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REVIEW PAPER

Dynamic photosynthesis in different environmental conditions

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Abstract

Incident irradiance on plant leaves often fluctuates, causing dynamic photosynthesis. Whereas steady-state photosynthetic responses to environmental factors have been extensively studied, knowledge of dynamic modulation of photosynthesis remains scarce and scattered. This review addresses this discrepancy by summarizing available data and identifying the research questions necessary to advance our understanding of interactions between environmental factors and dynamic behaviour of photosynthesis using a mechanistic framework. Firstly, dynamic photosynthesis is separated into sub-processes related to proton and electron transport, non-photochemical quenching, control of metabolite flux through the Calvin cycle (activation states of Rubisco and RuBP regeneration, and post-illumination metabolite turnover), and control of CO_2 supply to Rubisco (stomatal and mesophyll conductance changes). Secondly, the modulation of dynamic photosynthesis and its sub-processes by environmental factors is described. Increases in ambient CO_2 concentration and temperature (up to ~35°C) enhance rates of photosynthetic induction and decrease its loss, facilitating more efficient dynamic photosynthesis. Depending on the sensitivity of stomatal conductance, dynamic photosynthesis may additionally be modulated by air humidity. Major knowledge gaps exist regarding environmental modulation of loss of photosynthetic induction, dynamic changes in mesophyll conductance, and the extent of limitations imposed by stomatal conductance for different species and environmental conditions. The study of mutants or genetic transformants for specific processes under various environmental conditions could provide significant progress in understanding the control of dynamic photosynthesis.

Key words: Carbon dioxide, CO_2 assimilation, fluctuating irradiance, light transients, lightfleck, sunfleck, temperature, vapour pressure deficit.

Introduction

Photosynthesis is mostly studied using controlled, steady-state conditions. In nature, steady states are rare, and environmental factors, especially irradiance, change rapidly. Assimilation rates in nature result from those factors that

Abbreviations: C_a, ambient CO_2 concentration; CA1P, 2-carboxy-D-arabinitol 1-phosphate; C_c, chloroplast CO_2 concentration; C_i, substomatal cavity CO_2 concentration; ETC, electron transport chain; ETR, electron transport rate; FBPase, fructose-1,6-bisphosphatase; Fd, ferredoxin; GAPDH, glyceraldehyde-3-phosphate dehydrogenase; g_m, mesophyll conductance; g_s, stomatal conductance; I, irradiance; NPQ, non-photochemical quenching; PGA, 3-phosphoglycerate; PGCA, 2-phosphoglycolate; pmf, proton motive force; PRK, phosphoribulokinase; PS, photosystem; PsbS, photosystem II pigment-binding protein subunit; qE, energy-dependent quenching of photosystem II; Rca, Rubisco activase; Rubisco, ribulose-1,5-bisphosphate carboxylase oxygenase; RuBP, ribulose-1,5-bisphosphate; S7P, sedoheptulose-7-phosphate; SBPase, sedoheptulose-1,7-bisphosphatase; T, leaf temperature; t_{50}, time required to reach 50% of full photosynthetic induction; t_{90}, time required to reach 90% of full photosynthetic induction; VPD_{air}, air vapour pressure deficit; $VPD_{leaf-air}$, leaf-to-air vapour pressure deficit; XuBP, xylulose-1,5-bisphosphate; ΔpH, *trans*-thylakoid pH gradient; ΔΨ, *trans*-thylakoid electrical potential.

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limit steady-state photosynthesis as well as those that constrain the speed of response to environmental fluctuations (Naumburg and Ellsworth, 2002; Way and Pearcy, 2012). So, to understand photosynthesis in natural conditions we need to understand photosynthesis in fluctuating irradiance, i.e. dynamic photosynthesis.

Previous research on dynamic photosynthesis has focused on the kinetics of underlying processes and interspecific variation in response to fluctuating irradiance (Pearcy and Way, 2012). In contrast, no clear picture of the effects of ambient CO_2 concentration ([CO_2]), temperature, and leaf-to-air vapour pressure deficit ($VPD_{leaf-air}$) on dynamic photosynthesis exists (Way and Pearcy 2012). These environmental factors influence the rate constants and rates of processes that limit the response of photosynthesis to fluctuating irradiance. As leaf temperature and $VPD_{leaf-air}$ often change in parallel with irradiance (Peak and Mott, 2011; Schymanski *et al.*, 2013), transient rates of photosynthesis are affected by simultaneous changes in several factors. Atmospheric [CO_2] changes more slowly, currently rising by ~2 μmol mol^{-1} $year^{-1}$ (IPCC, 2013). Apart from influencing photosynthesis on its own, this increase in [CO_2] is likely to affect air temperature and humidity (IPCC, 2013). Knowledge of dynamic photosynthesis is good with respect to responses to changing irradiance, but much less developed regarding modulation by other environmental factors, even when these factors are held constant while irradiance fluctuates. This weakness impacts upon models of photosynthesis.

Vegetation and crop science relies heavily on models to predict photosynthesis. Models of steady-state photosynthesis are often sophisticated and useful, but tend to overestimate integrated photosynthesis in fluctuating irradiance (Naumburg and Ellsworth, 2002; Timm *et al.*, 2004). The degree of overestimation depends on average irradiance intensity and species-specific responses to fluctuating irradiance (Pearcy *et al.*, 1997; Naumburg *et al.*, 2001; Naumburg and Ellsworth, 2002), but can be as much as 35% per day (Naumburg and Ellsworth, 2002). Models of dynamic photosynthesis, on the other hand, account for the kinetics of photosynthesis as it responds to fluctuating light. Of the dynamic models that exist, none account for all environmental factors mentioned, while some account for the effects of [CO_2] (Kirschbaum *et al.*, 1998; Naumburg *et al.*, 2001; Vico *et al.*, 2011), leaf temperature (Pepin and Livingston, 1997; Ozturk *et al.*, 2012), and air humidity (Pepin and Livingston, 1997; Vico *et al.*, 2011). To improve models of dynamic photosynthesis, we need a better understanding of how environmental factors other than irradiance, even when they are constant, modulate the kinetics of responses to changes in irradiance.

Patterns of fluctuating irradiance can be classified as lightflecks and sunflecks. While lightflecks are artificial increases in irradiance with defined intensity, duration, and spectrum (Pearcy *et al.*, 1996), sunflecks are natural increases in irradiance above a threshold intensity, with great temporal, spatial, and spectral heterogeneity (Smith and Berry, 2013).

Steady-state responses of photosynthesis to [CO_2], leaf temperature, and $VPD_{leaf-air}$ are well understood, which makes analysing gas exchange dynamics in response to fluctuating irradiance easier. In this review, we consider environmental factors besides irradiance to be constant when we look at their role as modulators of dynamic photosynthesis, because (i) there are empirical data available on this situation, and (ii) considering two or more factors as changing dynamically would make this already complex process overly complicated. We review the modulation of dynamic photosynthesis by [CO_2], leaf temperature, and $VPD_{leaf-air}$, by (i) building a framework of all processes that may affect dynamic photosynthesis at the levels of electron transport, flux of metabolites through the Calvin cycle, and leaf CO_2 diffusion; and (ii) examining the effects of [CO_2], leaf temperature, and $VPD_{leaf-air}$ on underlying processes and dynamic gas exchange parameters. Using this structure, the reader is first introduced to the 'machinery' of dynamic photosynthesis in a mechanistic way, making the analysis which follows of modulation of dynamic photosynthesis by environmental factors much simpler to understand.

Dynamic control of photosynthetic gas exchange

The complex process of dynamic photosynthesis can be deconstructed into three major processes: photosynthetic induction, post-illumination CO_2 fixation, and the post-illumination CO_2 burst (Fig. 1). Photosynthetic induction itself is driven by sub-processes such as RuBP regeneration, Rubisco activation, and stomatal movement. Changes of mesophyll conductance (g_m) and non-photochemical quenching (NPQ) in response to irradiance may further modulate dynamic photosynthesis, and are affected by [CO_2] and leaf temperature. All of these processes are described below, in a framework (Fig. 2) that will help in understanding the modulation of dynamic photosynthesis by [CO_2], leaf temperature, and $VPD_{leaf-air}$.

Control of electron transport

Electron and proton transport

Light-driven charge separation in the reaction centres of photosystems I and II (PSI and PSII) initiates an electron transport process that results in the oxidation of water on the lumenal side and reduction of ferredoxin on the stromal side of the thylakoid, reducing $NADP^+$ to NADPH (Cruz *et al.*, 2001; Foyer *et al.*, 2012). Electron transport processes are coupled to proton transport across the thylakoid membrane. Proton transport builds up the proton motive force (pmf) which, after dark-light transitions, mainly consists of a *trans*-thylakoid electrical potential (ΔΨ), but partitions into ΔΨ and a pH gradient across the thylakoid membrane (ΔpH) after several seconds (Cruz *et al.*, 2001). The pmf affects (i) ATP synthesis, (ii) NPQ via ΔpH, (iii) maximum electron transport rate (ETR) through the cytochrome b_6f complex, and (iv) movement of Mg^{2+} ions across the thylakoid membrane into the stroma due to ΔΨ (Cruz *et al.*, 2001; Foyer *et al.*, 2012). Regulatory mechanisms of electron and proton

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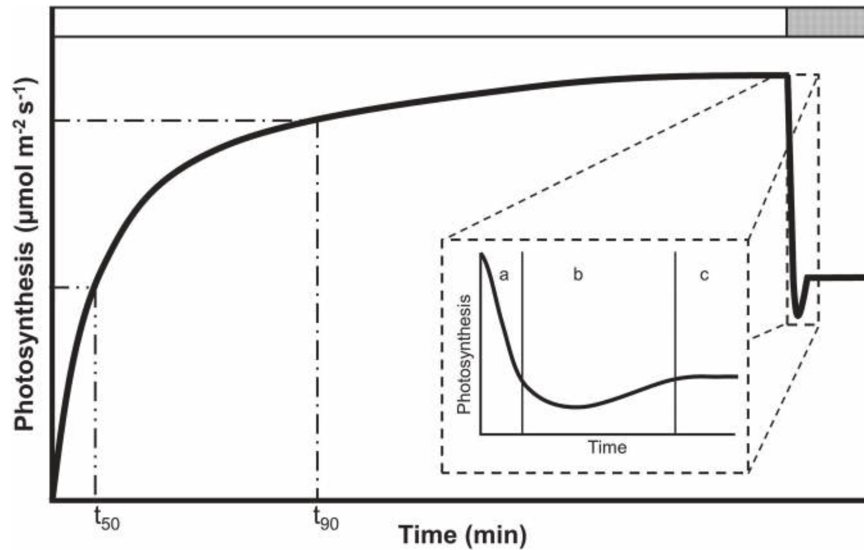

Fig. 1. Schematic diagram of transient net photosynthetic phenomena upon increase and decrease in irradiance: photosynthetic induction in a dark-adapted leaf during a lightfleck (white bar: high irradiance, e.g. 1000 µmol m^{-2} s^{-1}), followed by post-illumination CO_2 fixation and the post-illumination CO_2 burst after a lightfleck (grey bar: low irradiance, e.g. 200 µmol m^{-2} s^{-1}). t_{50}, t_{90}: time required to reach 50 and 90% of full photosynthetic induction, respectively. Inset: (a) post-illumination CO_2 fixation, (b) the post-illumination CO_2 burst, and (c) new steady-state photosynthesis after a lightfleck.

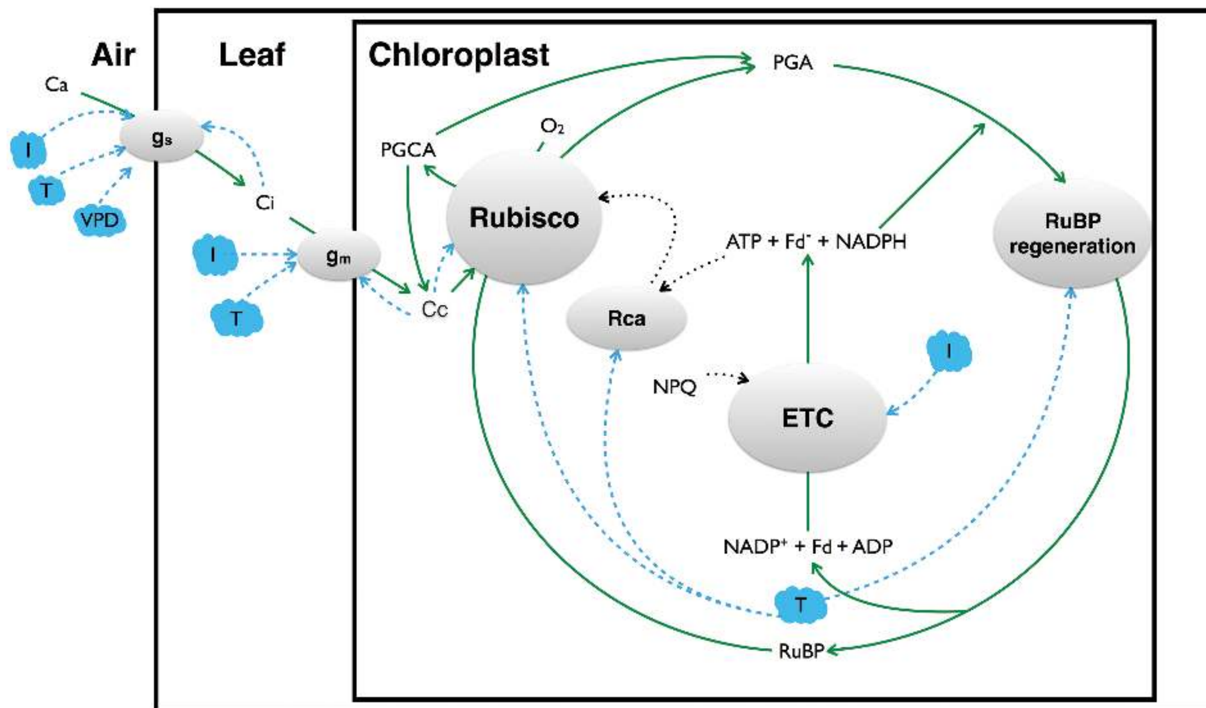

Fig. 2. Depiction of major components and processes of dynamic photosynthesis (grey circles), and main effects of environmental factors (blue clouds). Material flows are shown as green solid arrows, information flows between processes as dotted arrows, and information flows from environmental factors towards processes as blue, dashed arrows. Depending on its location, CO_2 is named either C_a (ambient CO_2 concentration), C_i (substomatal cavity CO_2 concentration), or C_c (chloroplast CO_2 concentration). Further abbreviations: ETC, electron transport chain; Fd, ferredoxin; g_m, mesophyll conductance; g_s, stomatal conductance; I, irradiance; NPQ, non-photochemical quenching; PGA, 3-phosphoglycerate; PGCA, 2-phosphoglycolate; Rca, Rubisco activase; Rubisco, ribulose-1,5-bisphosphate carboxylase oxygenase; RuBP, ribulose-1,5-bisphosphate; T, temperature; VPD, leaf-to-air vapour pressure deficit.

transport currently receive a lot of attention due to their pivotal role in protecting the photosynthetic apparatus and in balancing ATP/NADPH ratios in fluctuating light. They are dealt with in great detail in recent reviews (Kramer and Evans, 2011; Foyer *et al.*, 2012; Tikkanen *et al.*, 2012; Kono and Terashima, 2014; Shikanai, 2014). In the context of this review, electron and proton transport are mostly important in regulating NPQ and the thioredoxin-ferredoxin system, which in turn activates several of the light-regulated Calvin cycle enzymes.

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Non-photochemical quenching

Protecting PSII from damage by absorbed excess energy, NPQ is the result of up to four processes that operate at different time-scales. These processes include energy-dependent quenching (qE), state transitions, zeaxanthin-dependent quenching, and photoinhibition (Nilkens *et al.*, 2010; Ruban *et al.*, 2012; Jahns and Holzwarth, 2012). The most important process with regards to fluctuating irradiance is qE, as it responds most quickly to changes in irradiance. Additionally, it normally accounts for the largest fraction of NPQ (Ruban *et al.*, 2012). The formation of qE is strictly dependent on the build-up of ΔpH and its sensing by the PSII protein PsbS (Li *et al.*, 2000; 2004). The PsbS protein is most likely to be a catalyst of qE (Goral *et al.*, 2012; Hubbart *et al.*, 2012). Furthermore, qE is modulated by the amount of zeaxanthin and antheraxanthin (Johnson *et al.*, 2011), carotenoids that are formed from violaxanthin in the xanthophyll cycle; the exact role of the xanthophyll cycle in qE is still under debate (Jahns and Holzwarth, 2012).

Half-times for induction and relaxation of qE are between 15 and 60 s (Walters and Horton, 1991; Nilkens *et al.*, 2010; Peguero-Pina *et al.*, 2013). Because the relaxation kinetics of qE are slower than the rate of change of irradiance, qE transiently competes with ETR after lightflecks and could decrease integrated daily photosynthesis by 13–32% compared to the hypothetical situation of instant relaxation of qE (Zhu *et al.*, 2004). Relative losses due to downregulated ETR are greater in low irradiance (Tausz *et al.*, 2005). Furthermore, Zhu *et al.* (2004) assumed qE to be strongly affected by leaf temperature, making it a process that could impact on dynamic photosynthesis and be modulated by other environmental factors. In transgenic *Oryza sativa* plants overexpressing PsbS, photosynthetic induction was slower because of decreased ETR (Hubbart *et al.*, 2012). Unfortunately, no data were presented that linked qE relaxation kinetics after decreases in irradiance to rates of photosynthesis. Considering the extent of hypothesized effects of slow qE relaxation kinetics on plant productivity (Zhu *et al.*, 2004), it seems worthwhile to underpin these with experimental evidence.

Control of metabolite flux through the Calvin cycle

RuBP regeneration activation state

At low irradiance, pools of RuBP and its precursors are small (Sassenrath-Cole and Pearcy, 1992), but increase in higher irradiance. It is assumed that RuBP concentrations are non-limiting when they are 1.5–2 times the active site concentration of Rubisco (Woodrow and Mott, 1989; Sassenrath-Cole and Pearcy, 1992 Pearcy *et al.*, 1996), a level which is reached or exceeded 1 min after illumination (Sassenrath-Cole and Pearcy, 1992). Measured half-times of activation and deactivation of RuBP regeneration are in the range 2–3 min (Kirschbaum and Pearcy, 1988; Sassenrath-Cole and Pearcy, 1994). In dark-adapted leaves, the overall limitation due to inactive RuBP regeneration is small compared to limitations imposed by inactive Rubisco and closed stomata. However, because RuBP regeneration deactivates more quickly in low irradiance than Rubisco (Sassenrath-Cole and Pearcy, 1992), it can impose large limitations on integrated rates of photosynthesis in naturally fluctuating irradiance.

Chloroplast fructose-1,6-bisphosphatase (FBPase) and sedoheptulose-1,7-bisphosphatase (SBPase) activity limit RuBP regeneration activation (Stitt *et al.*, 1980; Prinsley and Leegood, 1986; Sassenrath-Cole and Pearcy, 1992; 1994; Sassenrath-Cole *et al.*, 1994). Also, phosphoribulokinase (PRK) may limit the activation of RuBP regeneration (Sassenrath-Cole and Pearcy, 1992; Sassenrath-Cole *et al.*, 1994). Activation of PRK saturated at much lower irradiance than FBPase (Sassenrath-Cole and Pearcy, 1994). Also, PRK activated more quickly than FBPase and SBPase in lightflecks (Champigny and Bismuth, 1976; Laing *et al.*, 1981; Kobza and Edwards, 1987) and deactivated comparably slowly thereafter (Avron and Gibbs, 1974). Altogether, FBPase and SBPase limit the activation of RuBP regeneration more strongly than PRK.

FBPase and SBPase are directly regulated by the thioredoxin-ferredoxin system (Raines *et al.*, 1999; Ruelland and Miginiac-Maslow, 1999). They are oxidized, and therefore inactive, in the dark. Upon illumination, reducing power is transferred from PSI via ferredoxin to thioredoxin, which reduces and thus activates the enzymes (Ruelland and Miginiac-Maslow, 1999). FBPase is further stabilized and positively regulated by its substrate fructose-1,6-bisphosphate (Scheibe, 2004), stromal pH, and Mg^{2+} (Ishijima *et al.*, 2003), and inhibited by glycerate and its product fructose-6-phosphate (Gardemann *et al.*, 1986; Schimkat *et al.*, 1990). Also, SBPase activity is positively regulated by Mg^{2+}, stromal pH, and its substrate sedoheptulose-1,7-bisphosphate (Schimkat *et al.*, 1990), and negatively by inorganic phosphate, glycerate, RuBP, and its product sedoheptulose-7-phosphate (Schimkat *et al.*, 1990; Ishijima *et al.*, 2003).

PRK can form a complex with the enzyme glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and a chloroplast protein, CP12, in darkness (Wedel *et al.*, 1997; Howard *et al.*, 2008). In *Pisum sativum* leaves, the complex dissociated within minutes of illumination; the extent of dissociation increased with irradiance up to 300 μmol m^{-2} s^{-1} (Howard *et al.*, 2008), providing flexible regulation of PRK. However, in dark-adapted leaves of other species (*Vicia faba*, *Solanum tuberosum*, *Solanum lycopersicon*, and *Spinacia oleracea*), enzymes existed both bound by the PRK/GAPDH/CP12 complex and as free enzymes, while in others (*Phaseolus vulgaris*, *Nicotiana tabacum*, and *Arabidopsis thaliana*) the enzymatic complex was almost absent (Howard *et al.*, 2011). Thus, the regulation of PRK and GAPDH activity by CP12 is far from universal among species. It is not clear whether the interspecific differences in PRK regulation impact on RuBP regeneration activation.

Rubisco activation state

To fix carbon, Rubisco must be carbamylated, i.e. Rubisco (E) needs to form a complex (ECM) with CO_2 and Mg^{2+} (Woodrow *et al.*, 1996). For carboxylation, RuBP (R) and another CO_2 molecule need to bind to ECM. Several inhibitory sugar phosphates can bind to Rubisco, preventing ECM formation, or to ECM, preventing carboxylation (Salvucci and Crafts-Brandner, 2004). Firstly, RuBP can bind to uncarbamylated Rubisco and form a stable but inactive ER complex (Salvucci and Crafts-Brandner, 2004); it may

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also bind to EC (McNevin *et al.*, 2006). Secondly, by misprotonation of RuBP during carboxylation or oxygenation, inhibitory sugar phosphates (X) such as D-glycero-2,3-pentodiulose-1,5-bisphosphate, 3-ketoarabinitol bisphosphate, or xylulose-1,5-bisphosphate are formed, which can bind to carbamylated Rubisco (Salvucci and Crafts-Brandner, 2004; Andralojc *et al.*, 2012). They might also bind to E and EC complexes (McNevin *et al.*, 2006). Thirdly, CA1P (2-carboxy-D-arabinitol 1-phosphate) can bind to ECM instead of RuBP in low irradiance or darkness (Parry *et al.*, 2013). CA1P is probably present in most species, but not always in concentrations high enough to take effect (Andralojc *et al.*, 2012). In darkness, the activation state of Rubisco can be strongly [CO_2]-dependent, as long as Rubisco is unaffected by CA1P. Namely, the Rubisco activation state can be higher in darkness than in low irradiance, since newly formed RuBP in low irradiance can bind to uncarbamylated Rubisco sites, while in darkness no RuBP is formed and CO_2 binds instead, keeping Rubisco carbamylated (Carmo-Silva and Salvucci, 2013).

To keep ECM catalytically competent and to free inactive ER, EX, ECR, and ECX complexes, the chaperone Rubisco activase (Rca) is required (Salvucci *et al.*, 1985; Portis *et al.*, 1986). Rca is inactive in darkness and activated upon illumination (Portis, 2003). Alternative splicing of the Rca gene results in two isoforms: the α-isoform in *A. thaliana* is regulated by the thioredoxin-ferredoxin system, while regulation of the smaller β-Rca is unclear and differs across species (Portis, 2003; Carmo-Silva and Salvucci, 2013). When both isoforms are present, α-Rca controls β-Rca (Zhang and Portis, 1999). Rca requires ATP for catalytic activity and is inhibited by ADP (Zhang and Portis, 1999; Portis, 2003). However, in a recent study using *A. thaliana* mutants, plants containing only β-Rca did not exhibit ADP sensitivity, and kept Rubisco almost fully activated in low irradiance (Carmo-Silva and Salvucci, 2013). Consequently, photosynthetic induction was much faster. In transgenic *N. tabacum* plants with substantially decreased Rca levels, no decreases were found in steady-state Rubisco activation state (Mate *et al.*, 1993). It was inferred that, theoretically, a concentration of Rca 200 times lower than Rubisco could suffice to keep Rubisco activated (Mate *et al.*, 1993), although this would slow down the rate of activation significantly. Naturally occurring Rca concentrations are much higher than this, which may help in using fluctuating irradiance more efficiently. The optimal allocation of nitrogen between Rubisco and Rca could therefore depend on a plant's microclimate (Mott and Woodrow, 2000). For more extensive reviews of Rubisco activation, see Parry *et al.* (2013) and Tcherkez (2013). For the kinetics of Rubisco activation and deactivation, see Pearcy *et al.* (1996).

Generally, the irradiance-dependent regulation of Rubisco is pivotal to dynamic photosynthesis. The activation state of Rubisco is strongly dependent on the functioning of Rca and is further modulated by [CO_2] and temperature.

Post-illumination CO_2 fixation

After decreases in irradiance, it can be observed in rapid gas exchange measurements that assimilation rates do not directly 'fall' to a new steady state, but that their decrease lags behind for a few seconds (Fig. 1, inset a). This phenomenon, termed post-illumination CO_2 fixation, increases the integrated carbon assimilation of a lightfleck and can substantially increase average photosynthetic rates of leaves in sunfleck environments (Pons and Pearcy, 1992; Roden and Pearcy, 1993; Roden, 2003). Post-illumination CO_2 fixation is driven by pools of Calvin cycle intermediates as well as NADPH, ATP, and pmf (Laisk *et al.*, 1984; Sharkey *et al.*, 1986). These pools build up within seconds (Sharkey *et al.*, 1986) and their size increases with irradiance intensity in parallel with photosynthetic rates (Laisk *et al.*, 1984), creating a linear relationship between photosynthetic rates and post-illumination CO_2 fixation (Kirschbaum *et al.*, 2005). Integrated post-illumination CO_2 fixation has been shown to correlate well with RuBP pools over various [CO_2] levels (Ruuska *et al.*, 1998), and has been used to estimate RuBP pools (Osmond *et al.*, 1988; Kirschbaum *et al.*, 1998). As metabolite pool sizes are often proportional to photosynthetic capacity, so are rates of post-illumination CO_2 fixation (Sharkey *et al.*, 1986; Osmond *et al.*, 1988; Pearcy *et al.*, 1996). Effects of post-illumination CO_2 fixation on integrated photosynthesis are often negligible (Pearcy *et al.*, 1994). However, as its fraction of integrated dynamic photosynthesis is inversely related to lightfleck length (Roden and Pearcy, 1993), it could increase photosynthesis in species with strongly fluttering leaves (by 5–15%, as estimated by Roden, 2003), as leaf flutter can facilitate extremely short lightflecks.

Post-illumination CO_2 burst

After post-illumination CO_2 fixation, a dip in net rates of photosynthesis, termed the post-illumination CO_2 burst (Decker, 1955), may be visible in gas exchange data (Fig. 1, inset b). Post-illumination CO_2 bursts of different kinetics occur in C_3, CAM, and some C_4 plants. Different origins of these bursts related to photorespiration (C_3 and CAM plants; Crews *et al.*, 1975; Vines *et al.*, 1983), overshoots in sucrose synthesis (C_3 plants; Prinsley *et al.*, 1986), phosphoenolpyruvate carboxykinase activity (CAM plants; Crews *et al.*, 1975), and differences in the activity of malate dehydrogenase (C_4 plants; Downton, 1970) have been reported. In this review, only the photorespiratory CO_2 burst will be considered, as it is most pronounced and most strongly modulated by [CO_2] and temperature.

The photorespiratory post-illumination CO_2 burst is caused by a transient rise in photorespiratory CO_2 production (Vines *et al.*, 1983; Prinsley *et al.*, 1986). This is usually explained by a lag time between adjustment of photorespiratory 2-phosphoglycolate (PGCA) recycling relative to Calvin cycle cycling. After lightflecks, PGCA is recycled into 3-phosphoglycerate (PGA) at a rate which is temporarily higher than at steady state; the corresponding consumption of ATP and reductant as well as CO_2 evolution during glycine decarboxylation cause the burst (Rawsthorne and Hylton, 1991). In *Pelargonium* × *hortorum*, lightflecks of at least 5 min duration were required to maximize the burst (Vines *et al.*, 1983). Further, a positive correlation of photosynthetic rates after lightflecks and burst magnitude suggests that this phenomenon requires energy (Vines *et al.*, 1983).

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Control of CO_2 supply to Rubisco

Stomatal conductance

Stomatal conductance (g_s) often decreases in low irradiance, which, together with slow stomatal opening during lightflecks, may limit dynamic photosynthesis. Stomatal limitation during induction can be calculated by correcting assimilation rates for the change in concentration of CO_2 in the substomatal cavity (C_i) (Woodrow and Mott, 1989; Tinoco-Ojanguren and Pearcy, 1993a; Allen and Pearcy, 2000). It is often assumed that g_s always limits induction, despite reports to the contrary (Ögren and Sundin, 1996; Tausz *et al.*, 2005; Tomimatsu and Tang, 2012). There may be two reasons for this. Firstly, stomatal limitations have often not been analysed, even though the necessary data (dynamic CO_2 exchange and g_s) were available (e.g. Chazdon and Pearcy, 1986; Roden and Pearcy, 1993; Pearcy *et al.*, 1997; Pepin and Livingston, 1997; Naumburg and Ellsworth, 2000; Leakey *et al.*, 2002, 2003). Secondly, many studies focus on forest understorey species, which may not be representative of other plant functional types. Re-evaluation of published data sets and genotypes with contrasting stomatal behaviour (Tomimatsu and Tang, 2012) may help to quantify stomatal limitations on dynamic photosynthesis.

Rates of stomatal opening and closure after changes in irradiance are highly heterogeneous between species, environmental conditions, and plant functional types. In several closely related *Banksia* trees, smaller stomata opened and closed faster in response to lightflecks than larger stomata, possibly due to their larger membrane surface area to volume ratio (Drake *et al.*, 2013). Two meta-analyses found that, on average, stomatal opening in lightflecks was faster than stomatal closure after lightflecks (Ooba and Takahashi, 2003; Vico *et al.*, 2011). However, there was large variation in these traits. In fact, several data sets showed faster stomatal closure than opening (Ooba and Takahashi, 2003; Vico *et al.*, 2011), which could be due to different environmental conditions between experiments.

Stomata respond to a myriad of intrinsic and extrinsic factors, among them all environmental factors discussed in this review. For changes in a single factor, the response is often well known. Far less work has been done on the kinetics of the response (Lawson and Blatt, 2014) or simultaneous changes in several factors, which are likely in nature (e.g. increase in irradiance and leaf temperature, or decrease in C_i and $VPD_{leaf\text{-}air}$). Recently, Merilo *et al.* (2014) have shown that effects of different environmental factors on g_s are non-multiplicative, rarely predictable, and strongly species-dependent. This challenges the often-held model assumption that effects of single factors are multiplicative and uniform across species (summarized in Damour *et al.*, 2010).

Mesophyll conductance

Mesophyll conductance, mediating CO_2 diffusion from the substomatal cavity to the chloroplast, can be a substantial limitation to photosynthesis. It can vary within minutes, and is affected by changes in irradiance, [CO_2], and temperature (Flexas *et al.*, 2007, 2008; Tholen *et al.*, 2008, Evans and von Caemmerer, 2013), making it a potentially important process within the framework of this review. The possible components of g_m, its short-term variability in response to environmental factors, and possible artefacts of methods used for its estimation are under ongoing discussion (Tholen *et al.*, 2012; Griffiths and Helliker, 2013). Relevant factors that may potentially contribute to variations in g_m are carbonic anhydrase, aquaporins, anatomical properties of leaves and cells (Flexas *et al.*, 2012), and the area of chloroplasts facing intercellular spaces (Tholen *et al.*, 2008). Of these, all but the basic anatomical properties of leaves and cells may be affected by short-term changes in environmental factors. Estimating g_m correctly is difficult, and every method has different drawbacks and underlying assumptions. Therefore, using at least two methods simultaneously is recommended (Flexas *et al.*, 2013). Two methods are currently available for measuring rapidly changing g_m: the 'variable J method', using simultaneous gas exchange and chlorophyll fluorescence (Harley *et al.*, 1992), and online carbon isotope discrimination, using tunable diode laser absorption spectroscopy (e.g. Evans and von Caemmerer, 2013). Combining these methods under various environmental factors should be of great use for determining the dynamics of mesophyll conductance in fluctuating irradiance and underpinning theories regarding its regulation.

Environmental factors influencing dynamic photosynthesis

In the remainder of this review, the effects of [CO_2], leaf temperature, and $VPD_{leaf\text{-}air}$ on the processes driving dynamic photosynthesis are discussed; they are summarized in Table 1. While changes in [CO_2] are normally gradual, leaf temperature and $VPD_{leaf\text{-}air}$ fluctuate almost as rapidly as irradiance itself. Thus, findings with regard to the effects of [CO_2] presented here may be used for future climate change scenarios, while findings regarding the other two factors can be used with regard to current natural conditions.

CO_2 concentration

Increased [CO_2] generally stimulates rates of photosynthetic induction, and enhances photosynthesis and growth in fluctuating irradiance (Leakey *et al.*, 2002). In previous work, [CO_2] was manipulated either during measurements (Chazdon and Pearcy, 1986) or continuously during plant growth (Naumburg and Ellsworth, 2000; Leakey *et al.*, 2002; Tomimatsu and Tang, 2012; Holišová *et al.*, 2012). In three out of five studies, elevated [CO_2] led to faster photosynthetic induction (Chazdon and Pearcy, 1986; Leakey *et al.*, 2002; Tomimatsu and Tang, 2012). Naumburg and Ellsworth (2000) found no differences in induction rates, while Holišová *et al.* (2012) reported faster induction for one of two species in elevated [CO_2]. The difference in outcomes between studies may be explained by [CO_2] treatment levels {Naumburg and Ellsworth (2000) and Holišová *et al.* (2012) used the narrowest range between [CO_2] treatments of the studies mentioned}, experimental procedures, or species differences.

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Table 1. *Effects of environmental factors on processes controlling dynamic photosynthesis after increases or decreases in irradiance*[a]

Change in irradiance	Process	Environmental factor			
		$[CO_2]$	Leaf Temperature		$VPD_{leaf\text{-}air}$
			Medium[b]	High[c]	
Increase	RuBP regeneration activation	–	↑	⬏	–
	Rubisco activation	~	↑	↓	⬎
	Stomatal opening	~	~	~	↓
	qE buildup	⬎	⬎	⬎	–
	Mesophyll conductance increase	?	↑	~	~
Decrease	RuBP regeneration deactivation	–	?	?	–
	Rubisco deactivation	↓	?	↑	⬏
	Stomatal closure	↑	?	?	↑
	Post-illumination CO_2 fixation	↓	↑	↓	?
	Post-illumination CO_2 burst	↓	↑	↑	?

[a] Symbols: ↑/↓, increase or decrease in the rate of the process when environmental factor increases; ⬏/⬎, hypothesized increase and decrease; –, no effect; ~, conflicting relationship throughout literature;?, unknown relationship.
[b] Temperature range: 5 to ~30°C.
[c] Temperature range: >30°C.

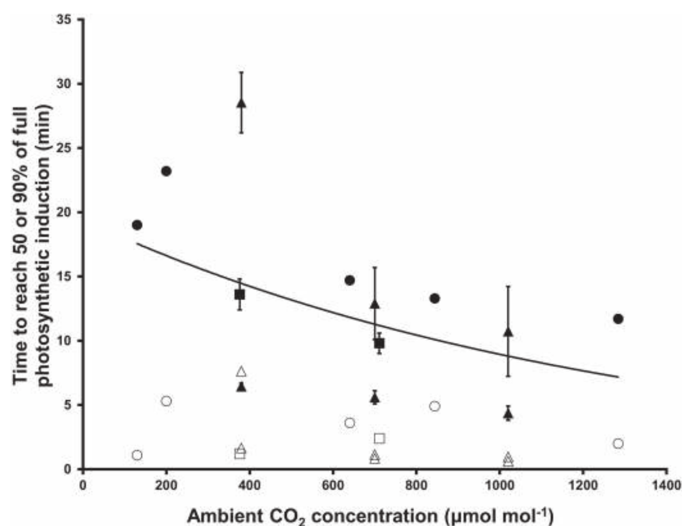

Fig. 3. Time (min) required to reach 50% (t_{50}, open symbols) and 90% (t_{90}, closed symbols) of full photosynthetic induction after a step increase in irradiance, as affected by C_a (µmol mol^{-1}). Data: Chazdon and Pearcy, 1986 (circles); Leakey *et al.*, 2002 (squares); and Tomimatsu and Tang, 2012 (triangles). Species included *Alocasia macrorriza* (circles), *S. leprosula* (squares), and *Populus koreana* × *trichocarpa* as well as *P. euramericana* (triangles). Error bars (±SE) are shown if supplied in the original publication. The negative exponential relationship (R^2 = 0.51) between t_{90} and $[CO_2]$ is described by: $t_{90} = 22.7e^{-7E-04[CO2]}$. No relationship between t_{50} and $[CO_2]$ was found.

Combining data from several experiments (Chazdon and Pearcy, 1986; Leakey *et al.*, 2002; Tomimatsu and Tang, 2012) revealed that the time required to reach 90% of full induction (t_{90}, visualized in Fig. 1) decreased with increasing $[CO_2]$ (Fig. 3; R^2 = 0.51). This effect was more pronounced between 200 and 600 µmol mol^{-1}. Because average t_{90} was 16 min, this indicates positive effects of $[CO_2]$ on stomatal limitations. No trend was observed for the time to reach 50% of full induction (t_{50}; Fig. 3). As average t_{50} was 3 min, a time range in which Rubisco activity is normally most limiting, this suggests that $[CO_2]$ did not affect this limitation. The overall effect of $[CO_2]$ on t_{90} was visible for every data set in Fig. 3, suggesting that decreasing t_{90} with increasing $[CO_2]$ is a general response among plants. Induction data from Naumburg and Ellsworth (2000) and Holišová *et al.* (2012) were not included here, as they were not provided in the original studies.

In *Spinacia oleracea* leaves, after small increases in irradiance, Rubisco activation was highly sensitive to $[CO_2]$. However, after large irradiance increases, it was $[CO_2]$-insensitive ($[CO_2]$ range: 100–300 µmol mol^{-1}; Woodrow *et al.*, 1996). Woodrow and colleagues assumed that $[CO_2]$-sensitive activation reflected a limitation by Rubisco carbamylation, while $[CO_2]$-insensitive activation reflected Rca limitation. Elevated $[CO_2]$ reduced the loss of induction (i.e. the deactivation of Calvin cycle enzymes and stomatal closure) in low irradiance after 5 (Leakey *et al.*, 2002), 6, and 12 min (Naumburg and Ellsworth, 2000), probably slowing down Rubisco deactivation. The relationship between low irradiance and $[CO_2]$ affecting the loss of induction needs further exploration, as deactivation of Rubisco can be different between low irradiance and darkness.

High $[CO_2]$ generally reduces g_s. However, effects of $[CO_2]$ on g_s dynamics in fluctuating irradiance are less clear: While stomatal opening rates during lightflecks in elevated $[CO_2]$ were shown to increase by Naumburg *et al.* (2001) and Leakey *et al.* (2002), they were shown to decrease by Tomimatsu and Tang (2012). Stomata closed faster after lightflecks in elevated $[CO_2]$ (Naumburg *et al.*, 2001). Elevated $[CO_2]$ also appears to decrease mesophyll conductance in various plant species (Flexas *et al.*, 2007, 2008), although this apparent change may be due to changes in reassimilation of CO_2 emitted from the mitochondria (Tholen *et al.*, 2012). Elevated $[CO_2]$ decreased steady-state NPQ at various irradiance levels in *Quercus ilex* (Arena *et al.*, 2005), and during long-term exposure in *Betula pendula* (Riikonen *et al.*, 2005). Additionally, elevated $[CO_2]$ increased the overall efficiency of electron transport through PSII (Riikonen *et al.*, 2005),

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which should lead to smaller transient limitations of ETR after decreases in irradiance. Increasing [CO_2] decreases post-illumination CO_2 fixation (Laisk *et al.*, 1984; Ruuska *et al.*, 1998; Sun *et al.*, 1999) and suppresses photorespiration and associated post-illumination CO_2 burst (Vines *et al.*, 1983; Leakey *et al.*, 2002).

To summarize, elevated [CO_2] increases photosynthetic induction rates in C_3 plants, and leads to slower loss of induction. More work is needed to confirm previous data on mesophyll conductance dynamics as affected by both irradiance and [CO_2] (Flexas *et al.*, 2007), and to quantify interactions between irradiance and [CO_2] during loss of induction.

Temperature

The temperature response of net photosynthesis generally follows a parabolic curve, often with an optimum at the growth temperature (e.g. Yamori *et al.*, 2014). Leaf temperature affects dynamic photosynthesis on many levels, due to temperature sensitivity of Rca and of the enzymes involved (Rubisco, FBPase, SBPase, and PRK). Between 5 and 30°C, net photosynthetic rates (Bernacchi *et al.*, 2013) and enzyme turnover generally increase. Increased turnover possibly reduces limitations due to the activation of RuBP-regeneration and Rubisco.

Combining data from photosynthetic induction experiments with various leaf temperatures during measurements (Küppers and Schneider, 1993; Pepin and Livingston, 1997; Leakey *et al.*, 2003; Yamori *et al.*, 2012; Carmo-Silva and Salvucci, 2013) revealed that the response of t_{50} and t_{90} to leaf temperature was best described by parabolic relationships (Fig. 4), albeit with strong scatter. The optimum temperature for rate of photosynthetic induction was ~30°C (Fig. 4). However, some data sets did not follow this trend (e.g. increasing t_{90} between 15 and 25°C; closed diamonds in Fig. 4), leading to a less uniform response of induction rates to temperature than to [CO_2] (Fig. 3). Interestingly though, the parabolic effects of temperature on induction rates found here matched those for rates of Rubisco activation by Rca for *A. thaliana*, *Camelina sativa*, *N. tabacum* and *Gossypium hirsutum* (Carmo-Silva and Salvucci, 2011). At 38°C compared to 28°C, *Shorea leprosula* showed faster loss of photosynthetic induction, and photosynthesis was more strongly reduced in fluctuating (59% reduction) than in constant irradiance (40% reduction; Leakey *et al.*, 2003).

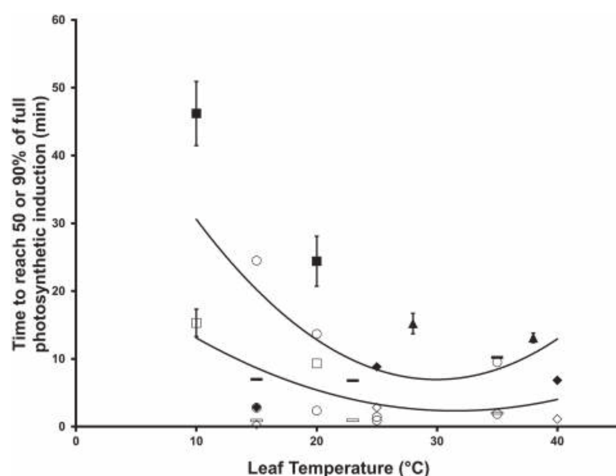

Fig. 4. Time (min) required to reach 50% (t_{50}, open symbols) and 90% (t_{90}, closed symbols) of full photosynthetic induction after a step increase in irradiance, as affected by leaf temperature (T, °C). Data: Küppers and Schneider, 1993 (circles); Pepin and Livingston, 1997 (squares); Leakey *et al.*, 2003 (triangles); Yamori *et al.*, 2012 (diamonds); and Carmo-Silva and Salvucci, 2013 (bars). Species included *Fagus sylvatica* (circles), *Thuja plicata* (squares), *S. leprosula* (triangles), *O. sativa* (diamonds), and *A. thaliana* (bars). Error bars (±SE) are shown if supplied in the original publication. Second order polynomials were fitted. $t_{90} = 0.06T^2 - 3.55T + 60.19$; $R^2 = 0.34$ and $t_{50} = 0.023T^2 - 1.47T + 25.41$; $R^2 = 0.19$.

At moderately high temperatures (above 30–35°C), Rubisco activity decreases (Eckardt and Portis, 1997) due to lowered Rca activity and faster formation of inhibitory sugar phosphates (Feller *et al.*, 1998; Salvucci and Crafts-Brandner, 2004; Yamori *et al.*, 2006). In most species, Rca forms high-molecular-weight aggregates that are catalytically incompetent above 30–35°C (Feller *et al.*, 1998). However, examples of functioning photosynthesis at higher temperatures exist: The desert plant *Rhazya stricta* maintained irradiance- and CO_2-saturated net photosynthetic rates up to 43°C, which may be due to differences between the two isoforms of the plant's Rca (Lawson *et al.*, 2014). Transgenic *O. sativa* plants with increased Rca contents showed faster photosynthetic induction at 15, 25 and 40°C due to higher Rubisco activation state at low irradiance (Yamori *et al.*, 2012). Thus, increased Rca contents or different Rca isoforms can greatly enhance dynamic photosynthesis across a large temperature range.

Photorespiration, and hence the post-illumination CO_2 burst, increases with temperature (Peterson, 1983), because the ratio [CO_2]/[O_2] in the chloroplast decreases, and because Rubisco specificity for O_2 increases (Foyer *et al.*, 2009). In *O. sativa*, post-illumination CO_2 fixation showed a parabolic response to leaf temperature, increasing in the range 10–30°C and decreasing at higher leaf temperatures (Sun *et al.*, 1999).

No straightforward relationship exists between g_s and temperature. While rising temperatures increase net rates of photosynthesis and guard cell metabolic activity (stimulating stomatal opening), increased C_i from higher respiration and photorespiration may have a diminishing effect on stomatal opening (Willmer and Fricker, 1996). Additionally, $VPD_{leaf-air}$ increases concomitantly with leaf temperature, which is likely to decrease g_s. Thus, there is strong variation in optimum temperatures for maximum g_s (Willmer and Fricker, 1996). Mesophyll conductance, on the other hand, increases in many plant species between 5 and 20°C and is either constant or decreases at higher temperatures (Flexas *et al.*, 2008). However, in *N. tabacum*, g_m and temperature were linearly correlated up to 40°C (Evans and von Caemmerer, 2013).

In irradiance above 1000 µmol m^{-2} s^{-1}, there was no relationship between NPQ and temperature (Bilger and Björkman, 1991; Clarke and Johnson, 2001), while in lower irradiances, steady-state NPQ decreased with increasing temperature (Clarke and Johnson, 2001). Furthermore, relaxation of NPQ after light-dark transitions was severely slowed down at temperatures below 20°C (Bilger and Björkman, 1991; Gilmore and Björkman, 1995). Overall, this suggests small initial and quickly relaxing NPQ with increasing temperatures, and therefore reduced limitation of ETR after lightflecks.

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Currently, there is a lack of knowledge about how Rubisco deactivation, and decreases in g_s and mesophyll conductance after lightflecks, are influenced by temperature. Furthermore, it is unclear how activation of RuBP regeneration and Rubisco are affected, and which of these processes might consequently limit dynamic photosynthesis more strongly at a given temperature. This knowledge is especially important between 10 and 30°C, as it is in this temperature range that most global plant productivity takes place.

To summarize, photosynthetic induction rates follow a parabolic response to temperature, with the fastest induction occurring around 30°C, despite large variation between studies. Above 35°C, photosynthesis suffers more from high temperature in fluctuating than in constant irradiance. Knowledge is lacking regarding the effects of temperature on the loss of photosynthetic induction and the temperature dependencies of RuBP regeneration activation and Rubisco activation in fluctuating irradiance.

Air humidity

Air humidity can affect photosynthesis indirectly through C_i, as stomata tend to close in dry air. Even though g_s generally decreases with increasing VPD_{air}, the extent of stomatal control over transpiration rates differs strongly between species (Monteith, 1995). Whether changes in VPD_{air} affect rates of dynamic photosynthesis depends on the extent to which g_s, and consequently C_i, change in response to VPD_{air}, which in turn depends on species and leaf water status. The only study on $VPD_{leaf\text{-}air}$ in dynamic photosynthesis (using *Piper aequale* and *P. auritum*) showed that decreases in g_s and C_i in elevated $VPD_{leaf\text{-}air}$ coincided with lowered photosynthetic induction rates and increased stomatal limitation during induction (Tinoco-Ojanguren and Pearcy, 1993b). Of course, this may not be representative for all plants and growth conditions. Upon illumination, stomata of *P. aequale* and *P. auritum* in elevated $VPD_{leaf\text{-}air}$ exhibited longer lag times in opening, and shorter lag times for closure, thus following a 'water conservation' response (Tinoco-Ojanguren and Pearcy, 1993a,b). In *Sambucus nigra* and *Aegopodium podagraria* leaves, stomata both opened and closed faster in elevated $VPD_{leaf\text{-}air}$; additionally, stomatal aperture showed stronger oscillations during lightflecks in elevated $VPD_{leaf\text{-}air}$ (Kaiser and Kappen, 2000; Kaiser and Kappen, 2001).

Decreased C_i between subsequent lightflecks might reduce Rubisco activation state, which would lead to slower Rubisco activation during lightflecks, as well as reduced carboxylation rates due to lower substrate availability. Very little is known about $VPD_{leaf\text{-}air}$ effects on mesophyll conductance, and some of the existing data are inconsistent (Flexas *et al.*, 2008). We hypothesize that $VPD_{leaf\text{-}air}$ does not affect the other sub-processes in our framework.

In summary, elevated $VPD_{leaf\text{-}air}$ lowers g_s to a variable extent, which might decrease C_i, affecting both carboxylation rates and Rubisco activation in fluctuating irradiance. Knowledge is particularly lacking on the sensitivity of changes in dynamic g_s to $VPD_{leaf\text{-}air}$ between species and its consequences for dynamic photosynthesis.

Conclusions

The sub-processes of dynamic photosynthesis are affected differently by the climate: the activation state of RuBP-regeneration is only influenced by temperature, while the activation state of Rubisco is directly affected by [CO_2] and temperature, and indirectly (via C_i) by $VPD_{leaf\text{-}air}$. Steady-state g_s is affected by all environmental factors. However, reported effects of [CO_2] on g_s in fluctuating light are contradictory. In the case of temperature and $VPD_{leaf\text{-}air}$ effects on dynamic g_s, almost no knowledge exists. Additionally, understanding the roles of mesophyll conductance and NPQ in dynamic photosynthesis needs more work.

Leaf temperature and [CO_2] affect rates of dynamic photosynthesis more strongly than $VPD_{leaf\text{-}air}$; however, leaf temperature and [CO_2] effects have been studied more often, such that this conclusion may shift with more experimental evidence. Data comparison revealed similar directionality for [CO_2] effects across studies (Fig. 3), while leaf temperature effects were more scattered and non-uniform (Fig. 4). $VPD_{leaf\text{-}air}$ may affect dynamic photosynthesis indirectly through C_i. However, its relative impact on photosynthetic gas exchange probably depends on the sensitivity of g_s to $VPD_{leaf\text{-}air}$. Further, in order to fully understand and quantify dynamic photosynthesis, loss is just as important as gain of photosynthetic induction. Much less literature is available on the former, as loss of induction studies are more time consuming. Loss of induction was diminished in elevated [CO_2], and enhanced in elevated temperatures, while effects of $VPD_{leaf\text{-}air}$ have not been reported.

Large leaps forward in knowledge were recently made by using genetic transformants or mutants of underlying processes of dynamic photosynthesis, e.g. Rubisco activation by Rca (Yamori *et al.*, 2012; Carmo-Silva and Salvucci, 2013) and the regulation of NPQ (Hubbart *et al.*, 2012; Suorsa *et al.*, 2012). Affecting one sub-process of dynamic photosynthesis at a time, as can be done using mutants or genetic transformants, can help our understanding of the regulation of the system and quantify the effects that one sub-process has on dynamic photosynthesis, possibly in various environmental conditions.

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