

Opportunities to improve our understanding of the impact of photosynthetic acclimation on terrestrial ecosystem processes under global change

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Carbon assimilated through photosynthesis provides the foundation for ecosystem productivity and functioning. At the global scale, photosynthesis is the largest carbon flux between the atmosphere and the Earth's surface and is 10 times greater than emissions from fossil fuel and land-use combined (Friedlingstein et al., 2023). Photosynthesis is a dynamic process that is influenced by current and projected future global changes. Thus, understanding how photosynthesis will respond to these changes is critical for predicting services provided by terrestrial ecosystems.

The short-term (i.e., seconds to minutes) response of photosynthesis to environmental change is generally well understood, and long-established theoretical models (e.g., Farquhar et al., 1980) can predict these responses. However, these short-term responses can change as a result of longer-term (i.e., days to weeks) exposure to new environmental conditions through a process called acclimation. Seminal papers have reviewed photosynthetic acclimation to light (Boardman, 1977), temperature (Berry and Bjorkman, 1980), and atmospheric carbon dioxide (CO₂) concentration (Bazzaz, 1990), and more recent reviews and syntheses have expanded our understanding of the topic (e.g., Smith and Dukes, 2013; Niinemets et al., 2015; Dusenage et al., 2019). Modeling studies have shown that processes related to photosynthetic acclimation can have outsized impacts on simulations of terrestrial carbon cycling (e.g., Booth et al., 2012).

Despite being well-known, predictive models of photosynthetic acclimation have generally relied on statistical representations of only a few aspects of acclimation (Smith and Dukes, 2013), with more comprehensive theoretical models only recently being developed (e.g., Stocker et al., 2020). Nonetheless, these theoretical models have limitations

due to a lack of mechanistic understanding in a few key areas that impede development. Here, I discuss two questions that highlight opportunities to address these limitations.

TO WHAT ASPECTS(S) OF ENVIRONMENTAL VARIABILITY DOES PHOTOSYNTHESIS ACCLIMATE AND HOW LONG DOES IT TAKE?

All models of photosynthetic acclimation must prescribe a timescale by which any photosynthetic process acclimates. However, while photosynthetic acclimation is ubiquitous, the timescale of acclimation is not well known (Smith and Dukes, 2013). Previous studies, using differing approaches, have suggested that photosynthetic acclimation occurs over days to weeks (Veres and Williams, 1984; Mengoli et al., 2022). However, other studies suggest that acclimation may take longer, as indicated by the faster acclimation of leaves of an individual plant developed under new conditions than those previously developed and transferred to new conditions (Campbell et al., 2007). Additionally, models must make an assumption about the conditions to which plants acclimate (Smith and Dukes, 2013). Plants experience variability in environmental conditions across many different scales, including diurnal, seasonal, and interannual variation. However, it is unclear to what aspect(s) of this variability photosynthetic traits acclimate, and studies designed to answer this question are rare. The timescale and component of variability to which plants acclimate are likely dependent on, among other things, the specific

photosynthetic process involved and the environmental change to which the plant is acclimating.

Some photosynthetic processes may acclimate faster than others. For instance, biochemical processes involved with the recycling of proteins may occur faster than those that involve anatomical changes. For example, photosynthetic traits show many acclimation responses to an increase in light availability (Poorter et al., 2019), but the upregulation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) may occur more quickly than a change in leaf morphology due to the greater resource requirement and, thus, greater time required to obtain those resources.

The environmental change to which the plant is acclimating may also influence the acclimation speed. Specifically, an acclimation response that requires the acquisition or reallocation of additional resources (e.g., an “upregulation”) may take longer than a response that reduces resource demand (e.g., a “downregulation”). Again, using light availability as an example (Poorter et al., 2019), acclimation to high light may be expected to be slower than acclimation to low light as the former tends to require an increase in

resources needs (“up-regulation”), while the latter tends to require a reduction in resource needs (“down-regulation”) to satisfy the demand from acclimation.

For environmental conditions that change relatively quickly (e.g., diurnally or seasonally), such as light availability and temperature, the component of variation (e.g., maximum, minimum, mean) to which the plant acclimates is also unknown. For example, in many places, light and temperature show an umbrella-shaped diurnal pattern that tends to peak during the middle of the day. If a plant acclimates its photosynthetic biochemistry to average daytime conditions, it will result in optimal acclimation at points before and after the peak. However, if acclimation is to midday conditions, as some studies have suggested (Mengoli et al., 2022), then the optimal acclimation will occur only at a single point during the middle of the day.

Experiments are needed to examine the component of variability to which photosynthetic traits acclimate and/or the rate of acclimation because these factors are likely to have large influences on model predictions in a rapidly changing world (Figure 1). Nonetheless, these experiments are difficult to design, given that acclimation may occur alongside other

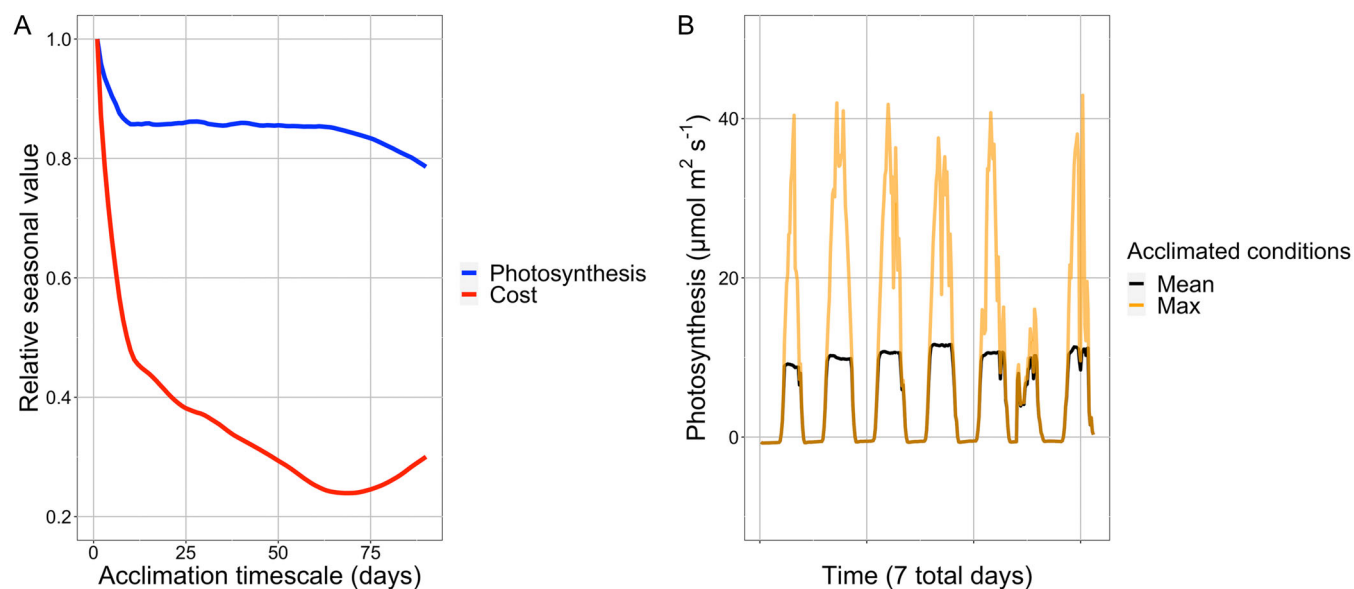


FIGURE 1 Simplified examples to show the photosynthetic benefit and cost of different timescales of photosynthetic acclimation (A) and acclimation to different aspects of environmental variability (B). (A) Simulated relative photosynthetic carbon assimilation and photosynthetic cost in plants acclimated to light, temperature, CO_2 , and vapor pressure deficit (VPD) across different timescales. Photosynthetic carbon assimilation values were simulated using a modified version of the model presented by Smith and Keenan (2020). The photosynthetic cost was estimated as the standard deviation of the maximum rate of Rubisco carboxylation (V_{cmax}) across the season. The model used environmental variables from the Harvard Forest National Ecological Observatory Network (NEON) site in 2017, assuming a growing season of 1 May to 30 September. Harvard Forest is a mesic, temperate forest. Simulations were performed with 1–90 acclimation timescales, with shorter timescales (left side of figure) indicative of faster acclimation times. Both lines are relativized to their values under a 1-day acclimation timescale. Note that the increased photosynthesis with fast acclimation is accompanied by a greater cost. The reduction in photosynthesis with longer acclimation timescales is the result of greater offset between current and acclimated conditions and not the result of downregulation. The increased cost of faster acclimation is due to increased need to adjust to changing conditions. (B) Simulated photosynthetic carbon assimilation over 7 days, assuming plants acclimate to mean daytime light availability (black line) or maximum daytime light availability (orange, semitransparent line). Simulations were done as in (A) using Harvard Forest NEON data from 30 June 2017 to 6 July 2017. Note that acclimation to maximum light conditions (orange) allows for greater photosynthesis during high light portions of days where midday light availability is high, but the stimulation of photosynthesis decreases during days where midday light availability is lower (e.g., day 6 in panel B). Also, note that investment in photosynthetic biochemistry is greater under the assumption that the plants acclimate to maximum (orange line; average acclimated $V_{\text{cmax}} = 178 \mu\text{mol m}^{-2} \text{s}^{-1}$) rather than mean (black line; average acclimated $V_{\text{cmax}} = 43 \mu\text{mol m}^{-2} \text{s}^{-1}$) conditions.

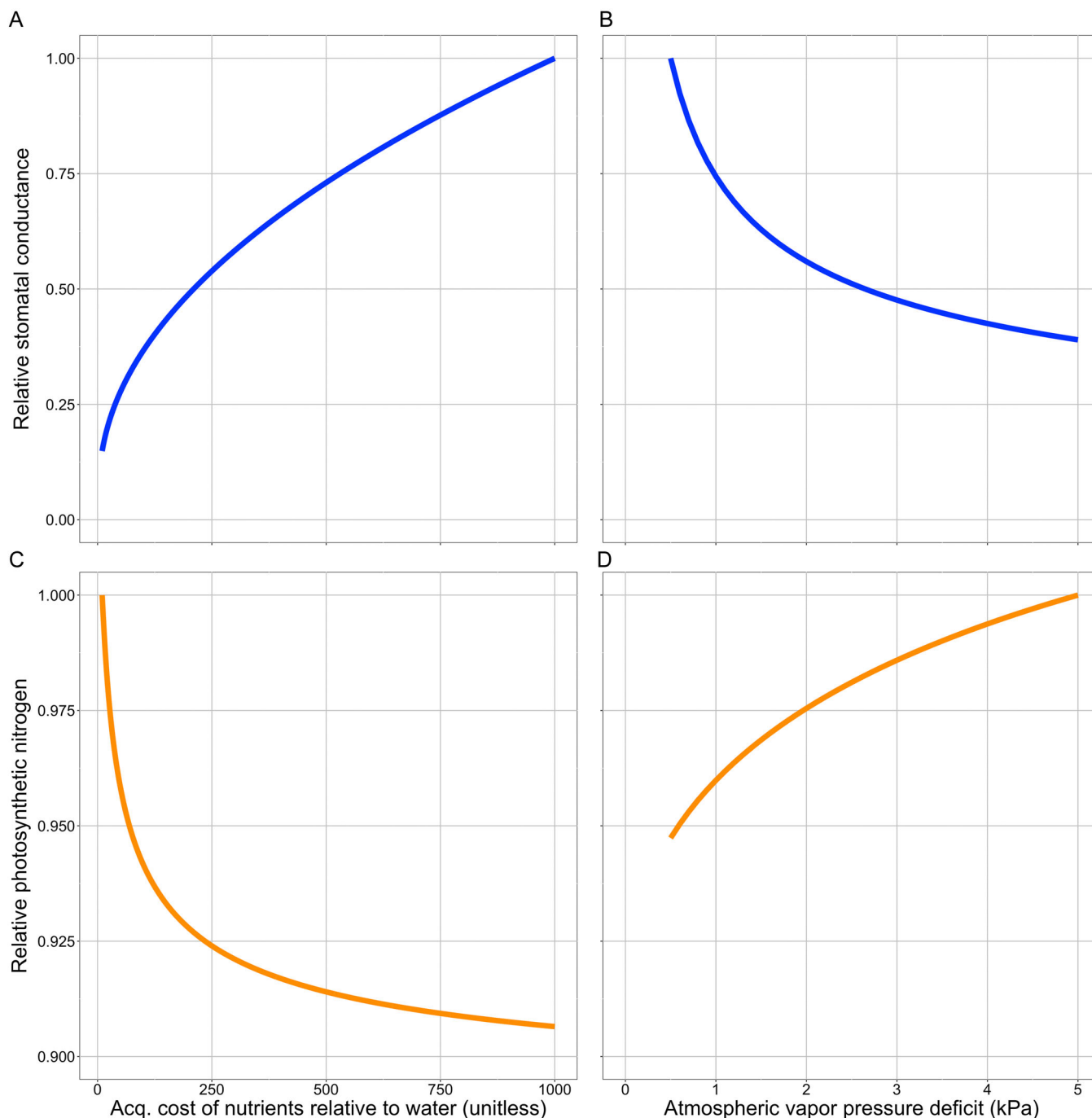


FIGURE 2 Simulated (A, B) relative stomatal conductance and (C, D) photosynthetic nitrogen as a function of (A, C) soil resource supply (reflected as the cost of acquiring nutrients relative to water) and (B, D) soil resource demand (reflected as the atmospheric vapor pressure deficit). Values were simulated using a modified version of the model presented in Smith and Keenan (2020). The x -axis in A and C is unitless and represents the relative carbon costs of acquiring and using nutrients for photosynthesis relative to the carbon costs of acquiring and using water for photosynthesis. This value is termed β in the model presented by Smith and Keenan (2020), developed from the least-cost model presented by Prentice et al. (2014). Thus, scenarios on the left side of panels A and C represent conditions where nutrient acquisition and use is costly relative to water acquisition and use, whereas values on the right side of the panels represent conditions where water acquisition and use is costly relative to nutrient acquisition and use. This can also be thought of as high nutrient and/or low water environments on the left side of panels A and C and low nutrient and/or high water environments on the right side of panels A and C. In panels B and D, rising VPD causes a reduction in stomatal conductance to minimize water loss, which is accompanied by an increase in photosynthetic nitrogen to maintain photosynthesis at low stomatal conductance. All y -axis values are relativized by their maximum value.

developmental and ontogenetic changes. A combination of manipulative experimental (e.g., Veres and Williams, 1984) and modeling (e.g., Mengoli et al., 2022) may be beneficial for addressing limitations to any one approach. It is also

important to consider the cost and benefits of acclimation (Figure 1). For instance, in Figure 1, both the timescale and component of acclimation impact the benefit (i.e., carbon assimilation) and cost (i.e., resource use to support

acclimation) of photosynthetic acclimation. Acclimation involves physiological processes that have some cost. Examining these costs in relation to the benefits gained by acclimation might provide a path toward greater understanding and better prediction.

HOW DOES THE INTERPLAY BETWEEN RESOURCE SUPPLY AND DEMAND INFLUENCE PHOTOSYNTHETIC ACCLIMATION?

Most studies on photosynthetic acclimation have tended to focus on responses to aboveground conditions (Boardman, 1977; Berry and Bjorkman, 1980; Bazzaz, 1990; Smith and Dukes, 2013; Niinemets et al., 2015; Dusenke et al., 2019). The focus on aboveground conditions is intuitive given that photosynthetic organs exist above the soil surface. In simplified terms, aboveground conditions influence demand for resources needed to acclimate. However, the availability of soil resources necessary to perform photosynthesis, namely water and nutrients, is known to influence photosynthetic traits (Smith et al., 2014; Liang et al., 2020), indicating a role of both soil resource demand from aboveground conditions and soil resource supply. Some models represent the influence of soil resource supply on photosynthetic acclimation using statistical relationships (Smith and Dukes, 2013; Smith et al., 2014), but theory development still lags behind.

Least-cost optimization theory provides a framework for understanding the interplay between soil resource supply and photosynthetic resource demand (Figure 2). Briefly, the theory suggests that soil water and nutrients can be substituted to support photosynthesis. That is, when water is relatively scarcer than nutrients, plants will increase nutrient use to perform photosynthesis at higher water-use efficiency and lower nutrient-use efficiency. The reverse is true when nutrient limitation increases relative to water limitation (Wright et al., 2003). Figure 2 shows least-cost predictions for photosynthetic trait responses to soil resource supply (reflected in the relative cost to acquire nutrients versus water) and soil resource demand (that result from changing atmospheric vapor pressure deficit). Least-cost theory has more recently been translated into a predictive mathematical formulation (Prentice et al., 2014), but analyses that use the theory to understand the impact of belowground drivers of photosynthetic acclimation are lacking (but see Waring et al., 2023). Photosynthetic optimization theories such as least-cost can be used to examine when and where soil resource supply is able to meet demand and how soil resource supply influences the acclimation of photosynthetic traits. For instance, deviation in traits from those expected from optimality may indicate instances where supply is not able to meet demand. Targeted manipulative experiments may be able to elucidate how these dynamics play out in individuals and communities.

CONCLUSIONS

Photosynthetic carbon assimilation is a key driver of ecosystem processes and heavily influences the services ecosystems provide. Photosynthesis is a dynamic process that acclimates to environmental conditions over space and time. While photosynthetic acclimation has been well studied, key uncertainties still remain that will require multiple approaches (e.g., observations, experiments, theory development, model simulations) to reconcile. Among these uncertainties are the temporal nature of acclimation (i.e., to what does photosynthesis acclimate and how long does it take?) and the role of belowground resource availability (i.e., how does the interplay between resource supply and demand impact acclimation?). There is a need to understand any species-specificity of responses to better characterize their role in influencing plant community dynamics and a need for appropriate across-species generalizations that can facilitate incorporation of photosynthetic acclimation processes into regional and global scale models. There are opportunities for the botanical, ecological, biogeochemical, and Earth system communities to work together to close these gaps.

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DATA AVAILABILITY STATEMENT

All code to create figures in this manuscript can be found at https://github.com/SmithEcophysLab/otnot_2024 (doi: <https://doi.org/10.5281/zenodo.10607779>).

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