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Into the Shadows and Back into Sunlight: Photosynthesis in Fluctuating Light

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Abstract

Photosynthesis is an important remaining opportunity for further improvement in the genetic yield potential of our major crops. Measurement, analysis, and improvement of leaf CO_2 assimilation (A) have focused largely on photosynthetic rates under light-saturated steady-state conditions. However, in modern crop canopies of several leaf layers, light is rarely constant, and the majority of leaves experience marked light fluctuations throughout the day. It takes several minutes for photosynthesis to regain efficiency in both sun-shade and shade-sun transitions, costing a calculated 10–40% of potential crop CO_2 assimilation. Transgenic manipulations to accelerate the adjustment in sun-shade transitions have already shown a substantial productivity increase in field trials. Here, we explore means to further accelerate these adjustments and minimize these losses through transgenic manipulation, gene editing, and exploitation of natural variation. Measurement and

analysis of photosynthesis in sun-shade and shade-sun transitions are explained. Factors limiting speeds of adjustment and how they could be modified to effect improved efficiency are reviewed, specifically nonphotochemical quenching (NPQ), Rubisco activation, and stomatal responses.

Contents

1. INTRODUCTION

Sink capacity: the plant's capability to utilize photosynthetically assimilated carbon in respiration and growth, including the formation of seed, fruit, and storage organs such as tubers

In silico: experimentation performed by computer simulation

Leaf CO_2 assimilation (A): the net rate of CO_2 uptake per unit leaf area ($\mu mol\ m^{-2}\ s^{-1}$)

Our title, "Into the Shadows and Back into Sunlight," describes the progression of this review of photosynthetic efficiency in fluctuating light but is also a metaphor for the attention that photosynthesis has received in crop improvement over the last few decades. Photosynthesis was viewed as a means to improve both food and energy supply in the 1960s and 1970s (196). However, failure to make progress, plus the views that the ability of a plant to utilize additional photosynthate, i.e., sink capacity, was likely limiting and that highly selected elite cultivars showed no better leaf photosynthetic rates than wild ancestors, placed a shadow over further work (68, 79, 188). In the intervening period, rapid progress in understanding limitations to photosynthesis at the biochemical and molecular levels, in addition to improved tools for measuring and analyzing photosynthesis in vivo and the emergence of the ability to probe the process in silico through high performance computing (16, 18, 66, 67, 166, 246, 253, 256, 266, 282, 288, 295, 305), opened the door to new approaches to engineering improved photosynthetic efficiency (163, 177, 242, 244). The bioengineered improvements in photosynthetic efficiency that have increased productivity and sustainability in replicated field trials (137, 165, 254, 298) have given further vigor to this effort. New among current approaches is a focus on nonsteady-state photosynthesis (191, 193, 249, 260, 307). Overwhelmingly, measurement and analysis of leaf CO_2 assimilation (A) have focused on steady-state photosynthesis under conditions of constant high light. For leaves within a crop canopy in the field, light is never constant. Here, leaves are subject to rapid changes in light due to intermittent cloud cover, dynamic self-shading caused by the movement of overlying leaves, and

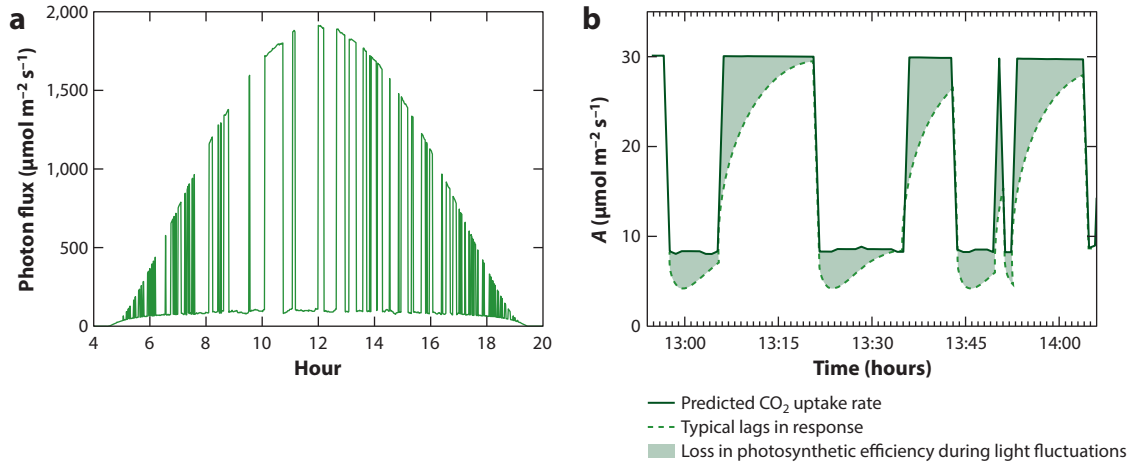

Figure 1

(*a*) Light at a point on a leaf in the second layer of a crop canopy. (*b*) Solid line shows the predicted leaf CO_2 uptake rate (*A*) from the light levels illustrated in panel *a*, assuming an instantaneous response. Dashed lines illustrate the typical lags in response. The differences between the solid and dashed lines represent the loss in photosynthetic efficiency during light fluctuations. Accumulated over one day for a crop canopy, these losses may amount to 10–40% (263, 281, 307). Data shown in graphs are from Reference 307.

the passage of the sun across the sky (249, 260, 281, 307). Adjustment to fluctuations in light is at the level of the individual chloroplast and stoma. At this resolution, fluctuations in light are almost instantaneous. In a canopy on a clear sky day, as the sun crosses the sky, one second a stoma or chloroplast is in full sunlight, the next in the shade of an overlying leaf. Yet adjustment of CO_2 assimilation to the change will take minutes (**Figure 1**). A leaf in the shadow of a single overlying leaf will typically receive only one-tenth of direct sunlight. Because of the slow adjustment of photosynthesis and stomata to these changes, leaves and canopies operate at an efficiency well below that achieved at steady state. Addressing this opens new opportunities for improving crop photosynthesis and sustainability in terms of water use and crop yield; some of these opportunities have now been achieved in field trials of engineered plants (137). This, however, is just a starting point, and the purpose of this review is to highlight further opportunities.

Why is this increased crop productivity needed? From the 1970s until 2014, the proportion of the global population that was calorie insufficient declined steadily. In 2014, this reversed and has steadily risen since, approaching one billion malnourished people, nearly 10% of the world population, in 2021. While such food shortages could be expected in conflict zones, numbers are also rising in nonconflict zones (64). The world is forecast to need 60% more food in 2050 than today, and, at current rates of increase in food crop yields per hectare, there could be a very substantial shortfall in supply (226, 227). Particularly affected are countries of sub-Saharan Africa and lower-income countries in Southeast Asia. Ironically, these are among the countries forecast to experience some of the greatest population growth and where agricultural production has already been most impacted by climate change (203). A further irony is that many of the food insufficient are farmers, feeding their families from a quarter- to half-hectare plot. One reliable way to ensure future supply and reverse the current rise in food insufficiency is to provide these farmers with seed that will increase sustainable yields per hectare (63, 267).

Steady state: constant environmental conditions, as opposed to nonsteady state

The 1950s and early 1960s saw large-scale famines, some due to conflict and poor policies, but others because regions simply could not produce enough food to support growing populations and demand. The Green Revolution provided the means to grow sufficient food and was the major

contributor to ensuring supply could meet demand for the next few decades. It was a genetic revolution, providing farmers with seed with a higher genetic yield potential and agronomy to realize the increased potential (62, 211). However, the technologies of the Green Revolution are meeting their biological limits (227). The major advance of the Green Revolution was breeding cultivars that partitioned more of their biomass into the part of the crop that is eaten, for example, the grains of major cereals. Much was achieved by dwarfing cultivars to invest less in stems and more in grain (211). Before the Green Revolution, the major grains had a harvest index of about 30% (i.e., 30% of their shoot biomass was grain). By the turn of this century, more typical harvest indices were 50–65%. If grain is to continue to be supported by some form of stem and structure, it is hard to see how much further improvement in harvest index can be achieved (61). In his 1997 address to the Royal Society, wheat physiologist Lloyd Evans looked at the prospect of doubling the food supply by the middle of this century and noted that "it is not apparent how a doubling of yield potential can be achieved unless crop photosynthesis can be substantially enhanced by genetic engineering" (61, p. 901). Photosynthesis, directly or indirectly the source of all of our food, is an obvious target. However, photosynthetic efficiency, even in the best elite cultivars, is less than one-third of its theoretical efficiency (306), so we are far from its biological limits. Further, the photosynthetic efficiency of elite cultivars today is not substantially different from that of their wild relatives and pre–Green Revolution cultivars, indicating that breeder selection has done little to improve this (79, 131). So why is there now a chance to improve photosynthesis?

While the pathways of photosynthetic electron transport (*J*), carbon metabolism, and nitrogen metabolism were largely elucidated more than half a century ago, innovations of the last two to three decades have allowed the identification of points of limitation and means to address these. Sufficient data have accrued to allow mathematical descriptions of all of the discrete steps, computational simulations, and in silico optimizations (120, 305, 308). In parallel, genomics, transcriptomics, metabolomics, and fluxomics have also provided insight into limitations and the means to address them (13, 25, 58, 120). Here, we assess the progress and potential in engineering improved photosynthetic efficiency within the leaf, first in sun-shade transitions and then in shade-sun transitions (**Figure 1*b***). We then consider the action of stomata, which frequently co-limit speeds of induction of photosynthesis on shade-sun transitions, while their slow rate of closure following sun-shade transitions lowers water-use efficiency.

Harvest index: the proportion of the shoot biomass that represents the harvested product

Electron transport (*J*): the rate of whole-chain photosynthetic electron transport in vivo (μmol m^{-2} s^{-1})

Induction: the rise in CO_2 uptake (*A*) of a leaf upon transfer from darkness or shade to a higher light level

Reactive oxygen species (ROS): unstable molecules that contain oxygen that can easily oxidize cellular components, such as hydrogen peroxide, singlet oxygen, and many organic peroxides

Nonphotochemical quenching (NPQ): the dissipation of absorbed light energy as heat

2. INTO THE SHADOWS

2.1. Nonphotochemical Quenching

In full sunlight, leaves receive more light energy than may be used in photosynthesis. If this excess energy is not dissipated, then a buildup of excited chlorophylls and highly reduced electron carriers in the photosynthetic electron transport chain occurs, leading to the formation of harmful reactive oxygen species (ROS) (136, 183, 259). Mechanisms collectively referred to as nonphotochemical quenching (NPQ) have evolved to dissipate this excess energy as heat, protecting the photosynthetic apparatus from such damage (44, 101, 159, 189, 194, 199, 230). The major form of and fastest-relaxing NPQ is energy-dependent quenching (*qE*) (135). Other processes contributing to NPQ that relax progressively more slowly (**Figure 2**) are zeaxanthin-dependent quenching (*qZ*) (198), state transitions (*qT*) (221), photoinhibition (*qI*) and photoinhibition-independent quenching processes such as *qH* (8, 170).

In a field canopy, *qE* is activated when the amount of incoming energy exceeds the capacity of electron sinks, as occurs during sunflecks. The threshold light level inducing this process is lowered when stresses, such as drought, nutrient deficiency, or temperature extremes, further limit photosynthesis (162). *qE* is therefore important for plant fitness (139), and its enhancement will

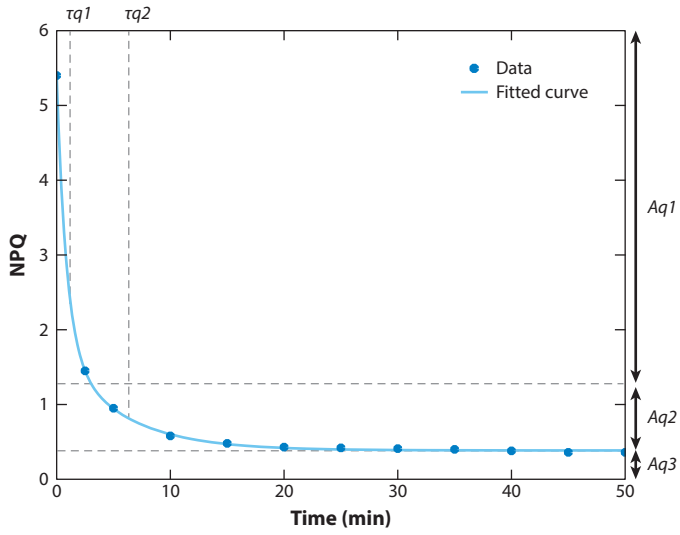

Figure 2

Calculating nonphotochemical quenching (NPQ) relaxation parameters. The graph depicts the relaxation of NPQ during 50 min of dark relaxation following high light treatment. Relaxation kinetics can be calculated by fitting a double exponential function (*blue line*), where components describe connected biological processes, with *Aq1* corresponding to fast-relaxing energy-dependent quenching (*qE*), *Aq2* capturing *qZ* and *qT*, and the constant *Aq3* representing long-term quenching, including *qI*. The half-lives of relaxation of *Aq1* and *Aq2* are determined by the parameters $\tau q1$ and $\tau q2$, such that $\text{NPQ} = Aq1^{(-\frac{1}{\tau q1})} + Aq2^{(-\frac{1}{\tau q2})} + Aq3$.

reduce photoinhibition (*qI*) (123, 158) and increase biomass production (102). However, too much *qE* can compromise photosynthesis by converting excitation energy that could be used for CO_2 assimilation into heat (102, 190, 193, 194, 224). The ancestors of today's crops largely evolved in resource-limited open habitats where there would be little self-shading. Today, most crops are grown at high population densities and produce canopies of several layers, such that most leaves will experience considerable intermittent self-shading (**Figure 1*a***). As a result, optimizing the amount of NPQ and the speed of its response to fluctuating light is an effective strategy to improve crop performance (190, 307). **Figure 1*b*** illustrates the cost this has on *A* during sun-shade transitions. Modeling of canopy lighting suggests an accumulated 10–40% loss of potential crop canopy CO_2 assimilation over the course of a day, compared to an instantaneous cessation of NPQ on the transition (281, 308).

2.2. Mechanism of Nonphotochemical Quenching

Detailed understanding of the mechanisms of NPQ is required to guide engineering approaches. The precise mechanism of *qE* remains controversial. However, knowledge of the molecular components involved in *qE* is sufficient to enable initial efforts at optimizing performance. *qE* is mediated by photosystem II subunit S (PsbS) (157), lumen pH, and a VAZ cycle involving interconversion of the xanthophylls: violaxanthin, antheraxanthin, and zeaxanthin. Activation and relaxation are modulated by changes in the thylakoid proton motive force, composed of a proton gradient (ΔpH) and electric field (Δψ) (257). Accordingly, proton motive force is controlled by the activity of the proton-pumping chloroplast adenosine triphosphate (ATP) synthase (119) and thylakoid ion transporters including K^+ efflux antiporter 3 (KEA3) (9), Voltage-dependent

Photosystem II subunit S (PsbS): a chlorophyll *a*/*b*–binding protein and an intrinsic component of photosystem II that strongly affects the amplitudes of nonphotochemical quenching

chloride channel 1 (VCCN1) and VCCN2 (52), Chloride channel e (ClCe) (93), and Phosphate transporter 4 family member 1 (PHT4;1) (10, 122, 219, 255). A ΔpH develops across the thylakoid lumen (27) on illumination, leading to protonation of PsbS (158) and activation of violaxanthin de-epoxidase (VDE) (83), in turn triggering the conversion of violaxanthin to zeaxanthin via antheraxanthin to activate quenching (42, 108).

Violaxanthin de-epoxidase (VDE): the enzyme that catalyzes the de-epoxidation of violaxanthin to zeaxanthin via intermediate antheraxanthin

Manipulation of ion transporters has therefore been suggested as a means of optimizing NPQ in a fluctuating light environment. Accordingly, overexpression of ion transporter KEA3 increased the rate of NPQ relaxation by accelerating the dissipation of ΔpH through the export of protons from the lumen (11). However, a constitutive increase in ion flow would reduce NPQ and linear electron flow by reducing ΔpH, decreasing protonation of PsbS and slowing proton pumping by the ATP synthase complex (37). Consequently, deregulation of KEA3 increased short-term carbon assimilation by reducing NPQ, but at the cost of photodamage during prolonged exposure to high light (271). It is therefore unclear that manipulation of the rate of formation of proton motive force could benefit crop growth, and these data emphasize the importance of continuing to advance modeling in concert with experimentation and measurement of NPQ to guide engineering efforts.

2.3. Measuring Nonphotochemical Quenching

A variety of spectroscopic methods have been developed to probe NPQ (19, 119, 181, 192). Most commonly, the different NPQ components (*qE*, *qT*, and *qI*) are determined by applying repetitive saturating light pulses during the transition from high light to dark and observing the decay kinetics during the quenching relaxation (**Figure 2**). Measurements of NPQ components are frequently based on the Stern-Volmer equation since this method is preferred in studies that evaluate plant stress physiology (134). Such measurements are traditionally done with the pulse-amplitude-modulated fluorometers that can work alone or be coupled with portable gas exchange systems, allowing the acquisition of chlorophyll fluorescence and gas exchange parameters simultaneously (137). However, these approaches are low throughput, and the increased need for high-throughput phenotyping to screen germplasm or multiple genetic transformation events has driven the development of chlorophyll fluorescence imaging techniques, which include systems based on pulse-amplitude-modulated imaging (204, 243), such as FluorCam (197), CF Imager (192), and other light-emitting diode (LED)-induced fluorescence imaging systems (109, 138).

2.4. Modeling Nonphotochemical Quenching

Modeling approaches have been used to clarify the mechanism of NPQ, simulate the influence of NPQ on photosynthetic efficiency, and estimate the loss of carbon assimilation by crop canopies. Mechanistic models have been used to simulate short-term NPQ, which induce and relax within a few minutes (**Figure 2**). Models found this type of NPQ to be associated with the content of PsbS (157), zeaxanthin, antheraxanthin (47, 162), lumen pH (112), and accumulation of lutein (176). However, some of the molecular mechanisms, and the interactions between components, remain unclear. Several mechanistic models were developed to study photosynthetic electron transport and short-term NPQ dynamics using differential equations (53, 141, 176, 250, 299, 308), where *qE* is assumed to be activated by zeaxanthin (52), de-epoxidized xanthophylls (zeaxanthin + antheraxanthin), protonated PsbS (52, 179, 299), and components triggered by lumen pH, including PsbS and VDE, described by a Hill equation. These models indicate that PsbS contributes to the fast response of NPQ to light fluctuations, while the xanthophyll cycle is more closely related to the slower, intermediate phase of NPQ (**Figure 2**). The further addition of lutein-dependent NPQ into a simplified biochemical model (155) suggested that both zeaxanthin and lutein affect NPQ independently.

As structural details of the photosystem II supercomplex were revealed, *qE* was incorporated within a membrane structure model of excitation transfer (20), which demonstrated that two-dimensional diffusion is needed to accurately simulate *qE* and the quantum yield of photosystem II primary photochemistry, where excitation energy is converted into chemical energy by charge separation. Although these models effectively explain dynamic chlorophyll fluorescence signals, without the restrictions on the use of electron transport products, ATP, and reduced nicotinamide adenine dinucleotide phosphate (NADPH) by carbon metabolism, the models were not able to directly estimate the effect of NPQ on CO_2 assimilation. Therefore, more comprehensive models (141, 180, 185, 186, 308) integrating the NPQ process into the whole photosynthetic system establish the relationship between NPQ and leaf CO_2 assimilation required to predict the effects on crop carbon gain and productivity.

Zeaxanthin epoxidase (ZEP): the enzyme that catalyzes the epoxidation of xanthophyll zeaxanthin to violaxanthin via intermediate antheraxanthin

Although some mechanisms are not fully understood, such as how lumen pH, PsbS, and lutein affect NPQ kinetics and how slower components emerge after *qE*, with better understanding of NPQ, mechanistic models continue to improve. Empirical models of *qI* and hypothetical canopy models have been used to estimate the loss of crop canopy CO_2 assimilation due to the slow relaxation of NPQ on sun-shade transitions. They suggest that *qI* reduces carbon fixation between 5% and 30% over a diurnal course (162, 285, 307). The significant limitation indicates a large potential for increasing canopy photosynthesis by optimizing NPQ. However, the accuracy of previous estimates was limited by simplified canopy structures and light distributions, and short-term NPQ dynamics were not incorporated. More recently, an actual three-dimensional canopy structure of soybean was integrated with forward ray tracing to predict the spatial dynamics of lighting across the canopy. With this dynamic lighting, combined short-term NPQ and *qI* limitations resulted in a predicted 9% and 11% reduction in canopy carbon assimilation on cloudy and sunny days, respectively (281). The three-dimensional canopy structure was also used to evaluate the role of PsbS in a rice canopy, accounting for altered canopy structure and the light environment (72). The simulation predicted an early growth advantage of PsbS overexpression and that manipulating photoprotective mechanisms can impact whole-canopy function. These models show that acceleration of the relaxation of NPQ on sun-shade transitions would potentially give large gains in crop canopy CO_2 assimilation.

2.5. Variation in Nonphotochemical Quenching as a Source for Crop Improvement

Models and measurements show that NPQ is sustained longer than necessary in the shade after a transition from direct sunlight at the cost of photosynthetic efficiency (306, 307). This may be overcome by accelerating the rate of NPQ relaxation through increase in the rate of conversion of zeaxanthin to violaxanthin on the transition from sun to shade. This could be achieved by increasing the activity of zeaxanthin epoxidase (ZEP). However, such an increase would also lower zeaxanthin content in full sunlight, remove protection against photodamage, and lessen capacity for scavenging of ROS. Researchers therefore reasoned that VDE and PsbS would also need to be upregulated to maintain protection in high light, while allowing faster relaxation of NPQ during sun-shade transitions (137). Subsequent combined overexpression of ZEP, PsbS and VDE in *Nicotiana tabacum* proved to accelerate both the induction of NPQ during a shade-sun transition and its relaxation during a sun-shade transition, resulting in an approximately 15% improvement in photosynthetic efficiency, measured as mol CO_2 assimilated per mol photon absorbed. In a replicated field trial, three independent transformation events showed significant 14–21% increases in productivity (137). This proof of principle spurred further interest in engineering this change in

crops and was subsequently demonstrated to provide substantial yield increases in maize, rice, and soybean (269). It has also raised the question of whether there is natural variation in the speed of NPQ relaxation that can potentially be exploited in breeding (279).

Studies on diverse genotypes of rice (123, 279), *Arabidopsis* (113, 116, 231, 272), and soybean (94, 95) have demonstrated the existence of substantial intraspecific variation in NPQ. In a genome-wide association study of NPQ capacity across a rice diversity set of 529 accessions, OsPsbS1 accounted for 40% of the variation in NPQ (279) with a mutator-like transposable element (MULE) in the promoter region associated with increased transcription appearing as a major factor (123, 201). However, differences in PsbS are insufficient to account for variation in other populations, and manipulating the VAZ cycle may not always result in increased performance (77). A greater understanding of the diversity of mechanisms driving variation and the conditions where VAZ manipulation would be beneficial is therefore required to assess the potential for this approach to improve crop plants (137). Given the dual role of de-epoxidated xanthophylls in both NPQ and ROS scavenging, impacts of manipulation on the latter role need to be understood.

Lutein epoxide cycle (LxL cycle): the interconversion of the de-epoxidated lutein with its epoxidated form, lutein epoxide

Photosynthetic photon flux density (PPFD): light expressed as photons (400–700 nm) reaching the leaf surface (μmol m^{-2} s^{-1})

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco): the enzyme that catalyzes the carboxylation and oxygenation of ribulose-1,5 bisphosphate (RuBP); all carbon assimilated in plant photosynthesis is through this enzyme

Stomatal conductance (g_s): quantifies the ease with which CO_2 can enter the leaf via the variable pores in the epidermis (stomata)

Mesophyll conductance (g_m): quantifies the ease with which CO_2 can move from the substomatal cavity to the site of carboxylation within the mesophyll

2.6. Diversity of Nonphotochemical Quenching Mechanisms

A wide diversity of NPQ mechanisms and responses have been described between photosynthetic organisms, allowing adaptation to ecological niches (15, 43, 45, 46, 127). In some plants, a second xanthophyll cycle, the lutein epoxide cycle (LxL cycle), operates in tandem with the universal VAZ cycle (29, 78, 124, 175, 176). Similar to the VAZ cycle, the LxL cycle is regulated by the antagonistic activities of VDE and ZEP, which also drive the interconversion between lutein epoxide (Lx) and lutein (98, 293). Both xanthophyll cycles respond to changes in photosynthetic photon flux density (PPFD) by modulating light harvesting and energy dissipation in photosynthetic antenna complexes; however, the LxL cycle operates on a much slower timescale, and its contribution to these processes is difficult to untangle from rapid VAZ-mediated responses (173). Introduction of the LxL cycle to *Arabidopsis* mutants lacking the VAZ cycle demonstrated the role of lutein in photoprotection and showed the role of Lx-enhanced light harvesting in low light (154, 155). Natural variations of the LxL cycle exist in a range of shade-tolerant, taxonomically diverse plants (175, 176), but most crops appear to lack an active LxL cycle and incorporate lutein in their photosystems despite the deep shade of their lower canopy. This inability to relax lutein-mediated photoprotection in low light reduces the efficiency of energy transfer to photosystem II reaction centers, causing dissipation of excitation energy that could be used in photosynthesis in the lower canopy (60, 110, 174). Engineering crops to accumulate Lx in the lower canopy to promote relaxation of photoprotective mechanisms conferred by lutein accumulation is therefore a promising target for further efforts to improve photosynthetic efficiency.

3. BACK INTO THE SUNSHINE: INDUCTION OF PHOTOSYNTHESIS ON SHADE-SUN TRANSITIONS

Induction describes the rise in photosynthesis to a new steady state as a leaf goes back into the sun after darkness or a period of shading (**Figures 1*b*** and **3*a***). During this phase, by definition, A is less than it is at steady state and therefore represents a loss of potential efficiency that may be described as forgone CO_2 assimilation. The speed of induction is affected by many processes, requiring increases in ribulose-1,5-biphosphate (RuBP) regeneration, RuBP carboxylase/oxygenase (Rubisco) activity, stomatal conductance (g_s) and mesophyll conductance (g_m). Simultaneously, there is need to avoid the damaging consequences of overexcitation of the photosynthetic apparatus. So here, induction of NPQ and capacity for removing ROS to a level sufficient to deal with the effects

of excess absorbed light energy are also critical (32, 114, 115, 210). Induction is a particularly vulnerable period since photosynthesis is removing less of the absorbed light energy than at steady state, and therefore speeding induction in itself will improve photoprotection. Rapid induction improves the margin of net CO_2 gain from intercepted quanta, i.e., radiation-use efficiency (306), by minimizing the CO_2 assimilation that is forgone when induction is slower (290).

3.1. Measuring and Analyzing Limitations in Induction

Photosynthetic induction can be conceived as the repeatable set of responses to an increase in PPFD and is usually measured in the context of step changes in PPFD from strongly light-limited (darkness or shade) to light-saturated (sun) photosynthesis (**Figure 3*a*,*b***; **Tables 1–3**).

Comparative measures of the impact of forgone A can be obtained from time series by establishing the time dependence of A as it responds to a step change in PPFD from shade to sun (**Figure 3**). Forgone A can be integrated across the induction, or comparisons can be made

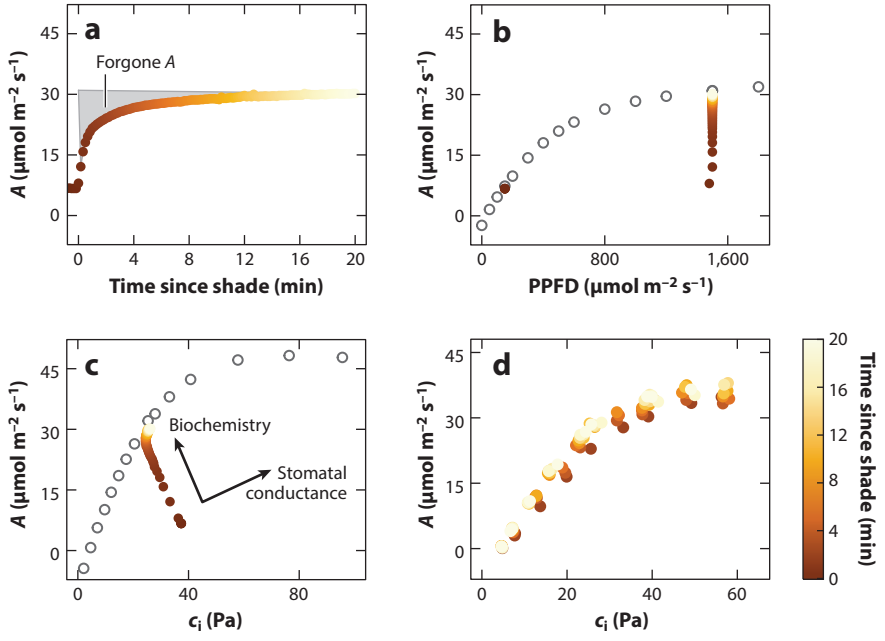

Figure 3

Induction (*a*) measured as a time series following a step change in photosynthetic photon flux density (PPFD) and indicating the concept of forgone assimilation that could have been achieved through instantaneous physiological adjustment. (*b*) The same induction sequence is shown but plotted onto the plane of the steady-state light response, where open symbols show the rate achieved at completion of induction at each light level. (*c*) The same induction replotted on the plane of the leaf CO_2 uptake (A)/intercellular CO_2 concentration (c_i) response. In this example, the initial, rapid phase of the sequence runs along a diagonal line that if drawn through the data would intersect the x axis at a CO_2 partial pressure in Pascals (Pa) equivalent to that outside the leaf, the supply function. The open symbols show the photosynthetic rate achieved at steady state for each c_i (67). Arrows show how this indicates a biochemical control over induction with little influence of stomatal conductance. Following the initial rapid phase, there is an extended period in which biochemistry and stomatal conductance act in conjunction to control the trajectory of the return to steady state. (*d*) Measurements made on a separate leaf demonstrate the shift in the A/c_i response, with measurements made at 2 min intervals from 2–20 min after shade, color coded to match timings in panels *a–c*. Data are for *Brassica oleracea*, from Reference 264.

Table 1 Analyses of crop plant induction using dynamic A/c_i approaches with parameters obtained

Reference	Species	Accessions per species	Preshade treatment	A/c_i parameters reported
252	*Glycine max*	2	Dark	$V_{c,max}$, J_{max}, c_i, l_s
251	*Glycine max*	3	Dark	$V_{c,max}$
263	*Triticum aestivum*	1	Fully induced	$V_{c,max}$, J, L_s, $c_{i,trans}$
236	*Triticum aestivum*	10	Fully induced	$V_{c,max}$, J, $c_{i,trans}$
264	*Brassica napus*, *Brassica oleracea*, *Brassica rapa*	1	Fully induced	$V_{c,max}$, $c_{i,trans}$
2	*Oryza sativa*	3	Dark	$V_{c,max}$, L_{SN}
39	*Manihot esculenta*	3	Dark	$V_{c,max}$, l_s

Abbreviations: A, leaf net CO_2 assimilation; c_i, intercellular [CO_2]; $c_{i,trans}$, c_i at which limitation transitions away from $V_{c,max}$; J, rate of electron transport; J_{max}, maximum rate of electron transport; l_s, stomatal limitation by differential method; L_s, stomatal limitation following Reference 67; L_{SN}, partitioning of stomatal and nonstomatal limitation following Reference 114; $V_{c,max}$, maximum Rubisco carboxylation rate.

based on the time taken to obtain, e.g., 50% or 90% of the steady-state A. Point comparisons are commonly expressed as induction states; however, alongside differences in experimental protocols, alternative normalizations to final A or the difference between sun and shade values of A (7, 210) make values for forgone A and induction states difficult to compare across studies. Induction can also be probed to evaluate its constituent processes. Key approaches using gas exchange measurements are partitioning of forgone A between stomatal and biochemical components (41, 270) and probing limitations due to Rubisco versus RuBP regeneration using induction under

Table 2 Studies and methodologies used to evaluate the contributions of biochemical and stomatal limitations during induction in crops

Reference	Crop species	PPFD sequence ($\mu mol\ m^{-2}\ s^{-1}$)	Analytical method
202	*Hordeum vulgare*	25 (>120 min); 800	Assumes a linear A/c_i response in calculating photosynthetic CO_2-use efficiency: $(A + R_d)/(c_i - \Gamma^*)$
171	*Coffea arabica*	Dark (360 min); 20 (5 min); 1,500	Assumes a linear A/c_i response to correct A to c_i observed at full induction using $A^* = [(A + R_d)(c_{i,f} - \Gamma^*)]/(c_i - \Gamma^*) - R_d$. Diffusional limitation ($A^* - A$) and biochemical limitation ($A_f - A^*$) are normalized to steady-state gross assimilation ($A_f + R_d$)
114	*Solanum lycopersicum*	Dark (60–120 min); 1,000	Nonlinear steady-state A/c_i response used to correct A to atmospheric [CO_2] (diffusional limitation) or final steady-state c_i (biochemical limitation), normalized to the change in A during induction ($A_f - A_i$)
277	*Helianthus annuus*	Dark (not specified, likely various); 1,000	Follows Reference 202
40; see also 41	*Gossypium hirsutum*, *Spinacia oleracea*, *Vicia faba*, *Vitis vinifera*	Dark (overnight); 25 (until steady state); 1,000	Differential method, partitioning limitation due to $V_{c,max}$ (one-point estimate assuming infinite g_m and Rubisco limited A) and g_{sc}
3	*Oryza sativa*	Dark (30 min); 50 (9 min); 1,500	Graphical comparison of $A^* = A(300/c_i)$. Simplified method assuming a linear A/c_i response through origin

Abbreviations: A, leaf net CO_2 assimilation; A^*, A corrected for limitation by stomatal diffusion; A_f, final A at the end of the induction period; A_i, initial A at the start of the induction; c_i, intercellular CO_2 concentration; $c_{i,f}$, final c_i at the end of the induction period; [CO_2], CO_2 concentration; Γ^*, CO_2 compensation point in the absence of R_d; g_m, mesophyll conductance; g_{sc}, stomatal conductance to CO_2; PPFD, photosynthetic photon flux density; R_d, day respiration; $V_{c,max}$; maximum Rubisco carboxylation rate.

Table 3 Gas exchange studies that have evaluated the kinetics of increasing Rubisco activity during induction in food crops

Reference	Crop species	Accessions per species	PPFD sequence ($\mu mol\ m^{-2}\ s^{-1}$)	Analytical method	Mean τ (s) (range given where there are multiple accessions/conditions)
290	*Spinacia oleracea*	1	690 (60 min); dark (10–60 min); 690	Analytical method of Reference 290	300
107	*Spinacia oleracea*	1	690 (60 min); dark-135 (45 min); 690	Analytical method of Reference 290	104–228
291	*Spinacia oleracea*	1	160 (45 min); various	Analytical method of Reference 290	103–298
187	*Spinacia oleracea*	1	Dark or 180 (>60 min); 1,200 [various c_i]	Analytical method of Reference 290	94–425
289	*Spinacia oleracea*	1	1,200 (60 min); various (30 min); 1,200	Analytical method of Reference 290	90–153
59	*Ocimum basilicum*	1	1,180 (steady state); 180 (0–40); 1,180 (c_a 25 Pa)	Analytical method of Reference 290	246 (199–338)
85	*Nicotiana tabacum*	1 (+antisense Rca)	110 (30 min); 1,200	Analytical method of Reference 290	118 (857)
86	*Nicotiana tabacum*	1	1,200 (60 min); 105 (30 min); 1,200	Equation of Reference 290 fit using nonlinear least squares	119
105	*Oryza sativa*	1 (+transgenic RbcS × 2)	1,800 (30 min); 60 (45 min); 1,800 (noting subambient inlet c_a of 25 Pa)	Analytical method of Reference 290	148 (161, 172)
294	*Oryza sativa*	1 (+2 transgenic overexpressing Rca; antisense Rca)	1,500 (30 min); 60 (45 min); 1,500	Analytical method of Reference 290	135–257 (94–174; 194–395)
76	*Oryza sativa*	1 (+transgenic: overexpressing Rca × 2)	1,800 (30 min); 60 (45 min); 1,800 (noting subambient inlet c_a of 25 Pa)	Analytical method of Reference 290	152 (130, 132)
252	*Glycine max*	7	Dark (overnight); 50 (steady state); 2,000	Diffusion-corrected $A^* = A(300/c_i)$: simplified method assuming a linear A/c_i response through origin	149–307
117	*Solanum lycopersicum*	1	Dark-200 (steady state); 1,000 (c_a varied: 20–80 Pa)	Diffusion-corrected A^* based on A/c_c response	76–256
263	*Triticum aestivum*	1	1,200 (steady state); 50 (30 min); 1,200	Analytical method of Reference 290	180–240
303	*Oryza sativa*	8	10 (assumed steady state); 1,200	Analytical method of Reference 290	132–1,369

Abbreviations: A^*, A corrected for limitation by stomatal diffusion; c_a, CO_2 concentration of air external to the leaf; c_c, chloroplast concentration; c_i, intercellular CO_2 concentration; Pa, Pascal; PPFD, photosynthetic photon flux density; Rca, Rubisco activase; RbcS, small subunit of Rubisco.

different CO_2 concentrations ($[CO_2]$) (35, 130). Common to these approaches is an interpretation of induction as a dynamic change in the response of A to intercellular CO_2 concentration (c_i), hereafter referred to as an A/c_i response (17, 128, 130, 202) (**Figure 3*c***; **Tables 1** and **2**).

Intercellular CO_2 concentration (c_i): the CO_2 concentration within the air spaces of the leaf

Maximum rate of carboxylation at Rubisco in vivo ($V_{c,max}$): the highest rate of CO_2 assimilation at Rubisco that a unit of leaf area can support in vivo under a given set of conditions ($\mu mol\ m^{-2}\ s^{-1}$)

Rubisco activase (Rca): the enzyme that activates Rubisco by removing sugar phosphate inhibitors from its catalytic sites

Gas exchange measurements that directly evaluate how the A/c_i response changes during induction (35) have recently been implemented in several crop species (**Table 1**). Details vary between experiments, but the common approach is to make a series of induction measurements, each at a different chamber inlet $[CO_2]$, allowing the construction of so-called dynamic A/c_i responses for different time points through induction (**Figure 3*c,d***). The approach enables the separation of stomatal limitations from those within the mesophyll through the induction, where biochemical limitations can be separated between the maximum rate of carboxylation $[CO_2]$ ($V_{c,max}$) equating to the maximum in vivo Rubisco activity, J, and triose-phosphate utilization (T_P) (263). The benefit of identifying such subprocesses or separating stomatal and biochemical limitations is that physiological targets for intervention are narrowed. This approach has shown differences between and within crop species in the key factors limiting speed of induction (202, 264).

Dynamic A/c_i measurements, while conceptually simple and providing a rich parameterization for understanding induction responses, are arduous to implement (252, 263). Where the primary biochemical limitation can be inferred or assumed, gas exchange time series can alternatively be used to good effect. Applications in crop species include partitioning or comparison of biochemical and stomatal limitations (**Table 2**). The slow phase biochemical limitation affecting photosynthesis during induction (**Table 3**) that is linked with the activity of the molecular chaperone Rubisco activase (Rca) (32, 85) can be modeled by predicting diffusion-corrected values for A. Classic, simplified approaches that obtain diffusion-corrected A by assuming linearity of the A/c_i response (85) have shown a reasonable match to dynamic A/c_i and Rubisco activity assays (263, 290). More accurate and powerful approaches are now being implemented by inversion of leaf photosynthesis models (41).

Practically, three significant complications impact data quality from leaf gas exchange measurements during induction. First, large step changes in irradiance affect the energy input to the leaf and therefore leaf temperature. This destabilizes both leaf temperature and the calculated vapor pressure deficit, with consequences for gas exchange system control loop feedback and estimates of g_s and, in turn, accuracy of c_i determination. Second, standard simplifications used to establish c_i based on leaf conductance to CO_2 assume that stomata are the primary pathway of both CO_2 and H_2O exchange, conditions that may be violated by stomatal closure during shade (87). Finally, in commonly used commercial open gas exchange systems, standard equation sets are used that assume a steady state in terms of gas concentrations measured from the leaf cuvette and/or reference air stream. During fast phases of induction, in particular the initial rise in assimilation that has been attributed to recovery of RuBP concentration (130, 239, 240), the $[CO_2]$ inside the gas exchange system cuvette can change so rapidly that longer system averaging times will smooth out substantial change and introduce lags in apparent cuvette $[CO_2]$ because of incomplete air turnover. Chamber air turnover in particular can be an issue where chamber volumes are relatively large, flow rates are low, and leaves are small or have low rates of CO_2 assimilation. Remedies include adjustment to limit the magnitude of PPFD change during sun-shade transitions while still ensuring a shift from subsaturating to saturating irradiance, which has the additional benefit that photoinhibition will be limited (114); calculation of chamber turnover times; and adjustment of protocols, including use of appropriate time windows in postprocessing to emphasize the process of interest. The duration, PPFD, and $[CO_2]$ during shade all affect initial g_s during induction. In protocols focused on biochemical limitations, adjusting these factors can be useful in establishing good initial conditions of adequate g_s for accurate and meaningful measurements (263, 264). Errors will be least when large leaf areas and minimal chamber volumes are used.

Time series measured during induction provide a wealth of physiological information. However, understanding speed of recovery on a shade-sun transition also requires understanding of speeds of deactivation on sun-shade transitions. On transfer back to shade, photosynthesis is no longer limited by the processes affecting light-saturated photosynthesis, yet changes in the capacity of these processes need to be measured to predict speeds of recovery after different durations of shade. For example, to quantify the rate of decrease in Rubisco activity or capacity for RuBP regeneration during shade, gas exchange measurements need to be made for a series of shade durations, and the post-shade induction state must be used to infer declines in the relevant processes (129, 290). Gas exchange equipment is more widely available to the plant physiology community, but in lab settings where enzyme activity assays are available, destructive sampling during shade may provide more direct data with similar efficiency (240). A recent study using high-throughput in vitro measurement of Rubisco activity in multiple leaf discs sampled with time after transfer to shade has shown the deactivation of Rubisco to be between two and seven times faster than previously assumed from indirect gas exchange measurements (262, 263). This suggests underestimation of the forgone A due to slow induction, since it shows that Rubisco deactivation occurs on a shorter timescale than previously realized, meaning that even with one minute of shade, A will require a significant time to recover on return to high light.

A significant limitation to direct estimates of in vivo induction of Rubisco activity has been the availability of methods for establishing g_m and therefore the response of A to chloroplast [CO_2] under dynamic conditions. Low precision and other methodological challenges mean that attempts to constrain g_m during induction using combined gas exchange and chlorophyll fluorescence through the variable J method (114) have so far lacked the accuracy needed to clearly identify induction dynamics. More promisingly, the use of isotope discrimination has recently provided a detailed analysis of g_m during shade-sun transitions in tobacco and *Arabidopsis* (233). Because methods of preconditioning are diverse, and bifurcate in particular within dynamic A/c_i studies (**Table 1**), it is particularly interesting that g_m responses measured by isotope discrimination were strongly affected by the preceding light environment. Relatively weak responses are observed when previously sun-exposed leaves are shaded, and strong g_m responses are observed in dark-adapted leaves that transition to shade before measuring induction (233).

3.2. Activation of Rubisco

The complex regulation of Rubisco activity involves carbamylation of catalytic sites, inhibition by certain sugar phosphates, and activation by Rca. In this section, the changes in the chloroplast stroma that occur when a leaf transitions from shade-sun-shade that directly impact Rubisco activity are discussed. Early in vitro studies showed that to efficiently catalyze the carboxylation and oxygenation of RuBP, Rubisco must be carbamylated. Carbamylation depends on the pH, [CO_2], and magnesium concentration ([Mg^{2+}]) of the chloroplast stroma (140, 166). The first step of carbamylation is binding of CO_2 to the ε-amino group of lysine 201 in the Rubisco catalytic site (168). CO_2 binding to this amino group is highly pH dependent, with binding almost nonexistent at pH 7.0 yet optimal above pH 8.0, thus corresponding to the pH changes of the stroma on transition from darkness to full sunlight (14, 167). It is unlikely that [CO_2] for carbamylation is limiting in the shade, since c_i is constant or rises slightly with decreasing light levels (286). This bound CO_2 is referred to as activator CO_2, distinct from the substrate CO_2. The carbamate formed by CO_2 binding creates an anionic amino group to which Mg^{2+} binds rapidly and stabilizes the otherwise unstable carbamate. Binding of both CO_2 and Mg^{2+} forms the catalytically competent carbamylated form of Rubisco. This is referred to as ECM, the enzyme catalytic site bound to activator CO_2 and Mg^{2+}, and is functionally distinct from the catalytic site free of CO_2 and Mg^{2+} (E). When

a leaf transitions from shade to sun, there is an increase in proton pumping from the chloroplast stroma to the thylakoid lumen, coupled with an increased flux of counterion Mg^{2+} from the lumen to the stroma (104, 133, 142, 156, 205, 215, 216, 245). These ion fluxes result in a more alkaline pH and increased [Mg^{2+}] local to Rubisco, promoting formation of ECM. These conditions are rapidly reversed, promoting decarbamylation to produce E, upon transition to low light (54, 262, 304). Importantly, the carbamylation of Rubisco catalytic sites in vivo is also dependent on RuBP concentration ([RuBP]) and the activity of Rca (218).

2-Carboxy-D-arabinitol 1-phosphate (CA1P): a sugar phosphate that inhibits the activity of Rubisco and plays a key role in its regulation

Water vapor pressure deficit (VPD): the difference (deficit) between the amount of moisture in the air and the amount the air at leaf temperature can hold

In addition to binding ECM prior to catalysis, the sugar phosphate substrate RuBP binds tightly and unproductively to the uncarbamylated catalytic site of E. Its concentration is saturating at moderate to high light but declines to subsaturating levels at low light and in darkness (32, 212). Subsaturating [RuBP] promotes Rubisco deactivation through dissociation of Mg^{2+} and CO_2 from catalytic sites (172, 217, 237). Tight binding of certain phosphorylated compounds to catalytic sites also inhibits Rubisco activity (reviewed in 26, 208). The best-known of these inhibitors is 2-carboxy-D-arabinitol 1-phosphate (CA1P), which in some species accumulates after at least one-hour exposure to low light and darkness (82, 184, 232). However, CA1P is not ubiquitous and is unlikely to accumulate to levels that cause significant inhibition of Rubisco when leaves are exposed to shade for shorter periods (<30 min). Thus, Rubisco can deactivate by decarbamylation (E) or formation of a dead-end complex by tight binding of RuBP to the uncarbamylated enzyme (E + RuBP = ER), depending on the balance between [RuBP] and [Mg^{2+}] and the ability of Rca to activate Rubisco.

Rca catalyzes the ATP-dependent removal of inhibitory compounds, such as RuBP or CA1P, from Rubisco catalytic sites that can then be carbamylated (228). The activity of Rca is regulated by the redox potential, adenosine diphosphate (ADP) to ATP ratio, and [Mg^{2+}] of the chloroplast stroma (90, 229, 301, 302), all of which change in response to the prevailing light level. Most plant species characterized to date contain more than one isoform of Rca (238). In both *Arabidopsis* and wheat, the Rca isoforms differ in their regulatory properties (32, 213, 241). *Arabidopsis* plants expressing only the Rca isoforms that are insensitive to redox modulation or inhibition by ADP (33, 300) and rice plants overexpressing Rca (76, 294) showed faster photosynthetic induction in low-to-high light transitions and grew faster under fluctuating light conditions than the wild-type forms from which they were derived.

The rate of CO_2 assimilation by Rubisco in a leaf is determined by its catalytic properties, abundance, and regulation. Previous efforts to enhance photosynthetic capacity by overexpressing Rubisco (235, 258), Rca (75, 76), or a CA1P phosphatase that dephosphorylates Rubisco inhibitors (160) have shown limited success, likely due in part to the negative correlation between Rubisco abundance and activation state (33). However, overexpression of both Rubisco and Rca resulted in enhanced photosynthesis and biomass production in rice at high temperature (220, 258). Careful selection of the Rca isoforms to overexpress will be necessary to efficiently activate Rubisco and increase photosynthesis in the fluctuating light of a crop canopy.

4. OPEN AND CLOSE THOSE DOORS FASTER BUT NOT SO WIDE

Stomata are the doors to gaseous exchange between a plant and the atmosphere, and they adjust aperture in response to both external and internal cues. Increasing light, lowering [CO_2], and lowering water vapor pressure deficit (VPD) are some of the stimuli that encourage stomatal opening. Closure is driven by low or decreasing light levels, high [CO_2] (5), and high VPD, as well as plant hormones such as abscisic acid, ROS, nitric oxide, Ca^{2+}, and pH signals (5, 30, 97, 146, 280, 296). However, these triggers rarely occur in isolation; therefore, stomatal responses are the results of an

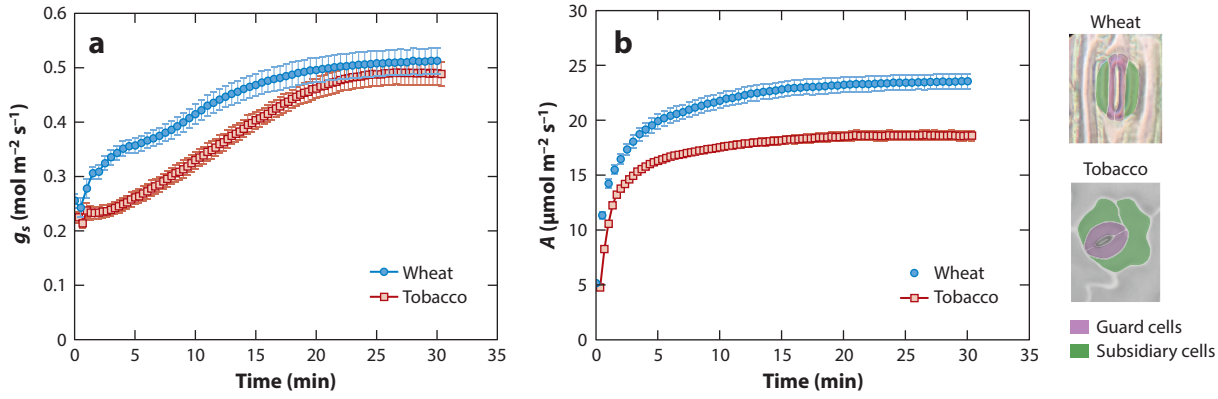

Figure 4

(*a*) Stomatal conductance (g_s) and (*b*) photosynthesis (A) in wheat (*blue circles*) and tobacco (*red squares*) in response to a step change in photosynthetic photon flux density (PPFD). Tobacco leaves were subjected to a step change in light from 100 μmol m^{-2} s^{-1} PPFD to 1,500 μmol m^{-2} s^{-1}, while wheat leaves were subjected to a step change in light from 100 μmol m^{-2} s^{-1} PPFD to 1,000 μmol m^{-2} s^{-1}. $n = 5$; error bars represent standard error. Guard cells (*purple*) and subsidiary cells (*green*) in the leaf epidermis of wheat and tobacco are shown.

integration of multiple signals in a hierarchical manner (143, 147, 151). Additionally, considerable variation in response times and magnitude of change exists both between and within species and leaves within the plant (1, 2, 39, 182). As noted above, stomata along with activation of Rubisco appear to be the major factors limiting the speed of induction of photosynthesis on shade-sun transitions and are thus the major causes of forgone CO_2 assimilation due to light fluctuation in crop canopies (**Figure 4**). Further, balancing stomatal opening with induction of photosynthesis within the mesophyll is clearly critical to water-use efficiency. If stomata open more rapidly than photosynthetic induction within the mesophyll, then more water will be lost than necessary; if too slowly, CO_2 assimilation will be forgone. Crops and their cultivars clearly differ in the extent to which stomatal opening limits photosynthetic induction (1, 2, 39, 182). The speed of stomatal closure on a sun-shade transition is typically an order of magnitude slower than the drop in CO_2 assimilation. This therefore has no effect on CO_2 assimilation but will sharply lower water-use efficiency in a crop canopy in the field.

Changes in stomatal aperture, and hence g_s, are brought about by modifications in guard cell turgor, driven by osmoregulatory pathways that move solutes and ions in and out of the cells, as explained in detail in Section 4.1. This alters solute and water potential, facilitating the movement of water into guard cells, causing them to swell and thus counteract the pressure exerted on them by surrounding epidermal cells (74). Mechanically, the asymmetric thickening of their walls causes paired guard cells to move away from each other, opening the stoma as their turgor pressure increases and closing the stoma as turgor decreases. The capacity of stomata to allow CO_2 and H_2O into and out of the leaf, expressed as g_s, is influenced by both anatomical features and biochemical processes (146, 178). The close relationship between photosynthesis and g_s is well established (80, 287); however, in a dynamic environment, such as the field, stomatal responses to changing conditions can be out of sync with photosynthesis (145, 209, 270). This will lower A (39, 182) and erode intrinsic water-use efficiency (iWUE) (51, 73, 96, 150, 151, 182). Therefore, increasing the rapidity of the response of g_s and optimizing the coordination between g_s and mesophyll demands for CO_2 in fluctuating light are gaining increasing attention as unexploited avenues to increase photosynthesis, crop water-use efficiency and productivity.

Intrinsic water-use efficiency (iWUE): the CO_2 gained by a leaf relative to water lost through the stomata, where iWUE = A/g_s

4.1. What Influences the Speed of Stomatal Responses?

Stomatal density (SD): the number of stomata per unit leaf area

Epidermal patterning factor (EPF): encodes plant-specific secretory peptides, several of which play a role in controlling stomatal density and patterning in the epidermis

The rapidity of stomatal responses is governed by a combination of biochemical, anatomical, and structural components of the guard cells, as noted above. Changes in guard cell turgor are driven by the uptake and release of solutes and ions, typically K^+, malate, and sucrose, which alter osmotic potential and water influx (22). The number and activity of transporters and/or ion channels determine the capacity for solute transport and therefore influence the rapidity of stomatal movements (23, 24, 38, 84, 144, 219, 265). Anatomical features, including stomatal density (SD), the presence or absence of subsidiary cells, and the size and geometry of guard cells, also impact stomatal responses (21, 88, 146). Smaller stomata, frequently associated with higher SD, often exhibit faster responses than larger stomata (65, 73, 121), although this is most evident when comparing closely related species (57, 182). The relationship between size and speed is based on a greater surface-area-to-volume ratio in smaller stomata, which lowers the solute flux requirement for movement (65, 73, 225). The dumbbell shape of grass guard cells also results in a high surface-area-to-volume ratio, allowing faster movement than the kidney-shaped guard cells of dicotyledonous plants (31, 81, 96, 118, 182). Smaller guard cells in C_4 crops may bring a double benefit. Unlike those of C_3 crops, leaves of C_4 crops are saturated by the elevated $[CO_2]$ of today's atmosphere, so g_s can be reduced to lower water loss without affecting CO_2 uptake (164, 214). Engineering or breeding for smaller stomata in these species would increase water-use efficiency in both steady-state and nonsteady-state conditions (152). Adjacent subsidiary cells are key to faster movement in the dumbbell-shaped guard cells of grasses, acting as a local reservoir of solutes and ions that can move rapidly between the two cell types. This gives a rapid alteration of turgor pressure in the guard cells while simultaneously removing the back pressure from the subsidiary cells (73, 222). Finally, structural components, including actin filaments (56, 99, 103, 125) and cell wall properties (34, 292) that influence the shape of the guard cells, also affect the rapidity and magnitude of change in g_s. Carter et al. (34) argued that stomatal cell wall thickening at the poles is more important for efficient stomatal opening than the commonly accepted view that radial thickening is the key structural factor regulating stomatal aperture. Additionally, actin filaments within guard cells, which control fusion of smaller vacuoles into a large vacuole, as found in some species and required for osmoregulation, also influence the speed of stomatal responses and overall g_s (106, 111).

4.2. Can the Speed of Stomatal Responses Be Manipulated?

Several laboratories have produced plants with differences in SD that have translated into different g_s responses to changing conditions (e.g., 21, 48, 92, 261); however, these studies have often only considered steady-state g_s, and only a handful have investigated the impact on stomatal kinetics in fluctuating light. By overexpressing epidermal patterning factor 9 (EPF9) or knocking out EPF1 in rice, plants with greater stomatal densities and faster stomatal responses to changes in light intensity were produced (234). Among EPFs, stomatal size was only reduced in the EPF9-overexpressing plants, supporting the theory that smaller stomata are not a prerequisite for fast responses (146, 182, 303). Alterations in SD can also influence stomatal patterning and clustering, which can be detrimental to stomatal function and rapidity (50, 153, 207) due to decreased capacity for solute fluxes (206), higher metabolic cost (144, 207, 225, 276), and water uptake requirements (91). On the other hand, the stomata of the patterning mutant *wer1-1*, in which the surface location of the guard cells is elevated above the subsidiary, open and close much faster than those of the wild type (275). This was attributed to the ectopic nature of the guard cells, which removed back pressure from adjacent cells. All of these studies suggest the existence of optimal SD, size, and positioning to facilitate rapid stomatal movement. However, genetic manipulations that produced large changes in SD in *Arabidopsis* were counterbalanced by changes in aperture such that

steady-state g_s was unaffected (33). A reasonable assumption would be that such compensatory mechanisms also hold true for the speed of response, and it may therefore be more appropriate to focus on functional/metabolic targets. For example, *Arabidopsis* was engineered to overexpress PATROL1 (126), which encodes a factor that regulates the localization of the guard cell plasma membrane H^+-ATPase (89). Because PATROL1 is essential for ion fluxes, its overexpression resulted in faster stomatal responses to changes in PPFD.

Manipulation of solute transfer and ion channels within the stomatal complex represents another possible target to improve the speed of stomatal responses. For example, knockout mutants of the Slow anion channel 1 gene (SLAC1), which encodes a stomatal anion channel involved in stomatal closure, exhibited higher rates of stomatal opening in rice (294). A further example includes monosaccharide/proton symporters in the plasma membrane in *Arabidopsis*, which are required for glucose imports from the mesophyll into the guard cells and are linked to rapid stomatal movements (70). However, the correlation between the speed of stomatal response and the speed of solute flux and accumulation may not be direct (146). A systems modeling approach (36, 100, 273, 278, 283) has demonstrated that manipulating a single channel or transporter might not be sufficient to achieve the desired changes in rapidity, as fluxes or transport of ionic species is often linked to other channels and membrane voltage changes. Therefore, multiple channel manipulation may be required, along with the consideration that increasing solute flux for rapid stomatal movement also required a balanced and coordinated ionic exchange at both the plasma membrane and tonoplast (144). This modeling approach provides a useful tool for identifying multiple and/or novel targets for manipulation as well as a platform for testing potential synthetic biology strategies. For example, guard cell expression of a synthetic light-gated K^+ channel (BLINK1) resulted in the production of plants with faster stomatal opening and, in turn, faster photosynthetic induction (207).

In subsidiary cells, K^+ channels in the plasma membrane inversely polarized with guard cells facilitate rapid K^+ fluxes during stomatal movements (169). Reciprocal concentration gradients of abscisic acid between the two cell types also appear to be involved in the more rapid stomatal responses of grasses to changes in light intensity (200, 223). Subsidiary cells also play an important role in signaling, for example, via stomatal closure in maize leaves through drought-induced H_2O_2 accumulation (297), while another study showed feedback regulation between stomatal movements and photosynthesis via a subsidiary cell glucose transporter (CST1) (278). These studies suggest that alterations to fluxes or signaling pathways linking guard and subsidiary cells represent another unexploited target to increase the speed of g_s response in induction of photosynthesis (28, 146, 200, 222).

Several studies have shown that photorespiratory processes are involved in modifying g_s (55, 69, 268), suggesting that manipulation of the photorespiratory pathway could be useful to explore stomatal kinetics and coordination between g_s and A. Direct manipulation of guard cell–specific metabolism may increase the speed of g_s, as demonstrated by modified starch breakdown in guard cells, which has been shown to be essential for rapid, blue-light-dependent opening early in the day (71). Blue light is 20 times more effective in inducing opening compared to red light, and recent work has demonstrated that it not only causes faster opening but also effects a wider opening (247, 274). However, this may not be the case for all species (49, 274). These findings suggest strengthening the blue light response as a route to increasing the speed of stomatal opening, although the biological components of these pathways and species-specific regulatory mechanisms may first need to be understood before these approaches can be exploited.

In summary, there are several routes for the potential manipulation of stomatal behavior, in terms of both the magnitude and rapidity of response, to improve photosynthetic induction. These involve adjustments to guard cell or stomatal anatomy; solute flux; and signaling, biochemical, and

osmoregulatory pathways. In addition, the underlying mesophyll photosynthetic capacity needs consideration because the mesophyll itself could provide a signal and trigger for stomatal responses (80, 149), along with guard cell photosynthesis (148). The close coordination between mesophyll demands for CO_2 and stomatal behavior is critical for both carbon capture and water-use efficiency. Improving the rapidity of stomatal responses to changing stimuli is a novel and mostly unexploited target for improving crop production and resource use; however, further research is needed on which target or combination of targets is required to fully exploit this in bioengineering and breeding.

5. CONCLUSION

Early research described the induction of photosynthesis on dark/shade-sun transitions, and provided means to analyze some of the limitations. However, only recently has the importance of nonsteady-state responses to light intensity fluctuations for improving crop photosynthesis and resource-use efficiency been recognized. Manipulations, some resulting in successful field demonstrations of productivity, are now proving the value of this recognition. The previous sections have highlighted the many opportunities to be exploited. Most so far have involved the transgenic upregulation of enzymes and other proteins. With rapid improvements in in silico engineering of proteins through atomistic simulation (6), coupled with accelerating editing capabilities (12, 195, 284), improving the kinetics and properties of native proteins may replace upregulation of gene expression. Investigation of natural variation may deliver two benefits. First, the application of genome-wide association studies can identify genetic elements affecting increased speeds of adjustment of photosynthesis to sun-shade and shade-sun transitions. Second, by identifying such elements, research will facilitate genomic selection of improved germplasm.

To further advance improvements in efficiency under nonsteady-state light conditions, important knowledge gaps need to be filled. The slow phases of NPQ relaxation account for a long tail on the recovery of CO_2 assimilation to its steady-state level in the shade. Determining the key processes, particularly in crops, will be important to further improvements. In partially limiting the speed of induction of CO_2 assimilation (233), g_m appears important, but from a very limited number of studies focused on model systems. Its importance in crops and degree of variation within crop germplasm needs to be established. At the same time, a better fundamental understanding of the dominant control, within the mesophyll, affecting g_m is needed if it is to be manipulated in crops. Rca clearly plays a key role in induction, and considerable progress has been made in understanding its isoforms and how these might be manipulated. Its efficacy clearly varies between and within species. Understanding the basis of efficacy differences will again inform editing. What makes faster stomata and the genes that affect stomatal size and number are understood but now need to be tested in crops.

Finally, to return to why photosynthesis as a means to improve crop production fell into the shadows, improved efficiency of carbon assimilation is only of benefit if the crop can use it to make more of the harvested product (248). Evidence that modern cultivars would benefit strongly from an increased supply of photosynthate comes from season-long open-air [CO_2] enrichment experiments, in free-air CO_2 enrichment (FACE) facilities. Because C_3 photosynthesis is CO_2 limited, the elevation of [CO_2] increases net photosynthesis (161). In both rice and soybean, a general trend was found in that older varieties did indeed appear to be sink limited with little yield response, while the most recent and productive varieties showed strong yield responses with approximately 20% increases in grain per unit ground area (reviewed in 4). This provides strong evidence that breeders have, or are able, to develop yield potential to utilize increased photosynthate supply. Obtaining yield potential, the maximum yield a crop can produce at a location when

in the absence of biotic and abiotic stresses, is perhaps a rare situation. However, the experience of the Green Revolution and beyond is that raising genetic yield potential on average raises achieved yields, not only in years with the best growing conditions but also in the worst years (e.g., 132). In summary, addressing the efficiency of crop photosynthesis in conditions of fluctuating light has much previously overlooked promise in providing improved sustainable crop yields.

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