Blonder Benjamin (Orcid ID: 0000-0002-5061-2385)
Michaletz Sean (Orcid ID: 0000-0003-2158-6525)
Posch Bradley Cooper (Orcid ID: 0000-0003-0924-6608)
Slot Martijn (Orcid ID: 0000-0002-5558-1792)
Winter Klaus (Orcid ID: 0000-0002-0448-2807)

Viewpoint

Plant water use theory should incorporate hypotheses about extreme environments, population ecology, and community ecology

Summary

Plant water use theory has largely been developed within a plant-performance paradigm that conceptualizes water use in terms of value for carbon gain, and that sits within a neoclassical economic framework. This theory works very well in many contexts but does not consider other values of water to plants that could impact their fitness. Here we survey a range of alternative hypotheses for drivers of water use and stomatal regulation. These hypotheses are organized around relevance to extreme environments, life history and population ecology, and species interactions within a community context. Most of these hypotheses are not yet empirically tested and some are controversial (e.g., requiring more agency and behavior than is commonly believed possible for plants). Some hypotheses, especially those focused around using water to avoid thermal stress, using water to promote reproduction instead of growth, and hoarding water, may be useful to incorporate into theory or to implement in Earth System Models.

Introduction

Predicting plant water use for species with differing traits and across environmental conditions is a central challenge for ecophysiology (Venturas *et al.* 2017; Kannenberg *et al.* 2022). Accurate predictions are critical for fundamental knowledge of plant biology, as well as for upscaling to ecosystem fluxes, e.g., via Earth System Models (Christoffersen *et al.* 2016; Fisher *et al.* 2018). Current *marginal gain theory* for water use (Wang *et al.* 2020) has been developed from a foundation of stomatal optimization framed in terms of maximizing carbon gain (Cowan & Farquhar 1977). This theory proposes that plants maximize $A - \Theta$, where A represents carbon gain and Θ represents some carbon penalties or costs, e.g., relating to soil drying, or hydraulic failure. Both. If E is the amount of water plants use, then mathematically, maximization occurs when $\frac{\partial A}{\partial E} = \frac{\partial \Theta}{\partial E}$, i.e. when the marginal gain equals the marginal penalty (Wang *et al.* 2020). Implementations of theory make divergent assumptions about A and Θ, e.g., whether the

timescale of each is instantaneous or temporally extended (i.e. whether A and Θ are defined as a rate or a quantity), whether the biological scale is a single leaf or a whole plant, whether the environment is constant or variable, etc. Often, E is assumed to depend only on stomatal opening, so the term 'stomatal optimization theory' is commonly used interchangeably with 'marginal gain theory'.

Current iterations of marginal gain theory are widely considered reliable and generally suggest that the penalty depends on vapor pressure deficit, or soil water potential, or other similar variables (Wang *et al.* 2020; Kannenberg *et al.* 2022), leading to the development of marginal gain models that consider the entire soil-plant-atmosphere-continuum (Sperry *et al.* 2016; Wolf *et al.* 2016). For example, some empirical models based on vapor pressure deficit (Leuning 1995; Medlyn *et al.* 2011) are widely used to parameterize Earth System Models, and predictions are often reliable at leaf and ecosystem scale (Franks *et al.* 2018). Nevertheless, substantial uncertainty remains about the biological and temporal scales over which this optimization is valid (Feng *et al.* 2022).

Optimal plant water use may be more complex than what most implementations of marginal gain theory indicate. As a first example, theory often fails in hot environments. Previous efforts to model gas exchange at higher thermal stresses (Franks *et al.* 1997; Eamus *et al.* 2008) have yielded results that are at odds with stomatal optimization theory thought to apply at short timescales (Medlyn *et al.* 2011). Heat avoidance can occur, where water use is optimized not to maximize instantaneous carbon gain per unit water loss (i.e. *marginal gain theory*), but instead to prioritize evaporative cooling that avoids thermal stress/mortality at high temperatures (Chaves *et al.* 2016; Slot *et al.* 2016; Urban *et al.* 2017; Blonder & Michaletz 2018; Aparecido *et al.* 2020; Marchin *et al.* 2022a) and thus enables sustained long-term carbon gain. As a second example, stomatal optimization theory thought to apply to isolated individuals can fail when plants are measured in community contexts. Recent models of stomatal optimization under competition (Wolf *et al.* 2016; Lu *et al.* 2020) indicate that water use strategies should change when neighbors compete for water. This prediction of water use shifting when growing with competitors vs. alone has been upheld in at least two sets of experiments (Vysotskaya *et al.* 2011; Zenes *et al.* 2020).

Conceptual framing

Marginal gain theory has been limited in four practical ways. First, validations of theory have been carried out primarily on a limited set of species, often crops (von Caemmerer & Evans 1991; Harley *et al.* 1992). While these cases are clearly of high interest, they represent a limited and biased subset of plant functional and evolutionary diversity. Second, tests of theory have been limited in extreme (very hot and concurrently very wet or very dry) environments (Schulze *et al.* 1973; Aparecido *et al.* 2020; Grossiord *et al.* 2020). This limitation is especially critical for accurate predictions in response to novel environmental conditions (Williams & Jackson 2007) projected under global change. Third, most data come from measurements of leaves, isolated from the whole-plant context, or individual plants, isolated from their population or community contexts. While such data provide snapshots of behavior under controlled conditions, they may not accurately represent behavior in complex natural conditions. Fourth, theory may not yet provide a sufficient description of all the biological processes affecting water use. This reflects either a tradeoff between model complexity and usefulness (Harrison *et al.* 2021), or alternatively, incomplete process knowledge or data for parameterizing models.

Marginal gain theory is also limited by its foundational assumption that plant water use is a problem analogous to the rational actor problem in classical (Smith 1776) and neoclassical economics (Jevons 1879). Both propose that the leaf or plant (analogously, the individual) has evolved mechanisms (chooses actions) that maximize performance (maximize utility or diminish marginal utility) due to natural selection (self-interest). Both also assume that the optimization can be conceived in terms of a single measure and store of value, carbon (money). This assumption has been widely critiqued in economics (Hollis & Nell 1975; Sen 1977), as it leads to both inaccurate predictions of human behavior (Veblen 1898; Fullbrook 2004), and also negates the possibility of considering cooperative behavior and multiple incommensurable types of values relevant to decision-making (e.g., 'human wellbeing' or 'ecosystem health') (Jackson 2016). Marginal gain theory for plant water use draws from this economic heritage, and implicitly requires us to accept the premise that plant behavior can be collapsed to the single currency of carbon, and the single objective of getting as much of it as possible. This logic also produces the concepts of ecosystem service valuation (Reid *et al.* 2005) and natural capital

(Costanza *et al.* 1997), which propose that money-based prices or valuations can be given to values that may actually not be commensurable. Returning to plant water use, it therefore may be useful to cast off the shackles of old economic ideas, and embrace a broader perspective on the values of water to plants that are not defined as, or priced in terms of, carbon gain.

Our central hypothesis is that the value of water to a plant extends far beyond its immediate value for instantaneous carbon gain, requiring either extension of marginal gain theory to more biological and temporal contexts, or alternatively development of new theory that asks how water use influences fitness–not ecophysiological performance. We survey hypotheses that operate at different biological and temporal scales (illustrated in **Figure 1**) that might cause current theory to fail, which are linked to performance in extreme environments ('E' hypotheses), to life history and population ecology ('P' hypotheses), and to species interactions and community context ('C' hypotheses). We then sketch a range of observed and yet unobserved hypotheses that are still on the frontier of current theory and that may run contrary to current theory's predictions.

Some of the hypotheses we propose are at odds with current understandings of how plants process information and ascribes a level of agency to plants that is not widely considered reasonable at individual or population scale. There is also little evidence to date that plants have evolved mechanisms to enable such complex behavior. Nevertheless, these strategies remain an under-investigated conceptual possibility. We used agentive terms within these hypotheses below because they are standard within game theory and computer science. Additionally, the limits of plant agency, behavior, communication/sensing, and social interactions remain poorly studied (Silvertown & Gordon 1989; Karban 2015; van Loon 2016).

Hypotheses relating to extreme environments

E1. Avoiding thermal damage or mortality

High transpiration may reflect prioritization of leaf cooling to avoid heat damage or death in thermally extreme environments (**Figure 2A**). This appears contrary to the stomatal optimization prediction (over short timescales) that stomata should close to prevent hydraulic failure, and also appears maladaptive because of the reduced efficiency of photosynthesis at high temperatures.

However, increasing transpiration at high temperatures actually can be optimal over long timescales if water is available and doing so prevents leaf thermal damage or mortality, i.e. if it promotes future carbon gain, and offsets the loss of carbon invested in the construction of the leaf (Blonder & Michaletz 2018). This type of optimization is difficult to capture in analytic models because leaf mortality is not reversible: if a leaf has exceeded a critical temperature even once, its future carbon gain is zero, regardless of the temperature the leaf later obtains.

Low transpiration rates prevent evaporative cooling and lead to high temperatures in leaves (Gates 1968; Monteith & Unsworth 2013) and also limit advective heat transfer by xylem sap, which can lead to high temperatures in branch and stem phloem, xylem, and sapwood (Swanson 1994). High leaf and branch temperatures, if sustained, could cause permanent (or costly-to-repair) biochemical damage, structural changes and reduced hydraulic conductivity of xylem (Michaletz *et al.* 2012), or cell and tissue necrosis (Teskey *et al.* 2015). Failure to evaporatively cool can also cause mortality. For example, during a hot drought in Australia, crown dieback in urban trees was negatively correlated with the critical temperatures for photosystem II dysfunction, while leaf water potentials showed trees were not severely water stressed (Marchin *et al.* 2022b). This suggests that dieback was driven by heat stress (not embolism) resulting from reduced transpirational cooling that enabled leaf temperatures to exceed a critical threshold.

Cooling is likely to be important in plants with relatively carbon-expensive and/or evergreen leaves, in environments that experience transiently high temperatures, especially when combined with high soil water availability (Aparecido *et al.* 2020). For example, stomatal responses to vapor pressure deficit and temperature can become decoupled in some desert plants (Schulze *et al.* 1973). There are likely more efficient ways to keep leaves cool via trait evolution over longer timescales, or alternatively higher thermal tolerances to occur via phenotypic plasticity or evolution. These latter approaches are likely taken by many hot-adapted species, which can see leaf temperatures reach 48-49 °C associated with midday depressions of photosynthesis and transpiration, while CAM plants can exceed 50 °C leaf temperature during mid-day, and some cacti obtain temperatures >50 °C, with heat tolerances up to 69 °C (Smith *et al.* 1984). For example, the Rubisco activase isoform in *Agave* remains active at up to 50 °C, 10° C higher than *Oryza* isoforms (Shivhare & Mueller-Cajar 2017).

Several underlying physiological processes could generate this cooling response. The most straightforward possibility is stomatal opening at high temperatures. Sensory mechanisms remain unknown, but may include detection of unfolded proteins, and changes in membrane fluidity (Hayes *et al.* 2021). Abscisic acid (ABA) may play a role, as its accumulation is linked to reduced transpiration and increased hydraulic conductivity during drought stress (Muhammad Aslam *et al.* 2022). Alternatively, other signal transduction mechanisms could cause high temperature stomatal opening (Kostaki *et al.* 2020). Another speculative possibility is stomatal popping, in which pressurized hot air in intercellular spaces forces guard cell opening (Brix *et al.* 1992; Aparecido *et al.* 2020). This is unlikely because such popping would occur only once, after which depressurization would occur and prevent further water flux. Alternatively, transpiration fluxes could arise from high cuticular conductance, which is known to increase at higher leaf temperatures, due to changes in the physical properties of cuticular waxes. This last cooling mechanism seems most plausible and has been described in desert (Bueno *et al.* 2019) and tropical (Slot *et al.* 2021) species, though it is unclear yet whether it is adaptive.

Cooling can also occur via leaf positioning rather than transpiration. For example, in *Piper auritum,* a tropical species associated with high light conditions in canopy gaps (Chiariello *et al.* 1987), high water use results in mid-day wilting. This reduces the direct sunlight that hits the leaves in their exposed habitat, which in turn decreases leaf temperatures. The reduction in incident irradiance caused photosynthesis to decrease, but less so than transpiration, so water use efficiency is improved by the avoidance of mid-day sun. The continued photosynthesis, albeit at reduced rate, suggests that this strategy enables optimization of time-integrated carbon capture. Similar behavior is observed in wheat, where leaf erectness and leaf rolling behavior are breeding targets for improving heat tolerance (Hunt *et al.* 2018).

Cooling requires available water, which can depend both on precipitation, but also species properties like maximum rooting depths and capacitance. For example, in hot conditions, deeply rooted evergreen woody plant taxa, *Quercus turbinella* and *Rhus ovata,* were shown to achieve high leaf-level transpiration rates that were decoupled from rates of carbon uptake (Aparecido *et al.* 2020). Similarly, stem gas exchange measurements conducted on mature *Carnegiea gigantea*

(saguaro cactus) in the Sonoran Desert during midsummer yielded daytime transpiration rates that at times equaled nighttime transpiration rates during Phase I of the CAM cycle (Bronson *et al.* 2011). These patterns indicate that under heat stress, giant saguaros either actively transpire water stored in their succulent stems by opening their stomata during the day, in turn losing carbon fixed at night – potentially as a mechanism to reduce stem surface temperatures – or experience daytime water loss through the cuticle as surface temperatures increase. As another example, transient shallow soil moisture conditions enable the desert shrub, creosote (*Larrea tridentata*) to take a riskier, anisohydric hydraulic strategy following precipitation pulses in both winter and summer; while adopting a more conservative, isohydric strategy in other periods when shallow soil moisture is absent (Guo *et al.* 2020). Likewise, warm-adapted cottonwood (*Populus fremontii*) – a desert riparian tree species – increases stomatal conductance during the warmest time of the year, unlike cool-adapted genotypes that show no seasonal changes in stomatal conductance (Blasini *et al.* 2022). Consequently, warm-adapted genotypes maintain cooler leaves than cool-adapted genotypes, which improves carbon balance and protects against leaf thermal damage.

E2. Minimizing respiration costs

Nighttime transpiration is observed in many species when environments are hot (Dawson *et al.* 2007; Yu *et al.* 2019). Reduced nighttime transpiration is recognized as a valuable target trait for breeding crops with high water use efficiency, e.g., (Coupel-Ledru *et al.* 2016). Nighttime transpiration in C_3 and C_4 plants is challenging to explain from an optimality perspective as it results in high water costs and no instantaneous carbon gain. An alternative explanation for this observation involves optimization of carbon gain over longer timescales. Cooling leaves at night via transpiration may reduce respiration rates, which increase exponentially with temperature. This strategy may complement or trade off with acclimation of respiration to elevated nighttime temperature (Reich *et al.* 2021). While the amount of cooling achieved by low rates of nighttime transpiration is likely small, the effect on carbon flux may nonetheless be significant. Reductions in nighttime carbon losses from respiration may offset low net carbon gains during the daytime when photosynthesis is limited at high temperatures and respiration is high. This might occur in hot environments where nighttime respiration is a major cost, and only for C_3 and C_4 species (Wang *et al.* 2021). Nighttime transpiration has also been linked to refilling of xylem embolisms

(Zeppel *et al.* 2014), though this may occur only under high water potentials (Klein *et al.* 2018). Such an effect would in turn benefit daytime carbon fixation, as it would enable more sustained stomatal opening.

E3. Shading via parasol effects

In extremely hot or bright environments, upper canopy sun leaves may photosynthesize sub-optimally at the leaf level, but still contribute significantly to overall plant carbon assimilation (Ishii *et al.* 2004) (**Figure 2B**). While the morphology of sun leaves often helps maximize convective heat losses to the atmosphere (Vogel 2009), such leaves may become too hot or light-saturated to efficiently carry out photosynthesis for much of the daylight hours, and may also require a high water supply in order to maintain open stomata, cool via transpiration, and avoid thermal mortality. However, this upper canopy layer may provide sufficient shading and associated cooling benefits to produce a canopy microclimate that enables lower-canopy shade leaves to photosynthesize at a lower water cost. This hypothesis has been supported in computer models of woody species architecture (de Haldat du Lys *et al.* 2022).

There is limited empirical support for positive effects on carbon gain of shading in a Puerto Rican tropical wet forest (Miller *et al.* 2021) and also in a temperate tree experiment (Kothari *et al.* 2021). While leaves under moderate shade may have lower maximum photosynthesis rates, the lower maximum tissue temperature and lower leaf-to-air vapor pressure deficit may enable them to avoid midday stomatal depression and maintain photosynthesis during most of the day. Thus, in this case, the standard carbon-for-water optimization still occurs, but at the scale of the whole plant, not the scale of a single leaf. This strategy might occur if the relative benefit of lower-canopy leaves exceeds the relative cost of sacrificial upper canopy leaves that act as a parasol for the overall plant. Alternatively, sun leaves, which are typically much shorter-lived than shade leaves (Reich *et al.* 2004), might operate at high photosynthetic rate for a while when they are young, and then continue their role in the parasol function until they are replaced by new leaves. Regardless, measurements of photosynthetic capacity that focus on sun leaves may obscure optimization occurring at whole-plant level.

Hypotheses relating to population ecology

P1. Time discounting

In plants with 'fast' life histories or strong competition among species over a common growing season, there may be substantial benefits to carbon gained earlier in ontogeny (e.g., photosynthetic cotyledons, early leaf flushes). Carbon acquired earlier in life can be re-invested in the deployment of additional photosynthetic tissue, which further accelerates growth (Chabot & Hicks 1982). This is because, from an economic perspective, the time discounting rate for carbon could be large, and costs incurred later may not be as important as benefits obtained earlier (Westoby *et al.* 2000). This perspective is widely discussed in the leaf lifespan literature(Kikuzawa & Lechowicz 2006; Falster *et al.* 2012; Castorena *et al.* 2022) and can be incorporated into stomatal optimization models, though most models do not include it (Wang *et al.* 2020). Thus, high water use early on in a life cycle or in a growing season may be optimal, even if it later leads to drawdowns in soil moisture, stem hydraulic failure, or leaf mortality. For example, many facultative CAM plants begin life using C_3 photosynthesis, because they prioritize rapid early growth over water use efficiency (Winter *et al.* 2011).

P2. Deadline effects

Related to the time discounting mechanisms, species may sometimes maximize fitness by exploiting limited resources as rapidly as possible, e.g., desert winter annuals where lifespans are limited by the onset of an arid foresummer, or in a savanna where locust outbreaks may occur driving fatal levels of herbivory (**Figure 2C**). As in a workplace analogy, any species that meets its deadline (completes its life cycle) is a winner, while all others that cannot meet the deadline are losers (Aronson *et al.* 1992; Peñuelas *et al.* 2004). This is effectively a special case of time discounting where the discount rate becomes infinite after a certain amount of time. In such a case, water use may reach levels high enough to exhaust water resources and risk vegetative tissue damage or death, so long as it leads to successful reproduction within a minimum time interval.

P3. Leaf lifespan effects

Species differing in their leaf lifespan (deciduous vs. evergreen) may have different water use strategies (Schulze 1982). In tropical species, there is often a tradeoff between drought avoidance (deciduousness) and hydraulic safety (Oliveira *et al.* 2021). However, much of this data comes

from seedlings, so empirical knowledge remains limited. Deciduousness may also influence water use in ways unrelated to hydraulic safety. Drought-deciduous species do not have leaves for part of the year, and benefit from not needing to pay the water and carbon costs of maintaining them (via transpiration and respiration respectively) (Vico *et al.* 2017). However, they also lose out on the opportunity to use water at other times of year to support carbon uptake, as well as on the opportunity to vegetatively compete with other species that could otherwise use the same shared pool of soil water (note that this argument is reversed when snowy/wintry conditions rather than drought are considered). Deciduous species also may take more aggressive water use strategies (Zeppel *et al.* 2014) when in the presence of evergreen species or when they have evolved under competition from evergreen species.

P4. Tradeoffs among fitness components

In plants where fitness is most demographically sensitive to variation in reproduction or survival, rather than to growth, water may be used in ways that deprioritize carbon gain in leaves (**Figure 2D**). This could drive apparently non-optimal stomatal regulation at the leaf level if allocation is not correlated with signals known to drive stomatal regulation, such as variation in stem water potential. For example, allocation of carbon towards osmotic regulation (e.g., for freezing responses) or storage (at the end of a season), or allocation of water towards fruit production, could lead to low leaf water use or leaf death, even when this strategy is optimal for fitness overall.

Some of these strategies might be expected to be more common in species where selection may be stronger for non-growth fitness components. During drought, plants might be more limited by water than by carbon, so they may prioritize allocation to reproduction over that to leaves, not only because of fitness, but also because water loss may be higher from leaves than from flowers or fruits. In stressful conditions, prioritization of water for fruit growth has been reported in *Solanum lycopersicum* (tomato) (Harrison Day *et al.* 2022) while prioritization of transpiration in flowers occurs in *Glycine max* (soybean) (Sinha *et al.* 2022), and prioritization of storage occurs in *Picea abies* (spruce). There is also increased allocation to reproduction when water is limited during seasonal and El Niño drought in tropical forest (Detto *et al.* 2018). Similarly, some annual (monocarpic) crop species need to initiate whole-plant senescence to remobilize and transfer

assimilates to grains (Yang & Zhang 2006). The amount of carbohydrates fixed prior to senescence can be particularly important for grain filling (Asseng & Van Herwaarden 2003). Therefore, leaves of annual plants may maximize short-term assimilation in the phase just before grain filling and senescence.

Additionally, selection may favor whole-plant survival even when it impacts leaf performance. For example, using advective heat transfer of xylem sap described above, *Pinus ponderosa* seedlings have been observed to maintain stem temperatures as much as 15 °C below ambient air temperature, enabling them to survive in open forests where soil surface temperatures could exceed 75 °C (Kolb & Robberecht 1996). The lethal temperature for stems was 63 °C, so the elevated stomatal conductance found in needles of surviving plants appears critical for whole-plant survival. As another example, *Helianthemum squamatum* switches between surface and deep water sources in dry conditions. This reduces water use efficiency from expected values, because the switching behavior has high costs that lead to reduced nutrient uptake, which then reduces leaf photosynthetic efficiency (Querejeta *et al.* 2021).

P5. Non-adaptive mechanisms

It is also possible that very high or low water use may be maladaptive and occur as a necessary cost driven by other processes that influence population fitness. A range of mechanisms are possible, and increasingly being recognized. Limited phloem export capacity or sink limitation may mean that water is often not transpired when it is available and could be used (Fatichi *et al.* 2014), because any resulting carbon gain would result in accumulation of reaction products and inhibit further reactions (e.g., driving the commonly-observed late afternoon depression in photosynthesis). This also could occur if plants are adapted to lower levels of atmospheric $[CO_2]$ than they currently experience. The same outcome can result from sink limitation; reduced sink activity results in carbohydrate accumulation in leaves, which triggers downregulation of photosynthesis and transpiration (Quereix *et al.* 2001; Li *et al.* 2007).

Additionally, the temperature dependence of cuticular conductance described above could lead to higher water use than would be adaptive, either because it is an unavoidable biophysical reality (Slot *et al.* 2021) or because of tradeoffs with photosynthetic capacity (Machado *et al.* 2021).

Alternatively, correlated selection (e.g., due to genetic linkage) could occur, resulting in non-optimal water use being a necessary consequence of strong selection for other traits. However there seems to be limited evidence for this given the omnigenic basis of many complex traits in plants (Boyle *et al.* 2017). Or, in some abiotically non-stressful environments, neither water use nor carbon gain may be limiting to performance, when for example, competition for pollinators or dispersers may be a priority. In such cases, water use strategies may be variable and inexplicable from a Panglossian optimality perspective (Gould & Lewontin 1979). While it seems unlikely that selection does not act strongly on water use, the alternative hypothesis should be rejected based on evidence rather than assumption.

Hypotheses relating to community ecology

C1. Mechanisms that promote coexistence

The fitness of a population may be influenced by community context. Mechanisms that promote coexistence effectively increase the long-term fitness of a population. Therefore, mechanisms influencing coexistence may lead to selection on water use behavior for species when they occur with other species, whether the underlying species interactions are positive or negative. Coexistence mechanisms are processes that yield higher intraspecific competition relative to interspecific competition when each species is rare, meaning that species are able to recover from low densities without becoming extinct (Chesson 2000). These coexistence mechanisms necessarily operate at scales beyond that of the individual or population.

Temporal niche partitioning is one such mechanism. If water is a key resource, then some species may perform better only when water availability is consistent over time and space, while others may perform better when water availability is variable over time and space. Thus, some species may appear to use non-optimal water use strategies when measured in a constant environment, when in fact their strategy is optimal for population dynamics when environments fluctuate (Chesson *et al.* 2004).

Spatial niche partitioning is another mechanism. If species exploit water at different soil depths, there may be reductions in interspecific competition mediated by shifts in species' water use

efficiencies or timing of water use (as droughts affect each depth differently) and potential impacts on ecosystem water use and community diversity. Evidence for complementarity and partitioning remains mixed (Verheyen *et al.* 2008; Bachmann *et al.* 2015; Guderle *et al.* 2018). Alternatively, hydraulic redistribution of moisture between soil depths (Richards & Caldwell 1987; Caldwell *et al.* 1998) could instead drive facilitation or increased interspecific competition (Dawson 1993). Deeply-rooted plants have the potential to engineer the thermal environment of whole communities, not only by providing added soil water via hydraulic lift (Dawson 1993), but also by modifying the humidity of the shared near-surface environment in a community.

The storage effect is an additional mechanism that can operate if water availability varies over time or space. If some species have differential responses to water availability, then in 'good' years they may be able to store these gains as larger population sizes or seedbanks, while having a relatively small negative effect on their populations in 'bad' years. This mechanism is known to operate in Sonoran Desert annual plants (Venable & Pake 1999), which vary widely in their water use efficiency (Angert *et al.* 2009). Succulents might also be able to store water for multiple months or years before using it, yielding a lagged version of the storage effect. This population buffering mechanism means that species that have non-optimal water use within bad years may be buffered from negative consequences due to their success in good years.

C2. Hoarding and spite

In other cases, fitness may not be maximized by coexistence, but rather by resource preemption (**Figure 2E**). Species may succeed by using soil water to cause the local extinction of other species. The balance between facilitation and competition is known to shift as soil water becomes more limiting (Holmgren *et al.* 1997; Haberstroh & Werner 2022). Resource preemption may thus arise only under stressful circumstances (i.e. not likely in very wet environments, or in those with many species present, or for small-sized plants).

Resource preemption can occur via hoarding. Plants could rapidly acquire soil moisture, then store it in tissues or via capacitance, after which they can transpire it at any future time while also preventing other plants from using it, as might occur for desert plants like agaves, various columnar cacti, or baobabs. Alternatively, they could redistribute it to deeper soil (hydraulic

descent) and make it unavailable to shallow-rooted competitors but available to themselves. This may occur primarily in environments where precipitation events are rare. Hoarding does occur for carbon and other nutrients in plant-fungal interactions, wherein fungi withhold transfer of mineral nutrients until the plant provides a higher amount of carbon in return (van't Padje *et al.* 2021b, a), suggesting hoarding may also occur among plants.

Resource preemption can also occur via spite. Aggressive water use can manifest as exuberant transpiration. General theory for spite has been developed (Hamilton 1970), but these ideas are not yet included in models of plant water use. However, if a species uses soil water quickly, it could make that water unavailable to other species. Spite would only be successful in cases where one species is able to cause greater harm to all other species than it causes to itself through such aggressive soil water use. Such an idea is consistent with the minimum resource level concepts in R* resource competition theory (Tilman 1982). A consequential hypothesis is that high nighttime transpiration (Wang *et al.* 2021) or hydraulic descent (Hultine *et al.* 2003) may be examples of spiteful water use by drought-tolerant species to harm drought-intolerant species.

C3. Bluffing and learning

In a community context, if all species benefit from using a common resource (water), the optimal strategies (at individual or population level) may differ strongly from those in a single-species context. From this perspective, water use strategies could be viewed as a game in which the opponent's strategy is only partially observable. The game can have a Nash equilibrium, i.e. a stable outcome where each species is better off retaining its strategy than switching to a different strategy. This has been demonstrated in one stomatal regulation model (Wolf *et al.* 2016) where competition causes changes in water use efficiency under drought, and has been considered in other allocation models (Farrior *et al.* 2013; Lu *et al.* 2020). It has also been shown empirically in several species, *Pinus taeda* (Zenes *et al.* 2020) and in *Lactuca sativa* (lettuce) and *Solanum lycopersicum* (tomato) (Vysotskaya *et al.* 2011). The broader game theory of competitive or cooperative depletion of water resources has also been considered in human contexts (Madani 2010) but not widely applied to plants.

In a Nash equilibrium, the optimal strategies are often mixed, in that they involve randomizing choice of action over some probability distribution. This occurs because the actions taken by other species may influence the value of the actions taken by a focal species; additionally, each individual may have limited information available about the resources available to other individuals and may not know their actual strategy. Rather, each individual may only be able to respond to observed sequences of actions taken by another individual, e.g., via rhizosphere processes including sensing soil moisture drawdown near roots, or chemosensing of other species' root hormones and exudates (Jackson 1997; Hinsinger *et al.* 2005) or of other volatile cues (Jin *et al.* 2021).

In simple terms this means that, in community contexts, species may deploy unusual behaviors. They may bluff with their water use, by using more or less water than they would otherwise, to send a false signal to others or force others to take certain actions. They may also invest in learning, by exploring the environment through yet-unknown means to better predict the current or future levels of water availability. For example, species that pre-form buds years in advance like *Veratrum tenuipetalum* (Iler & Inouye 2013) are effectively gambling on the future state of the environment being favorable for photosynthesis.

C4. Positive species interactions

A fundamental premise of much water use theory and the ideas outlined above is that the most common interactions among plant species are negative and often competitive. However, the assumption of competition as the fundamental process may reflect our biases more than reality (Simha *et al.* 2022). Instead, beginning from a viewpoint of abundance (Kimmerer 2020) and mutualism (Bronstein 2015), sharing water may actually be mutually beneficial in many cases, especially when indirect interactions between plants occur that are mediated by other species (**Figure 2F**). As conceptual examples, a first species could provide water to a second species that in turn transpires it and provides beneficial cool and shaded conditions to the first species; or the second species could attract insects that would also pollinate or defend the first species.

Species may use water in ways that appear non-optimal from an individual performance perspective or from a competitive perspective, because they produce cooperative (positive)

interactions. Species that are most able to access water could redistribute it to other species that need it (e.g., via hydraulic lift, or evaporative cooling affecting a whole community), and in turn receive a non-water benefit they cannot provide for themself. Temperate trees using water to support their own growth provide shade to some other species that in turn grow faster than they would alone (Kothari *et al.* 2021). Or, savanna trees bring up water from deeper soil layers and redistribute it in the more superficial root zone (i.e., hydraulic lift), improving grass quality and attracting herbivores (Treydte *et al.* 2007, 2011). Grass decomposition and addition of urine and feces may in turn improve the nutrient availability for the trees.

C5. Negative species interactions

Mycorrhizal fungi have been implicated in changes in various aspects of plant water use, including increased aquaporin function, and increased root hydraulic conductivity, generally resulting in improved performance of mycorrhizal plants under drought (Lehto & Zwiazek 2011). They thus generally are considered to yield positive interactions with plants. However, in the process of maximizing their own fitness, these fungi could lead a plant into adopting a non-optimal water use strategy in a parasitic interaction. Mycorrhizal fungi are known to exploit multiple species of plants to extract the best price for their mineral nutrients when demand is highest (Whiteside *et al.* 2019). Direct transfer of water taken up by arbuscular mycorrhizal fungi to host plants has also recently been demonstrated (Kakouridis *et al.* 2022). Increases in plant transpiration and photosynthesis also have been observed when fungal partners are present for *Linum usitatissimum* (flax) (Drüge & Schonbeck 1993) and *Citrus jambhiri* (rough lemon) (Levy *et al.* 1983), suggesting that some aspects of plant water use may be mediated by exchanges with fungal partners. Whether and when these interactions are negative instead of positive remains under-explored.

Endophytes, organisms living inside leaves, may also have negative interactions with host plants through causing non-optimal water use for their hosts. Minimum leaf conductance is almost twice as high in *Theobroma cacao* (cacao) leaves with natural abundances of endophytes than in leaves without endophytes (Arnold & Engelbrecht 2007). All plants in natural ecosystems contain leaf endophytes (Rodriguez *et al.* 2009), but densities and species assemblages vary widely, even across leaves within individual trees (Arnold & Herre 2003). Water loss through

leaf cuticles or from leaky stomata may thus be affected by the abundance and perhaps identity and functional properties of leaf endophytes, independent of the short-term carbon economy of the leaves.

Epiphylls, plants growing on top of the leaf surface, can also have negative interactions with their host plants through water use. As leaves of evergreen plants age, they may accumulate epiphylls to the extent that exposed leaves only receive 15-45% of the sunlight they would receive in the absence of epiphylls (Coley *et al.* 1993). As a result, the photosynthetic capacity of these shaded leaves is reduced (Anthony *et al.* 2002), and presumably also their water use. The retention of such leaves that are unlikely to fix significantly more carbon than they use in respiration appears non-optimal from both a carbon and water use perspective, unless there are other not yet understood benefits of epiphyll presence, e.g., uptake of foliar water (Rosado & Almeida 2020) or nitrogen (Bentley 1987), or benefits of maintaining old leaves, e.g., taking up space and shading competitors.

Implications for leaf and earth system models under climate change

These hypotheses, if supported widely by empirical data, would require substantial revisions to extant water use theory and the leaf and earth system models they are used within. Many process-based leaf models use the Ball *et al.* (1987) or Medlyn *et al.* (2011) representation of stomatal conductance, in which stomatal conductance is calculated based on a suite of environmental variables, and notably, the photosynthetic rate and a parameter that identifies the relationship between stomatal conductance and photosynthesis (often referred to as g_1 in these models, representing the inverse of water use efficiency). The g_1 value can change within and across species, and by plant functional category if used in a larger-scale model. The value may also respond to processes described by any of the above hypotheses, though such effects are not yet implemented.

Errors in the plant water use theory currently used in many Earth System Models (ESMs) can have important consequences for understanding changes in water resources, heat and precipitation extremes, and ecosystem functioning under changing climate . This is because the soil-plant-atmosphere continuum representations in ESMs often uses similar or the same

marginal gain theory used in leaf-scale models to calculate ecosystem stomatal conductance (Clark *et al.* 2011; Massoud *et al.* 2019; Koven *et al.* 2020). There are known inaccuracies in ecosystem water fluxes simulated by ESMs (Li *et al.* 2021), which ultimately can influence other simulated quantities like soil moisture and precipitation. Even when average patterns and trends are simulated reasonably well, inaccuracies can manifest in other functions and time scales, such as predicting future heatwave intensities and durations (Kala *et al.* 2016).

A key question is whether adding complexity to ESMs would be useful when upscaled predictions of water flux are needed (Medlyn *et al.* 2017). Because ecosystem scale predictions are already usually successful and are made without including detailed vegetation dynamics, it is unlikely that the population and community ecology hypotheses we outlined would require incorporation into theory used in ESMs. However, the extreme environment hypotheses should likely be integrated into water use theory given existing evidence that current theory fails in some of these cases, and because of the forecasted higher prevalence of extreme environments in the near future. We suggest that incorporation of cooling (E1) into theory will be most productive. However, as ESMs continue to be used to answer more complex questions related to feedback between vegetation and climate, some of the population and community context hypotheses may also become relevant. We speculate that tradeoffs among fitness components (P4) and resource hoarding (C2) are the two highest priorities.

Conclusion

We have highlighted numerous hypotheses that indicate the multiple values of water to plants, and that have varying degrees of support based on empirical observations. Not all these hypotheses may be common, nor equally important. However, in rejecting or supporting the hypotheses underlying them, we may come closer to a more complete theory of plant water use. More significantly, many of these hypotheses may be relevant for some species and not others, or in some environments or communities and not others, suggesting that it will be difficult to generate a single water use theory applicable in all situations.

We are not seeking to challenge the relevance of extant theory. It is correct, or close enough to correct, for most scenarios that have been of interest to date. Rather, we aim to highlight the

many additional values of water relevant to more types of plants and environments than this theory has considered, and in doing so, to challenge the implicit use of simple economic ideas within ecophysiology. The alternative ideas we proposed may have potentially large consequences for individual plants, for community dynamics, and for ecosystem fluxes. By expanding beyond ecophysiology to incorporate population and community ecology – with all their uncertainties and complexities, we may achieve a more complete understanding of plant water use.

Competing interests

The authors have no conflicts of interest to declare.

Author contributions

BWB conceived the manuscript and wrote the first draft. BCP, MS, and BWB created the figures. LA, KH, DL, SM, BCP, MS, and KW contributed sections of the text.

ORCID

Benjamin Wong Blonder (ORCID: 0000-0002-5061-2385)

Luiza Aparecido (ORCID: 0000-0001-8642-6632)

Kevin Hultine (ORCID: 0000-0001-9747-6037)

Danica Lombardozzi (ORCID: 0000-0003-3557-7929)

Sean Michaletz (ORCID: 0000-0003-2158-6525)

Bradley C. Posch (ORCID: 0000-0003-0924-6608)

Martijn Slot (ORCID: 0000-0002-5558-1792)

Klaus Winter (ORCID: 0000-0002-0448-2807)

Benjamin Wong Blonder 1 *, Luiza Aparecido 2,3, Kevin Hultine 3, Danica Lombardozzi 4, Sean Michaletz 5, Bradley C. Posch 3,6, Martijn Slot 7, Klaus Winter 7

1: Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, CA, 94720 United States

2: School of Earth and Space Exploration, Arizona State University, Tempe, AZ, 85287 United States

3: Department of Research, Conservation and Collections, Desert Botanical Garden, Phoenix, AZ, 85008 United States

4: National Center for Atmospheric Research: Boulder, CO, 80305 United States

5: Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, V6T 1Z4 Canada

6: Department of Biological Sciences, Texas Tech University, Lubbock, TX, 79409 United States

7: Smithsonian Tropical Research Institute, Balboa, Ancón, 0843-03092 Republic of Panama

(*: Corresponding author, benjamin.blonder@berkeley.edu)

References

Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106, 11641.

Anthony, P.A., Holtum, J.A.M. & Jackes, B.R. (2002). Shade acclimation of rainforest leaves to colonization by lichens. *Functional Ecology*, 16, 808–816.

Aparecido, L.M., Woo, S., Suazo, C., Hultine, K.R. & Blonder, B. (2020). High water use in desert plants exposed to extreme heat. *Ecology Letters*, 23, 1189–1200.

Arnold, A.E. & Engelbrecht, B.M. (2007). Fungal endophytes nearly double minimum leaf conductance in seedlings of a neotropical tree species. *Journal of Tropical Ecology*, 23, 369–372.

Arnold, A.E. & Herre, E.A. (2003). Canopy cover and leaf age affect colonization by tropical fungal endophytes: Ecological pattern and process in Theobroma cacao (Malvaceae). *Mycologia*, 95, 388–398.

Aronson, J., Kigel, J., Shmida, A. & Klein, J. (1992). Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia*, 89, 17–26.

Asseng, S. & Van Herwaarden, A.F. (2003). Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. *Plant and Soil*, 256, 217–229.

Bachmann, D., Gockele, A., Ravenek, J.M., Roscher, C., Strecker, T., Weigelt, A., *et al.* (2015). No evidence of complementary water use along a plant species richness gradient in temperate experimental grasslands. *PloS one*, 10, e0116367.

Ball, J.T., Woodrow, I.E. & Berry, J.A. (1987). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: *Progress in Photosynthesis Research*. Springer, pp. 221–224.

Bentley, B.L. (1987). Nitrogen fixation by epiphylls in a tropical rainforest. *Annals of the Missouri Botanical Garden*, 74, 234–241.

Blasini, D.E., Koepke, D.F., Bush, S.E., Allan, G.J., Gehring, C.A., Whitham, T.G., *et al.* (2022). Tradeoffs between leaf cooling and hydraulic safety in a dominant arid land riparian tree species. *Plant, Cell & Environment*, 45, 1664–1681.

Blonder, B. & Michaletz, S.T. (2018). A model for leaf temperature decoupling from air temperature. *Agricultural and Forest Meteorology*, 262, 354–360.

Boyle, E.A., Li, Y.I. & Pritchard, J.K. (2017). An expanded view of complex traits: from polygenic to omnigenic. *Cell*, 169, 1177–1186.

Brix, H., Sorrell, B.K. & Orr, P.T. (1992). Internal pressurization and convective gas flow in some emergent freshwater macrophytes. *Limnology and Oceanography*, 37, 1420–1433.

Bronson, D.R., English, N.B., Dettman, D.L. & Williams, D.G. (2011). Seasonal photosynthetic gas exchange and water-use efficiency in a constitutive CAM plant, the giant saguaro cactus (Carnegiea gigantea). *Oecologia*, 167, 861–871.

Bronstein, J.L. (2015). *Mutualism*. Oxford University Press, USA.

Bueno, A., Alfarhan, A., Arand, K., Burghardt, M., Deininger, A.-C., Hedrich, R., *et al.* (2019). Temperature effects on the cuticular transpiration barrier of two desert plants with water-spender and water-saver life strategies. *Journal of Experimental Botany*.

von Caemmerer, S. & Evans, J.R. (1991). Determination of the average partial pressure of CO2 in chloroplasts from leaves of several C3 plants. *Functional Plant Biology*, 18, 287–305.

Caldwell, M.M., Dawson, T.E. & Richards, J.H. (1998). Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, 113, 151–161.

Castorena, M., Olson, M.E., Enquist, B.J. & Fajardo, A. (2022). Toward a general theory of plant carbon economics. *Trends in Ecology & Evolution*.

Chabot, B.F. & Hicks, D.J. (1982). The ecology of leaf life spans. *Annual Review of Ecology and Systematics*, 13, 229–259.

Chaves, M.M., Costa, J.M., Zarrouk, O., Pinheiro, C., Lopes, C.M. & Pereira, J.S. (2016). Controlling stomatal aperture in semi-arid regions—the dilemma of saving water or being cool? *Plant Science*, 251, 54–64.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31, 343–366.

Chesson, P., Gebauer, R.L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S., *et al.* (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.

Chiariello, N.R., Field, C.B. & Mooney, H.A. (1987). Midday wilting in a tropical pioneer tree. *Functional Ecology*, 1, 3–11.

Christoffersen, B.O., Gloor, M., Fauset, S., Fyllas, N.M., Galbraith, D.R., Baker, T.R., *et al.* (2016). Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v. 1-Hydro). *Geoscientific Model Development*, 9, 4227–4255.

Clark, D., Mercado, L., Sitch, S., Jones, C., Gedney, N., Best, M., *et al.* (2011). The Joint UK Land Environment Simulator (JULES), model description–Part 2: carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, 4, 701–722.

Coley, P.D., Kursar, T.A. & Machado, J.-L. (1993). Colonization of tropical rain forest leaves by epiphylls: effects of site and host plant leaf lifetime. *Ecology*, 74, 619–623.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., *et al.* (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.

Coupel-Ledru, A., Lebon, E., Christophe, A., Gallo, A., Gago, P., Pantin, F., *et al.* (2016). Reduced nighttime transpiration is a relevant breeding target for high water-use efficiency in grapevine. *Proceedings of the National Academy of Sciences*, 113, 8963–8968.

Cowan, I.R. & Farquhar, G.D. (1977). Stomatal function in relation to leaf metabolism and environment. In: *Symposia of the Society for Experimental Biology*. p. 471.

Dawson, T.E. (1993). Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, 95, 565–574.

Dawson, T.E., Burgess, S.S., Tu, K.P., Oliveira, R.S., Santiago, L.S., Fisher, J.B., *et al.* (2007). Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiology*, 27, 561–575.

Detto, M., Wright, S.J., Calderón, O. & Muller-Landau, H.C. (2018). Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation. *Nature Communications*, 9, 1–8.

Drüge, U. & Schonbeck, F. (1993). Effect of vesicular-arbuscular mycorrhizal infection on transpiration, photosynthesis and growth of flax (Linum usitatissimum L.) in relation to cytokinin levels. *Journal of Plant Physiology*, 141, 40–48.

Eamus, D., Taylor, D.T., Macinnis-Ng, C., Shanahan, S. & De Silva, L. (2008). Comparing model predictions and experimental data for the response of stomatal conductance and guard cell turgor to manipulations of cuticular conductance, leaf-to-air vapour pressure

difference and temperature: feedback mechanisms are able to account for all observations. *Plant, Cell & Environment*, 31, 269–277.

Falster, D.S., Reich, P.B., Ellsworth, D.S., Wright, I.J., Westoby, M., Oleksyn, J., *et al.* (2012). Lifetime return on investment increases with leaf lifespan among 10 Australian woodland species. *New Phytologist*, 193, 409–419.

Farrior, C.E., Dybzinski, R., Levin, S.A. & Pacala, S.W. (2013). Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *American Naturalist*, 181, 314–330.

Fatichi, S., Leuzinger, S. & Körner, C. (2014). Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist*, 201, 1086–1095.

Feng, X., Lu, Y., Jiang, M., Katul, G., Manzoni, S., Mrad, A., *et al.* (2022). Instantaneous stomatal optimization results in suboptimal carbon gain due to legacy effects. *Plant, Cell & Environment*, 45, 3189–3204.

Fisher, R.A., Koven, C.D., Anderegg, W.R., Christoffersen, B.O., Dietze, M.C., Farrior, C.E., *et al.* (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, 24, 35–54.

Franks, P.J., Bonan, G.B., Berry, J.A., Lombardozzi, D.L., Holbrook, N.M., Herold, N., *et al.* (2018). Comparing optimal and empirical stomatal conductance models for application in Earth system models. *Global Change Biology*, 24, 5708–5723.

Franks, P.J., Cowan, I.R. & Farquhar, G.D. (1997). The apparent feedforward response of stomata to air vapour pressure deficit: information revealed by different experimental procedures with two rainforest trees. *Plant, Cell & Environment*, 20, 142–145.

Fullbrook, E. (2004). *A guide to what's wrong with economics*. Anthem Press.

Gates, D.M. (1968). Transpiration and leaf temperature. *Annual Review of Plant Physiology*, 19, 211–238.

Gould, S.J. & Lewontin, R.C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 205, 581–598.

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T., *et al.* (2020). Plant responses to rising vapor pressure deficit. *New Phytologist*, 226, 1550–1566.

Guderle, M., Bachmann, D., Milcu, A., Gockele, A., Bechmann, M., Fischer, C., *et al.* (2018). Dynamic niche partitioning in root water uptake facilitates efficient water use in more diverse grassland plant communities. *Functional Ecology*, 32, 214–227.

Guo, J.S., Hultine, K.R., Koch, G.W., Kropp, H. & Ogle, K. (2020). Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. *New Phytologist*, 225, 713–726.

Haberstroh, S. & Werner, C. (2022). The role of species interactions for forest resilience to drought. *Plant Biology*, 24, 1098–1107.

de Haldat du Lys, A., Millan, M., Barczi, J.-F., Caraglio, Y., Midgley, G.F. & Charles-Dominique, T. (2022). If self-shading is so bad, why is there so much? Short shoots reconcile costs and benefits. *New Phytologist*.

Hamilton, W.D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature*, 228, 1218–1220.

Harley, P.C., Thomas, R.B., Reynolds, J.F. & Strain, B.R. (1992). Modelling photosynthesis of cotton grown in elevated CO_2. *Plant, Cell & Environment*, 15, 271–282.

Harrison Day, B.L., Carins-Murphy, M.R. & Brodribb, T.J. (2022). Reproductive water supply is prioritized during drought in tomato. *Plant, Cell & Environment*, 45, 69–79.

Harrison, S.P., Cramer, W., Franklin, O., Prentice, I.C., Wang, H., Brännström, Å., *et al.* (2021). Eco-evolutionary optimality as a means to improve vegetation and land-surface models. *New Phytologist*, 231, 2125–2141.

Hayes, S., Schachtschabel, J., Mishkind, M., Munnik, T. & Arisz, S.A. (2021). Hot topic: Thermosensing in plants. *Plant, Cell & Environment*, 44, 2018–2033.

Hinsinger, P., Gobran, G.R., Gregory, P.J. & Wenzel, W.W. (2005). Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. *New Phytologist*, 168, 293–303.

Hollis, M. & Nell, E. (1975). *Rational Economic Man: A Philosophical Critique of Neo-Classical Economics*. Cambridge University Press, Cambridge, UK.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997). The interplay of facilitation and competition in plant communities. *Ecology*, 78, 1966–1975.

Hultine, K.R., Cable, W.L., Burgess, S.S.O. & Williams, D.G. (2003). Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology*, 23, 353–360.

Hunt, J.R., Hayman, P.T., Richards, R.A. & Passioura, J.B. (2018). Opportunities to reduce heat damage in rain-fed wheat crops based on plant breeding and agronomic management. *Field Crops Research*, 224, 126–138.

Iler, A.M. & Inouye, D.W. (2013). Effects of climate change on mast-flowering cues in a clonal montane herb, Veratrum tenuipetalum (Melanthiaceae). *American Journal of Botany*, 100, 519–525.

Ishii, H.T., Tanabe, S. & Hiura, T. (2004). Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science*, 50, 342–355.

Jackson, M. (1997). Hormones from roots as signals for the shoots of stressed plants. *Trends in Plant Science*, 2, 22–28.

Jackson, T. (2016). *Prosperity without growth: Foundations for the economy of tomorrow*. Routledge.

Jevons, W.S. (1879). *The theory of political economy*. Macmillan and Company.

Jin, J., Zhao, M., Gao, T., Jing, T., Zhang, N., Wang, J., *et al.* (2021). Amplification of early drought responses caused by volatile cues emitted from neighboring tea plants. *Horticulture Research*, 8, 243.

Kakouridis, A., Hagen, J.A., Kan, M.P., Mambelli, S., Feldman, L.J., Herman, D.J., *et al.* (2022). Routes to roots: direct evidence of water transport by arbuscular mycorrhizal fungi to host plants. *New Phytologist*, 236, 210–221.

Kala, J., De Kauwe, M.G., Pitman, A.J., Medlyn, B.E., Wang, Y.-P., Lorenz, R., *et al.* (2016). Impact of the representation of stomatal conductance on model projections of heatwave intensity. *Scientific Reports*, 6, 23418.

Kannenberg, S.A., Guo, J.S., Novick, K.A., Anderegg, W.R., Feng, X., Kennedy, D., *et al.* (2022). Opportunities, challenges and pitfalls in characterizing plant water-use strategies. *Functional Ecology*, 36, 24–37.

Karban, R. (2015). Plant sensing and communication. In: *Plant Sensing and Communication*. University of Chicago Press.

Kikuzawa, K. & Lechowicz, M.J. (2006). Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *American Naturalist*, 168, 373–383.

Kimmerer, R.W. (2020). The serviceberry: An economy of abundance. *Emergence Magazine*.

Klein, T., Zeppel, M.J.B., Anderegg, W.R.L., Bloemen, J., De Kauwe, M.G., Hudson, P., *et al.* (2018). Xylem embolism refilling and resilience against drought-induced mortality in woody plants: processes and trade-offs. *Ecological Research*, 33, 839–855.

Kolb, P.F. & Robberecht, R. (1996). High temperature and drought stress effects on survival of Pinus ponderosa seedlings. *Tree Physiology*, 16, 665–672.

Kostaki, K.-I., Coupel-Ledru, A., Bonnell, V.C., Gustavsson, M., Sun, P., McLaughlin, F.J., *et al.* (2020). Guard cells integrate light and temperature signals to control stomatal aperture. *Plant Physiology*, 182, 1404–1419.

Kothari, S., Montgomery, R.A. & Cavender-Bares, J. (2021). Physiological responses to light explain competition and facilitation in a tree diversity experiment. *Journal of Ecology*, 109, 2000–2018.

Koven, C.D., Knox, R.G., Fisher, R.A., Chambers, J.Q., Christoffersen, B.O., Davies, S.J., *et al.* (2020). Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama. *Biogeosciences*, 17, 3017–3044.

Lehto, T. & Zwiazek, J.J. (2011). Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*, 21, 71–90.

Leuning, R. (1995). A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant, Cell & Environment*, 18, 339–355.

Levy, Y., Syvertsen, J.P. & Nemec, S. (1983). Effect of drought stress and vesicular–arbuscular mycorrhiza on citrus transpiration and hydraulic conductivity of roots. *New Phytologist*, 93, 61–66.

Li, J., Miao, C., Wei, W., Zhang, G., Hua, L., Chen, Y., *et al.* (2021). Evaluation of CMIP6 global climate models for simulating land surface energy and water fluxes during 1979–2014. *Journal of Advances in Modeling Earth Systems*, 13, e2021MS002515.

Li, W.D., Duan, W., Fan, P.G., Yan, S.T. & Li, S.H. (2007). Photosynthesis in response to sink—source activity and in relation to end products and activities of metabolic enzymes in peach trees. *Tree physiology*, 27, 1307–1318.

van Loon, L.C. (2016). The intelligent behavior of plants. *Trends in Plant Science*, 21, 286–294.

Lu, Y., Duursma, R.A., Farrior, C.E., Medlyn, B.E. & Feng, X. (2020). Optimal stomatal drought response shaped by competition for water and hydraulic risk can explain plant trait covariation. *New Phytologist*, 225, 1206–1217.

Machado, R., Loram-Lourenço, L., Farnese, F.S., Alves, R.D.F.B., de Sousa, L.F., Silva, F.G., *et al.* (2021). Where do leaf water leaks come from? Trade-offs underlying the variability in minimum conductance across tropical savanna species with contrasting growth strategies. *New Phytologist*, 229, 1415–1430.

Madani, K. (2010). Game theory and water resources. *Journal of Hydrology*, 381, 225–238.

Marchin, R.M., Backes, D., Ossola, A., Leishman, M.R., Tjoelker, M.G. & Ellsworth, D.S. (2022a). Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. *Global Change Biology*, 28, 1133–1146.

Marchin, R.M., Esperon-Rodriguez, M., Tjoelker, M.G. & Ellsworth, D.S. (2022b). Crown dieback and mortality of urban trees linked to heatwaves during extreme drought. *Science of The Total Environment*, 157915.

Massoud, E.C., Xu, C., Fisher, R.A., Knox, R.G., Walker, A.P., Serbin, S.P., *et al.* (2019). Identification of key parameters controlling demographically structured vegetation dynamics in a land surface model: CLM4. 5 (FATES). *Geoscientific Model Development*, 12, 4133–4164.

Medlyn, B.E., De Kauwe, M.G., Lin, Y.-S., Knauer, J., Duursma, R.A., Williams, C.A., *et al.* (2017). How do leaf and ecosystem measures of water-use efficiency compare? *New Phytologist*, 216, 758–770.

Medlyn, B.E., Duursma, R.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Barton, C.V., *et al.* (2011). Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology*, 17, 2134–2144.

Michaletz, S.T., Johnson, E.A. & Tyree, M.T. (2012). Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist*, 194, 254–263.

Miller, B.D., Carter, K.R., Reed, S.C., Wood, T.E. & Cavaleri, M.A. (2021). Only sun-lit leaves of the uppermost canopy exceed both air temperature and photosynthetic thermal optima in a wet tropical forest. *Agricultural and Forest Meteorology*, 301, 108347.

Monteith, J.L. & Unsworth, M.H. (2013). *Principles of Environmental Physics (Fourth Edition)*. Academic Press, Boston.

Muhammad Aslam, M., Waseem, M., Jakada, B.H., Okal, E.J., Lei, Z., Saqib, H.S.A., *et al.* (2022). Mechanisms of abscisic acid-mediated drought stress responses in plants. *International Journal of Molecular Sciences*, 23, 1084.

Oliveira, R.S., Eller, C.B., Barros, F. de V., Hirota, M., Brum, M. & Bittencourt, P. (2021). Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist*, 230, 904–923.

van't Padje, A., Oyarte Galvez, L., Klein, M., Hink, M.A., Postma, M., Shimizu, T., *et al.* (2021a). Temporal tracking of quantum-dot apatite across in vitro mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. *The ISME Journal*, 15, 435–449.

van't Padje, A., Werner, G.D.A. & Kiers, E.T. (2021b). Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt 'crashes' and 'booms' of resource availability. *New Phytologist*, 229, 2933–2944.

Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., *et al.* (2004). Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist*, 161, 837–846.

Quereix, A., Dewar, R.C., Gaudillere, J.-P., Dayau, S. & Valancogne, C. (2001). Sink feedback regulation of photosynthesis in vines: measurements and a model. *Journal of Experimental Botany*, 52, 2313–2322.

Querejeta, J.I., Ren, W. & Prieto, I. (2021). Vertical decoupling of soil nutrients and water under climate warming reduces plant cumulative nutrient uptake, water-use efficiency and productivity. *New Phytologist*, 230, 1378–1393.

Reich, P.B., Stefanski, A., Rich, R.L., Sendall, K.M., Wei, X., Zhao, C., *et al.* (2021). Assessing the relevant time frame for temperature acclimation of leaf dark respiration: A test with 10 boreal and temperate species. *Global Change Biology*, 27, 2945–2958.

Reich, P.B., Uhl, C., Walters, M.B., Prugh, L. & Ellsworth, D.S. (2004). Leaf demography and phenology in Amazonian rain forest: a census of 40 000 leaves of 23 tree species. *Ecological Monographs*, 74, 3–23.

Reid, W.V., Mooney, H.A., Cropper, A., Capistrano, D., Carpenter, S.R., Chopra, K., *et al.* (2005). *Ecosystems and human well-being-Synthesis: A report of the Millennium Ecosystem Assessment.* Island Press.

Richards, J.H. & Caldwell, M.M. (1987). Hydraulic lift: substantial nocturnal water transport between soil layers by Artemisia tridentata roots. *Oecologia*, 73, 486–489.

Rodriguez, R.J., White Jr, J.F., Arnold, A.E. & Redman, a R. and. (2009). Fungal endophytes: diversity and functional roles. *New Phytologist*, 182, 314–330.

Rosado, B.H.P. & Almeida, L.C. (2020). The importance of phyllosphere on foliar water uptake. *Trends in Plant Science*, 25, 1058–1060.

Schulze, E.D. (1982). Plant life forms and their carbon, water and nutrient relations. In: *Physiological plant ecology II*. Springer, pp. 615–676.

Schulze, E.-D., Lange, O.L., Kappen, L., Buschbom, U. & Evenari, M. (1973). Stomatal responses to changes in temperature at increasing water stress. *Planta*, 110, 29–42.

Sen, A.K. (1977). Rational fools: A critique of the behavioral foundations of economic theory. *Philosophy & Public Affairs*, 317–344.

Shivhare, D. & Mueller-Cajar, O. (2017). In vitro characterization of thermostable CAM Rubisco activase reveals a Rubisco interacting surface loop. *Plant Physiology*, 174, 1505–1516.

Silvertown, J. & Gordon, D.M. (1989). A framework for plant behavior. *Annual Review of Ecology and Systematics*, 349–366.

Simha, A., Hoz, C.P.-D. la & Carley, L. (2022). Moving beyond the "diversity paradox": the limitations of competition-based frameworks in understanding species diversity. *American Naturalist*.

Sinha, R., Zandalinas, S.I., Fichman, Y., Sen, S., Zeng, S., Gómez-Cadenas, A., *et al.* (2022). Differential regulation of flower transpiration during abiotic stress in annual plants. *New Phytologist*, 235, 611–629.

Slot, M., Garcia, M.N. & Winter, K. (2016). Temperature response of CO_2 exchange in three tropical tree species. *Functional Plant Biology*, 43, 468–478.

Slot, M., Nardwattanawong, T., Hernández, G.G., Bueno, A., Riederer, M. & Winter, K. (2021). Large differences in leaf cuticle conductance and its temperature response among 24 tropical tree species from across a rainfall gradient. *New Phytologist*, 232, 1618–1631.

Smith, A. (1776). *The Wealth of Nations*. W. Strahan and T. Cadell, London.

Smith, S.D., Didden-Zopfy, B. & Nobel, P.S. (1984). High-temperature responses of North American cacti. *Ecology*, 65, 643–651.

Sperry, J.S., Wang, Y., Wolfe, B.T., Mackay, D.S., Anderegg, W.R., McDowell, N.G., *et al.* (2016). Pragmatic hydraulic theory predicts stomatal responses to climatic water deficits. *New Phytologist*, 212, 577–589.

Swanson, R.H. (1994). Significant historical developments in thermal methods for measuring sap flow in trees. *Agricultural and Forest Meteorology*, 72, 113–132.

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M.A. & Steppe, K. (2015). Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699–1712.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton.

Treydte, A.C., van der Beek, J.G., Perdok, A.A. & van Wieren, S.E. (2011). Grazing ungulates select for grasses growing beneath trees in African savannas. *Mammalian Biology*, 76, 345–350.

Treydte, A.C., Heitkönig, I.M., Prins, H.H. & Ludwig, F. (2007). Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics*, 8, 197–205.

Urban, J., Ingwers, M.W., McGuire, M.A. & Teskey, R.O. (2017). Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in Pinus taeda and Populus deltoides x nigra. *Journal of Experimental Botany*, 68, 1757–1767.

Veblen, T. (1898). Why is economics not an evolutionary science? *The quarterly journal of economics*, 12, 373–397.

Venable, D.L. & Pake, C.E. (1999). Population ecology of Sonoran Desert annual plants. In: *The ecology of Sonoran Desert plants and plant communities*. University of Arizona Press, Tucson, pp. 115–142.

Venturas, M.D., Sperry, J.S. & Hacke, U.G. (2017). Plant xylem hydraulics: what we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, 59, 356–389.

Verheyen, K., Bulteel, H., Palmborg, C., Olivié, B., Nijs, I., Raes, D., *et al.* (2008). Can complementarity in water use help to explain diversity–productivity relationships in experimental grassland plots? *Oecologia*, 156, 351–361.

Vico, G., Dralle, D., Feng, X., Thompson, S. & Manzoni, S. (2017). How competitive is drought deciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach. *Environmental Research Letters*, 12, 065006.

Vogel, S. (2009). Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist*, 183, 13–26.

Vysotskaya, L., Wilkinson, S., Davies, W.J., Arkhivpova, T. & Kudoyarova, G. (2011). The effect of competition from neighbours on stomatal conductance in lettuce and tomato plants. *Plant, Cell & Environment*, 34, 729–737.

Wang, Y., Anderegg, W.R., Venturas, M.D., Trugman, A.T., Yu, K. & Frankenberg, C. (2021). Optimization theory explains nighttime stomatal responses. *New Phytologist*, 230, 1550–1561.

Wang, Y., Sperry, J.S., Anderegg, W.R., Venturas, M.D. & Trugman, A.T. (2020). A theoretical and empirical assessment of stomatal optimization modeling. *New Phytologist*, 227, 311–325.

Westoby, M., Warton, D., Reich, P.B. & Associate Editor: James, B.G. (2000). The time value of leaf area. *American Naturalist*, 155, 649–656.

Whiteside, M.D., Werner, G.D., Caldas, V.E., van't Padje, A., Dupin, S.E., Elbers, B., *et al.* (2019). Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. *Current Biology*, 29, 2043-2050. e8.

Williams, J.W. & Jackson, S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475–482.

Winter, K., Garcia, M. & Holtum, J.A. (2011). Drought-stress-induced up-regulation of CAM in seedlings of a tropical cactus, Opuntia elatior, operating predominantly in the C3 mode. *Journal of Experimental Botany*, 62, 4037–4042.

Wolf, A., Anderegg, W.R. & Pacala, S.W. (2016). Optimal stomatal behavior with competition for water and risk of hydraulic impairment. *Proceedings of the National Academy of Sciences*, 113, E7222–E7230.

Yang, J. & Zhang, J. (2006). Grain filling of cereals under soil drying. *New Phytologist*, 169, 223–236.

Yu, K., Goldsmith, G.R., Wang, Y. & Anderegg, W.R.L. (2019). Phylogenetic and biogeographic controls of plant nighttime stomatal conductance. *New Phytologist*, 222, 1778–1788.

Zenes, N., Kerr, K.L., Trugman, A.T. & Anderegg, W.R. (2020). Competition and drought alter optimal stomatal strategy in tree seedlings. *Frontiers in Plant Science*, 11, 478.

Zeppel, M.J.B., Lewis, J.D., Phillips, N.G. & Tissue, D.T. (2014). Consequences of nocturnal water loss: a synthesis of regulating factors and implications for capacitance, embolism and use in models. *Tree Physiology*, 34, 1047–1055.

Figures

Figure 1. Overview of hypotheses considered in this manuscript. Hypotheses are arranged by biological scale (vertical) and temporal scale (horizontal) at which they might operate. They are colored by category: E, extreme environments (orange); P, population ecology (green); C, community ecology (purple) and contrasted with extant theory: M, marginal gain (red).

Figure 2. Speculative examples of the multiple values of water to plants. Photos are selected to illustrate concepts, not necessarily because they directly confirm a hypothesis. **A)** In southeastern Arizona, a cottonwood tree (*Populus fremontii*) growing in hot conditions with abundant water may use water for evaporative cooling instead of photosynthesis (Hypothesis E1). **B)** In a moist tropical forest in Borneo, water used to maintain the top layer of a forest canopy may provide shading to photosynthetically active leaves in lower layers (Hypothesis E3). **C)** In the northern Sonoran Desert where winter rain is the only moisture source before spring/foresummer drought, water may be used as quickly as possible to support seed production before the drought deadline occurs (Hypothesis P2). **D)** In a tomato plant, fitness may be enhanced by allocating water to higher fruit production even if it reduces water available for photosynthesis and growth (Hypothesis P4). Image in public domain. **E)** In the southern Sonoran Desert, succulent or deep-rooted plants may hoard water (via vegetative storage or hydraulic descent) to prevent it from being used by competitors (Hypothesis C2). **F)** In the alpine zone of the Rocky Mountains, plants may use water to help neighbors in a facilitative or mutualistic relationship, e.g., by leaf transpiration that co-creates a more humid microclimate in dry sites, or via investment in flowers and flower transpiration that attracts shared pollinators (Hypothesis C4). Photo credits: A: Kevin Hultine; B,C,E,F: Benjamin Blonder; D: public domain.

Categories of plant water use hypotheses

E: Extreme environments
P: Population ecology
C: Community ecology
M: Marginal gain

Temporal scale
Biological scale

Instantaneous — Seasonal — Lifetime

Leaf
Individual
Population
Community

E1. Avoiding thermal damage and mortality
E2. Minimizing respiration costs
E3. Shading via parasol effects

M. Extant theory

P1. Time discounting
P2. Deadline effects
P3. Leaf lifespan effects
P4. Tradeoffs among fitness components
P5. Non-adaptive mechanisms

C1. Mechanisms that promote coexistence
C2. Hoarding and spite
C3. Bluffing and learning
C4. Positive species interactions
C5. Negative species interactions

A) Avoiding thermal damage and mortality (E1)

B) Shading via parasol effects (E3)

C) Deadline effects (P2)

D) Tradeoffs among fitness components (P4)

E) Hoarding and spite (C2)

F) Positive species interactions (C4)