Rethinking economic theories of plant water use

Adam B. Roddy

Institute of Environment, Department of Biological Sciences, Florida International University, Miami, FL, USA

aroddy@fiu.edu ORCID: 0000-0002-4423-8729

A central assumption in plant ecophysiology is that carbon is the primary currency for plant fitness. To this end, plants are thought to maximize carbon gain and any deviations from maximum carbon gain are ascribed to resource limitations (e.g. temperature, drought), biophysical limitations (e.g. biophysical limits on cell size), or variation in plant life history that may prioritize future carbon gain over current carbon gain (i.e. applying an economic discount rate to carbon). Compared to living in water, living on land made accessing CO_2 substantially easier: CO_2 diffuses approximately 10,000 times faster in air than in water. However, because this CO_2 must diffuse into the aqueous environment of the living mesophyll cells where photosynthetic metabolism occurs (Théroux-Rancourt *et al.* 2021), the greater CO_2 supply of the terrestrial lifestyle also comes with a cost: losing approximately 200–400 molecules of water by transpiration for every molecule of CO_2 fixed by photosynthesis (Nobel *et al.* 2005). Water, therefore, is considered a valuable resource to be conserved and not wasted. As such, much of the field of plant ecophysiology posits carbon as the central currency for which water is traded.

Our conceptual framing of water and carbon is based in Neoclassical economic theory. By expending water to enable photosynthesis, the traditional thinking goes, then the fixed carbon can be allocated to the three components of individual fitness: growth, reproduction, and survival (Violle *et al.* 2007). However, in a recent review, Blonder *et al.* (2023) argue that this framing ignores important uses of water that may not be directly linked to carbon and certainly not to short-term carbon gain. Blonder *et al.* (2023) point out various functions of water itself, separate from its exchange rate for carbon. Elevating water use to be on par in importance with carbon allocation may illuminate critical plant ecological strategies and behaviors that may otherwise be easy to ignore.

While carbon is undoubtedly important to plant function, can it be the metric of fitness so often assumed by ecophysiologists? Most ecophysiologists would agree that the ultimate goal of all resource allocation is integrated lifetime reproductive fitness. While it is typically assumed that short-term transpiration to support more carbon uptake allows for greater investment in reproduction, water is expended to support reproductive functions directly and independently of carbon. For example, water is critical for building flowers that are cheap but nonetheless attractive and biomechanically robust (Olson and Pittermann 2019; Roddy *et al.* 2019; Roddy *et al.* 2023) and for attracting and rewarding pollinators (De la Barrera and Nobel 2004; von Arx *et al.* 2012; Dahake *et al.* 2022). Water may be preferentially directed towards reproductive organs over vegetative organs, particularly under conditions of water scarcity (Harrison Day *et al.* 2022; Sinha *et al.* 2022).

Beyond reproduction, water is used for means other than promoting individual carbon gain and may be lost inadvertently because of either unavoidable tradeoffs or constraints due to other plant functions or limitations. As a major source of latent heat loss, transpired water can be critical to maintaining plant leaves and reproductive organs within safe operating temperatures (Patiño and Grace 2002; Borges *et al.* 2016; Roddy 2019; Kullberg *et al.* 2023). This effect may extend beyond the individual leaf-level to include the whole canopy, as excessive transpiration by sun leaves may provide a cooler, darker microclimate for shade leaves so that they may photosynthesize closer to their light optimum at lower water cost (Blonder *et al.* 2023). But Blonder *et al.* (2023) move beyond the individual leaf- or plant-level to suggest how individual plant water use influences populations and communities. The capitalist underpinnings of Neoclassical economic thinking assumes that most interactions between plants have negative outcomes (Simha *et al.* 2022). However, given that plants almost universally have evolved while embedded within communities, mutually beneficial interactions that reduce the costs of competition may have been particularly advantageous. Blonder *et al.* (2023) point to hydraulic redistribution as one example: deep-rooted trees may passively move water into shallower soil layers, which improves growth of shallow-rooted species and can have positive feedbacks on deep-rooted plants, such as increasing nutrient availability (Dawson 1993). Importantly, Blonder *et al.* (2023) note that while many of the various types of water use they detail may be under selection, there are also some non-adaptive processes that use water. For example, it is impossible to completely stop water loss because cuticles covering the epidermis are inherently permeable. How much plants invest in limiting cuticular water loss could depend on a variety of factors, and the conductance of the cuticle is thought to be a critical trait affecting drought tolerance and water use (Roddy *et al.* 2016, 2023; Duursma *et al.* 2019). Broadening our thinking about how water is used by plants, as Blonder *et al.* (2023) argue, is vital to explaining observed hydraulic behavior and predicting plant responses to climate change.

Furthermore, the review by Blonder *et al.* (2023) begs us to consider more broadly how our understanding of plants (and biology more generally) may be limited not only by Neoclassical economics but by historical contingency, dominant sociopolitical paradigms, and self-interested bias (Simha *et al.* 2022). If we insist upon applying economic theory to plant ecophysiology, then we should at the very least update our heuristics to account for more developments in economic theory. One of the major advances in economics over the last half century has been the recognition of the role of individual psychology in economic behavior. The foundational work of Kahneman and Tversky starting in the 1970s showed that humans often make economic decisions that prioritize desires and values beyond just monetary gain and that are limited by incomplete information and their psychology (Kahneman and Tversky 1979; Camerer *et al.* 2004). People's short-term economic decisions often depend on their financial context: their monetary wealth and whether they have experienced financial instability (Piff *et al.* 2012; Côté *et al.* 2015). For example, people often save money more effectively when they have the stability of wealth but spend any new income more readily when they lack wealth, such that a psychology of scarcity–and the material constraints imposed by scarcity–traps people into making financial decisions that do not prioritize their long-term financial well-being. Plant water use strategies can be similarly variable within species due to resource availability (Guo *et al.*

2020; Driscoll *et al.* 2020) and among species due to the history of selection that has shaped individual traits and overall physiological and life history strategies (Silvertown and Doust 1993; Martínez-Vilalta *et al.* 2014; Meinzer *et al.* 2016; Roddy *et al.* 2020).

The predominant thinking among plant biologists is that plants are mere biophysical reactors to their environments that lack cognitive capacity (Mallatt *et al.* 2021). However, plants, like all biological systems, must store, process, perceive, and transmit information as an inherent part of converting energy and matter and make consequential decisions about their short-term and long-term well-being (Gagliano *et al.* 2016; Gagliano 2017; Hoke *et al.* 2021). Thus, they may be strategic, optimizing among multiple functions (e.g. carbon uptake or reproduction), planning for the future depending on their experience of resource availability (e.g. switching between monocarpy and polycarpy; Cotado and Munné-Bosch (2020)), and expressing some sense of agency or action regarding other individuals in the population or community (as discussed by Blonder *et al.*, 2023), or even–like humans–making seemingly poor water use decisions based on incomplete information or their past history of resource scarcity. Maintaining some level of imperfection in water use may actually be under selection: just as genetic mutations–though often detrimental–are the source of innovation and maintained by selection (Orr 2000; Swings *et al.* 2017), so too may seemingly detrimental water use by plants be beneficial in some contexts, particularly when there is increasing unpredictability in conditions due to climate change.

Human economics may not be the best analogy for plant water use. Selection acts on reproductive success and only on plant water use insofar as it maximizes reproductive success–be it through increased carbon uptake, reproductive assurance, or supporting other individuals in the population and community. By contrast, in human societies subject to Neoclassical economics greater monetary wealth is largely unrelated to reproductive fitness. Seeing the strengths and also the weaknesses of the metaphors and analogies we use to understand biological systems is critical to better understanding these systems. Blonder *et al.* (2023) should remind us to more fully embrace and enact objectivity in our work by acknowledging our own subjectivity (Intemann 2016). Science is, after all, a social endeavor performed by people embedded in social contexts. Despite our proclaimed objectivity, scientific knowledge is subject to who does science, what questions they ask, and how that knowledge is perceived. Moving out of the shadow of dominant economic theories that have shaped plant biology would allow for a more nuanced, more complete understanding of the future functioning of plants and ecosystems under ever-more varied and unpredictable environments.

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