

The Dynamic Plant: Capture, Transformation, and Management of Energy¹

Plants are exquisite in their capacity to convert photons of *light* through photosynthetic carbon dioxide (CO₂) fixation into carbohydrate resources that are assimilated and partitioned from photosynthetic source to sink tissues. The chemical *energy* gained from photosynthesis includes ATP and NADPH that along with sugars are vital to biosynthetic processes, cell proliferation, biomass production, and reproductive fitness. As in all eukaryotes, plants are dependent upon *dioxygen* (O₂) for efficient production of ATP through aerobic respiration by mitochondria. Therefore, O₂ is crucial for the efficient catabolism of carbohydrates, lipids, and protein into chemical energy in leaves in the light and darkness, as well as in sink tissues. In this Focus Issue, numerous reviews and research articles explore the integration of light, O₂, and energy metabolism from the cellular to the whole-plant level. The articles analyze molecular, biochemical, physiological, and developmental mechanisms that contribute to the plant's energy balance. A recurrent theme is the integration of light, O₂, and sugar sensing with signal transduction and gene regulation, resulting in metabolic and developmental plasticity that maximizes available energy for growth. This knowledge expands opportunities to enhance photosynthetic efficiency and fine-tune energy allocation to maximize yields of crops.

LET THERE BE LIGHT: DYNAMICS OF CHLOROPLAST BIOGENESIS AND DIFFERENTIATION

The biogenesis of photosynthetically active chloroplasts involves the coordinated regulation of the nuclear and proplastid genomes. This synchronization involves both anterograde (nucleus to plastid) and retrograde (plastid to nucleus or another compartment) signaling (de Souza et al., 2017; Hernández-Verdeja and Strand, 2018). Using a single-cell system of *Arabidopsis* (*Arabidopsis thaliana*), Dubreuil et al. (2018) tracked dynamics in transcripts and metabolites to refine the definition of the early light-induced anterograde phase that includes chlorophyll

synthesis and rudimentary thylakoid membrane formation. Their analysis resolved a second phase that is characterized by retrograde signaling from the plastid to the nucleus that dramatically bolsters the expression of nucleus-encoded photosynthetic genes and the transition to photosynthetic competence. Modeling confirmed that this second phase involves positive feedback from the plastid itself. The two-phase biogenesis is demarked by distinct morphological changes, including movement of chloroplasts to the cell periphery. Intriguingly, the retrograde phase is inhibited by high levels of Suc, indicating that a surplus of carbon restricts the maturation of chloroplasts.

Chloroplasts coordinate a range of cellular and developmental processes, as covered in two reviews (de Souza et al., 2017; Hernández-Verdeja and Strand, 2018). These processes include signaling through the production of photosynthesis-derived reactive oxygen species (ROS) that cause inhibition of PSII (photoinhibition). The ephemeral superoxide and more enduring hydrogen peroxide generated by photooxidative stress have well-studied impacts on signaling and physiology in leaves. These active oxygens also act as signaling molecules during development of flowers and fruits that may augment photoprotection, stimulate pigment production, and trigger chloroplast differentiation to chromoplasts and other forms with specific biochemical activities and structural features (Muñoz and Munné-Bosch, 2018).

PHOTOSYNTHESIS: MAXIMIZING FLEXIBILITY AND OUTPUT

Photosynthesis takes place under variable light intensity, humidity, temperature, and CO₂. The optimization of photosynthesis along with use of water, nitrogen, and other limiting factors is a key opportunity for crop improvement. Such improvements can be pursued through modeling of steady-state and dynamic physiological data, and the targeted engineering of specific metabolic processes. Advances in monitoring photosynthetic parameters continue to benefit modeling. In a pioneering study, Lichtenberg et al. (2017) performed laser light sheet microscopy with defined spectra on the thalli of the aquatic macrophyte *Fucus* to improve the estimation of PSII efficiency. To better understand photosynthetic electron transport, Morales et al. (2018) leveraged an extensive published dataset for the C₃ species *Arabidopsis*, including gas exchange, chlorophyll fluorescence, light intensity, and CO₂ availability, to model interactions between multiple mechanisms and reactions. These interactions include regulation of cyclic and noncyclic alternative electron transport and

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Rubisco activity. Their simulations exposed flexibility in the coordination of photosynthesis in fluctuating environments that can be tested with specific genotypes. Over the past decade, several studies have manipulated enzymes to bolster photosynthesis and increase the acquisition of biomass (Long et al., 2015). One such study in this issue found that overexpression of the RieskeFeS protein, a component of the cytochrome *b₆f* complex that connects the two photosystem reaction centers, significantly increased PSI and PSII electron transport efficiency, CO₂ assimilation, and yield in *Arabidopsis* (Simkin et al., 2017).

Two must-read *Updates* on photosynthetic dynamics caused by fluctuations in irradiance review the salient physiology and promising strategies for improving photosynthesis in crop canopies (Kaiser et al., 2018; Slattery et al., 2018). One possible strategy is to optimize the use of sunflecks within the lower part of the canopy. The approach is addressed by Townsend et al. (2018) through modeling of photosynthesis within a 3D reconstruction of light rays in field-grown wheat (*Triticum aestivum*). Their results underscore the disparity between the brevity of photosynthetic activity and the maintenance of photosynthetic capacity in leaves as they become progressively shaded. These shaded leaves of wheat contain the majority (80%) of total shoot nitrogen, a repository that is underutilized in the production of photosynthate at current planting densities and is not fully remobilized to the seed during maturation.

On the flipside, Walker et al. (2018) address the long-held hypothesis that photosynthesis can be increased by limiting the chlorophyll content of upper leaves of the canopy, where photosynthetic activity is readily maximized at low levels of solar radiation. Their simulations for soybean (*Glycine max*) predict that reductions in chlorophyll can provide a savings of nearly 10% of leaf nitrogen without compromising photosynthetic assimilation at the canopy scale. However, computing with the leaf optical properties collected in the field for 67 chlorophyll-deficient genotypes, their empirical model failed to predict an overall enhancement of photosynthesis in chlorophyll-deficient soybean. Despite this, modeling coupled with manipulation of three enzymes that allow chloroplasts to release excess light as heat through nonphotochemical quenching of chlorophyll fluorescence provided a 15% increase in biomass in field-grown tobacco (*Nicotiana tabacum*; Kromdijk et al., 2016). Thus, manipulation of photosynthesis, photoprotection, and development is a promising solution to biomass improvement across crop species (Slattery et al., 2018).

PHYTOCHROME CENTRAL: TUNING LIGHT RESPONSES AND RESOURCE MANAGEMENT

Light is the plant's source of energy, harnessed through photosynthesis, but light also has pivotal signaling functions for growth and development. Different wavelengths are sensed through different

photoreceptors, including UV-A and blue light-sensitive cryptochromes and phototropins and the red (R)/far-red (FR)-reversible phytochromes (briefly reviewed by van Gelderen et al. [2018]). The *Update* by Krahmer et al. (2018) posits that phytochromes are central regulators of photosynthetic capacity and resource management. This calls for an important broadening of our views on phytochrome activity to integrate their signaling function for development and for resource management, the latter being indispensable for the first. In the process of photosynthesis, photoinhibition can occur when normally shaded leaves experience high light conditions. Phytochrome A of *Arabidopsis* was shown by Wang et al. (2018) to be involved in the protective effect of a low R/FR light ratio, via control of the ELONGATED HYPOCOTYL5 (HY5) transcription factor. Phytochromes mediate their regulation primarily via Phytochrome Interacting Factors (PIFs), a subgroup of basic helix-loop-helix transcription factors (Leivar and Quail, 2011; Leivar and Monte, 2014). The latest insights about this interaction are discussed in Pham et al. (2018), including recent insights into multiple kinases and ubiquitin ligases that control PIF activity.

Plants express multiple photoreceptors with different light quality sensitivities to monitor different features of their light environment. Mechanisms of phototropin signal transduction, focusing particularly on the roles of NON-PHOTOTROPIC HYPOCOTYL3 and ROOT PHOTOTROPISM2-LIKE proteins are reviewed by Christie et al. (2018). Photoreceptors have a wide variety of functions in plant growth and development, including the transition to an autotrophic lifestyle of recently germinated seedlings, circadian clock input, flowering time control, and responses to the environment, such as shade avoidance. Gommers and Monte (2018) review the latest insights in light control of seedling establishment, considering the subtleties from dark to light and proposing darkness, and thus photoreceptor inactivity, as an important information state.

The CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1)-SUPPRESSOR OF PHYTOCHROME A (SPA) E3 ligase is a key suppressor of light signaling that controls the abundance of several central regulators, such as HY5 and CONSTANS (CO). CO regulates photoperiodic control of flowering time; Ordoñez-Herrera et al. (2018) provide new experimental data showing that 14 CO-LIKE (COL) proteins also are COP1-SPA targets in *Arabidopsis*. Among those, COL12 is shown to be a regulator of both flowering time and plant architecture. HY5 regulates photomorphogenesis and plant architecture. In their study of HY5 homologs in monocots, Burman et al. (2018) provide experimental evidence that HY5 functions in the monocot rice (*Oryza sativa*) may be more diverse than observed in the dicot *Arabidopsis*.

Although photomorphogenic responses are broadly considered to be a suite of responses that occur above ground to ensure light capture, van Gelderen et al. (2018) stress the impact of photoreceptor activity for root development. They discuss the different mechanisms

through which light signaling may exert this control, including photoreceptor activity in the shoot and root, signal transmission from shoot to root, and consequences for, among others, shade avoidance. Shade avoidance is dominantly regulated by PIF-dependent control of auxin homeostasis (de Wit et al., 2016) and refers to a suite of elongation responses that consolidate light capture in dense stands (Ballaré and Pierik, 2017). Interesting experimental data from a research paper by Peng et al. (2018) provide evidence for a novel link between PIFs and histone modifications during shade avoidance in *Arabidopsis*. Additionally, Zhou et al. (2018) explore the involvement of the *TEOSINTE BRANCHED1*, *CYCLOIDEA*, and *PCF* (TCP) transcription factors in shade avoidance control of the *Arabidopsis* hypocotyl. They provide evidence for direct binding of TCP17 to promoters encoding PIFs and YUCCAs, the latter encoding auxin biosynthesis enzymes that also are direct targets of PIFs.

The examples above are cases of light acting as a signal, through photoreceptors, to control plant development. A process in which light acts both as a signal and, through photosynthates, as a resource is the regulation of axillary bud outgrowth. Signorelli et al. (2018) discuss the various functions of light signaling, including roles of cryptochromes and HY5, in the outgrowth of axillary buds of perennials, and integrate these with energy and oxygen signaling.

ENERGY NEXUS: DYNAMIC SUGAR SENSING METERS CARBON ALLOCATION FOR GROWTH AND DEVELOPMENT

The energy status of plants is reflected in the availability of energy-rich photosynthetic products such as ATP, reducing power, carbohydrates (including sugars), and lipids. Plants can adjust growth and development by sensing the availability of these molecules. Sugars and sugar phosphates (in particular the low-abundance metabolite trehalose-6-P, T6P) play an important role in signaling energy availability in plants (Wingler, 2018). Key energy signaling pathways include the protein kinases SNF1-related protein kinase 1 (SnRK1; low energy signaling) and Target of Rapamycin (TOR; high energy signaling), with interactions between them. Regulation of these pathways is complex, but recent findings have made important contributions to our understanding of their downstream actions. One of the key questions is how SnRK1 communicates a low energy state to adjust metabolism in plant organelles. In their *Update*, Wurzinger et al. (2018) discuss a role of SnRK1 in phosphorylating transcription factors that may regulate metabolic pathways in mitochondria and chloroplasts, although the effect of phosphorylation of these on the expression of their target genes remains to be demonstrated. TOR activates protein synthesis and stimulates cell proliferation and growth when energy supply is high. Recent discoveries on the role of TOR in mRNA

translation are discussed by Schepetilnikov and Ryabova (2018), who present a model showing how plant TOR promotes reinitiation of translation of a subset of transcripts with small upstream open reading frames in their 5' leaders. Several of these encode Auxin Response Factors, which drive transcription in response to auxin. In summary, SnRK1 and TOR signaling act antithetically to meter energy use in plant cells.

While the photosynthetic organs of plants are not short of energy during the day, a continuous supply of energy for growth and maintenance processes is required in source and sink tissues and also during the night. This necessitates not just sensing of the energy status throughout the day/night cycle, but also adjustment of metabolic processes for careful management of energy reserves, for example, by T6P-dependent control of starch metabolism (Martins et al., 2013). While the traditional view is that starch produced during the day is only degraded to provide sugars at night, Fernandez et al. (2017) show that starch degradation starts in parallel with photosynthesis at the end of long days and in evening twilight, in a manner influenced by the circadian clock. Thereby, starch degradation may supplement sugar synthesis to provide a steady supply of carbon skeletons and energy for biosynthetic pathways and growth.

Photosynthetically derived sugar provides the carbon skeletons that drive nutrient acquisition in roots, organ growth, and reserves to developing seeds. Fatty acid (FA) and triacylglycerol (TGA) biosynthesis requires that Suc is abundant and biosynthetic pathways are activated by sugar signaling. Zhai et al. (2017) achieve significant increases in FA and TGA content with genotypes defective in starch biosynthesis and the export of sugar from leaves. Contents of these lipid molecules were further bolstered by overexpression of three genes associated with the "push," "pull," and "protection" stages of lipid synthesis and accumulation (Vanhercke et al., 2014). These were the *WRINKLED1* transcription factor that regulates genes involved in FA biosynthesis, a diacylglycerol acetyltransferase that promotes TAG production, and *OLEOSIN1*, a protein that determines oil body size.

Individual enzymes also can have a major impact on partitioning carbon reserves between pathways controlling growth. This is demonstrated by mutation of individual isoforms of phosphoglycerate kinase (PGK), an enzyme that converts 1,3-bisphosphoglycerate into 3-phosphoglycerate in glycolysis but catalyzes the reverse reaction in photosynthesis (Rosa-Téllez et al., 2018). Interestingly, a double mutant in the chloroplastic (photosynthetic) and cytosolic (glycolytic) isoforms of PGK is less impaired in growth than the single mutant in cytosolic PGK, demonstrating the importance of balancing photosynthetic and glycolytic reactions for growth.

Developmental transitions such as germination, flowering, and seed development require a sufficient supply of energy. While there is considerable knowledge of the role of sugars as signals in developmental

transitions, interactions of sugar signals with other developmental regulators, such as microRNA miR156, are less well explored (Wingler, 2018). In *Arabidopsis* seedlings, Suc supply induces hypocotyl elongation under short-day conditions, suggesting that a minimum supply of energy is required for hypocotyl elongation (Simon et al., 2018). This response is dependent on T6P synthase but inhibited by overexpression of the SnRK1 catalytic subunit, which is in agreement with the opposite effects of T6P and SnRK1 in energy signaling.

How energy signaling controls leaf initiation and expansion is explored by Mohammed et al. (2018), who demonstrate the importance of integration of multiple energy signals, including light, Suc, and hormones. Whereas TOR can integrate sugar and auxin signals (Schepetilnikov and Ryabova, 2018) to stimulate cell proliferation, photomorphogenesis is required for formation of the leaf lamina (Mohammed et al., 2018). Shoot branching is another developmental process that relies on energy supply in the form of sugars. Salam et al. (2017) show that sugar supply induces the branching of sprouts growing from potato (*Solanum tuberosum*) tubers. The silencing of a gene encoding a vacuolar invertase, which converts Suc to Glc and Fru, enhanced sprout branching, suggesting that Suc is an important signal for this developmental decision. Suc also may be involved in perennial bud burst after dormancy, although its role as carbon source versus its signaling function remains unresolved (Signorelli et al., 2018). Recent research has demonstrated a function of T6P in pea (*Pisum sativum*) shoot branching in response to Suc availability (Fichtner et al., 2017), and it is therefore possible that T6P also is the signal inducing the branching of potato sprouts and perennial bud burst.

OXYGEN: BOTH METABOLIC NECESSITY AND DEVELOPMENTAL CUE

O₂ is essential for aerobic energy production. When cellular O₂ levels decline due to limited gas diffusion as a consequence of tissue density or the external environment, a cellular energy crisis can ensue (Bailey-Serres and Voeselek, 2008). Cellular hypoxia or anoxia can rapidly damage cells, leading to organ or plant death. *Updates* in this issue consider how O₂ deficiency is managed through integrated signaling and response networks that reconfigure gene expression and metabolism and promote changes in anatomy or morphology that enhance aeration. These involve both direct and indirect sensing of changes in cellular O₂ homeostasis, with the latter involving the mitochondrion and both anterograde and retrograde signaling (Schmidt et al., 2018; Wagner et al., 2018). The low O₂ levels intrinsic to some developmental zones, such as meristems, also guide developmental processes in consort with light and carbon availability, as described for seasonal progressions in axillary buds (Signorelli et al., 2018).

The *Update* by Sasidharan et al. (2018) surveys signatures of gaseous signals (O₂, CO₂, ethylene, and

nitric oxide), as well as ROS for flooding conditions, including soil waterlogging and complete submergence. When gas exchange with the atmosphere is limited, the constitutive production of ethylene ensures a robust early signal of coming limitations in O₂ as well as CO₂. In waterlogged to completely submerged plants, increases in ethylene drive changes in the anatomy and morphology of root systems that enhance tissue aeration, including the enhancement of root aerenchyma in a number of species (Yamauchi et al., 2018). Once O₂ levels fall beyond an undetermined cellular threshold, transcriptional activators of the group VII subclass of Ethylene Responsive Factors (ERF-VIIs) that are constitutively synthesized become stabilized, as reviewed in detail by Giuntoli and Perata (2018). This is due to a reduction in their conversion into an N-terminal degron that targets degradation by the N-end rule pathway of proteolysis (Gibbs et al., 2011; Licausi et al., 2011). ERF-VIIs activate the transcription of a number of genes, including enzymes of anaerobic metabolism, regulators of ROS, and plant-specific PLANT CYSTEINE OXIDASEs. The latter catalyze the first step in ERF-VII turnover through oxidation of an evolutionarily conserved N-terminal Cys to a Cys-sulfonic acid residue (White et al., 2017). Nitric oxide also is important in the conditional regulation of ERF-VII abundance (Giuntoli and Perata, 2018; Sasidharan et al., 2018; Wagner et al., 2018).

ERF-VIIs, ethylene, and other factors influence physiology and development under flooded conditions. The role of ERFs in an ethylene-activated developmental pathway was first shown in rice for the SNORKEL1/2 and SUBMERGENCE1 ERF-VIIs that promote or limit underwater shoot elongation growth, respectively (Xu et al., 2006; Hattori et al., 2009). *Arabidopsis* ERF-VIIs acting in conjunction with ethylene were shown to limit the transition from skoto- to photomorphogenesis, as well as the opening of the apical hook of seedlings (Abbas et al., 2015), a trait that could be advantageous in poorly aerated soil. New research from Eysholdt-Derzso and Sauter (2017) demonstrates that auxin-mediated upward bending of *Arabidopsis* roots under hypoxia is limited by the ERF-VII RAP2.12, revealing that they antagonize the establishment of an auxin gradient. Partially flooded semiaquatic plants typically develop highly porous adventitious roots that develop on stems of dicots or at the stem node of monocots (Yamauchi et al., 2018). These roots need to be near to the air-water interface to be well aerated. Remarkably, the young adventitious roots of partially submerged rice display strong upward growth due to a change in gravitational setpoint in the dark, but not in R, FR, or blue light (Lin and Sauter, 2018).

The importance of mitochondrial energy and redox state in signaling when O₂ is limiting is comprehensively discussed by Wagner et al. (2018). Their analysis complements the review by Schmidt et al. (2018) that highlights integration of responses to O₂ deficiency, including consequences of mitochondrial electron transport inhibition and ROS release. We are reminded that there are more than 200 proteins that are putative targets of the

O₂-dependent N-end rule pathway responsible for ERF-VII turnover and more than 350 O₂-dependent enzymes in Arabidopsis. The critical challenge of deciphering cellular dynamics in response to changing O₂ tension in a noninvasive manner for cellular and sub-cellular quantitation is discussed by Schmidt et al. (2018).

The decline in efficiency in ATP production per mol of Glc under low O₂ conditions is counterbalanced by catabolism of carbon skeletons. SnRK1-regulated endosperm starch catabolism is required to promote anaerobic metabolism during germination of rice seeds under extreme O₂ deficiency, and management of leaf starch catabolism is critical to submergence survival (Yu et al., 2015). The starchless plastidic *PHOSPHOGLUCOMUTASE* mutant was used in experiments that demonstrate a requirement for transitory leaf starch catabolism in submerged Arabidopsis rosettes that requires the ERF-VIIs but is independent of SnRK1 (Loreti et al., 2018).

CLOSING REMARKS

The increased understanding of the ability of plants to dynamically capture, transform, and manage energy to maximize growth provides avenues to meet the critical challenge of increasing yields in highly variable environments. Already, spatial regulation of T6P metabolism has been shown to improve the allocation of leaf photosynthate to developing kernels of maize (*Zea mays*) in varied environments (Nuccio et al., 2015). Advances based on computational modeling, precision monitoring, genotype characterization, gene manipulation, and metabolic engineering will accelerate progress toward these goals. We look forward to advancements centered on the plant's mastery of light and oxygen to fix carbon into energy to further benefit humanity.

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