Chapter 4

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

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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 CO_2 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 enironments 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 CO_2 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 CO_2 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., CO_2, 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 CO_2, 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 CO_2 and heat wave

The global change, leading to frequent occurrence of atmospheric CO_2 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 CO_2 has probably less effect on C_3 plants as compared to C_4 plants [10]. In fact, elevated CO_2 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 C_3 and 50% for C_4 species [10, 12, 13]. The lower g_s in C_4 plants may induce lower transpiration (water loss) and thus higher leaf temperatures, which may increase heat-related damage in C_4 plants as compared to C_3 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 CO_2 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 1hour[14]. Our previous finding showed that elevated CO_2, 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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

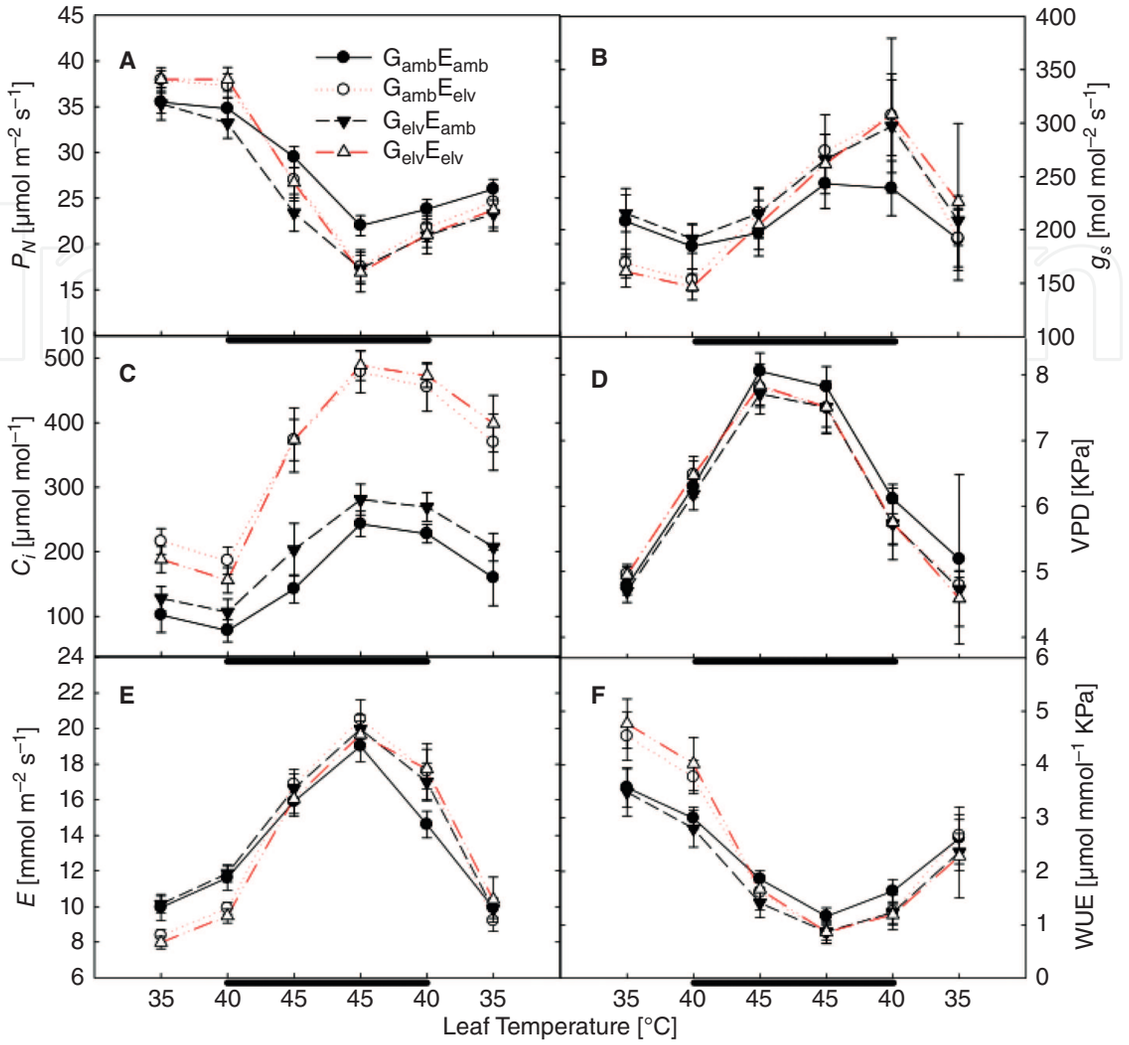

Figure 1. Dynamic changes of photosynthetic parameters during acute heat stress cycles. Lines with same color stand for treatment at same exposure CO_2 concentrations. Symbols $G_{amb}E_{amb}$, $G_{amb}E_{elv}$, $G_{elv}E_{amb}$, and $G_{elv}E_{elv}$ represent grown and exposed at ambient [CO_2], grown at ambient [CO_2] but exposed at elevated [CO_2], grown at elevated [CO_2] but exposed at ambient [CO_2], and both of grown and exposed at elevated [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-

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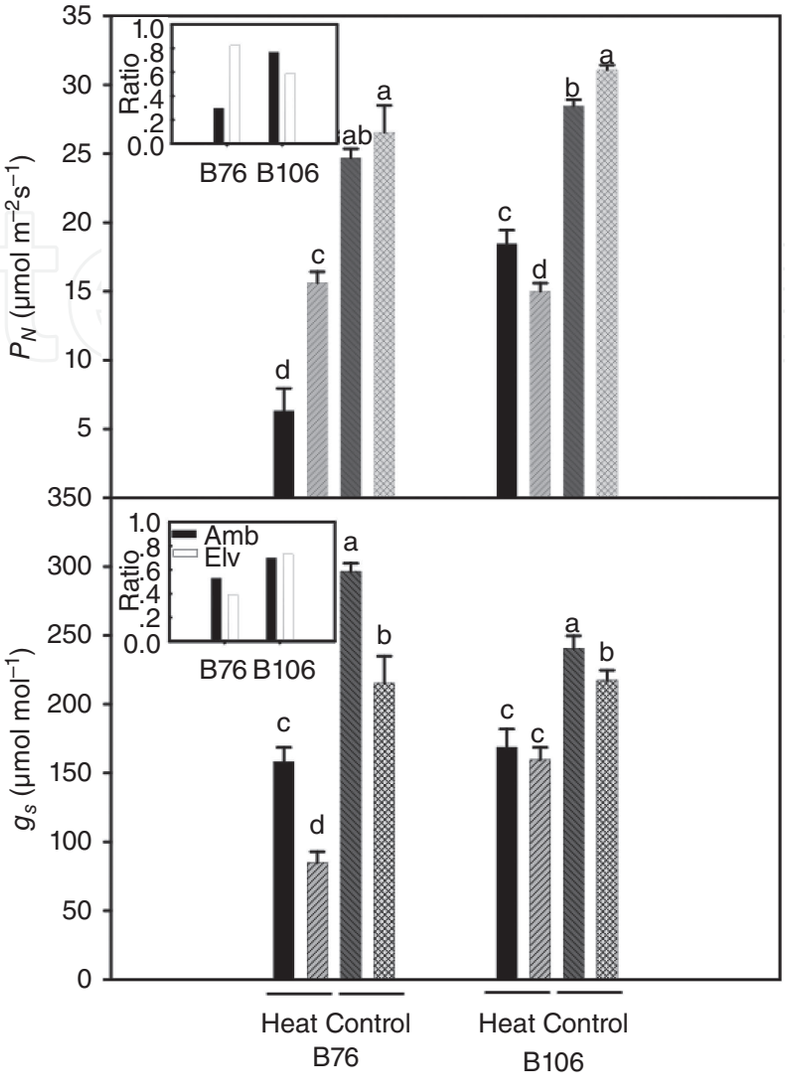

Figure 2. Heat induced decrease of photosynthesis and stomatal conductances in B76 and B106. Black and grid bars represent ambient and elevated [CO_2], respectively. Ratio of photosynthesis and stomatal conductances under heat stress over control in B76 and B106 was shown in inserted panel. (Qu et al. 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 (μmol m^{-2} s^{-1})	ME activity (μmol m^{-2} s^{-1})	MDH activity (μmol m^{-2} s^{-1})
Ambient[CO2]				
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
Elevated[CO2]				
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 [CO_2]. Values of control experiments were shown in brackets (Qu et al. 2016, unpublished data).

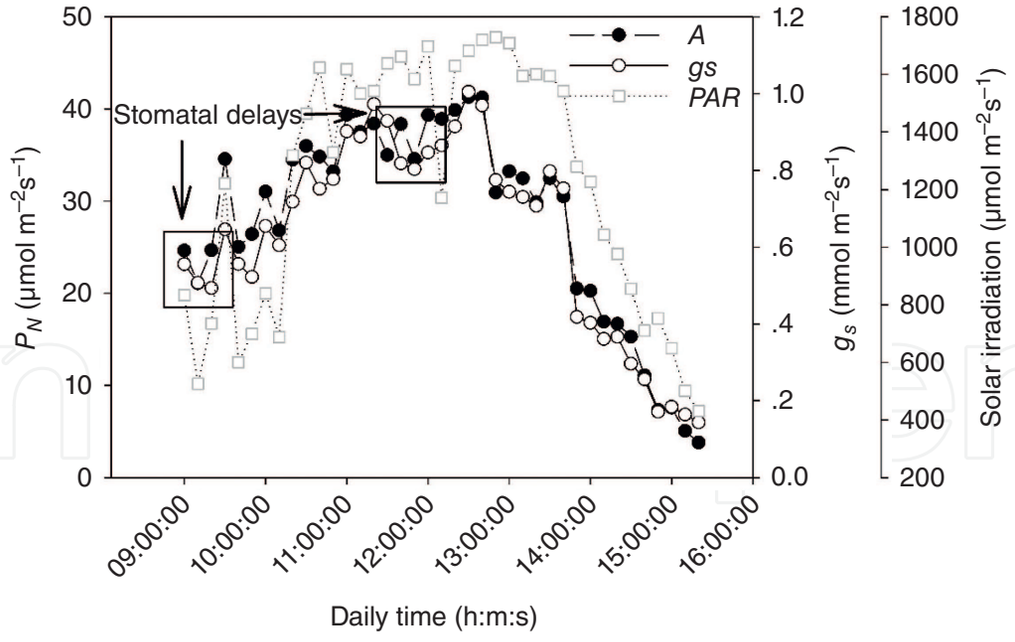

Figure 3. Photosynthesis and stomatal conductance in response to naturally light regime (Qu et al. 2016, unpublished data).

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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_{cl}) 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.

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