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Review

Tansley insight

Speedy stomata, photosynthesis and plant water use efficiency

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Summary

Stomatal movements control CO_2 uptake for photosynthesis and water loss through transpiration, and therefore play a key role in plant productivity and water use efficiency. The predicted doubling of global water usage by 2030 mean that stomatal behaviour is central to current efforts to increase photosynthesis and crop yields, particularly under conditions of reduced water availability. In the field, slow stomatal responses to dynamic environmental conditions add a temporal dimension to gaseous fluxes between the leaf and atmosphere. Here, we review recent work on the rapidity of stomatal responses and present some of the possible anatomical and biochemical mechanisms that influence the rapidity of stomatal movements.

I. Introduction

Stomata control gas exchange between the leaf interior and the external environment, and therefore adjustments in stomatal aperture in response to both environmental factors and internal signals determine CO_2 diffusion into the leaf and water loss via transpiration. Regulation of gaseous fluxes in and out of the leaf is essential to meet mesophyll demand for CO_2, maintaining appropriate leaf temperature, whilst conserving overall plant water status. Early work by Wong *et al.* (1979) demonstrated a close relationship between photosynthesis A and stomatal conductance g_s; however, stomatal responses to changing conditions are generally an order of magnitude slower than photosynthetic responses (see Lawson & Blatt, 2014). Sluggish stomata can cause nonsynchronous behaviour between A and g_s, which under dynamic conditions can result in far from optimal intrinsic water use efficiency ($W_i = A/g_s$; Matthews *et al.*, 2017; Vialet-Chabrand *et al.*, 2017). The quantification of stomatal kinetics has recently received a great deal of attention; however, the majority of this work focused on the consequences and has provided little mechanistic understanding of the underlying causes. Our review will centre on the physical and metabolic constraints that influence the speed at which stomatal aperture responds to changing conditions; and while we will exemplify dynamic responses using photosynthetic photon flux density (PPFD)-driven changes, we acknowledge that other environmental factors greatly influence kinetics.

II. Influence of the speed of g_s responses on A and W_i

Light is one of the most dynamic environmental signals that influence both photosynthetic rate A and stomatal conductance g_s. Passing clouds and overlapping leaves in a canopy result in leaves experiencing 'sun flecks' and 'shade flecks' that can occur in timeframes of seconds to hours. Additionally, the variation in light

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energy received by the plant can create rapid and extreme fluctuations in leaf temperature and leaf–air vapour pressure deficit to which stomata will respond in conjunction with other environmental cues. However, plant responses do not all occur within the same timescale: PPFD-driven changing in A responding and reaching a new steady state within several tens of seconds to minutes, whereas changes in g_s can take minutes to hours (Barradas & Jones, 1996; Lawson & Morison, 2004; Lawson *et al.*, 2010; Vico *et al.*, 2011; McAusland *et al.*, 2016). The slow g_s increase often limits A, whilst the slow g_s decreases result in a lag between the drop in A and the g_s response, which can result in unnecessary water loss for a limited carbon gain, reducing W_i (Hetherington & Woodward, 2003; Franks & Farquhar, 2007; Brodribb *et al.*, 2009; Vico *et al.*, 2011; Lawson *et al.*, 2012; Drake *et al.*, 2013; McAusland *et al.*, 2016). The disconnection between A and g_s and resulting g_s limitation of A depends on the change in PPFD, the photosynthetic capacity of the plant, the initial and final g_s and the speed of the stomatal response. This is illustrated in Fig. 1, which shows the relationship between A and g_s at different light intensities and the possible trajectories of A and g_s following a step change in light. In this example, the red line illustrates a typical temporal response of A, in which A rapidly increases to a new steady state (determined by the initial g_s value), with any further increase in A dependent upon the rapidity of the g_s response. The blue line represents the theoretical g_s required to achieve 95% A, and the trajectory if A and g_s were fully synchronized, and could represent a target for improved stomatal behaviour. Values to the left of the trajectory (blue line) represent g_s limitation of A (red shading), whilst those to the right (blue shading) represent unnecessary water loss relative to CO_2 gain.

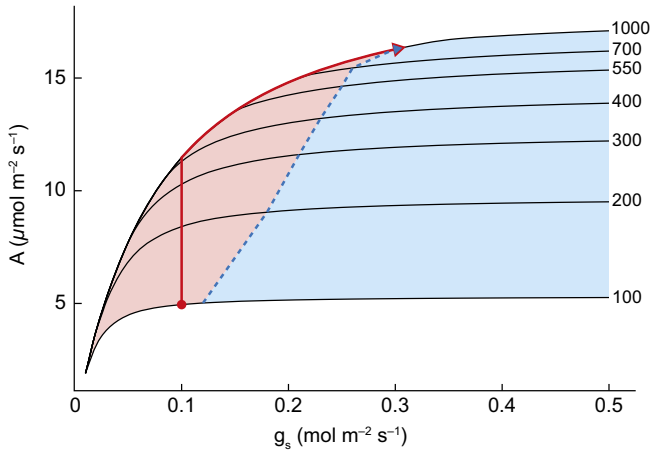

Fig. 1 Relationship between net CO_2 assimilation $A$and stomatal conductance g_s as a function of light intensity (indicated on each line, μmol m^{-2} s^{-1}), under constant temperature and air relative humidity. Each line represents the value of A if light intensity was kept constant and only g_s varied. Net CO_2 assimilation was calculated using the equations provided by Wang & Jarvis (1993). The red line illustrates the trajectory of A after a step change in irradiance (from 100 to 1000 μmol m^{-2} s^{-1}), showing the instantaneous increase in A followed by a slow increase in A limited by the g_s response. The blue dashed line represents the g_s value required to achieved 95% of maximum A (depending on light intensity) and represents the trajectory if A and g_s were fully synchronized. Values to the left of the trajectory (blue line) represent g_s limitation of A (red shading), whilst those to the right (blue shading) represent unnecessary water loss relative to CO_2 gain. Red dots represent the initial g_s and the arrow the final steady-state g_s.

Considerable variation between species in both the rapidity and magnitude of g_s responses to changing PPFD has been reported in both laboratory (e.g. Elliott-Kingston *et al.*, 2016; McAusland *et al.*, 2016) and field studies (e.g. Cardon *et al.*, 1994, 1995; Barradas & Jones, 1996; Qu *et al.*, 2016), depending on guard cell type (Hetherington & Woodward, 2003; Franks & Farquhar, 2007; McAusland *et al.*, 2016), growth conditions (Elliott-Kingston *et al.*, 2016; Qu *et al.*, 2016; Matthews *et al.*, 2017; Hepworth *et al.*, 2018) and the magnitude and type of signal that initiates these responses (Elliott-Kingston *et al.*, 2016; Hepworth *et al.*, 2018). Fig. 2 provides an example of the diversity of A and g_s responses to a step change in irradiance in *Vicia faba* and *Avena sativa*. The difference between the initial and final steady-state g_s along with the rapidity of response resulted in different limitations on A and W_i. In *V. faba*, A took longer to reach a plateau due to the slow temporal response of g_s (Fig. 2a) limiting CO_2 diffusion, whilst slow stomatal closure in *A. sativa* resulted in unnecessary water loss (Fig. 2b). Modelled synchronous behaviour in g_s and A has been shown to theoretically increase W_i by 20% in *Phaseolus vulgaris* subjected to dynamic light (Lawson & Blatt, 2014).

Two important components of the PPFD signal that will determine the temporal response of A, g_s and W_i are the intensity of the new light level and its duration (Vialet-Chabrand *et al.*, 2016). The intensity impacts on the magnitude of the g_s response, whilst the duration determines the level that can be achieved within the timescale, as illustrated in Fig. 3. Owing to slow stomatal responses, variations in PPFD of a short duration or low magnitude do not significantly impact on g_s, despite a change in A (Lawson *et al.*, 2012). However, changes in light intensity of a greater magnitude and/or longer duration result in a typical exponential response of A and g_s that can be used to quantify the rapidity of g_s response, the degree of limitation of A and the impact on W_i (Fig. 3). In this example W_i is improved by the slow increase in g_s; however, this is at the expense of limiting A, which illustrates the challenge of optimizing W_i whilst maintaining high A. Slow reaction time of stomata can also result in a g_s continuing on the same trajectory even after the light stimulus has ceased (Kirschbaum *et al.*, 1988; Tinoco-Ojanguren & Pearcy, 1993), which can be defined as a stomatal 'overshoot'. Overshoots in stomatal opening are a common feature of well-watered plants, resulting in unnecessary water loss and decreasing W_i (McAusland *et al.*, 2016), but may be important for maintaining leaf temperature or maximizing A in a dynamic environment.

McAusland *et al.* (2016) showed significant variation in the opening and closing kinetics in a range of different species, reporting an average 10% stomatal limitation on A. Kaiser *et al.* (2015) suggested that stomatal limitation of A was minimal (1–3%) compared with the biochemical limitations imposed by activation of Rubisco. However, these findings could be due to the experimental protocol, as plants were dark adapted before being exposed to a step increase in illumination of 1000 μmol m^{-2} s^{-1} PPFD. Plants in a 'real' environment would never experience such extreme changes in light intensity, which could induce high levels of

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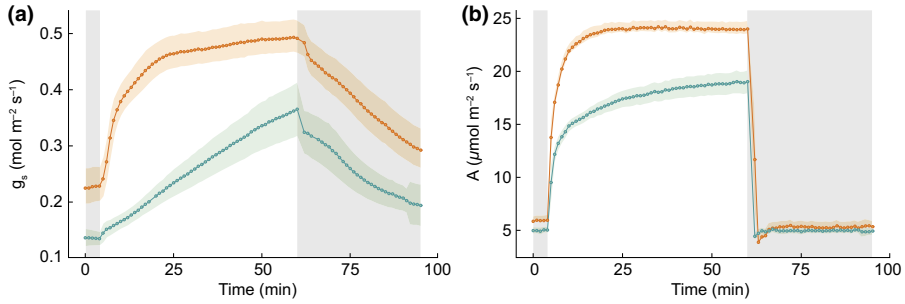

Fig. 2 Temporal responses of (a) stomatal conductance g_s and (b) net CO_2 assimilation A in *Vicia faba* (blue dots) and *Avena sativa* (red dots) to a step change increase followed by a decrease in irradiance. Values are an average of four replicates, and the coloured shading represents plus/minus SE. The shaded and white areas represent light intensities of 100 μmol m^{-2} s^{-1} and 1000 μmol m^{-2} s^{-1} respectively. Data redrawn from McAusland *et al.* (2016).

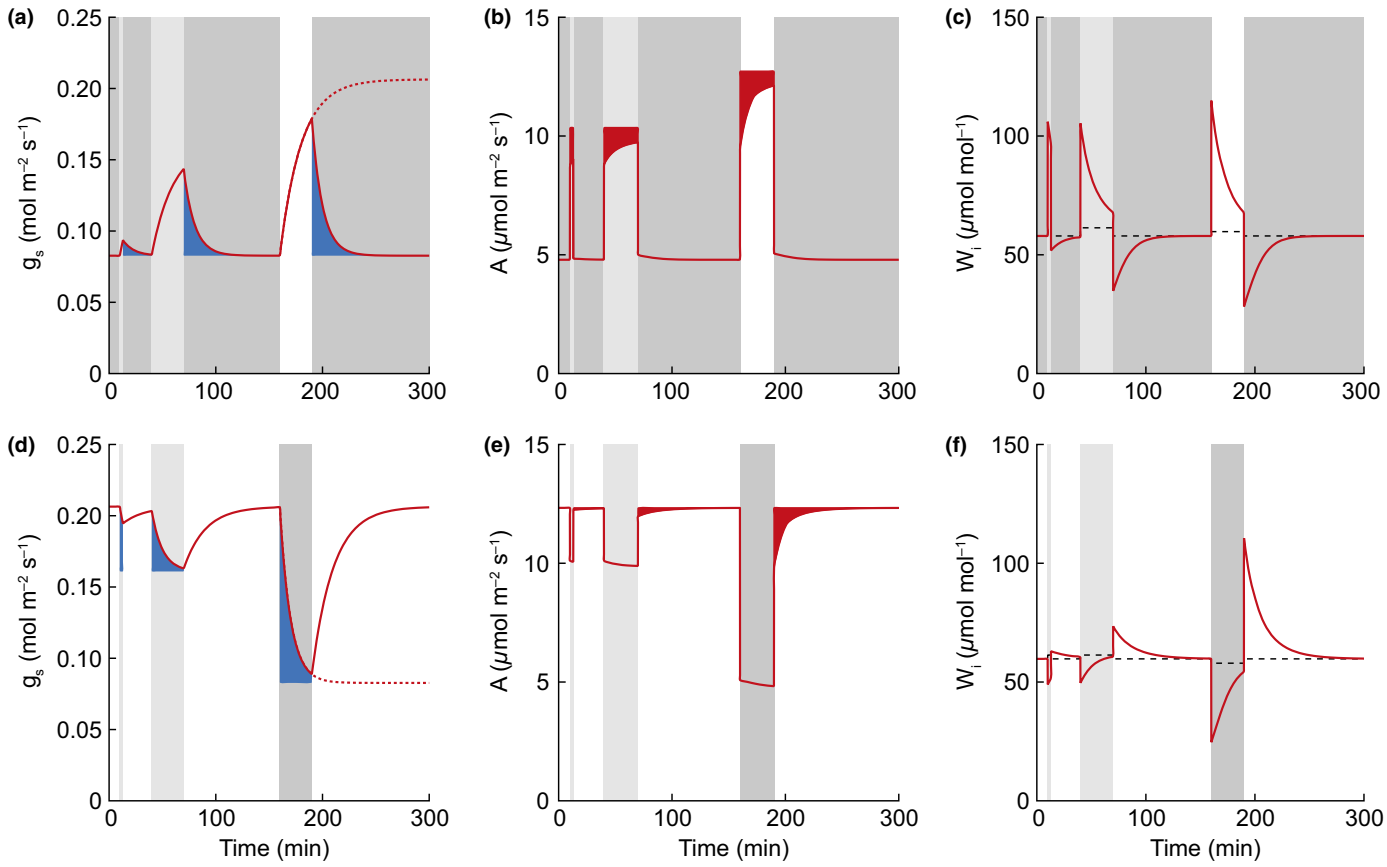

Fig. 3 Schematic representing the temporal response of stomatal conductance g_s, net CO_2 assimilation A and intrinsic water use efficiency W_i during (a–c) sun flecks or (d–f) shade flecks of different durations and changes in light intensity. The intensity of the shading (from grey to white) represents variation in light intensity, with white the highest intensity and dark grey the lowest. Blue shading represents unnecessary water loss (relative to A) due to the slow temporal responses in g_s, whilst red shading is the amount of A limitation by g_s. The red dashed line represents the g_s achieved if conditions were maintained constant for a long time period. The black dashed line (c, f) represents W_i in the case of an instantaneous response of g_s to variation in light intensity.

stress due to a lack of induction and activation of key photosynthetic enzymes.

III. Determinants of the rapidity of g_s responses

The determinants of the rapidity of the g_s response can be simply categorized into anatomical (e.g. density and size of stomata), structural (e.g. cytoskeleton and cell wall elasticity) and biochemical (e.g. number and activity of transporters or ion channels) features.

Anatomical considerations

Smaller stomata have often been proposed to have faster kinetics (Drake *et al.*, 2013), thought to be due to a greater guard cell membrane surface area to volume ratio, which enables more rapid

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changes in solutes than with larger guard cells (Hetherington & Woodward, 2003; Drake *et al.*, 2013; Raven, 2014). Although a relationship between size and speed holds up in closely related species of the same genus (Drake *et al.*, 2013), this is not conserved over a wide range of species (Elliott-Kingston *et al.*, 2016; McAusland *et al.*, 2016) and may only be valid within or between species with similar stomatal features. Whilst diverse species with different stomatal features may have mechanisms influencing the speed independently of the size (e.g. including the number and size of subsidiary cells for solutes exchange (Franks & Farquhar, 2007) and differences in biochemistry, gene expression and sensitivity). For example, Elliott-Kingston *et al.* (2016) examined rapidity of stomatal closure in an evolutionary diverse set of species (including fern, cycad, conifers and angiosperms) and found no relationship with size or density of stomata, but suggested that species diversification in low atmospheric [CO_2] led to faster stomatal responses (Elliott-Kingston *et al.*, 2016). The differences in the rapidity of g_s observed by McAusland *et al.* (2016) in a range of crop plants could also not be explained by the size of stomata in species with elliptical (or kidney-shaped) guard cells. However, in species with dumbbell-shaped guard cells, size impacted on the speed and amplitude of response, and generally resulted in faster g_s responses (McAusland *et al.*, 2016), suggesting involvement of biochemical mechanisms. Interestingly, the same authors also suggested that mesophyll photosynthetic metabolites might be important in the rapidity, as both opening and closing responses were faster in C_4 dumbbell species than in C_3 (McAusland *et al.*, 2016), although the exact mechanism that links these two processes has yet to be identified.

Franks & Farquhar (2007) illustrated that morphology of stomatal complexes, including guard cell shape and the presence or absence of subsidiary cells, also influences stomatal function. This research illustrated that fully turgid subsidiary cells convey a mechanical advantage, and maximum stomatal aperture in grass species such as *Triticum aestivum* cannot be achieved without reductions in subsidiary cell turgor pressure. The rapid exchange of osmotica between subsidiary cells and guard cells enables rapid switching of turgor pressure between these two cells, providing a possible mechanism for the rapid stomatal movement in grasses (Franks & Farquhar, 2007). A recent study supporting this mechanism, in which a transcription factor necessary for subsidiary cell development was manipulated in *Brachypodium distachyon*, has resulted in impaired stomatal kinetics and reduced g_s (Raissig *et al.*, 2017). The evolution of dumbbell-shaped guard cells in grass species (which includes a number of major crops) and the relationship between the guard cells and subsidiary cells has provided these species with the functional advantage of faster stomatal responses (Drake *et al.*, 2013; McAusland *et al.*, 2016; Chen *et al.*, 2017) and optimal patterning (Hepworth *et al.*, 2018) that has been attributed to the evolutionary success of these species (Chen *et al.*, 2017).

Structural considerations

Stomatal movements involve pronounced changes in the shape and volume of the guard cell that are partially controlled by the reorganization of actin filaments (Kim *et al.*, 1995; Hwang *et al.*, 1997; Higaki *et al.*, 2010; Eisinger *et al.*, 2012) and cell wall properties (Carter *et al.*, 2017; Woolfenden *et al.*, 2017). For example, Carter *et al.* (2017) recently proposed a new model of guard cell structural changes in response to turgor, involving a pectin-based pinning down of the guard cell ends that promotes increase in stomatal width during opening. The importance of these properties in the rapidity of guard cell movements has recently been assessed using actin-related protein 2 (arp2) and arp3 mutant, which showed impaired vacuolar fusion and slower opening than wild-type (WT) controls and complementation lines (Jiang *et al.*, 2012; Li *et al.*, 2013; Isner *et al.*, 2017).

Biochemical considerations

Stomatal movements result from changes in guard cell turgor due to osmotic adjustments in response to fluxes of potassium ions (K^+), chloride and organic anions (e.g. malate and sucrose), and their transport across the plasma membrane and tonoplast (Blatt, 2000). The extent and rapidity of stomatal movements is therefore intrinsically linked to the capacity for solute transport and the speed with which transport responds to environmental cues (reviewed by Lawson & Blatt, 2014). Transport capacity is determined by the density and activity of guard cell membrane transporters, which is connected to the surface area to volume ratio and has been suggested to relate stomatal size with speed (Franks & Farquhar, 2007; Raven, 2014). However, several studies have reported considerable variation in solute fluxes in different species independent of cell size (reviewed by Lawson & Blatt, 2014), which could explain the lack of correlation between the size of stomata and stomatal speed. In addition to the mechanical advantage provided by the four-celled stomatal complex, grass species exhibit the fastest response due to the rapid transport of ions and osmolytes between guard cells and subsidiary cells (see Cai *et al.*, 2017; Chen *et al.*, 2017; Jezek & Blatt, 2017). A systematic approach for exploring potential targets to manipulate solute fluxes and the speed of stomatal responses is the use of quantitative system modelling. For example, Wang *et al.* (2014a) used the OnGuard model and found that only primary hydrogen ion transport and transporters directly influencing calcium ion (Ca^{2+}) fluxes affected stomatal movements, and that modest changes of separate ion channels is largely ineffective. This study provided promising targets in the form of manipulation of the voltage-dependent characteristics of the K^+ channels of the plasma membrane in guard cells. The authors reported that a voltage shift in the gating of the outward-rectifying K^+ channel accelerated stomatal closure by 30%; however, the model found that doubling the number of channels actually resulted in a slower rate of closing. In complement, Vialet-Chabrand *et al.* (2017) analysed the synergies between transporters in different cellular compartments and identified subsets of transporters associated with [Ca^{2+}], which represent potential targets to enhance plant performance. These studies illustrate the complexity of stomatal osmoregulation and signal transduction pathways, highlighting the difficulty of finding viable targets for manipulating the rapidity of stomatal responses at a biochemical level. However, it emphasizes how reverse engineering may provide

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practical solutions for improving A and W_i in a dynamic environment. For example, McLachlan *et al.* (2016) demonstrated that the breakdown of triacylglycerols is required to supply ATP for hyperpolarization of the plasma membrane and K^+ uptake through inward-rectifying K^+ channels for stomatal opening. Wang *et al.* (2014b) overexpressed H^+-ATPase in the guard cells of Arabidopsis and reported greater g_s and A, which enhanced plant growth but at the expense of W_i. This suggested that stomatal closure rates did not parallel the accelerated stomatal opening (Lawson & Blatt, 2014). Asymmetry of opening and closing responses has been reported with longer delays in opening or slower opening responses relative to closure (Vico *et al.*, 2011), which may indicate water conservation strategies rather than optimizing carbon gain (Vico *et al.*, 2011; McAusland *et al.*, 2016). However, stomatal responses also depend on the growth environment, including the influence of water status (Qu *et al.*, 2016; Haworth *et al.*, 2018) and lighting regime (Matthews *et al.*, 2018), illustrating further complexities.

It is worth remembering that the cost of stomatal movements, in terms of energy and solute requirements, could be too great if stomata responded continuously to environmental changes to maximize photosynthesis and water use efficiency. Therefore, the more conservative (buffered) responses, as well as the reported asymmetry in the rapidity of stomatal opening and closing, could reflect a trade-off between cost of stomatal movements, CO_2 uptake and water loss under a specific environment.

IV. Conclusion

Improving the rapidity of stomatal responses could greatly improve A and W_i and aid plant productivity. Although many studies have investigated the rapidity of stomatal responses and attributed differences to anatomical features, a full mechanistic understanding is still lacking. Guard cell membrane transport and channel activity are key to balancing ionic fluxes for stomatal movement; however, the manipulation of a single channel is unlikely to increase the rapidity of g_s, as coordination of multiple channels is required, as well as coordination of fluxes at both the plasma membrane and tonoplast. Further studies are therefore needed to generate extensive data sets on stomatal kinetics from existing mutants, as well as the identification of new targets for guard cell manipulation. Restricting studies to a single genus will minimize genetic effects, reducing the complexity of responses, and may be the most effective procedure for screening and selecting for faster stomata (Drake *et al.*, 2013).

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