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The hare and the tortoise: stomatal kinetics under light change in *Poaceae* crops

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When plants first colonized land about 450 million years ago, they had to maintain diffusion of carbon dioxide CO₂ to chloroplasts while avoiding substantial water loss to dry air. The development of openings in the leaf epidermis, that is stomata, controlled gas exchange between the plant and the fluctuating conditions of the atmosphere (Harris et al., 2020). By modulating their shape, guard cells limit the opening of stomata and control the rate of gas exchange (including CO₂ and water vapor; Kirkham, 2014). Coordination of stomatal opening and closing with environmental conditions is therefore important for the plant to maximize the amount of carbon assimilated for a given amount of water transpired. This characteristic is reflected by water-use efficiency (WUE), which is the ratio of carbon assimilation to water transpiration.

Carbon atoms are integrated into organic molecules through the process of photosynthesis. Light energy, captured by the photosystems, is transformed into chemical energy in the form of organic molecules. Photosynthesis is often defined by the number of carbon atoms in the first fixation product, whether the C₃ product phosphoglycerate or the C₄ product oxaloacetate. Both C₃ and C₄ photosynthesis types are observed in *Poaceae* species, which represents more than 60% of the world's food production. C₃ plants generally grow in relatively mild conditions, with relative abundance of water and mild temperature, such as in temperate zone (Percy and Ehleringer, 1984). Under elevated temperature, the oxygenase activity of Rubisco (Ribulose-1,5-bisphosphate carboxylase oxygenase) is higher than the carboxylase activity, resulting in an imbalance between photorespiration and carbon fixation. In contrast, C₄ plants transfer C₄ products from the mesophyll cells to the vascular bundle sheath cells, where CO₂ is released to maintain a high CO₂ pressure and thus enhance carboxylase activity. The CO₂ concentration mechanism allows C₄ plants

to fix carbon even under warm temperatures, such as in tropical areas, or when stomata are closed due to water stress. Thus, C₄ species often have a higher WUE than C₃ species, but is this solely because of the CO₂ concentration mechanism? In the present issue of *Plant Physiology*, Ozeki et al. (2022) tested whether stomatal kinetics could also contribute to higher WUE in C₄ species.

Of the factors that control stomatal conductivity and photosynthetic efficiency, light is probably the most important. Light-induced stomatal opening maintains a high intercellular CO₂ concentration when photosystems are stimulated, while closing stomata in the dark avoids inefficient water loss. Characterizing the kinetics of stomata as light changes is therefore an important factor in WUE. Rapid opening upon illumination allows diffusion and assimilation of CO₂ (Figure 1). Rapid closure upon darkness blocks water loss when assimilation stops. Higher WUE is thus expected if the rate of stomatal closing and/or opening is rapid. An important factor in controlling maximum assimilation rate is the nitrogen content of the leaf, as it can be considered as a proxy for Rubisco content (Wright et al., 2004). Estimating whole-plant traits, such as transpiration ϵ and stomatal conductance (g_s), via high-throughput phenotyping is an interesting way to distinguish the influence of environmental and physiological parameters (Charrier et al., 2018).

Ozeki et al. (2022) investigated the dynamics of stomatal opening and closing under intermittent light in C₃ (wheat [*Triticum aestivum*], oat [*Avena sativa*], barley [*Hordeum vulgare*], and Ryegrass [*Lolium multiflorum*]) and C₄ crop species (finger millet [*Eleusine coracana*], sorghum [*Sorghum bicolor*], millet [*Panicum miliaceum*], and maize [*Zea mays*], and its wild relative *Zea nicaraguensis*) under high and low nitrogen conditions. Alternating between 100 and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density, they

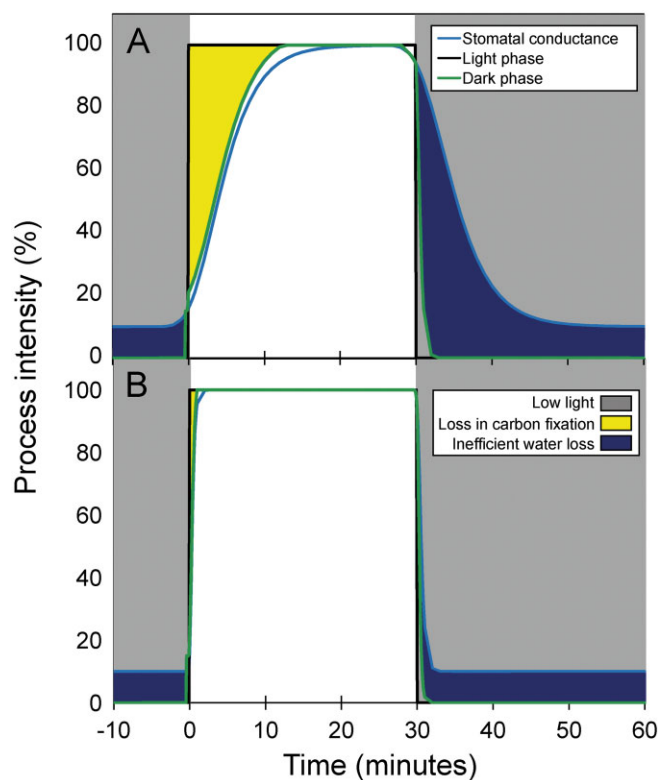


Figure 1 Stomatal kinetics during changes in light intensity. Stomatal conductance (blue line), light phase (black line) and dark phase of photosynthesis (green line) during changes in light regimes in C_3 (A) and C_4 species (B). The difference between light and dark phase corresponds to potential loss in carbon fixation when light turns on (yellow area). The difference between dark phase and stomatal conductance corresponds to inefficient water loss when light turns off (dark blue area). It should be noted that intercellular CO_2 is limited by the diffusion through stomata although CO_2 generated by maintenance respiration and photorespiration could modulate these patterns. Gray area corresponds to low light period.

estimated g_s by a continuous measurement of weight change. Fitting a sigmoid function to the stomatal response to the change in light regime provided time constant parameters, k_{open} and k_{close} , for opening and closure, respectively, which allowed comparison of species and fertilization treatments.

Both C_3 and C_4 species showed rapid changes in net assimilation (A_{net}) when irradiance was varied. However, the change in g_s was slower in C_3 compared with C_4 species, leading to a lower WUE during the transition phase. Overall, C_4 crops exhibited faster responses (smaller k_{open} and k_{close}), which contributed to a higher WUE in these species. All species showed consistent responses to change in light levels with a significant correlation between k_{open} and k_{close} . Under high nitrogen treatment, stomatal response correlated with morphological traits (leaf area, stomatal density, and length of the guard cells).

To assess the contribution of stomatal kinetic on WUE, Ozeki et al. (2022) performed a sensitivity analysis on a dynamic photosynthesis model. They simulated the effect of

independent and simultaneous changes in k_{open} and k_{close} on total assimilation (A_{total}), total transpiration (E_{total}), and WUE. Rapid stomatal opening increased A_{total} , providing better coordination between the light and dark phases, at the cost of higher E_{total} (Figure 1). The increase in A_{total} compared with E_{total} was lower in C_3 than in C_4 , resulting in a lower WUE in C_3 , while it was similar in C_4 . Rapid stomatal closure also allowed for better coordination between the light and dark phases with similar A_{total} , reducing inefficient water loss and therefore increasing WUE. Finally, the concomitant rapid opening and closing of stomata induced a higher A_{total} and similar E_{total} , therefore increasing WUE in both C_3 and C_4 .

The results from Ozeki et al. (2022) showed that higher WUE in C_4 species can be attributed not only to higher A_{net} and lower E but also to more rapid stomatal opening and closing. Rapid stomatal kinetics are linked to the shape of the guard cells, which are dumbbell-shaped in *Poaceae* crops (McAusland et al., 2016). However, why do C_4 *Poaceae* species exhibit a more rapid stomatal response compared with C_3 species? Ozeki et al. (2022) suggested that the smaller guard cells would be more flexible. Osmotic control of guard cell volume would therefore involve mobilizing smaller amounts of solutes and/or water (Drake et al., 2013). In addition, it should be noted that the relationship between morphological traits and stomatal response was only observed under high nitrogen treatment. As A_{net} positively correlated with leaf nitrogen content (Wright et al., 2004), nitrogen-depleted plants exhibited lower maximum A_{net} whereas maximum g_s was not systematically affected by the nitrogen treatment.

To improve WUE in the field and therefore decrease water consumption by food production of *Poaceae* crops, rapid stomatal closure seems to be a relevant avenue. Natural light fluctuations can induce substantial difference in WUE at different scales: at shorter timescales with the dynamic movement of sun/shade flecks in understory plants and at longer timescales along latitudinal gradients (Lawson and Blatt, 2014). During the early evolution of *Poaceae* in understory environment, a rapid stomatal response would have increased WUE in the early morning and under intermittent light (Hetherington and Woodward, 2003). In tropical areas, marked daily changes in light regimes may have generated important selective pressure in C_4 crops. In temperate zones, the daily light changes are milder, resulting in less selective pressure for C_3 crops.

Other related questions remain unanswered, such as does the carbon memory mechanism, that is a saturation of stomatal opening after successive open/close cycles, exist in *Poaceae* and differ across C_3 and C_4 crop species (Jezek et al., 2021)? And do stomatal response kinetics differ under drought stress, when guard cells are dehydrated and more reactive to vapor pressure deficit (Charrier et al., 2018)? A better understanding of the mechanisms of stomatal kinetics would help to understand whether k_{close} could be a relevant trait for the selection of *Poaceae* crops.

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