through starch degradation in vivo remains to be discovered. Elucidation of the signaling pathway that links the clock, located in the nucleus, to the posttranslational control of enzymes in the cell plastids presents an interesting challenge for the future.

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For Review

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<au>**Alexander Graf**

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For Review

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For Review