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EDITORIAL

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Photosynthesis and the stomatal nexus, past, present and future

The stomatal nexus is unique as a focal point that brings together knowledge across both research disciplines and purpose. Stomata are pores on the surfaces of terrestrial plants, formed between pairs specialised epidermal cells, the guard cells. They are vital as pathways across the impermeable cuticle barrier of the plant surface that enable CO_2 entry into the leaf for photosynthesis by the mesophyll. The open stoma also provides a pathway for transpirational water loss to the atmosphere from the near-saturated inner air space of leaves. Inevitably, diffusion of CO_2 into the leaf comes at the expense of water vapour diffusion from the leaf, and it is this exchange that has attracted much interest, from plant ecophysiology, photosynthetic and metabolic adaptations (Lawson et al., 2014; Long et al., 2022; Santelia & Lawson, 2016) to the molecular mechanics of guard cell signal transduction and bioengineering (Horaruang et al., 2022; Papanatsiou et al., 2019).

Stomata connect the carbon and water cycles across the globe through the activities of photosynthesis and they exert a major impact on both. We need only look at the success of atmospheric modelling, first introduced at the end of the 1980s to incorporate foliar water loss, that dramatically refined weather prediction over the past quarter of a century (Beljaars et al., 1996; Berry et al., 2010; Betts et al., 1996; Jasechko et al., 2013). By the same token, it has become abundantly clear that stomata are at the centre of the interlinked challenges of climate change, water availability and crop production that are unfolding now and are certain to become all the more urgent over the next 10–20 years. Fresh water usage across the globe increased sixfold over the 20th century, twice as fast as the human population, and is likely to double again before 2035, driven by agricultural demand (Unesco, 2015). Even in the United Kingdom, not generally considered a region of arid climate, irrigation has risen 10-fold in the past 30 years and this trend is expected to continue (Home Office Hadley, 2012).

The position of stomata, and the relative isolation of the guard cells at the leaf surface, also makes these cells unusually tractable targets for the most fundamental questions in plant physiology. How do guard cells control the osmotic solute and water fluxes that drive stomata to open and close? What are the molecular mechanics behind these fluxes? And how are these mechanisms coupled to environmental and physiological signals, and to other biophysical processes within the leaf? Indeed, many of the developments emerging into the mainstream of plant membrane research finds their roots in research into guard cells (Blatt, 2024).

It comes as no surprise, then, that the stomata continue to challenge thinking across disciplines, whether of fundamental or applied research, and to yield new insights into the life of plants in the global environment. This special issue offers a selection of reviews, and the viewpoints of some of the leading scientists in their fields, that address the stomatal nexus.

In addition to a number of primary research articles, this issue of Plant, Cell and Environment opens with four articles that review aspects of the common themes of development, evolution, and the interplay in stomatal characteristics within the leaf epidermis and their breadth of functional characteristics. Kim and Torii (2023) assess our present knowledge of how stomata arise, from initiation through commitment and differentiation of stem cells, highlighting how the timing of cell fate and identity decisions define the progression and differentiation of functional stomata and their neighbours. Much of recent knowledge here comes from single-cell and cell-type-specific transcriptomics, epigenomics and chromatin accessibility profiling that identifies the most important regulatory transcription factors and epigenetic machineries behind fate commitment and maintenance.

Chen et al. (2024) explore our understanding of how stomata evolved the diversity of functional behaviours with special emphasis on guard cell membrane transporters. Their analysis suggests that many of the core signalling processes arose before the evolution of anatomically-distinct stomata, by contrast with developmental genes that co-evolved with the earliest stomata. The two developments reflect distinct but parallel adaptive strategies behind land plant evolution. The complementary review by Nguyen and Blatt (2024) delves into questions of the development, evolution and function of the epidermal cells that surround stomatal guard cells. These surrounding cells, sometimes anatomically distinct as 'subsidiary' cells, impact on stomatal movements both as solute reservoirs and as kinetic moderators that affect stomatal kinetics through backpressure on the guard cells. Although poorly studied to date, the review highlights the few detailed studies that address their transport characteristics and indicate often complex contributions to stomatal physiology.

The fourth of these reviews from Ding et al. (2024) assembles the recent findings around the role of aquaporins in stomatal movements. Aquaporins have come to be recognised as important pathways for water flux behind stomatal opening and closing. The review addresses the interplay between the guard cells and their surrounding epidermals cells, with a special focus on the stomata of grasses. Here, as in ion transport, traffic, partner protein interactions and subcellular distributions are now recognised for their crucial roles in defining stomatal dynamics.

Moving to the whole plant, the review of Pelaez-Vico et al. (2024), published earlier this year, considers the growing evidence for systemic and long-distance coordination between stomata on a leaf and between leaves of a plant. These are phenomena that have intrigued researchers for almost four decades. Only now are some answers surfacing as to how they arise and the complex signalling events that lie behind them. The authors also address potential biotechnological implications of regulating systemic stomatal responses in a warmer and CO_2-enriched environment.

At the whole-plant and canopy levels, the technologies for quantifying stomatal function, photosynthesis and their entanglements have advanced substantially over the past two decades. Busch et al. (2024) outline much of the conceptual logic behind the biochemical and biophysical parameters defining photosynthesis and transpiration that are accessible to the experimenter through gas exchange measurements. They offer a step-by-step guide in gas exchange analysis that incorporates best practices for equipment usage, and they highlight some common pitfalls in experimental design and data interpretation.

Walker et al. (2024) review our knowledge of photorespiration, the bypass that accommodates fixation of O_2 rather than CO_2 by ribulose-bisphosphate carboxylase oxygenase. They discuss the consequent alterations in metabolic requirements for ATP and NADPH. New model treatments of metabolic flux lead to a conclusion that the energetic demands of photorespiration are highly sensitive to alternative flux, and they suggest alternative flows of carbon through photorespiration may require a reconsideration of the ATP and NADPH demands on linear electron transport.

Of course, the stomatal nexus connects directly with hydraulic water flux through the xylem that feeds the leaf, inorganic carbon flux within the leaf and mesophyll, and thermal exchange between the leaf and its environment. Jacobsen et al. (2024) highlight the difficulties around estimating and predicting xylem water flux, particularly as water demand means that plants regularly experience conditions that give rise to air gaps—embolisms—within at least some of the xylem conduits. Under these conditions, evaluating the network and the remaining functionalities of partially-embolized networks present important barriers to an understanding of how plants cope with stress.

In a complementary review, Marquez and Busch (2024) examine some of the recent advances in understanding CO_2 passage within the leaf and mesophyll, and the methodologies behind these developments. They emphasise the interactions between stomatal conductance and so-called mesophyll conductance that associates with CO_2 diffusion within the leaf and mesophyll, and they suggest that the two, at least in part, may be subject to independent controls. Leverett and Kromdijk (2024) approach some of the same issues but from the viewpoint of bioengineering. They examine the challenges of engineering crops with improved photosynthetic efficiencies by enhancing foliar mesophyll conductance. Their review explores the limitations and uncertainties behind estimates of this parameter to ask the question whether mesophyll conductance is a viable target for bioengineering.

Water flux through stomata is driven by evaporation within the leaf and its consequence is to transfer heat to water vapour as well as by the vapour pressure difference (VPD) between the inside and outside of the leaf, which is also subject to temperature. In short, transpiration is deeply entangled with leaf temperature at multiple levels. Mills et al. (2024) address the long-standing but poorly researched topic of thermo-responsiveness in stomata. They review the data available that separates temperature from changes in VPD as well as proposed biophysical mechanics of temperature sensitivity to assess the possible implications for whole-plant adaptation in a time of global climate change. Novick et al. (2024) take a considered look at VPD, the global pressures that affect it, and their impacts on water resources, crop yields and biodiversity. Their assessments lead to a set of recommendations for mitigating these impacts. Finally, Wilkening et al. (2024) examine the continuum of soil, plant and atmosphere from the different ecological perspectives of plant physiology and soil hydrology. They trace the origins and developments surrounding both that have led to commonalities in concept and quantitative analysis. The review makes a strong case for the integration of these disparate yet intertwined fields, pointing to the limitations of each approach in isolation as well as the benefits of work that straddles the two disciplines.

As a compendium and overview of the present research landscape, the articles that comprise this special issue offer deep and thoughtful dives into the advances in understanding that are possible when researchers appreciate the many linkages that cross boundaries from the cell and plant to the environment. Indeed, the issue is a fitting illustration of the value of Plant Cell and Environment, as it approaches 50 years of publication, and a showcase for some of the most important research in integrative and environmental plant physiology.

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