



Editorial: Transport and Membrane Traffic in Stomatal Biology

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Editorial on Research Topic

Transport and Membrane Traffic in Stomatal Biology

Global climate change and increasing atmospheric CO₂ are clearly set to impact precipitation and the availability of fresh water worldwide. Agricultural water usage is fundamentally connected to plant gas exchange and hence to the carbon cycle of the globe, thereby affecting agricultural productivity (Blatt et al., 2017). The stomata of plants are tiny pores that facilitate the gas exchange between plants and the environment. Their movements are regulated by dynamic changes in the volume of guard cells that line the stomatal pore. Guard cell volume is regulated in response to environmental cues, balancing leaf gas exchange. Stomatal opening facilitates CO₂ uptake for photosynthetic carbon assimilation and stomatal closing prevents water loss through transpiration (Lawson and Blatt, 2014). Although the total area of stomatal pores only represents <3% of the leaf surface, almost all CO₂ absorption and up to 95% of water loss from plants are through these pores in stomata-bearing plant species (Schroeder et al., 2001). Indeed, changes in stomatal behavior in response to changing climatic conditions will, in turn, affect global water and carbon cycles (Lawson and Blatt 2014). Moreover, stomatal guard cells respond to an array of extracellular and intracellular signals, including light and CO₂. In guard cells, ion transport and membrane vesicle traffic are coordinated for the regulation of stomatal aperture in response to environmental and endogenous cues (Sutter et al., 2007; Grefen et al., 2015; Jezek and Blatt, 2017; Xia et al., 2019). Thus, understanding stomatal function and their regulating mechanisms are vital for water use efficiency (WUE) in agriculture, and for the development of strategies for improved crops that are resilient to global climate changes.

In plants, water loss by transpiration occurs through the stomatal pore. WUE is calculated as a ratio of the amount of water used in metabolism to the water plant transpired and takes into account photosynthetic rate (A) to transpire rate (E), or the ratio of biomass produced by the plant to the rate of transpiration. However, improving WUE by enhancing plant A is difficult as enhancing CO₂ uptake comes at a cost of water loss in most plants. Thereby, accelerating stomatal responses to reduce transpirational water loss is considered an efficient way to improve WUE. In the past decades, efforts are ongoing to improve WUE in crops, and success in such technologies requires fundamental knowledge of stomatal regulation in plants.

Quantitative modeling is a potential strategy to solve the dilemma of balancing between WUE and A. It offers a promising *in silico* approach to investigate the stomatal function and its related WUE. The OnGuard model is the first quantitative guard cell model with a set of macroscopic descriptors of guard-cell-specific features (Chen et al., 2012; Hills et al., 2012). Experimental tests (Chen et al., 2012; Hills et al., 2012; Wang et al., 2012, 2014; Minguet-Parramona et al., 2016; Jezek et al., 2021) established the reliability of the representations encoded in the model across a wide

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range of experimentation and led to a more profound understanding of the complex mechanisms behind many of the responses of guard cells and stomata to environmental change (Wang et al., 2017). OnGuard model offers users an unprecedented tool with which to explore the mechanics of stomatal functions across scales from the molecule to the whole plant. In this Research Topic, Shafaque et al. describe a standard protocol for using OnGuard Software in studying stomatal physiology and its related ion transport and homeostasis. They provided comprehensive guidance to the fresh users to manipulate the function of each key option of the model and took several examples to show how to change parameters in ion transporter characters and humidity.

Recent studies have shown that enhanced stomatal kinetics for opening and closure can contribute to high WUE in plants (Lawson and Blatt, 2014). Papanatsiou et al. (2019) expressed a synthetic, light-gated K⁺ channel, BLINK1 in the guard cells of Arabidopsis to accelerate both stomatal opening under light exposure and closing after irradiation, driving a 2.2-fold increase in biomass in fluctuating light without cost in water use by the plant. These findings open a new avenue for strategies toward improving plant WUE by using optogenetic tools that enhance stomatal kinetics. In this Research Topic, Ding and Chaumont provide insights into the regulation of stomatal kinetics by optimizing the expression of water transporting aquaporin proteins in plants.

In addition to the stomatal kinetics, stomatal morphology is also a key factor to affect stomatal response and WUE. The Poaceae family have distinctive dumbbell-shaped guard cells and specialized subsidiary cells to form an efficient stomatal complex. These allow for a faster grass stomatal response than any other stomatal type (Chen et al., 2017). However, the molecular mechanism of Poaceae family stomatal regulation is not well characterized. In this Research Topic, Wang and Chen highlight the unique structure and developmental progress of grass stomata and outline the different guard cell signaling mechanisms in monocots and eudicots.

REFERENCES

- Blatt, M. R., Brodribb, T. J., and Torii, K. U. (2017). Small pores with a big impact. *Plant Physiol.* 174, 467–469. doi: 10.1104/pp.17.00642
- Chen, Z. H., Chen, G., Dai, F., Wang, Y., Hills, A., Ruan, Y. L., et al. (2017). Molecular evolution of grass stomata. *Trends Plant Sci.* 22, 124–139. doi: 10.1016/j.tplants.2016.09.005
- Chen, Z. H., Hills, A., Baetz, U., Amtmann, A., Lew, V. L., and Blatt, M. R. (2012). Systems dynamic modeling of the stomatal guard cell predicts emergent behaviors in transport, signaling, and volume control. *Plant Physiol.* 159, 1235–1251. doi: 10.1104/pp.112.197350
- Grefen, C., Karnik, R., Larson, E., Lefoulon, C., Wang, Y., Waghmare, S., et al. (2015). A vesicle-trafficking protein commandeers Kv channel voltage sensors for voltage-dependent secretion. *Nature Plants* 1, 15108. doi: 10.1038/nplants.2015.166
- Hills, A., Chen, Z. H., Amtmann, A., Blatt, M. R., and Lew, V. L. (2012). OnGuard, a computational platform for quantitative kinetic modeling of guard cell physiology. *Plant Physiol.* 159, 1026–1042. doi: 10.1104/pp.112.197244
- Jezek, M., and Blatt, M. R. (2017). The membrane transport system of the guard cell and its integration for stomatal dynamics. *Plant Physiol.* 174: 487–519. doi: 10.1104/pp.16.01949
- Jezek, M., Silva-Alvim, F., Hills, A., Donald, N., Ishka, M. R., Shadbolt, J., et al. (2021). Guard cell endomembrane Ca²⁺-ATPases underpin a 'carbon memory' of photosynthetic assimilation that impacts on water-use efficiency. *Nat. Plants.* 7:1301–1313. doi: 10.1038/s41477-021-00966-2
- Lawson, T., and Blatt, M. R. (2014). Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiol.* 164, 1556–1570. doi: 10.1104/pp.114.237107
- Minguet-Parramona, C., Wang, Y., Hills, A., Violet-Chabrand, S., Griffiths, H., Rogers, S., et al. (2016). An optimal frequency in Ca²⁺ oscillations for stomatal closure is an emergent property of ion transport in guard cells. *Plant Physiol.* 170, 33–42. doi: 10.1104/pp.15.01607
- Papanatsiou, M., Petersen, J., Henderson, L., Wang, Y., Christie, J. M., and Blatt, M. R. (2019). Optogenetic manipulation of stomatal kinetics improves carbon assimilation, water use, and growth. *Science.* 363:1456–1459. doi: 10.1126/science.aaw0046

In the last article of this Research Topic, Ren et al. provide us a mini-review on sulfur compounds in stomatal regulation. Sulfur is one of the essential elements for plants. It has important effects on plant growth, development, and abiotic and biotic responses. In recent studies, various sulfur compounds, including H₂S, SO₂, SO₃²⁻, etc., were reported to regulate stomatal movements. This mini-review offers us the detail of how these sulfur compounds affect stomatal movements.

To sum up, this Research Topic provides up-to-date stomatal knowledge using multi-disciplinary approaches, including computational biology, agricultural biology, and molecular and cellular biology. We believe that stomatal research will continue to flourish in the future as novel technologies emerge.

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- Schroeder, J. I., Allen, G. J., Hugouvieux, V., Kwak, J. M., and Waner, D. (2001). Guard cell signal transduction. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 52, 627–658. doi: 10.1146/annurev.arplant.52.1.627
- Sutter, J., Sieben, C., Hartel, A., Eisenach, C., Thiel, G., and Blatt, M. R. (2007). Abscisic acid triggers the endocytosis of the Arabidopsis KAT1 K⁺ channel and its recycling to the plasma membrane. *Curr. Biol.* 17, 1396–1402. doi: 10.1016/j.cub.2007.07.020
- Wang, Y., Hills, A., and Blatt, M. R. (2014). Systems analysis of guard cell membrane transport for enhanced stomatal dynamics and water use efficiency. *Plant Physiol.* 164, 1593–1599. doi: 10.1104/pp.113.233403
- Wang, Y., Hills, A., Vialet-Chabrand, S., Papanatsiou, M., Griffiths, H., Rogers, S., et al. (2017). Unexpected connections between humidity and ion transport discovered using a model to bridge guard cell-to-leaf scales. *Plant Cell* 29, 2921–2939. doi: 10.1105/tpc.17.00694
- Wang, Y., Papanatsiou, M., Eisenach, C., Karnik, R., Williams, M., Hills, A., et al. (2012). Systems dynamic modeling of a guard cell CL-channel mutant uncovers an emergent homeostatic network regulating stomatal transpiration. *Plant Physiol.* 160, 1956–1967. doi: 10.1104/pp.112.207704
- Xia, L., Marques-Bueno, M., Bruce, C., and Karnik, R. (2019). Unusual roles of secretory SNARE SYP132 in plasma membrane H⁺-ATPase traffic and vegetative plant growth. *Plant Physiol.* 180, 837–858. doi: 10.1104/pp.19.00266

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