Into the shadows and back into the sunlight – Photosynthesis in fluctuating light.

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Abstract

Photosynthesis appears the major remaining opportunity for further improvement the genetic yield potential of our major crops. The focus in measurement, analysis and improvement of leaf CO_2 uptake (*A*) has been on rates in steady-state and saturating light. However, in modern crop canopies of several leaf layers light is rarely constant. There are delays of several minutes in adjustment of efficiency both in sun-shade and shade-sun transitions, costing a calculated 10 – 40% of potential crop carbon uptake. Transgenic manipulations to accelerate the adjustment in sun-shade transitions have already shown substantial productivity increase in field trials. Here we explore means to accelerate these adjustments and minimize these losses, through transgenic up-regulations, editing and exploitation of natural variation. Measurement and analysis of photosynthesis in sun-shade and shade-sun transitions are explained. Factors, dominating these transitions and how they could be modified to effect improved efficiency are reviewed: non-photochemical quenching, Rubisco activase and stomatal apparatus.

Keywords: Photosynthesis, Crop productivity, Non-photochemical quenching, Rubisco, Stomata, Photosynthetic induction, genetic engineering, crop breeding

1. INTRODUCTION

Our title, into the shadows and back into the sun, describes the progression of this review in dealing with photosynthetic efficiency in fluctuating light. However, it is also a metaphor for the attention photosynthesis has received in crop improvement over the last few decades. Photosynthesis was viewed as a means to improve both food supply and energy in the 60s and 70s (200). However, failure to make progress, plus the view that ability of the 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 the wild ancestors, placed a shadow over further work (69; 80; 192). In the intervening period, rapid progress in understanding limitations to photosynthesis at the biochemical and molecular level, and improved tools for measuring and analyzing photosynthesis *in vivo* together with simulation of the process through high-performance computing(17; 19; 67; 68; 167; 251; 259; 262; 271; 286; 292; 299; 310), opened the door to new approaches to engineering improved photosynthetic efficiency(164; 179; 247; 249). The demonstration of bioengineered improvements in photosynthetic efficiency that have increased productivity and sustainability in replicated field trials(138; 166; 260; 302), has given further vigor to this effort. New among current approaches is a focus on non-steady-state photosynthesis (195; 197; 255; 266; 311). The overwhelming majority of measurement and analysis of leaf CO_2 uptake (*A*) has focused on steady-state photosynthesis, under conditions of constant high light. However, in a crop canopy in the field light is never constant. Most leaves in modern dense crop canopies are subject to rapid changes in light due to intermittent cloud cover, and dynamic self-shading caused by the movement of overlying leaves and the passage of the sun across the sky (255; 266; 285; 311). Adjustment to fluctuations in light is at the level of the individual chloroplast and individual stoma. At this resolution, fluctuations in light are rapid. When considering 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 to the change will take minutes (Fig. 1b). Moving into the shadow of a single overlying leaf will typically decrease light to about 1/10th of direct sunlight. Because of the slow adjustment of photosynthesis, leaves and canopies operate at an efficiency well below that achieved at steady-state. Addressing this, however, opens new opportunities for improving crop photosynthesis, sustainability and yield. Accelerating the ability of the leaf to adjust has improved photosynthetic efficiency and crop productivity in the field(138). This, however, is just a starting point and the purpose of this review is to highlight many further opportunities to gain much more.

What is the need for this? From the 70s until 2014 the proportion of the global population that were calorie insufficient declined. In 2014 this reversed and has steadily risen since, reaching 690

million or 8.9% of the world population by 2019. While such increases could be expected in conflict zones, numbers are also rising in non-conflict zones(65). 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 would be a very substantial shortfall in supply(230; 231). Particularly affected are countries of sub-Saharan Africa and poorer countries of SE 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(207). A further irony is that many of the food insufficient are farmers, feeding their families from a half- to one-acre plot. A certain way of insuring future supply and reversing the current rise in those that are food insufficient is to provide seed that will increase their crop production(64; 225). The 50s and early 60s 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; 214). However, the technologies of the Green Revolution are meeting their biological limits(231). The major Green Revolution advance was breeding our major crops so that more of their biomass was partitioned into the part of the crop we eat, for example the grains of our major cereals. Much was achieved by dwarfing; shorter stems and more grain(214). Before the Green Revolution the major grains had a harvest index of about 30%, that is to say 30% of their shoot biomass was grain. By the turn of this century, more typical harvest indices were 50-65%. If there is to be some stem and structure to support grain it is hard to see how further improvement in harvest index could be achieved(61). In his 1997 address to the Royal Society, the eminent wheat physiologist, Lloyd Evans, looked at the prospect of achieving the need for a doubling of food supply by the middle of this Century. To quote from his article "it is not apparent how a doubling of yield potential can be achieved unless crop photosynthesis can be substantially enhanced by genetic engineering". Photosynthesis would appear on the surface as an obvious target. It is directly or indirectly the source of all of our food. Further, its efficiency even in our best elite cultivars is less than 1/3 of theoretical(309), so we are a long way from its biological limits. Yet the photosynthetic efficiency of elite cultivars today is little different from that of their wild relatives and pre-green revolution cultivars(80; 132). So why is there now a chance to improve photosynthesis?

While the pathways of photosynthetic electron transport, carbon metabolism and nitrogen metabolism were largely elucidated more than a half-century ago, innovations of the last two to three

decades have allowed identification of points of limitation and means to address these. Sufficient data have accrued to allow mathematical description of all the discrete steps, computational simulation and *in silico* optimization (121; 310; 312). In parallel, genomics, transcriptomics, metabolomics and fluxomics have also provided insight to limitations and means to address these (14; 26; 58; 121). Great strides in the efficiency of genetic engineering of crops have allowed test-of-concept in crop field trials(138; 260; 302). Rapid advances in *in vivo* measurement and analysis of photosynthesis, in particular modulated chlorophyll fluorescence, now allows high-throughput analysis and selection of predicted photosynthetic phenotypes from multiple transformation events(17; 184; 185). This has proved particularly valuable in the case of photosynthetic efficiency in fluctuating light(138). Here we assess progress and potential in engineering improved photosynthetic efficiency within the leaf, first in sun-shade transitions and then in shade-sun transitions (Fig. 1b). We then consider the action of stomata, which frequently co-limit speeds of induction of photosynthesis on shade-to-sun transitions, while their slow rate of closure following sun-shade transitions, lowers water use efficiency.

2. INTO THE SHADOWS

Non-photochemical quenching (NPQ)

In full sunlight leaves receive more light energy than may be used in photosynthesis. If this excess energy is not dissipated, the result will be a build-up of highly reduced electron carriers in the photosynthetic electron transport chain, leading to the formation of harmful reactive oxygen species (137; 187; 265). Mechanisms have evolved to dissipate excess energy as heat, protecting the photosynthetic apparatus from damage, collectively referred to as non-photochemical quenching (NPQ) (45; 102; 160; 193; 198; 203; 234). The major form of NPQ, and fastest relaxing, is energy-dependent quenching (qE)(136). Other processes contributing to NPQ that relax progressively more slowly (Figure 2) are zeaxanthin-dependent quenching (qZ)(202), state transitions (qT)(224), and photoinhibition independent quenching (qH) (9; 171).

In chloroplasts in a field crop canopy, qE is activated when the amount of incoming energy exceeds the capacity of electron sinks, as occurs during sun flecks. 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 (140), and its enhancement can reduce photoinhibition (124; 159) and increase biomass production (103). However, too much qE can compromise photosynthesis, by converting excitation energy that could be used for CO_2 fixation into heat (103; 194; 197; 198; 228). The ancestors of today's crops largely evolved in resource limited open habitats

where there would be little self-shading. Today most are grown at high population densities and produce canopies of several layers, such that most leaves will experience considerable and often intermittent self-shading (Figure 1a). 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 (194; 311). Figure 1b illustrates the cost this has on the efficiency of CO_2 uptake on sun-shade transitions. Modeling of canopy lighting suggests an accumulated 15 – 40% loss of potential crop canopy carbon acquisition over the course of day, compared to an instantaneous cessation on NPQ on the transition (285; 312).

Mechanism of NPQ

Detailed understanding of the mechanisms of NPQ are required to guide engineering approaches. qE is mediated by PsbS (158), lumen pH and a VAZ cycle, involving interconversion of the xanthophylls violaxanthin (V) antheraxanthin (A) and zeaxanthin (Z). Build-up of a proton gradient (ΔpH) across the thylakoid lumen (28) leads to protonation of PsbS (159) and activation of violaxanthin de-epoxidase (84) triggering the conversion of V to Z via A to activate quenching (48; 109). The precise mechanism of qE remains controversial. However, sufficient progress has been made in understanding the molecular components involved in qE to enable initial efforts at optimizing performance.

Activation and relaxation of NPQ is not instantaneous, but modulated by changes in the thylakoid proton motive force (*pmf*)(263), which is controlled by the activity of the proton pumping chloroplast ATP Synthase (120), and thylakoid ion transporters including KEA3 (10), VCCN1/2 (53), ClCe (94) and PHT4;1 (123) as reviewed previously (11; 222; 261). Manipulation of ion transporters has therefore been suggested as a means of optimizing NPQ in a fluctuating light environment. Accordinlgly, overexpression of ion transporter KEA3, increased the rate of NPQ relaxation by speeding up dissipation of ΔpH through export of protons from the lumen (12). However, increasing the proportion of *pmf* stored as electric field can result in increased photodamage (38), and deregulation of KEA3 caused increased short term carbon assimilation at the cost of higher rates of photodamage (275). It is therefore unclear that manipulation of the rate of formation of *pmf* could benefit crop growth.

Measuring NPQ

A variety of spectroscopic methods have been developed to probe NPQ (21; 120; 183; 196). While NPQ values can be obtained with a saturating flash on dark-adapted leaves followed by a single saturating flash in illuminated leaves, 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 (135). Such measurements are traditionally done with the Pulse Amplitude Modulated (PAM) fluorometers that can work alone or be coupled with portable gas exchange systems, allowing the acquisition of chlorophyll fluorescence and gas exchange parameters simultaneously. However, the increased need for high-throughput phenotyping has driven the development of chlorophyll fluorescence imaging techniques, which include systems based on PAM imaging (208; 248), such as: FluorCam (201), CF Imager (196), and LED induced fluorescence (110; 139). These allow high-throughput imaging of speeds of relaxation of NPQ across germplasm panels in conventional breeding for improved speeds to relaxation and in screening multiple genetic transformation events where improved NPQ relaxation on sun-shade transitions is targeted.

Modeling NPQ

Modeling approaches have been used to further elucidate the mechanism of NPQ, simulate the influence of NPQ on the whole photosynthetic system, and estimate the loss of carbon fixation by crop canopies. Mechanistic models have been used to simulate the 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 (158), zeaxanthin (Z), antheroxanthin (A), (47; 162), lumen pH (113) and accumulation of lutein (178). 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 (54; 142; 178; 256; 303; 312), where qE is assumed to be activated by Z (53), de-epoxidized xanthophylls (Z+A), protonated PsbS (53; 181; 303), and components triggered by lumen pH described by a Hill equation. These models indicate PsbS to contribute to the fast response of NPQ to light fluctuations, while the xanthophyll cycle is more closely related to the slower response; early phase of qM (Figure 2). Further addition of lutein-dependent NPQ into a simplified biochemical model (156), suggested both zeaxanthin and lutein affect NPQ independently.

As structural details of the PSII supercomplex were revealed, qE was incorporated within a membrane structure model of excitation transfer (20), which demonstrated that two-dimensional diffusion is also important for accurately simulating qE and quantum yield. Although these models effectively explain dynamic chlorophyll fluorescence signals, without the restrictions on the use of

electron transport products, ATP and NAPH.H by carbon metabolism, the models were not able to directly estimate the effect of NPQ on CO_2 uptake. Therefore, more comprehensive models (142; 182; 189; 190; 312) integrating the NPQ process into the whole photosynthetic system, establish the relationship between NPQ and leaf carbon assimilation required to predict the effects on crop carbon gain and productivity.

Although some mechanisms are not fully understood, such as how lumen pH, PsbS and lutein affect NPQ kinetics, and how slower components emerge after the qE, with better understanding of NPQ, mechanistic models continue to improve. Empirical models of photoinhibition (qI) and hypothetical canopy models have been used to estimate the loss of carbon fixation in crop canopy, qI reduces carbon fixation between 5 to 30% over a diurnal course (162; 289; 311). The significant limitation indicated 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 3D 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 (285). The 3D canopy structure was also used to evaluate the role of PsbS in a rice canopy, accounting for altered canopy structure and the light environment (73). The simulation predicted an early growth advantage of PsbS over-expression 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 carbon assimilation by crop canopies.

Variation in NPQ as a source for crop improvement

Models and measurements show NPQ is sustained longer than necessary in the shade after a transition from direct sunlight at the cost of photosynthetic efficiency (309; 311). This could be overcome by accelerating the rate of NPQ relaxation by increasing 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, and remove protection against photodamage and lessen scavenging of reactive oxygen species (ROS). It was therefore reasoned that violaxanthin de-expoxidase (VDE) and PsbS would also need to be up-regulated to maintain protection in high light, while allowing faster relaxation of NPQ on a sun-shade

transitions(138). Subsequent over-expression of these three genes in *Nicotiana tabacum* proved to both accelerate induction of NPQ on a shade-sun transition and its relaxation on a sun-shade transition, resulting in a ca. 15% improvement in photosynthetic efficiency, measured as mol CO_2 assimilated per mol photon absorbed. In a replicated field trial, three independent events of this transformation showed significant 14 – 21% increases in productivity(138). This proof of principle spurred further interest in engineering this in crops and was subsequently demonstrated to provide substantial yield increases in maize, rice and soybean (273). It has also raised the question of whether there is natural variation in the speed of NPQ relaxation for potential exploitation in breeding(283).

Studies on diverse genotypes of rice (124; 283), Arabidopsis (114; 117; 235; 276) and soybean (95; 96) have demonstrated the existence of substantial variation in NPQ within species. The insertion of a MULE-like element in the promoter of OsPsbS1 in Japonica rice varieties, was found to account for 40% of the variation in NPQ found in rice populations (283) by increasing transcription of PsbS (124; 205). 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 (78). A greater understanding of the diversity of mechanisms driving variation and the conditions where VAZ manipulation would be beneficial are therefore required to assess the potential for this approach to improve crop plants. Given the dual role of de-epoxidated xanthophylls in both NPQ and ROS scavenging, impacts of manipulation on the latter role also need to be understood.

Diversity of NPQ mechanisms

A wide diversity of NPQ mechanisms and responses have been described between photosynthetic species, allowing adaptation to ecological niches (16; 43; 44; 46; 128). In some plants, a second xanthophyll cycle called the lutein epoxide cycle (LxL cycle) operates in tandem with the universal VAZ cycle (30; 79; 125; 177; 178). Similar to the VAZ cycle, the LxL cycle is regulated by the antagonistic activities of VDE and ZEP which drive the interconversion between lutein epoxide (Lx) and lutein (L)(99; 297). Both xanthophyll cycles respond to changes in light intensity 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 and robust VAZ-mediated responses (175). Introduction of the LxL cycle to Arabidopsis mutants lacking the VAZ cycle helped define the role of L in photoprotection and provides new evidence of Lx-enhanced light harvesting in low light (155; 156). Natural variations of the LxL cycle exist in a range of shade-tolerant, taxonomically

diverse plants (177; 178), but most crops lack an intact LxL cycle and incorporate L in their photosystems despite the deep shade of their lower canopy. This inability to relax L-mediated photoprotection in low light reduces the efficiency of energy transfer to PSII reaction centers causing dissipation of excitation energy that could be used in photosynthesis in the lower canopy (60; 111; 176). Engineering crops to accumulate Lx in the lower canopy to promote relaxation of photoprotective mechanisms conferred by L 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 steady-state as a leaf goes back into the sun after darkness or a period of shading (Figure 1b; 3a). During this phase, by definition, photosynthetic CO_2 uptake is less than at steady-state and therefore represents a loss of potential efficiency that may be described as forgone carbon loss. While loss of efficiency between a sun-shade transition and regaining steady-state is largely due to the time taken to remove NPQ, induction is affected by many processes. These include induction of photosynthetic electron transport rates in the thylakoid membrane; 2) light activation of Calvin-Benson cycle enzymes, in particular Rubisco; 3) accumulation of intermediates of carbon metabolism; 4) stomatal opening and 5) increasing mesophyll conductance(42).

Measuring and analyzing limitations in induction

Photosynthetic induction can be conceived as the repeatable set of responses to an increase in photosynthetic photon flux density (PPFD), and is usually measured in the context of step-changes in PPFD from strongly light-limited (shade) to light-saturated (sun) photosynthesis (Figure 3a & b). Consequently, 'induction' represents a series of compensatory changes necessary to achieve the full rate of CO_2 assimilation that the increase in light can support: increased RuBP regeneration, Rubisco activity, stomatal conductance and mesophyll conductance. These combine with increased protection against the damaging consequences of over-excitation of the photosynthetic apparatus that results from photon absorption in excess of capacity for photochemical quenching, i.e. it requires as increase in non-photochemical-quenching (NPQ) and availability of compounds that can remove reactive oxygen species (33; 115; 116; 213). The involvement of these explicitly protective processes, highlights that from a physiological perspective rapid induction can be viewed as a stress minimising process. The flipside, from the perspective of maximising crop efficiency, is that rapid induction improves the margin of net CO_2 gain from intercepted quanta, i.e., radiation use efficiency(309) by minimising CO_2 assimilation that is 'forgone' when induction is slower(294).

Comparative measures of the impact of forgone assimilation can be obtained from time series by establishing the time dependence of net CO_2 assimilation (A, µmol m^{-2} s^{-1}) as it responds to a step change in PPFD from shade to sun (Fig. 3). Forgone A can be integrated across the induction, or comparisons can be made 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 use of normalisations to final A or the difference between sun and shade values of A(8; 213) applied to forgone assimilation and induction states make values 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(42; 274), and probing limitations due to Rubisco or RuBP regeneration using induction under different [CO_2]s (36; 131). Common to these approaches is an interpretation of induction as a dynamic change in the response of A to [CO_2] (particularly intracellular [CO_2], c_i, hereafter referred to as an A/c_i response)(18; 129; 131; 206) (Figure 3c; Tables 1 & 2).

Gas exchange measurements that directly evaluate how the A/c_i response changes during induction (36) 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 at different chamber inlet [CO_2], allowing the construction of so-called dynamic A/c_i responses for different time points in induction (Figure 3c & d). The approach enables separation of stomatal limitations from those within the mesophyll through the induction, where biochemical limitations can be separated between $V_{c,max}$ (the maximum rate of carboxylation by Rubisco), J (the rate of electron transport limiting RuBP regeneration) and T_P (triose-phosphate utilization)(268). The benefit of identifying such sub processes or separating stomatal and biochemical limitations, is that physiological targets for intervention, for decreasing forgone CO_2 assimilation in crops, are narrowed down. There is evidence that biochemical limiting factors affecting induction and steady-state A, differ between plants, including among and within crop species (206; 269).

Dynamic A/c_i experiments, while conceptually simple and providing a rich parameterisation for understanding induction responses, are arduous to implement. 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 (Tables 2). Prediction of diffusion-corrected values for A that can be used to model the slow-phase biochemical limitation affecting photosynthesis during induction (Table 3) is linked with activity of the molecular chaperone Rubisco activase (*Rca*)(33; 86). Classic, simplified approaches that obtain diffusion-

corrected *A* by assuming linearity of the *A*/c_i response (86) have shown a reasonable match to dynamic *A*/c_i and Rubisco activity assays(268; 294); however, because the slope of the *A*/c_i response saturates as c_i increases, these approaches will be increasingly prone to error as ambient [CO_2] increases(115; 294). More accurate and powerful approaches are now being implemented by inversion of *A*/c_i equations (42).

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 vapour pressure deficit, with knock-on consequences for system control-loop feedback and estimates of stomatal conductance and particularly c_i. 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(88). 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, the initial rise in assimilation that has been attributed to recovery of RuBP turnover (131; 244; 245), the [CO_2] inside the cuvette can change so rapidly that longer system averaging times will average-out substantial change, or lags in apparent cuvette [CO_2] will arise because of incomplete turnover. Chamber 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 assimilation. Remedies include adjustment to limit the magnitude of PPFD change during sun-shade transitions to limit photoinhibition while still ensuring a shift from sub-saturating to saturating irradiance(115), calculation of chamber turnover times, and adjustment of protocols, including use of appropriate time-windows in post-processing to emphasize the process of interest. The duration, PPFD, and [CO_2] during shade all affect initial stomatal conductance during induction. In assays focused on biochemical limitations, manipulating these factors can be useful in establishing good initial conditions of adequate stomatal conductance for accurate and meaningful measurements(268; 269). Alternatively, explicit consideration of cuticular conductance can be used in sensitivity analyses or to more fully parameterise the gas exchange model for greater accuracy(131; 172)

Time series measured during induction provide a wealth of physiological information. By contrast, because shade results in an immediate transition to light-, rather than enzyme activity-limited photosynthesis, using gas exchange to understand loss of induction during shade requires more extensive experiments more closely resembling the effort needed to generate dynamic *A*/*c*i responses.

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 used to infer declines in the relevant processes(130; 294). 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 data with a similar degree of efficiency(245).

A significant limitation to direct estimates of *in vivo* induction of Rubisco activity has been the availability of methods for establishing mesophyll conductance (g_m) and therefore the response of A to chloroplast [CO_2] (c_c) 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(115)] have so far lacked the precision needed to clearly identify induction dynamics. More promisingly, use of isotope discrimination has recently provided a detailed analysis of g_m during shade-sun transitions in tobacco and Arabidopsis(237). Because methods of pre-conditioning 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(237).

Activation of Rubisco

The complex regulation of Rubisco activity involves carbamylation of catalytic sites, inhibition by certain sugar-phosphate derivatives and activation by the molecular chaperone Rubisco activase (Rca). Some additional cellular components are known to interact with and affect the activity of Rubisco. Here, the changes in the chloroplast stroma that occur when a leaf transitions from shade-sun-shade to directly impact Rubisco activity are discussed. As reviewed previously (241), the coordinated regulation of CO_2 fixation and electron transport activity enables plants to maintain metabolites at optimal levels and respond rapidly to changes in the prevailing environment. Recent evidence suggests that the regulation of primary metabolism would benefit from some adjustment to cope with the increasing environmental volatility (253). One avenue predicted to result in significant improvement in crop productivity is through maintaining high CO_2 assimilation of Rubisco and speeding the rate of adjustment of Rubisco activity in response to changes in PPFD.

Early in vitro studies on the biochemistry of Rubisco(141; 167), showed that to be catalytically competent to catalyze the carboxylation or oxygenation of ribulose-1,5-bisphosphate (RuBP), Rubisco must be carbamylated. Carbamylation depends on the pH, CO_2 and Mg^{2+} concentrations of the chloroplast stroma. The first step of carbamylation is the binding of CO_2 to the ε-amino group of lysine 201 in the Rubisco catalytic site (169). This amino group has a distinctly alkaline p*K*, meaning that binding of CO_2 is minimal at pH 7.0 and optimal above pH 8.0 (15; 168). It is unlikely that CO_2 for carbamylation is limiting in the shade, since intercellular [CO_2] (c_i) is constant or rises slightly with decreasing light levels (290), This binding of CO_2 to Rubisco is referred to as "activator" CO_2, distinct from the substrate CO_2, The carbamate formation by CO_2 binding promotes changes the charge of the amino group. The subsequent binding of Mg^{2+}, to the now anionic amino group, occurs rapidly and stabilizes the otherwise unstable carbamate. Binding of CO_2 and Mg^{2+} forms the catalytically competent carbamylated form of Rubisco. This is referred to as ECM: enzyme catalytic site bound to activator CO_2 and Mg^{2+}. 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 increased flux of Mg^{2+} from the lumen to the stroma (105; 134; 143; 157; 209; 218; 219; 250). These ion fluxes result in a more alkaline pH and increased [Mg^{2+}] at the site of Rubisco, promoting carbamylation. These conditions are rapidly reversed, promoting decarbamylation, upon transition to low light (55; 308). Importantly, the carbamylation of Rubisco catalytic sites *in vivo* is also dependent on [RuBP] and the activity of Rca (221)

In addition to binding ECM prior to catalysis, the sugar-phosphate substrate RuBP binds tightly and unproductively to the uncarbamylated catalytic site. Its concentration is saturating at moderate to high light but declines to sub-saturating levels at low light and in darkness (33; 215). Sub-saturating [RuBP] promote Rubisco deactivation through dissociation of Mg^{2+} and CO_2 from catalytic sites (174; 220; 242). Tight binding of certain phosphorylated compounds to catalytic sites can also inhibit Rubisco activity (reviewed in (27; 211)). 2-carboxy-D-arabinitol-1-phosphate (CA1P) accumulates in some plant species after relatively periods of at least 1h exposure to low light and darkness ((83; 188; 236)). 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, catalytic site free of CO_2 and Mg^{2+}) or formation of a dead-end complex by tight-binding of RuBP to the uncarbamylated enzyme (ER), depending on the balance between [RuBP] and [Mg^{2+}], and the ability of Rca to activate Rubisco.

Rca catalyses the ATP-dependent removal of inhibitory compounds from Rubisco catalytic sites, which can then be carbamylated (232). The activity of Rca is regulated by the redox potential, ADP/ATP ratio and [Mg^{2+}] of the chloroplast stroma (91; 233; 305; 306), all of which change in response to the prevailing light level. Most plant species characterized to date contain more than one isoform of Rca (243). In both Arabidopsis and wheat, the Rca isoforms differ in their regulatory properties (33; 216; 246). Arabidopsis plants expressing only the Rca isoforms that are insensitive to redox-modulation or inhibition by ADP (34; 304) and rice plants overexpressing Rca (77; 298) showed faster photosynthetic induction in low to high light transitions and grew faster under fluctuating light conditions.

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 (239; 264), Rca (76; 77) or a CA1P phosphatase that dephosphorylates Rubisco inhibitors (161) have shown limited success, partly due to the negative correlation between Rubisco abundance and activation state (34). However, overexpression of both Rubisco and Rca resulted in enhanced photosynthesis and biomass production in rice at high temperature (223; 264). 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. STOMATA

Stomata are the gatekeeper to gaseous exchange between the plant and the atmosphere, and adjust aperture in response to both external and internal cues. Increasing light, low [CO_2] and low 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] (6), high VPD as well plant hormones such as abscisic acid (ABA), reactive oxygen species (ROS), nitric oxide, Ca^{2+} and pH signals (6; 31; 98; 147; 284; 300). However, these triggers rarely occur in isolation and therefore stomatal responses are the results of an integration of multiple signals in a hierarchical manner (144; 148; 152). Additionally, considerable variation in response times and magnitude of change exists both between and within species, and leaves within the plant(2; 3; 40) (1; 52; 63; 66; 180; 186). As noted above, stomata along with activation of Rubisco, appear the major factors limiting the speed of induction of photosynthesis on shade to sun transitions, and are thus the major causes of forgone carbon fixation due to light fluctuation in crop canopies. 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, too slow and carbon assimilation will be forgone. Crops, and cultivars within crops, clearly differ in the extent to which stomatal opening limits photosynthetic induction (2; 3; 40; 186). While speed of stomatal closure on a sun-shade transition is unlikely to affect the typically order of magnitude faster drop in CO_2 assimilation, the speed with which stomatal closure adjusts, will have a strong effect on field canopy water use efficiency.

Changes in stomatal aperture are brought about by modifications in guard cell turgor, driven by sophisticated osmoregulatory pathways that move solutes and ions in and out of the cells. This alters solute and water potential facilitating the movement of water into the guard cells causing them to swell and thus overcome the pressure of the surrounding epidermal cells (75). Mechanically, the asymmetric thickening of the walls, causes the guard cells to move away from the stoma as their turgor pressure increases and close as it decreases. The capacity of stomata to allow CO_2 and H_2O into and out of the leaf is expressed as stomatal conductance (g_s) and is influenced by both anatomical features as well biochemical processes (147; 180). It is well-established that there is a close relationship between photosynthesis and g_s (81; 291), however in a dynamic environment such as the field, stomatal responses to changing conditions can be an order of magnitude slower than photosynthetic responses (146; 212; 274) which can limit carbon assimilation (40; 186) and erode intrinsic water use efficiency (iWUE). iWUE is a measure of CO_2 gained relative to water loss through stomata, $W_i = A/g_s$ at the leaf level (52; 74; 97; 151; 152; 186). Therefore, increasing the rapidity of stomatal and g_s responses and/or optimizing the co-ordination between g_s and mesophyll demands for CO_2 in light fluctuations is increasingly gaining attention as a currently unexploited avenue to increase photosynthesis, water use efficiency and crop productivity.

What influences the speed of stomatal responses?

The rapidity of stomatal responses is governed by a combination of anatomical, structural and biochemical components of the guard cells. Stomatal movements are caused by changes in guard cell turgor driven by the uptake and release of solutes and ions, typically K^+, Malate and sucrose, which alter osmotic potential and water influx (23). The number and activity of transporters and/or ion channels determine the capacity for solute transport and therefore influences the rapidity of stomatal movements (24; 25; 39; 85; 145; 222; 270). Anatomical or morphological features, including stomatal density, the presence or absence of subsidiary cells and the size and geometry of guard cells also impact stomata responses (22; 89; 147). Stomatal density (SD) is the number of stomata, per unit leaf surface

area. Smaller stomata, frequently associated with higher densities, often exhibit faster responses than larger stomata (66; 74; 122) although this may depend on how closely species are related (57; 186). 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 (66; 74; 229). This also allows the faster movement of the dumbbell shaped guard cells of grasses compared to the kidney shaped ones of dicotyledonous plants (32; 82; 97; 119; 186). Smaller guard cells in C4 crops may bring a double benefit. Unlike C3 crops, leaves of C4 crops are saturated by the elevated [CO_2] of today's atmosphere, such that g_s can be reduced to lower water loss without affecting CO_2 uptake (165; 217). Here engineered or bred smaller stomata could serve to increase efficiency of water use in both steady-state and non-steady-state conditions (153). The faster speed of movement in the dumbbell shaped guard cells of grasses is further enhanced by a local reservoir of solutes and ions, provided by adjacent subsidiary cells, which 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 (74; 226).

Structural components, including actin filaments (100; 104; 126)(Eisinger et al., 2012) and cell wall properties (35; 296) which influence the shape of the guard cells, also affect the rapidity and magnitude of change. Carter et al. (35) advocated that stomatal cell well thickening at the poles rather than the traditional idea of radial thickening is critical to facilitate rapid movements, whilst 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 (107; 112).

Can the speed of stomatal responses be manipulated?

Several laboratories have produced plants with differences in stomatal density that have translated into different g_s responses to changing conditions(e.g. (22; 49; 93; 267)), however these studies have often only considered "steady state" g_s values and only a handful have investigated the impact on stomatal kinetics, and particularly fluctuating light. Manipulating two members of Epidermal Patterning Family (over expressing EPF9 and knocking out EPF1) in rice, Sakoda et al. (238) produced plants with greater stomatal densities and reported faster stomatal responses to changes in light intensity in both mutants. Interestingly stomatal size was only reduced in the EPF9 OE plants, supporting the theory that smaller stomata are not a pre-requisite for fast responses (147; 186; 307). Alterations in SD can also influence stomatal patterning and clustering which can be detrimental to stomatal function and rapidity (51; 154; 210) through decreased capacity for solute fluxes (Papanatsiou et al., 2016),

higher metabolic cost (145; 210; 229; 280) and water uptake requirements (92). On the other hand, Vialet-Chabrand et al. (279) showed that the stomatal patterning mutant *wer1-1* (in which the surface location of the guard cells relative to the subsidiary is altered), open and close much faster than WT which was attributed to the ectopic nature of the guard cells relative to epidermal cells, removing back pressure. All of these studies suggest the existence of an optimal stomatal density and size to facilitate rapid stomatal movement. However, Bussis et al. (31) demonstrated that changes in aperture counterbalanced alterations in stomatal density, which resulted in similar steady state g_s. A reasonable assumption would be that such compensatory mechanisms also holds true for the speed of response and it may therefore be more appropriate to focus on functional/metabolic targets. For example, Kimura et al., (127) using Arabidopsis over-expressed PATROL1, which encodes a factor that regulates the localization of the guard cell plasma membrane H^+-ATPase (90). This is essential for ion fluxes and its over-expression resulted in faster stomatal responses to changes in light intensity.

Several studies have shown that photorespiratory processes are involved in modifying g_s (56; 70; 272), suggesting that manipulation of the photorespiratory pathway could be useful to explore stomatal kinetics and co-ordination between g_s and A. Direct manipulation to 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 opening early in the day (72). Blue light is 20x more effective inducing opening compared to red light driven stomatal behavior and recent work has demonstrated that it is not only faster, but of greater magnitude (252; 278). However, this may not be consistent across all species (50; 278). These findings suggest that strengthening the blue light response could also be a route to increasing the speed of stomatal opening, although the biological components of these pathways and species specific regulatory mechanisms need first to be understood before these approaches can be exploited.

Manipulation of solute transfer and ion channels within the stomatal complex represents another possible target to improve the speed of stomatal responses. For example, knock out mutants of SLAC1 which encodes a stomatal anion channel involved in stomatal closure exhibited higher rates of stomatal opening in rice (298). A further example includes monosccharide/proton symporters (STP1 and 4) in the plasma membrane in Arabidopsis which are required for glucose imports from mesophyll into the guard cells and are linked to rapid stomatal movements (71). However, the correlation between the speed of stomatal response and the speed of solute flux and accumulation may not be direct (147), with a systems modelling approach (37; 101; 277; 282; 287) demonstrating that manipulating a single channel or transporter might not be sufficient to achieve the desired changes in

rapidity. This model provides a useful tool for identifying multiple and/or novel targets for manipulation as well as providing 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 (210).

In subsidiary cells, K^+ channels in the plasma membrane inversely polarized with guard cells facilitate rapid K^+ fluxes during stomatal movements (170), and reciprocal concentration gradients of ABA between the two cell types appear also involved in the more rapid stomatal responses of grasses to changes in light intensity (204; 227). Subsidiary cells also play an important role in signaling, for example stomatal closure in maize leaves through drought induced H_2O_2 accumulation (301), and feedback regulation of stomatal behavior via a glucose transporter (cst1) (282). These studies suggest that alterations to fluxes between guard and subsidiary cells or signaling pathways represent another unexploited target to increase the speed of g_s response in induction of photosynthesis (29; 147; 204; 226).

In summary, there are several routes for potential manipulation of stomatal behavior in terms of both the magnitude and rapidity of response to increase photosynthetic induction. These involve adjustments to guard cell or stomatal anatomy, signaling, biochemistry and osmoregulatory pathways. However, there must be close account of underlying mesophyll photosynthetic rates and capacity. This is because the mesophyll itself could provide a signal and trigger for stomatal responses (150), along with guard cell photosynthesis (149). The close co-ordination 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 targets or combination of targets are required to fully exploit this for future breeding programs.

5. CONCLUSION

While early work described induction of photosynthesis on dark/shade-sun transitions, and provided means to analyze some of the limitations, only recently has the importance of non-steady-state responses for improving crop photosynthesis and resource use efficiency been recognized. Manipulations, some resulting in successful crop field demonstrations, are now proving the value of this recognition. The previous sections have highlighted the many opportunities to be exploited. Most so far have involved transgenic up-regulation of enzymes and other proteins. With rapid improvements in *in silico* engineering of proteins through atomistic simulation(7), coupled with accelerating editing capabilities(13; 199; 288), improving the kinetics and properties of native proteins may replace this.

Investigation of natural variation may deliver two benefits. First, by application of genome wide association study (GWAS) identify genetic elements affecting increased speeds of adjustment of photosynthesis to sun-shade and shade-sun transitions. Secondly, by identifying such elements allow genomic selection of improved germplasm.

To further advance improvements in efficiency under non-steady state light conditions, important knowledge gaps need to be filled. The slow phases on 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. Mesophyll conductance (g_m), appears important in partially limiting the speed of induction of CO_2 assimilation(237), but from a very limited number of studies, and these focused on Arabidopsis. 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 influence, within the mesophyll, of g_m is needed if it is to 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 from species to species and even within crops. Understanding the basis of efficacy differences will again inform editing. There is understanding of what makes faster stomata, and at least of the genes that affects stomatal size and number, which now clearly need to be tested in crops.

Finally, and to revert to the point made in our first paragraph as to why photosynthesis as a means to improve crop production fell into the shadows, improved efficiency of carbon gain is only of benefit if the crop can use it to make more of the harvested product(254). Evidence that modern cultivars would benefit strongly from increased supply of photosynthate comes from season-long open-air [CO_2] enrichment experiments, in so-called Free-Air CO_2 Enrichment (FACE) facilities. Because C3 photosynthesis is CO_2-limited, elevation of [CO_2] increases net photosynthesis (163). In both rice and soybean a general trend was found, in that older varieties did indeed appear sink-limited with little yield response, while the most recent and productive varieties showed strong yield responses with ca. 20% increases in grain per unit ground area (reviewed: (5)). This provides strong evidence, that breeders have, or are able, to develop yield potential to utilize increased photosynthate suppy. Yield potential, is the maximum yield a crop can produce at a location when in the absence of biotic and abiotic stresses, 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. the best years, but also in the worst achieved, but also the

minimum yields (e.g. (133)). In summary, addressing efficiency of crop photosynthesis in conditions of fluctuating light has much, and overlooked, promise in providing achieved improved crop yields.

Tables

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

Ref.	Species	Accessions per species	Pre-shade treatment	A/c_i parameters reported
(258)	*Glycine max*	2	Dark	$V_{c,max}$, J_{max}, c_i, l_s
(257)	*Glycine max*	3	Dark	$V_{c,max}$
(268)	*Triticum aestivum*	1	Fully induced	$V_{c,max}$, J, L_s, $c_{i,trans}$
(240)	*Triticum aestivum*	10	Fully induced	$V_{c,max}$, J, $c_{i,trans}$
(269)	*Brassica napus*, *B. oleracea*, *B. rapa*	1	Fully induced	$V_{c,max}$, $c_{i,trans}$
(3)	*Oryza sativa*	3	Dark	$V_{c,max}$, L_{SN}
(40)	*Manihot esculenta*	3	Dark	$V_{c,max}$, l_s

$V_{c,max}$, maximum Rubisco carboxylation rate; J_{max}, maximum rate of electron transport; c_i, intercellular [CO_2]; J, rate of electron transport; l_s, stomatal limitation by differential method; L_s, stomatal limitation following(68); L_{SN} partitioning of stomatal and non-stomatal limitation following (115); $c_{i,trans}$, c_i at which limitation transitions away from $V_{c,max}$

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

Ref.	Crop species	PPFD sequence (PPFD units: µmol m^{-2} s^{-1})	Analytical method
(206)	*Hordeum vulgare*	25 (>120 min); 800	Assumes linear A/c_i response in calculating photosynthetic CO_2 use efficiency: $(A + R_d)/(c_i - \Gamma^*)$
(173)	*Coffea arabica*	dark (360 min); 20 (5 min); 1500	Assumes linear A/c_i response to correct A to c_i observed at full induction using $A^* = (A + R_d)(c_i - \Gamma^*)/(c_i - \Gamma^*) - R_d$. Diffusional limitation (A* − A), and biochemical limitation ($A_{max} - A^*$) are normalised to steady-state gross assimilation
(115)	*Solanum lycopersicum*	dark (60-120 min); 1000	Non-linear steady-state A/c_i response used to correct A to atmospheric [CO_2] (diffusional limitation) or final steady-state c_i (biochemical limitation), normalised to the change in A during induction ($A_f - A_i$).
(281)	*Helianthus anuus*	dark (not specified, likely various); 1000	Follows Ögren & Sundin
(41) See also (42)	*Gossypium hirsutum*; *Spinacia oleracea*; *Vicia faba*; *Vitis vinifera*	dark (overnight); 25 (until steady-state); 1000	Differential method, partitioning limitation due to $V_{c,max}$ (one-point estimate assuming infinite g_m and Rubisco limited A) and g_{sc}
(4)	*Oryza sativa*	dark (30 min); 50 (9 min); 1500	Visual comparison of diffusion-corrected $A^* = A(300/c_i)$: simplified method assuming linear A/c_i response through origin

Table 3. Gas exchange studies that have evaluated the kinetics of increasing Rubisco activity during induction in food crops.					
Ref.	Crop species	Access-ions per species	PPFD sequence (PPFD units: µmol m^{-2} s^{-1})	Analytical method (if other than (294)	Mean τ (s) (range given where multiple accessions/ conditions)
(294)	*Spinacia oleracea*	1	690 (60 min) dark (10 – 60 min); 690	-	300
(108)	*Spinacia oleracea*	1	690 (60 min) dark-135 (45 min); 690		104-228
(295)	*Spinacia oleracea*	1	160 (45 min); various	-	103-298
(191)	*Spinacia oleracea*	1	Dark or 180 (> 60 min); 1200 [various c_i]	-	94-425
(293)	*Spinacia oleracea*	1	1200 (60 min); various (30 min); 1200	-	90-153
(59)	*Ocimum basilicum*	1	1180 (steady-state); 180 (0-40); 1180 [c_a 25 Pa]	-	246 (199-338)
(86)	*Nicotiana tabacum*	1 (+antisense Rca)	110 (30 min); 1200	-	118 (857)
(87)	*Nicotiana tabacum*	1	1200 (60 min); 105 (30 min); 1200	Equation of (294) fit using non-linear least squares	119
(106)	*Oryza sativa*	1 (+transgenic RbcS × 2)	1800 (30 min); 60 (45 min); 1800 [noting subambient inlet c_a of 25 Pa)	-	148 (161, 172)
(298)	*Oryza sativa*	1 (+transgenic: OE Rca; antisense Rca)	1500 (30 min); 60 (45 min); 1500	-	135-257 (94-174; 194-395)
(77)	*Oryza sativa*	1 (+transgenic: OE Rca × 2)	1800 (30 min); 60 (45 min); 1800 [noting subambient inlet c_a of 25 Pa)	-	152 (130, 132)
(258)	*Glycine max*	7	dark (overnight); 50 (steady-state); 2000	Diffusion-corrected $A^* = A(300/c_i)$: simplified method assuming linear A/c_i response through origin	149-307

(118)	*Solanum lycopersicum*	1	dark-200 (steady-state); 1000 [c_a varied: 20 – 80 Pa]	Diffusion corrected A* based on A/c_c response	76-256
(268)	*Triticum aestivum*	1	1200 (steady state); 50 (); 1200	-	180-240
(307)	*Oryza sativa*	8	10 (assumed steady-state); 1200	-	132-1369

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