

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

4,800

Open access books available

122,000

International authors and editors

135M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.

For more information visit www.intechopen.com



The physiology and genetics of stomatal adjustment under fluctuating and stressed environments

Mingnan Qu, Saber Hamdani and James A. Bunce

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/62223>

Abstract

Stomata are pores in the leaf that allow gas exchange where water vapor leaves the plant and carbon dioxide enters. Under natural condition, plants always experience at a fluctuating light regime (shade-/sun-fleck) and due to global climate change, occasionally extreme high temperature and CO₂ enrichment will be inevitable occurred, which dramatically affects stomatal response, and trade-off between water-use efficiency and photosynthesis. Response of stomata to fluctuating and stressed environments determines optimized strategy of plants directing to water save or photosynthesis. Dynamic adjustments of stomata play an equivalent role as steady-state stomatal characteristics. Evolutionary approach indicated that stomatal-dynamic adjustments interacting with historical environments or life histories could be genetically controlled and environmentally selected. In this article, we reviewed physiological response of stomatal dynamic to changing environments including our previous works, and discussed the possibility of genetic improvements on stomatal adjustments by estimating broad-sense heritability and SNP heritability of stomatal pattern. To gain insight into the framework of stomatal genetics, we highlighted the importance of combining multidisciplinary techniques, such as mathematic modeling, quantitative genetics, molecular biology and equipments developments.

Keywords: Stomatal dynamics, Changing environments, Photosynthesis, Evolution

1. Introduction

Stomata, from the Greek word “stoma” meaning mouth, are small pores that distributed on the epidermis of plant leaves. Their structures consist of two guard cells around a pore. For optimum efficiency, stomata must balance the gas exchange between inside and outside the leaf, in order

to maximize CO₂ uptake for photosynthetic carbon assimilation (P_N) and to minimize water loss through transpiration (E). Although the cumulative area of stomatal pores only represents a small fraction of the leaf surface, typically less than 3%, the CO₂ uptake and water loss pass through these pores. When fully open, they can promote water evaporation equivalent to one-half of a wet surface of the same area [1]. To cope with environmental stress during growth condition, plants must adjust and regulate the stomatal opening/closing process to obtain optimized transpiration and leaf water status.

On the other hand, studying the evolutionary adaptation and natural variation of stomata-related genes may represent an essential step for better understanding the mechanisms involved in the stomatal adjustment and regulation. In fact, stomata have probably undergone a crucial adaptation occurring 400 million years ago, it enabled plants to thrive on land. To survive in the dry atmosphere, plants must maintain a reasonable level of gas exchange necessary for P_N and E , in order to protect against desiccation [2]. In addition, the natural variation in stomata-related genes across different cultivars (from different origins) of particular species may indicate differing selection pressures allowing better adaptation against environmental stress [3].

To get a deeper understanding, the study of the relationship between genotype and phenotype at the organism–environment interface by identifying traits that respond to differing environmental pressures and uncovering the genetic basis for variability in these traits is highly requested. Recent researches have shown that the mode of action of stomatal movement depends on the combination of environmental and intracellular signals. These external factors (e.g., CO₂, biotic and abiotic stresses, and additionally different plant hormones) and internal signals (e.g., ion exchange, metabolites, catalyze of enzyme, and gene structure or expression) simultaneously affect stomatal dynamics, forming a complex framework behind acclimation responses of plants under fluctuating and stressed environments. The empirical evidences related to stomatal dynamics provide strong promotion for the development of model stimulating stomatal dynamics, which remains difficult to achieve so far. In this chapter, we aim to give a multidimensional review about recent works describing multiple environmental and internal factors, such as elevated CO₂, heat stress, light fluctuations, ion channel, and stomata-related genes [4–8]. Furthermore, we discussed expended research perspective regarding stomatal evolution, natural variations of stomatal traits, interactions with life history, and theoretical modeling.

2. External environments

2.1. Interactive effects of elevated CO₂ and heat wave

The global change, leading to frequent occurrence of atmospheric CO₂ enrichment and heat wave, inevitably affects the development and final productivity of plants. Most climate impact studies rely on changes in means of meteorological variables, such as temperature and rainfall, to estimate the potential climate impacts on agricultural production. However, extreme meteorological events, e.g., a short period of abnormally high temperatures, can have a

significant profound and lasting effect on canopy transpiration, crop growth, and final yield [9].

During heat stress, elevated CO₂ has probably less effect on C₃ plants as compared to C₄ plants [10]. In fact, elevated CO₂ can increase water-use efficiency (WUE) by decreasing stomatal conductance (g_s) and E [11], which may increase tolerance to acute heat. It was shown that the reduction in g_s (stomatal opening) is about 20% for C₃ and 50% for C₄ species [10, 12, 13]. The lower g_s in C₄ plants may induce lower transpiration (water loss) and thus higher leaf temperatures, which may increase heat-related damage in C₄ plants as compared to C₃ plants in the same habitat.

Since evaporative cooling is essential to avoid heat damage in leaves exposed to full sunlight, and time scales of stomatal adjustments are longer than fluctuations in solar irradiance within a canopy, the question arises whether elevated CO₂ can mitigate damage over transpiring leaves from extreme high temperature by decreasing g_s . If this is the case, then adaptation for cooling would appear as a more imperative driver for stomatal adjustments than the potential increase in carbon gain. To test this hypothesis, intact leaves of maize were subjected to a substantial reduction P_N due to 45°C heat stress cycle for 1 hour [14]. Our previous finding showed that elevated CO₂, either during plant growth or co-heat period, does not improve the foliar thermotolerance against heat stress (Figure 1). With the lower P_N and higher g_s and subcellular CO₂ pressure (C_i) following the acute heat stress treatment, a non-stomatal inhibition of g_s occurs, contrary to other studies showing a stomatal adjustments in response to high temperature stress in grape leaves [15, 16]. In the meantime, the sudden reversal of stomatal responses to leaf temperature and CO₂ between 40°C and 45°C (Figure 1) suggests that to avoid damage, plants enhance the stomatal opening, leading to an increase in evaporative cooling.

Some studies compared elevated CO₂ effects with tolerance to heat stress in relatively heat-sensitive vs. heat-tolerant species or in species with different photosynthetic pathways [4, 17–20]. As an example, two corn cultivars (B73 and B106) were previously reported as contrasting heat stress tolerance from field investigation and evaluations [21]. When comparing the effects of elevated CO₂ and heat stress from field-based investigation using these corn cultivars, our previous results showed a reversible response of two cultivars regarding to photosynthetic activity (Figure 2), which might be due to intricate reasons: 1) change in physical function of stomatal regulation by decreasing transpiration and optimized water conservation at intact leaves scales; 2) change in kinetic activities of photosynthetic regulatory enzymes, i.e., rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase), PEPase, and MDHase (Table 1), which agrees with some reports [22, 23]; and 3) disorder of metabolite flux in Calvin cycle due to heat stress.

2.2 Fluctuating light effects

Leaves are always subjected to rapidly fluctuating irradiance due to motion of sunflecks and clouds that may span two orders of magnitude from light compensation points of shade-adapted leaves to almost full irradiance intensities [25]. Such environmental fluctuations occur at second scales, which is much shorter than the time needed for stomatal adjustments (2–60

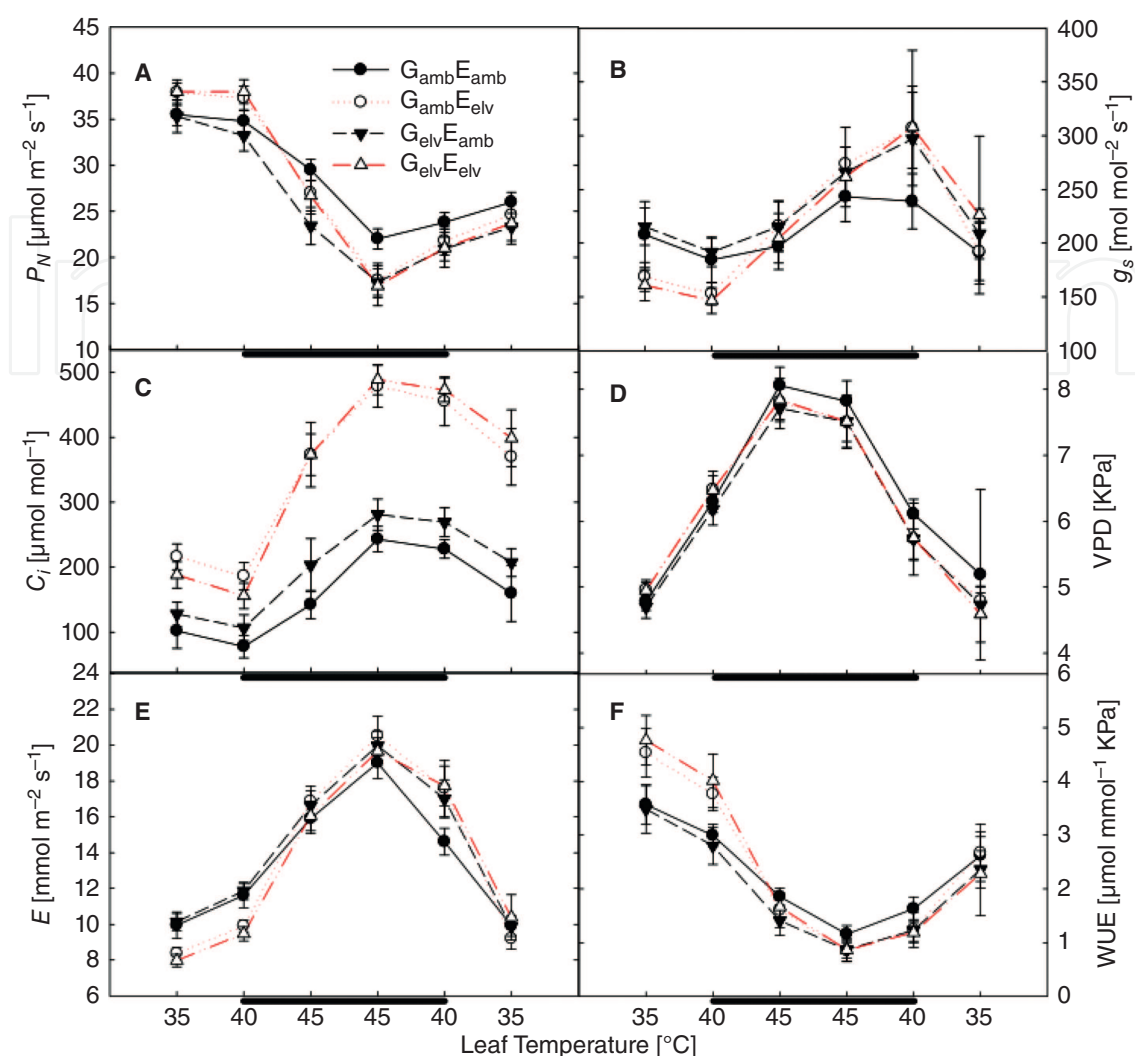


Figure 1. Dynamic changes of photosynthetic parameters during acute heat stress cycles. Lines with same color stand for treatment at same exposure CO_2 concentrations. Symbols $G_{\text{amb}}E_{\text{amb}}$, $G_{\text{amb}}E_{\text{elv}}$, $G_{\text{elv}}E_{\text{amb}}$, and $G_{\text{elv}}E_{\text{elv}}$ represent grown and exposed at ambient $[\text{CO}_2]$, grown at ambient $[\text{CO}_2]$ but exposed at elevated $[\text{CO}_2]$, grown at elevated $[\text{CO}_2]$ but exposed at ambient $[\text{CO}_2]$, and both of grown and exposed at elevated $[\text{CO}_2]$. Vertical bars represent S.E. for $n = 9$ (see [14]).

min.) [26]. For leaves with slowly adjusting stomata, rapid fluctuations at shorter time scales could push leaf hydraulic and thermal status beyond operational limits resulting in xylem cavitation, overheating, or wilting.

Although the phenomena underlying dynamic responses of photosynthesis to sunflecks (such as induction requirements) were studied by physiologists and biochemists earlier [26], their role in sunfleck utilization was not recognized until the early 1980s. Evidence for the light activation requirement of the primary carboxylating enzyme, Rubisco, was first uncovered in the 1960s [27]. The components underlying induction, especially stomatal behavior, are complex and are dependent on environmental and developmental factors as well transient light changes. It was reported that water stress could reduce g_s in shade-grown, but not in sun-

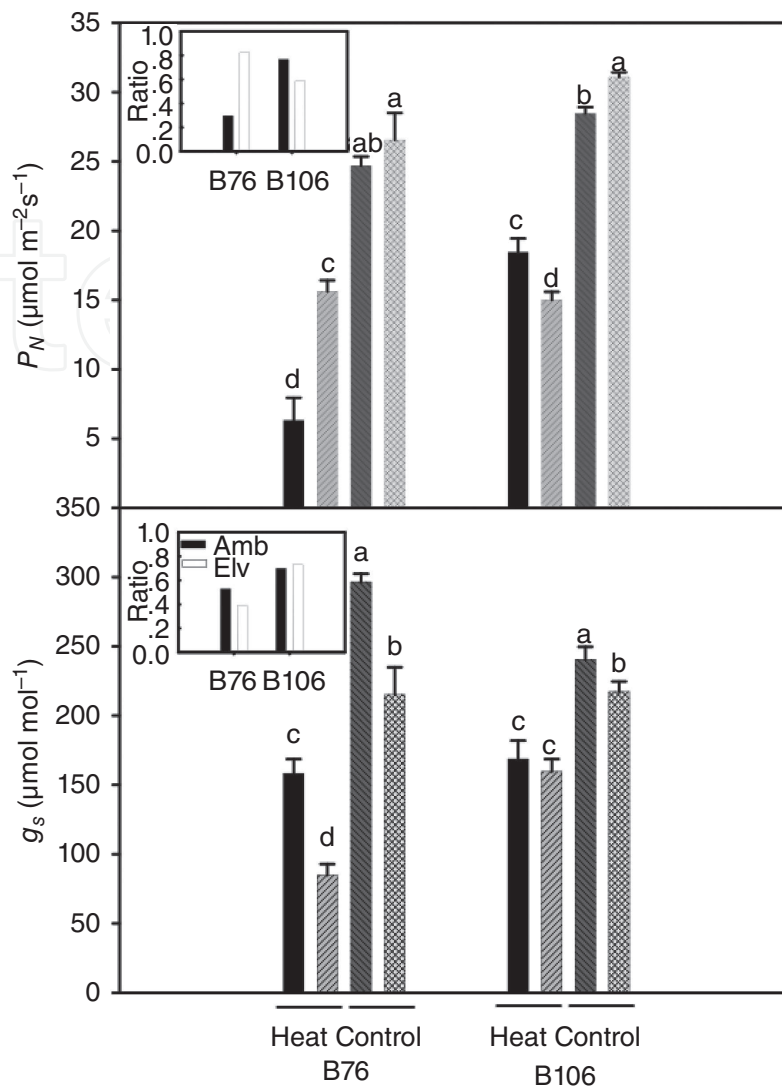


Figure 2. Heat induced decrease of photosynthesis and stomatal conductances in B76 and B106. Black and grid bars represent ambient and elevated [CO₂], respectively. Ratio of photosynthesis and stomatal conductances under heat stress over control in B76 and B106 was shown in inserted panel. (Qu et al. 2016, unpublished data).

grown for the leaves of a *Populus* species; drought also could lead to faster induction gain in shade-grown, but not in sun-grown for the leaves during simulated sunflecks [28].

In the naturally fluctuating environment, the temporal disconnect between g_s and P_N means the coordination between carbon gain and water loss (and, therefore, WUE) is far from optimal ([29]; Figure 3). Photosynthetic induction state is a complex function of light-dependent stomatal opening and closing responses and the time courses of light-regulated enzyme activation and deactivation. All these combined factors determine the potential light-saturated P_N at any given time and therefore the potential P_N that can be achieved during a fluctuating light (shade-fleck). Under this condition, responses of g_s and P_N are not always synchronized, as stomatal movements can be an order of magnitude slower than the more rapid photosynthetic response to the same environmental stimuli ([30, 31]; Figure 3).

OTCs	Heat	PEPC activity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	ME activity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	MDH activity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
<i>Ambient[CO₂]</i>				
B76	aft0	15.5 ± 0.5 (33.1 ± 1.6)	3.7 ± 0.4 (31.6 ± 0.5)	7.9 ± 3.4 (24.8 ± 3.3)
	aft4	19.7 ± 0.5 (36.5 ± 1.5)	20.6 ± 0.3 (29.0 ± 0.1)	14.9 ± 1.2 (26.5 ± 0.4)
	% Change	27.1	456.8	88.6
B106	aft0	13.3 ± 0.7 (32.8 ± 0.5)	12.4 ± 1.1 (24.6 ± 0.3)	17.2 ± 0.3 (26.1 ± 0.2)
	aft4	15.8 ± 0.7 (36.6 ± 1.4)	13.9 ± 0.7 (27.7 ± 0.3)	19.0 ± 2.7 (28.9 ± 0.4)
	% Change	18.8	12.1	10.5
<i>Elevated[CO₂]</i>				
B76	aft0	13.6 ± 1.5 (32.0 ± 0.7)	10.9 ± 0.2 (25.3 ± 0.4)	12.1 ± 1.7 (29.0 ± 1.2)
	aft4	17.9 ± 1.3 (34.4 ± 0.9)	18.1 ± 1.0 (26.3 ± 0.6)	20.9 ± 0.4 (28.8 ± 1.5)
	% Change	31.6	66.5	72.7
B106	aft0	10.5 ± 1.7 (32.2 ± 0.1)	9.0 ± 0.6 (26.7 ± 0.8)	14.6 ± 1.7 (28.6 ± 0.6)
	aft4	12.8 ± 1.0 (31.9 ± 1.0)	11.6 ± 1.6 (29.2 ± 0.5)	13.7 ± 0.9 (31.6 ± 1.1)
	% Change	21.9	29.1	-6.2

Table 1. Enzyme activities of PEPC, NADP-ME, and NADP-MDH for B76 vs. B106 grown ambient and elevated [CO₂]. Values of control experiments were shown in brackets (Qu et al. 2016, unpublished data).

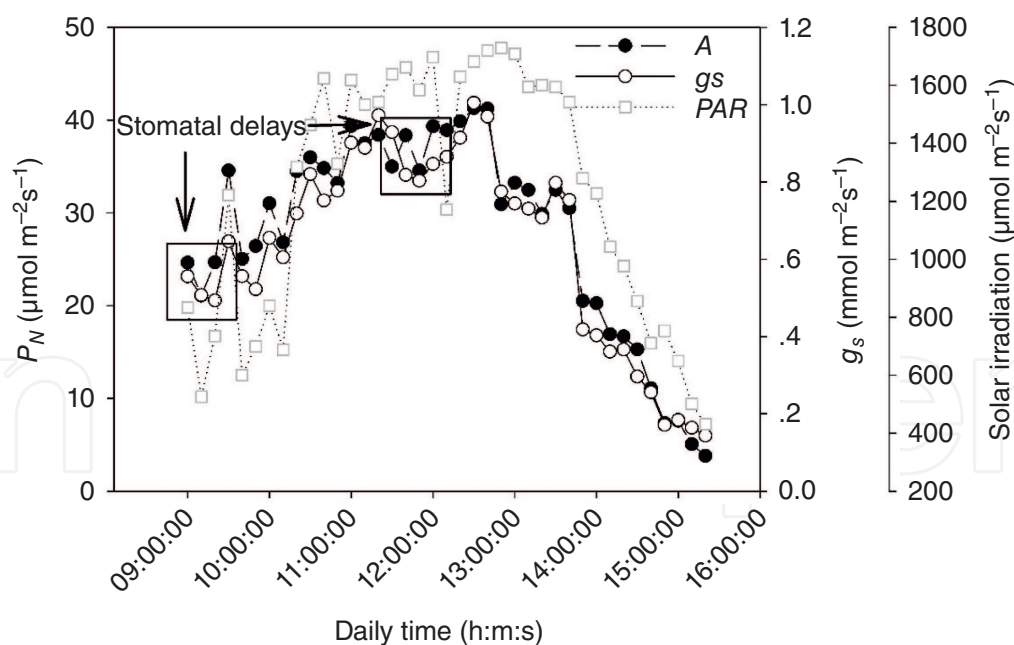


Figure 3. Photosynthesis and stomatal conductance in response to naturally light regime (Qu et al. 2016, unpublished data).

3. Internal signals

3.1 Ion channels and transmembrane antiporters

There is no question that stomatal movements (stomatal opening and closing) of seed plants, including crop plants, arise from the transport, accumulation, and release of osmotically active solutes (reviewed by [32]). It has been shown that the guard cell movement is controlled by movement of Cl^+ , Na^+ , K^+ , and also changes in the sucrose and malate levels [32, 33]. It is reasonable to give expectation that ion exchange, inducing change in pH, might indirectly determine response time of stomatal adjustments during light fluctuations based on previous literatures. For example, membrane depolarization in ABA stimulates K^+ efflux within seconds through outward-rectifying K^+ channels, in Arabidopsis the GORK K^+ channel [34, 35], and these K^+ currents are enhanced during the subsequent 3–5 min as a consequence of rise in cytosolic pH [36, 37]. Stomatal aperture responds more slowly, typically with half-times of 10–20 min, reaching a new stable, (near) closed state after 45–60 min [38–40]. Thus, making a connection of ion channel antiporters to the speed and efficacy of stomatal movements is necessarily important.

3.2 Anatomical features of stomata

Responsiveness of stomatal adjustments under changing environments is also dependent on anatomical characteristics. In fact, stomatal anatomical features define the maximum theoretical conductance and also influence the speed of response [41]. Many experimental evidences have demonstrated that stomatal density is negatively correlated with stomatal size [42, 43]. The interaction/correlation between stomatal size and density and the impact on stomatal function have received much attention [44]. The latest studies have also implied that physical attributes affect stomatal response times following environmental perturbations [45]. Therefore, it is possible to manipulate the stomatal structure, for example, we can take into consideration the interaction between stomatal size and number and its impact on rapidity of stomatal movement.

3.3 Casual genes of stomatal features

Engineering and breeding crops for enhanced drought resistance become a pressing task for plant biologists and breeders. Manipulation on functional genes underlying dynamics of stomatal responses and steady-state values of g_s would be helpful for optimizing WUE and drought resistance of plants [46–51]. For example, mutation in the *SLAC1* gene, which codes for an anion channel, causes slow stomatal opening by light, low CO_2 , and elevated air humidity in intact plants, due to severely reduced activity of inward K^+ channels in *slac1* guard cells [52]. Arabidopsis (*Arabidopsis thaliana*) stomatal density and distribution (*sdd1-1*) mutants, having a point mutation in a single gene that encodes a subtilisin-like Ser protease, exhibit a 2.5-fold higher stomatal density compared with their wild type [53]. Stomatal movements can also be stimulated by membrane fusion protein, soluble N-ethylmaleimide-sensitive fusion protein attachment protein receptor (SYP121), Eisenach et al. [54] demonstrated that stomatal

opening and the rise in stomatal transpiration of the *syp121* mutant were delayed in the dark–light transition and following the Ca^{2+} -evoked closure. The increase in stomatal density translates leads to an increase in g_s and 30% greater P_N under high light conditions [55]. Tanaka et al. [56] have used plants overexpressing STOMAGEN, a positive regulator of stomatal density, to produce transgenic plants with a two- to three fold greater stomatal density than the wild type. P_N in these plants is increased by 30% due to greater CO_2 diffusion into the leaf rather than changes in photosynthetic carboxylation capacity [56]. By contrast, some genes can induce low stomatal density and g_s at high light intensities, for example, upregulation of *sdd1* can restrict CO_2 diffusion limited P_N to 80% of the wild type [57].

These findings exemplify the role of both the physical and functional stomatal features in determining g_s . In particular, these works illustrate the importance of surrounding environmental conditions and ion exchange on stomatal behavior and the significance of examining g_s limitation on P_N at fluctuating light and elevated CO_2 and heat stress.

4. Natural variation and heritability of stomatal conductance

The analysis of evolution of stomata over species should depend on two strategies, i.e., fossil studies on ancestor plants and genetic studies on current plants. Fossil evidence shows that stomata have occurred in sporophytes and (briefly) gametophytes of embryophytes during the last 400 million years. Cladistic analyses with hornworts basal are consistent with a unique origin of stomata, although cladograms with hornworts as the deepest branching embryophytes require loss of stomata early in the evolution of liverworts (reviewed by [58]).

Genetic variation is a vital characteristic of every population that is required to adapt. Phenotypic trait variance within a population can be related to genetic variance as an estimation of broad-sense heritability (H^2). In theory, when a greater proportion of phenotypic variation is attributable to genetic variance, the corresponded trait is highly heritable. Exploring stomatal traits with high H^2 under multiple environments could provide strategy for artificial selection and improvements on stomatal traits. Although natural variation in photosynthetic capacity especially stomatal features is known to exist among different species [59–63], relatively few studies have examined natural variation among accessions of the same species [64–67]. Besides, studying the genetic variation of photosynthetic capacity of different rice accessions with diverse genetic background could be an effective way to improve the photosynthetic capacity of existing rice elite germplasm [67, 68].

In fact, mining natural variations of photosynthetic and stomatal parameters is regarded as a promising approach to identify new genes or alleles for crop improvement. Conventionally, the identification of genomic loci that govern complex traits has been extensively facilitated by the development of quantitative trait locus (QTL) mapping approaches. Recent advances in high-throughput and high-dimensional genotyping and phenotyping technologies enable us to reduce the gaps between genomics and phenomics using the principles of genome-wide association studies (GWAS). This biostatistic method has been widely used in food crops for identifying genes that underlie natural variation of various ecological and agricultural traits

[69–71]. Consequently, a combination of GWAS and QTL mapping as well as co-expression network would be a better option to obtain additive, dominance, and epistasis effects of genes, for example, in *Arabidopsis* [72] and soybean [73].

Therefore, understanding the mechanisms that underlie efficient carbon gain driven by stomatal adjustments in fluctuating light can open doors for increasing plant yields and, more broadly, can reveal fundamental principles to optimize the water cycle system in the biosphere.

5. Relation of stomatal profiling with life histories

Evolutionary responses of stomata to fluctuating light conditions are important because stomata in theory must have been subject to evolutionary pressures associated with highly variable conditions. This is always related to the life history of accession origins. Studying the evolution of photosynthesis is critical to understand how stomata or plants structure variation influence ecological interactions and adaptation to various environments [74]. Where an overlying geographical origin or environmental gradient exerts strong adaptive selection, the natural variation in both genotype and phenotype is predicted. However, this variation will depend on the relative strength of selection, demographic history, and levels of dispersal and/or gene flow among populations [75]. Differing selection pressures may include temperature, precipitation, and soil nutrient availability, growing season length, photoperiod, and biotic agents. Many of these factors are directly affected by geographic conditions and are therefore interrelated. This is already extensively reported in trees species. Genetic covariance among ecophysiological traits can be shaped by the past ecological and evolutionary processes [3]. However, for traits of ecological or evolutionary interest, studies must also address the extent to which population structure, trait variation, and genetic architecture covary along ecological gradients [3].

6. Theoretical modeling for describing stomatal delays

To describe the dynamics of g_s and P_N in response to an abrupt change in light, piecewise linear, logistic, and exponential models have been frequently employed [25, 76–78]. For instance, in terms of stomatal dynamics in time scales during closing (τ_d) and opening phases (τ_{op}), significant variation insensitivity and responsiveness is known to exist among different species [25, 32, 33]. As described above, when switching from high to low light, stomata always performed a lag relative to photosynthetic reduction, and to simplify, linearizing imputation between specific time period (stepwise) on photosynthetic dynamics could be a better option to define the amplitude and speed of stomata. In *Arabidopsis*, Wang et al. [79] have developed a dynamic model of stomatal responses, taking into consideration ion channel and kinetic effects as components controlling g_s under steady-state and dynamic conditions. This model integrated the biophysical, molecular, and biochemical characteristics of guard cell transport, malate metabolism, and H^+ and Ca^{2+} , to predict stomatal aperture, which can be used to explore

inherent interaction between different factors controlling g_s [79, 80]. This model provided a good framework to incorporate new knowledge about controls over guard cell movements and hence help design engineering options to gain optimal steady state g_s and also optimal dynamic responses of g_s to light levels.

Author details

Mingnan Qu^{1,2}, Saber Hamdani¹ and James A. Bunce²

1 CAS-Key Laboratory for Computational Biology, CAS-MPG Partner Institute for Computational Biology, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Shanghai, China

2 USDA ARS, Crop Systems and Global Change Laboratory, Beltsville, MD, USA

References

- [1] Willmer C, Fricker M. 1996. Stomata, 2nd edn. London: Chapman & Hall.
- [2] Peterson KM, Rychela AL, Toriia KU. Out of the mouths of plants: The molecular basis of the evolution and diversity of stomatal development. *The Plant Cell* 22: 296–306.
- [3] McKown AD, Guy RD, Klateps J, Gerald A, Friedmann M, Cronk QCB, El-Kassa YA, Mansfield SD, Douglas CJ. 2014a. Geographical and environmental gradients shape phenotypic trait variation and genetic structure in *Populus trichocarpa*. *The New Phytologist* 201: 1263–1276.
- [4] Taub DR, Seemann JR, Coleman JS. 2000. Growth in elevated CO₂ protects photosynthesis against high-temperature damage. *Plant, Cell & Environment* 23: 649–656.
- [5] Wang D, Heckathorn SA, Barua D, Joshi P, Hamilton EW, LaCroix JJ. 2008. Effects of elevated CO₂ on the tolerance of photosynthesis to acute heat stress in C₃, C₄, and CAM species. *American Journal of Botany* 95: 165–176.
- [6] Wang D, Heckathorn SA, Hamilton EW, Frantz J. 2014. Effects of CO₂ on the tolerance of photosynthesis to heat stress can be affected by photosynthetic pathway and nitrogen. *American Journal of Botany* 101: 34–44.
- [7] Yang Y, Han C, Liu Q, Lin B, Wang J. 2008. Effect of drought and low light on growth and enzymatic antioxidant system of *Picea asperata* seedlings. *Acta Physiologiae Plantarum* 30: 433–440.

- [8] Demmig B, Winter K, Kruger A, Czygan FC. 1988. Zeaxanthin and the heat dissipation of excess light energy in *Nerium oleander* exposed to a combination of high light and water stress. *Plant Physiology* 87: 17–24.
- [9] Mearns LO, Katz RW, Schneider SH. 1984. Extreme high temperature events: changes in their probabilities with changes in mean temperature. *Journal of Climate and Applied Meteorology* 23: 1601–1613.
- [10] Sage RF. 1994. Acclimation of photosynthesis to increasing atmospheric CO₂: The gas-exchange perspective. *Photosynthesis Research* 39: 351–368.
- [11] Ainsworth EA, Davey PA, Bernacchi CJ, Dermody OC, Heaton EA, Moore DJ, Morgan PB, Naidu SL, Ra HSY, Zhu XG, Gurtis PS, Long SP. 2002. A meta-analysis of elevated CO₂ effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biology* 8: 695–709.
- [12] Reich PB, Tilman D, Craine J, Ellsworth D, Tjoelker MG, Knops J, Wedin D, Naeem S, Bahaeddin D, Goth J, Bengtson W, Lee TD. 2001. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *The New Phytologist* 150: 435–448.
- [13] Maherali H, Reid CD, Polley HW, Johnson HB, Jackson RB. 2002. Stomatal acclimation over a subambient to elevated CO₂ gradient in a C₃/C₄ grassland. *Plant, Cell & Environment* 25: 557–566.
- [14] Qu M, Bunce JA, Shi ZS. 2014. Does elevated CO₂ protect photosynthesis from damage by high temperature via modifying leaf water status in maize seedlings? *Photosynthetica* 52: 211–216.
- [15] Luo HB, Ma L, Xi HF, Duan W, Li SH, Loescher W, Wang JF, Wang LJ. 2011. Photosynthetic responses to heat treatments at different temperatures and following recovery in grapevine (*Vitis amurensis* L.) leaves. *PLoS ONE* 6: e23033. doi:10.1371/journal.pone.0023033.
- [16] Hamilton EW, Heckathorn SA, Joshi P, Wang D, Barua D. 2008. Interactive effects of elevated CO₂ and growth temperature on the tolerance of photosynthesis to acute heat stress in C₃ and C₄ species. *Journal of Integrative Plant Biology* 50: 1375–1387.
- [17] Coleman JS, Rochefort L, Bazzaz , Woodward . 1991. Atmospheric CO₂, plant nitrogen status and the susceptibility of plants to acute heat stress. *Plant, Cell & Environment* 14: 667–674.
- [18] Bassow SL, McConnaughay KDM, Bazzaz FA. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* 4: 593–603.

- [19] Roden JS, Ball MC. 1996. Growth and photosynthesis of two eucalypt species during high temperature stress under ambient and elevated [CO₂]. *Global Change Biology* 2: 115–128.
- [20] Huxman TE, Hamerlynck EP, Loik ME, Smith SD. 1998. Gas exchange and chlorophyll fluorescence responses of three south-western Yucca species to elevated CO₂ and high temperature. *Plant, Cell & Environment* 21: 1275–1283.
- [21] Chen JP, Burke JJ, Xin ZG. 2010. Role of phosphatidic acid in high temperature tolerance in maize. *Crop Science* 50: 2506–2515.
- [22] Eckardt NA, Snyder GW, Portis AR Jr, Ogren WL. 1997. Growth and photosynthesis under high and low irradiance of Arabidopsis thaliana antisense mutants with reduced ribulose-1,5-bisphosphate carboxylase/oxygenase activase content. *Plant Physiology* 113: 575–586.
- [23] Crafts-Brandner SJ, Salvucci ME. 2002. Sensitivity of photosynthesis in a C₄ plant, maize, to heat stress. *Plant Physiology* 129: 1773–1780.
- [24] Chazdon RL. 1988. Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research* 18: 1–63.
- [25] Vico G, Manzoni S, Palmroth S, Katul G. 2011. Effects of stomatal delays on the economics of leaf gas exchange under intermittent light regimes. *The New Phytologist* 192: 640–652.
- [26] Osterhout WJV, Haas ARC. 1918. On the dynamics of photosynthesis. *The Journal of General Physiology* 1: 1–16.
- [27] Walker DA. 1973. Photosynthetic induction phenomena and the light activation of ribulose diphosphate carboxylase. *The New Phytologist* 72: 209–235.
- [28] Tang Y, Liang NS. 2000. Characterization of the photosynthetic induction response in a Populus species with stomata barely responding to light changes. *Tree Physiol* 20: 969–976.
- [29] Lawson T, Weyers JDB. 1999. Spatial and temporal variation in gas exchange over the lower surface of *Phaseolus vulgaris* primary leaves. *Journal of Experimental Botany* 50: 1381–1391.
- [30] Pearcy RW. 1990. Sunflecks and photosynthesis in plant canopies. *Annual Review of Plant Physiology and Plant Molecular Biology* 41: 421–453.
- [31] Lawson T, von Caemmerer S, Baroli I. 2010. Photosynthesis and stomatal behaviour. In: Luttge U, Beyschlag W, Budel B, Francis D, eds. *Progress in Botany*, Vol. 72. Heidelberg: Springer, 265–304.
- [32] Lawson T, Blatt MR. 2014. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiology* 164: 1556–1570.

- [33] Lawson T. 2009. Guard cell photosynthesis and stomatal function. *The New Phytologist* 181: 13–34.
- [34] Hosi E, Vavasseur A, Mouline K, Dreyer I, Gaymard F, Porée F, Boucherez J, Lebaudy A, Bouchez D, Very AA, . 2003. The Arabidopsis outward K⁺ channel GORK is involved in regulation of stomatal movements and plant transpiration. *Proceedings of the National Academy of Sciences of the United States of America* 100: 5549–5554.
- [35] Suhita D, Raghavendra AS, Kwak JM, Vavasseur A. 2004. Cytoplasmic alkalization precedes reactive oxygen species production during methyl jasmonate- and abscisic acid-induced stomatal closure. *Plant Physiology* 134: 1536–1545.
- [36] Blatt MR, Armstrong F. 1993. K⁺ channels of stomatal guard cells: abscisic acid-evoked control of the outward rectifier mediated by cytoplasmic pH. *Planta* 191: 330–341.
- [37] Grabov A, Blatt MR. 1997. Parallel control of the inward-rectifier K⁺ channel by cytosolic-free Ca²⁺ and pH in *Vicia* guard cells. *Planta* 201: 84–95.
- [38] Raschke K, Firm RD, Pierce M. 1975. Stomatal closure in response to xanthoxin and abscisic acid. *Planta* 125: 149–160.
- [39] Roelfsema MG, Prins HA. 1995. Effect of abscisic acid on stomatal opening in isolated epidermal strips of abi mutants of *Arabidopsis thaliana*. *Physiologia Plantarum* 95: 373–378.
- [40] Zhang X, Miao YC, An GY, Zhou Y, Shanguan ZP, Gao JF, Song CP. 2001. K⁺ channels inhibited by hydrogen peroxide mediate abscisic acid signaling in *Vicia* guard cells. *Cell Research* 11: 195–202.
- [41] Dow GJ, Bergmann DC, Berry JA. 2014. An integrated model of stomatal development and leaf physiology. *The New Phytologist* 201: 1218–1226.
- [42] Hetherington AM, Woodward FI. 2003. The role of stomata in sensing and driving environmental change. *Nature* 424: 901–908.
- [43] Franks PJ, Beerling DJ. 2009. CO₂-forced evolution of plant gas exchange capacity and water-use efficiency over the Phanerozoic. *Geobiology* 7: 227–236.
- [44] Franks PJ, Farquhar GD. 2007. The mechanical diversity of stomata and its significance in gas-exchange control. *Plant Physiology* 143: 78–87.
- [45] Drake PL, Froend RH, Franks PJ. 2013. Smaller, faster stomata: scaling of stomatal size, rate of response, and stomatal conductance. *Journal of Experimental Botany* 64: 495–505.
- [46] Negi J, Matsuda O, Nagasawa T, Oba Y, Takahashi H, Kawai-Yamada M, Uchimiya H, Hashimoto M, Iba K. 2008. CO₂ regulator *SLAC1* and its homologues are essential for anion homeostasis in plant cells. *Nature* 452: 483–486.

- [47] Wang D, Maughan MW, Sun J, Feng X, Miguez F, Lee D, Dietze MC. 2012. Impact of nitrogen allocation on growth and photosynthesis of *Miscanthus* (*Miscanthus × giganteus*). *GCB Bioenergy* 4: 688–697.
- [48] Merlot S, Leonhardt N, Fenzi F, Valon C, Costa M, Piette L, Vavasseur A, Genty B, Boivin K, Müller A. 2007. Constitutive activation of a plasma membrane H⁺-ATPase prevents abscisic acid-mediated stomatal closure. *The EMBO Journal* 26: 3216–3226.
- [49] De Angeli A, Monachello D, Ephritikhine G, Frachisse JM, Thomine S, Gambale F, Barbier-Brygoo H. 2009. Review: CLC-mediated anion transport in plant cells. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 195–201.
- [50] Gobert A, Isayenkov S, Voelker C, Czempinski K, Maathuis FJM. 2007. The two-pore channel TPK1 gene encodes the vacuolar K⁺ conductance and plays a role in K⁺ homeostasis. *Proceedings of the National Academy of Sciences of the United States of America* 104: 10726–10731.
- [51] Valliyodan B, Nguyen HT. 2006. Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Current Opinion in Biotechnology* 9: 189–195.
- [52] Laanemets K, Wang YF, Lindgren O, Wu J, Nishimura N, Lee S, Caddell D, Merilo E, Brosche M, Kilk K. 2013. Mutations in the *SLAC1* anion channel slow stomatal opening and severely reduce K_p uptake channel activity via enhanced cytosolic [Ca²⁺]_p and increased Ca²⁺_p sensitivity of K_p uptake channels. *The New Phytologist* 197: 88–98.
- [53] Berger D, Altmann T. 2000. A subtilisin-like serine protease involved in the regulation of stomatal density and distribution in *Arabidopsis thaliana*. *Genes & Development* 14: 1119–1131.
- [54] Eisenach C, Chen ZH, Grefen C, Blatt MR. 2012. The trafficking protein SYP121 of *Arabidopsis* connects programmed stomatal closure and K⁺ channel activity with vegetative growth. *The Plant Journal* 69, 241–251.
- [55] Schlüter U, Muschak M, Berger D, Altmann T. 2003. Photosynthetic performance of an *Arabidopsis* mutant with elevated stomatal density (*sdd1-1*) under different light regimes. *Journal of Experimental Botany* 54: 867–874.
- [56] Tanaka Y, Sugano SS, Shimada T, Hara-Nishimura I. 2013. Enhancement of leaf photosynthetic capacity through increased stomatal density in *Arabidopsis*. *The New Phytologist* 198: 757–764.
- [57] Büssis D, von Groll U, Fisahn J, Altmann TA. 2006. Stomatal aperture can compensate altered stomatal density in *Arabidopsis thaliana* at growth light conditions. *Funct Plant Biol* 33: 1037–1043.
- [58] Raven JA. 2002. Selection pressures on stomatal evolution. *The New Phytologist* 153: 371–386.

- [59] Wullschlegel SD. 1993. Biochemical limitations to carbon assimilation in C₃ plants – a retrospective analysis of the A/C_i curves from 109 species. *Journal of Experimental Botany* 44: 907–920.
- [60] Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N, Poorter H, Villar R, Warton DI, Westoby M. 2005. Assessing the generality of the global leaf trait relationships. *The New Phytologist* 166: 485–496.
- [61] Hikosaka K, Shigeno A. 2009. The role of Rubisco and cell walls in the interspecific variation in photosynthetic capacity. *Oecologia* 160, 443–451.
- [62] Hikosaka K. 2010. Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species. *Plant Biotechnology* 27: 223–229.
- [63] Lawson T, Kramer DM, Raines CA. 2012. Improving yield by exploiting mechanisms underlying natural variation of photosynthesis. *Current Opinion in Biotechnology* 23: 215–220.
- [64] Pettigrew WT. 2004. Cotton genotypic variation in the photosynthetic response to irradiance. *Photosynthetica* 42: 567–571.
- [65] Gilbert ME, Zwieniecki MA, Holbrook NM. 2011. Independent variation in photosynthetic capacity and stomatal conductance leads to differences in intrinsic water use efficiency in 11 soybean genotypes before and during mild drought. *Journal of Experimental Botany* 62: 2875–2887.
- [66] Flood PJ, Harbinson J, Aarts MGM. 2011. Natural genetic variation in plant photosynthesis. *Trends in Plant Science* 16: 327–335.
- [67] Gu J, Yin X, Stomph T-J, Struik PC. 2014. Can exploiting natural genetic variation in leaf photosynthesis contribute to increasing rice productivity? A simulation analysis. *Plant, Cell & Environment* 37: 22–34.
- [68] Hamdani S, Qu M, Xin CP, Li M, Chu C, Govindjee, Zhu XG. 2015. Variations between the photosynthetic properties of elite and landrace Chinese rice cultivars revealed by simultaneous measurements of 820 nm transmission signal and chlorophyll a fluorescence induction. *Journal of Plant Physiology* 177: 128–138.
- [69] Huang X, Wei X, Sang T, Zhao Q, Feng Q, Zhao Y, Li C, Zhu C, Lu T, Zhang Z, Li M, Fan D, Guo Y, Wang A, Wang L, Deng L, Li W, Lu Y, Weng Q, Liu K, Huang T, Zhou T, Jing Y, Li W, Lin Z, Buckler ES, Qian Q, Zhang QF, Li J, Han B. 2010. Genome-wide association studies of 14 agronomic traits in rice landraces. *Nature Genetics* 42: 961–967.
- [70] Huang X, Zhao Y, Wei X, Li C, Wang A, Zhao Q, Li W, Guo Y, Deng L, Zhu C, Fan D, Lu Y, Weng Q, Liu K, Zhou T, Jing Y, Si L, Dong G, Huang T, Lu T. 2012. Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. *Nature Genetics* 44: 32–40.
- [71] Mckown AD, Guy RD, Quamme L, Klapste J, Mantia JL, Constabel CP, El-Kassaby YA, Hamelin RC, Zifkin M, Azam MS. 2014b. Association genetics, geography and eco-

- physiology link stomatal patterning in *Populus trichocarpa* with carbon gain and disease resistance trade-offs. *Molecular Ecology* 23: 5771–5790.
- [72] Brachi B, Faure N, Horton M, Flahauw E, Vazquez A, Nordborg M, Bergelson J, Cuguen J, Roux F. 2010. Linkage and association mapping of *Arabidopsis thaliana* flowering time in nature. *PLoS Genetics* 6: e1000940.
- [73] Sonah H, O'Donoghue L, Cober E, Rajcan I, Belzile F. 2014. Identification of loci governing eight agronomic traits using a GBS-GWAS approach and validation by QTL mapping in soybean. *Plant Biotechnology Journal*. doi: 10.1111/pbi.12249.
- [74] Eckert AJ, Dyer RJ. 2012. Defining the landscape of adaptive genetic diversity. *Molecular Ecology* 21: 2836–2838.
- [75] Savolainen O, Pyhajarvi T, Knurr T. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics* 38: 595–619.
- [76] Kirschbaum MUF, Gross LJ, Pearcy RW. 1988. Observed and modeled stomatal responses to dynamic light environments in the shade plant *Alocasia macrorrhiza*. *Plant, Cell & Environment* 11: 111–121.
- [77] Zipperlen SW, Press MC. 1997. Photosynthetic induction and stomatal oscillations in relation to the light environment of two *dipterocarp* rain forest tree species. *Journal of Ecology* 85: 491–503.
- [78] Naumburg E, Ellsworth DS, Katul GG. 2001. Modeling dynamic understory photosynthesis of contrasting species in ambient and elevated carbon dioxide. *Oecologia* 126: 487–499.
- [79] Wang Y, Papanatsiou M, Eisenach C, Karnik R, Williams M, Hills A, Lew VL, Blatt MR. 2012. Systems dynamic modeling of a guard cell Cl^- channel mutant uncovers an emergent homeostatic network regulating stomatal transpiration. *Plant Physiology* 160: 1956–1967.
- [80] Blatt MR, Wang YZ, Leonhardt N, Hills A. 2014. Exploring emergent properties in cellular homeostasis using OnGuard to model K^+ and other ion transport in guard cells. *Journal of Plant Physiology* 17: 1770–778.