Oecologia
https://doi.org/10.1007/s00442-023-05458-y

SPECIAL COLLECTION: CELEBRATING ON 200 VOLUMES OF OECOLOGIA

The carbon balance of plants: economics, optimization, and trait spectra in a historical perspective

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Received: 3 April 2023 / Accepted: 22 September 2023

Abstract

Over fifty years have passed since the publication of Harold Mooney's formative paper, "The Carbon Balance of Plants" on pages 315–346 of Volume 3 (1972) of *Annual Review of Ecology and Systematics*. Arguably, the conceptual framework presented in that paper, and the work by Mooney and his students leading up to the paper, provided the foundational principles from which core disciplines emerged in plant economic theory, functional trait theory and, more generally, plant physiological ecology. Here, we revisit the primary impacts of those early discoveries to understand how researchers constructed major concepts in our understanding of plant adaptations, and where those concepts are likely to take us in the near future. The discipline of functional trait ecology, which is rooted in the principles of evolutionary and economic optimization, has captured the imagination of the plant physiological ecology research community, though its emphasis has shifted toward predicting species distributions and ecological roles across resource gradients. In the face of 'big-data' research pursuits that are revealing trait expression patterns at the cellular level and mass and energy exchange patterns at the planetary scale, an opportunity exists to reconnect the principles of plant carbon balance and evolutionary optimization with trait origins at the genetic and cellular scales and trait impacts at the global scale.

Keywords Tradeoffs · Lifespan · Photosynthesis · Nitrogen · Spectrum

Introduction

The glasses of hindsight tend toward the rosy. Childhoods are remembered for their pleasant moments, early days in school for their novelties, and previous times in science for their frontier spirit and intellectual possibilities. Plant functional ecology is no exception to this historical red-shift, and looking back to the post-WWII period seems no different. In Germany and Austria, respectively, Heinrich Walter and Walter Tranquillini published detailed studies of plant distribution and function in relation to climate. Walter's collaborations with Forest Shreve and John Weaver before the war had helped ensure that European advances would be noticed in the United States, and Tranquillini's studies of conifers at their range boundaries set the stage for future mechanistic work. Just as importantly, insights were developing rapidly in a broad set of ecologically related fields, including ecological genetics (e.g., Clausen et al. 1940), population biology (e.g., Harper 1966), agronomy (e.g., Cohen 1966), and physiology (e.g., Slatyer 1967; Björkman and Holmgren 1963; Monsi and Saeki 1953; Hatch and Slack 1970).

By the end of the 1960s, optimality approaches using linear programming that had been championed by Herbert Simon (1959) had influenced a broad range of disciplines, especially in ecology through the work of Robert MacArthur and his students (MacArthur 1972). In plant functional ecology, however, despite the many detailed studies in both Europe and the USA, especially by Dwight Billings and his students (Billings and Mooney 1968), there was no coherent unifying theory that brought together the growing realization that, to paraphrase Dobzhansky, 'nothing in ecology

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Communicated by Melinda D. Smith.

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makes sense except in the light of evolution.' The discipline was progressing thanks to novel techniques to measure gas exchange and water relations in field settings and with the development of a focused comparative approach to assess adaptive patterns in distinct habitats; yet, with little means of anchoring observations to evolutionary theory. Into this void, with clear prose and compelling syntheses of data, came several key papers by Harold A. Mooney, his students, and colleagues (Mooney and Dunn 1970a; 1970b; Mooney and Kummerow 1971; Harrison and Mooney 1971; Mooney 1972; Morrow and Mooney 1974). The questions that were asked in these works concerned functional similarities between the floras of Chile and California within the context of convergent evolution and comparative physiology, and they laid the foundation for a long-lasting research legacy in what is now known as trait-based ecology. At an even more fundamental level, however, they established comparative studies of plant carbon balance as the unifying theme of an emergent new research discipline, plant physiological ecology.

Here, in recognition of 50 years since Mooney's classic paper (Mooney 1972; hereafter M72), we revisit the foundational breakthroughs of this early work and their roles in establishing current and future trends in comparative trait theory. In an era when many students identify the beginning of ecological trait theory as the formulation of the worldwide leaf economics spectrum (Wright et al. 2004; hereafter WLES), it is worth looking back to the roots of many of the ideas, especially in the realm of evolutionary and economic optimization, that led to that influential paper. At the same time, looking forward, we consider the opportunities that lie in front of us to understand the cellular and genetic mechanisms underlying the costs and benefits of trait expression, the means by which selection has reconciled those costs and benefits to produce observed patterns of trait correlation, and briefly, the potential applications of trait theory to broader applications in ecosystem ecology and global biogeochemistry.

In many ways, M72 represents the keystone of evolutionarily informed comparative ecophysiology. Given the extensive use of phylogeny in many of today's ecological studies, it is difficult to remember that not very long ago the fields of physiology, ecology, and evolution stood largely separate. In M72, Mooney brought together an array of papers across a range of disciplines to argue that an evolutionary approach to physiology, including metabolism, allocation, and chemistry, was both necessary and sufficient to understand the mechanistic bases of ecological patterns. Starting from simple, often implicit, assumptions about optimal acquisition and allocation and their evolutionary significance, he built a coherent model of plant ecological function that accounted for structures such as roots, stems, leaves, and seeds and for functions such as growth, defense, and reproduction. In laying out this framework, he brought together disparate elements and set the stage for scaling plant processes from organ to individual to community to landscape and to globe. This integrated approach was possible because of one crucial simplifying assumption that Mooney's Lab made about how these diverse parameters could be measured in a unified manner. Utilizing, though perhaps without realizing it, the ideas of Nicole Oresme from the fourteenth century (Fryde 1958; Woodhouse 2017), they proposed that carbon could be considered a common currency, a biological money.

The path to M72

By midway through the Twentieth Century, the role of individual organisms in plant ecological relations had been assigned the epithet 'autecology'. The essential textbook on this topic, *Plants and the Environment: A Textbook of Plant Autecology*, which was first published in 1947 by Rexford Daubenmire, advanced a perspective focused on the many different environmental factors that affect plant distributions, though with primary consideration of environmental pressures, and little attention to the evolutionary basis of plant responses. How selection shapes an individual's response to the environment had been well placed within topics concerning plant ecotypes, initially by Göte Turesson in the 1920s and 1930s in Sweden, and later by Clausen, Keck, and Heisey in the 1940s and 1950s in the United States. Even here, however, the focus was most clearly aimed at explaining the maintenance of genetic variation within species, with less emphasis on the adaptive scope of traits reflecting that variation. Thus, by the 1960s the pieces were in place for a novel synthesis with a focus on plant function and its adaptive underpinnings in the face of environmental variation. This was the setting for works to emerge by Milner et al. (1958), Mooney and Billings (1961), and Björkman and Holmgren (1963), in which the photosynthetic processes of ecotypic variants within species were examined in relation to their habitats of origin.

The emergence of evolutionary economics as a basis for the discipline

As the decade of the 1960s ended and rolled into the 1970s, Mooney and his students were putting together a series of observations on the photosynthetic and morphological attributes of Mediterranean-climate shrubs in California and Chile (Mooney and Dunn 1970a, b; Mooney and Kummerow 1971; Harrison and Mooney 1971; Morrow and Mooney 1974). Using principles of convergent evolution, they were able to explain repeated patterns in photosynthetic, phenological, and morphological traits across similar precipitation gradients in both locations. The most significant connection to plant function in these early papers was through the stomatal control over photosynthesis and transpiration and variation in these processes in relation to leaf longevity—specifically, a comparison between the evergreen and deciduous growth habits (Fig. 1). In these early studies, clear patterns were observed whereby deep-rooted, evergreen shrubs, and trees with lower photosynthesis and transpiration rates were found in habitats with access to deep soil water, whereas shallow-rooted, drought-deciduous shrubs with higher photosynthesis and transpiration rates were found in habitats with exposure to more frequent seasonal droughts. These patterns were repeated in both the Chilean and Californian Mediterranean-climate floras.

Central to the studies of Mooney and Dunn (1970a; hereafter MD70a, 1970b; hereafter MD70b) were those multiple selective forces (e.g., climate, nutrient availability, herbivory, and fire) that interacted in combination and constrained selection to favor a limited number of adaptive phenotypes and trait combinations. This theme was especially evident in MD70a, wherein they noted that the temperature regimes of Mediterranean climates are mild enough to permit year-round photosynthesis, leaving seasonal drought as the more likely climate factor determining the coexistence of species with divergent phenology patterns. They also recognized, however, that the benefits of a trait in the face of one environmental constraint come with a cost induced by a second concurrent constraint—leading to a tradeoff, or negative correlation between traits. This thinking was clearly reflected in one of the principal conclusions from MD70a:

> "The cost of maintaining evergreen leaves that can withstand periodic environmental stress is less than that of producing a new photosynthetic system annually which would only be present during completely favorable periods (as in deciduous species) … However, evergreeness introduces certain evolutionary problems. Evergreen leaves offer a year-round food source for herbivores and are thus subject to potentially high predation."

Mooney and Dunn 1970a (parenthetical phrase added for clarity).

In the two years following MD70a and MD70b, many of the ideas raised in these papers were organized as a general economic theory for the evolution of carbon balance strategies in plants in Mooney (1972). In M72, for example, we find him summarizing some of the past studies as follows:

> "Mooney and Dunn (1970b) have viewed the morphological variability of woody plants along aridity gradients in terms of optimization of carbon-gaining capacity."

Reading further we note that he links photosynthetic processes to leaf longevity and plant growth form in a dedicated section on 'morphological strategies', in which he states:

> "Thus, it is apparent that the annual productivity of a plant is set in part by the LAI (leaf area index) it can maintain, which in turn is set by the growth strategy of the plant (deciduous or evergreen herb, shrub, or tree). The leaf productivity must not only cover the maintenance and construction costs of the photosynthetic system, but also the entire shoot and root system."

Following the publication of M72, a series of papers were published by other labs, as well as the Mooney Lab, which together established the framework for an economic perspective on how selection shapes adaptive trait combinations in species, including the balancing of costs and benefits, the constraints imposed by trait tradeoffs, and the importance of marginal gain to fitness as the ultimate arbiter of trait expression. In these early-to-mid 1970s papers, we see an early expression of the 'fast-slow' (acquisitive-conservative) concept of plant trait associations (Grime

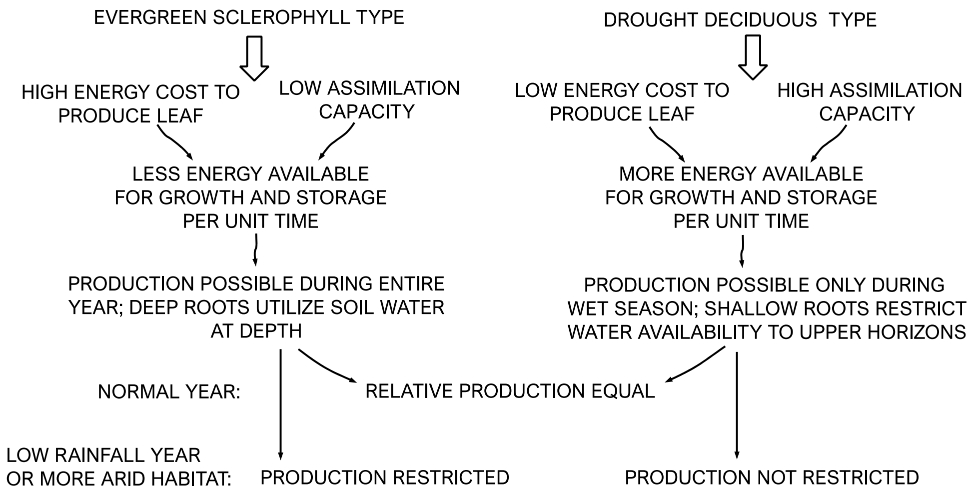

Fig. 1 Flow diagram redrawn from Mooney and Dunn (1970b) showing the conceptual linkages among traits in evergreen and deciduous Mediterranean shrubs and trees in response to moisture availability. The origins of traits partitioned into the 'fast' and 'slow' poles of the worldwide leaf economic spectrum (WLES) are evident in the associations of leaf lifespan, metabolic rates and growth habit

1974, 1977), which would be fully formalized in the later development of the WLES (Wright et al. 2004; Reich 2014). In its modern form, the 'fast-slow' spectrum of trait covariances refers to fast versus slow rates of resource acquisition and metabolic processing, with 'fast' traits generally associated with shorter leaf life spans, lower leaf mass-to-area ratios, and lesser resource allocation to herbivore defense, compared to 'slow' traits which are associated with longer leaf life spans, higher leaf mass-to-area ratios, and greater resource allocation to herbivore defense.

At about the same time as the publication of M72, three other fundamental concepts of gas exchange optimization emerged. First, Parkhurst and Loucks (1972; hereafter PL72) published a paper in which principles of evolutionary optimization were applied to the analysis of leaf size and shape. The authors focused on the quantitative relationships governing the leaf-diffusive exchanges of CO_2 and H_2O as a cost–benefit criterion. Optimization was defined as the point at which leaf size and shape (which influence the opposing diffusive resistances for CO_2 uptake and H_2O loss) result in a maximum water-use efficiency, and carbon assimilation/water loss (assimilation/transpiration, A/E). At optimization, the cost of losing H_2O is assumed to be at a minimum relative to the benefit of gaining CO_2. Second, using the economic framework of PL72, Givnish and Vermeij (1976; hereafter GV76) further explored the 'profit' (A, photosynthesis) and 'cost' (E, transpiration) ratio as a function of leaf size. In contrast to PL72, the optimization criterion in GV76 was set as the difference between A and E (i.e., profit), not their ratio (i.e., efficiency). Third, in Australia, Cowan and Farquhar (1977) proposed an approach whereby photosynthetic carbon gain and water loss were optimized at specific values. Their model proposed that stomatal conductance should be regulated to keep marginal water use efficiency ($\partial A/\partial E$) constant. An optimal photosynthetic water-use efficiency was assumed to be an important selective determinant of maximum plant fitness. These studies remained as the most prominent approaches until recent studies by Sperry et al (2016) and Wolf et al (2016) demonstrated that a more robust approach could be achieved based on maximizing carbon gain while considering the impacts of limited water and hydraulic features. These models provide a more integrated insight into plant carbon gain responses in a dynamic and water competitive environment.

At about the same time the Cowan and Farquhar (1977) paper appeared, Orians and Solbrig (1977; hereafter OS77) published a broader ecophysiological treatment with more direct linkages of plant growth strategies to fitness, going beyond diffusive fluxes, while retaining recognition of fitness within context of the whole plant. In the introductory sections of OS77, the authors stated:

> "Any model of natural selection assumes both some "goal" that is being optimized (or maximized) and the constraints within which the organisms operate. A reasonable short-range goal for plants might be the maximization of photosynthetic rate; a plant capable of increasing photosynthesis within the constraints of its available resources and the physical environment should gain advantages in competition with other plants, defenses against herbivores, and should have more energy to devote to reproduction." (Here, photosynthetic rate is developed as a whole-plant concept, and one that is analogous to growth).

In OS77, the authors relied on optimization to explain the divergence of evergreen and deciduous leaf traits, which had been discussed extensively in MD70a, MD70b, and M72, including the covariance of maximum photosynthesis rate and leaf longevity. In OS77, one can recognize the expanding discussions that were occurring within the ecology community on the evolutionary underpinnings of observed patterns in functional trait expression. This would lead to a symposium at Cornell University in June 1977, organized by Otto Solbrig, and focused on 'the role of optimality thinking in current evolutionary thought' (as reviewed by Antonovics 1980). Mooney, Givnish, and Solbrig, along with others presented papers in one section of the conference on evolutionary topics within the field of plant physiological ecology. (In his review of the conference, Antonovics provides a relatively cautious view of optimization, tradeoffs, and cost–benefit analyses within the context of plant physiological ecology, commenting that: "these papers … inadequately discuss the genetic basis of such tradeoffs and how such costs and benefits can be translated into gains and losses in fitness"). Many papers from the Cornell conference were published as a book in 1979 (Solbrig et al. 1979).

Almost in parallel with the rise of optimality models of allocation in plants came a complementary approach that emphasized the importance of environmental interactions in determining plant strategies, Game Theory, which was developed within the context of economics (von Neumann and Morgenstern 1953) and applied soon after to evolution (Lewontin 1961; Slobodkin and Rapoport 1974; Maynard Smith 1982). In game theoretic approaches, context and constraints were paramount for determining optimal strategies, and the kinds of constraints discussed by these early workers are similar, and sometimes identical, to the issues discussed in criticisms of the adaptationist program (e.g., Gould and Lewontin 1979). As has often been the case in the development of ecological theory, the animal ecologists were ahead of the plant ecologists, and the first explicitly plant-focused game theoretic model did not appear until efforts to rewrite competition theory (Mirmirani and Oster 1978).

A watershed moment occurred in 1982 with the publication of the first game-theoretic plant allocation model (Givnish 1982). This model concentrates on the decision space of when a plant "should" grow taller and when it should extend leaf area horizontally and thus should have had direct relevance to the later development of functional trait theory. It emphasized light as the critical resource being sought and the role of neighbors in mediating light availability. It showed the importance of neighbors in changing optimal allocation strategy by altering light availability, and, critically, it showed how consideration of these neighbor effects on resources led to predictions that matched empirical data from the traits of wild-grown plants. Although Givnish's effort has been cited over 300 hundred times (Clarivate, Web of Science), the general impact of game theoretic approaches on our understanding of the carbon balance of plants has been considerably less than that of the simpler trait and resource-based optimality approaches. It is a worthy topic of investigation, but beyond the scope of this paper, to examine why explicitly game theoretic models have not been employed more extensively.

The maturation of an economic context for plant trait analysis

The emphasis on environmental constraints in OS77 brought to the forefront an important pattern that was originally observed by MD70b and discussed indirectly in M72, but which was not yet placed entirely within the context of natural selection. That is the question as to ***why species with longer leaf longevities tend to have lower maximum photosynthetic rates, even when growing in habitats or seasons with less drought stress***. Mooney and Dunn (1970a, b) had noted that the evergreen species they studied had leaves with greater mass per unit area (LMA) and that this morphological trait, while favorable to 'durability, water conservation and predator protection', was in some manner 'inimical to high leaf gas-exchange capacity'. Repeating the explanation proffered by Mooney and Dunn, OS77 hypothesized that the greater LMA, with smaller mesophyll cells and thicker cell walls, along with biochemical inhibition of photosynthesis by drought, prevented the expression of higher photosynthesis rates in xerophytic, evergreen leaves. In other words, in the prevailing view, it was the structure of sclerophyllous leaves, which was required for durability and protection, that limited the diffusion of atmospheric CO_2 to chloroplasts, and therefore prevented the expression of high photosynthetic rates, even when ample water resources were available.

A breakthrough toward understanding the selective constraints on photosynthetic capacity came, in part, following studies by Mooney during an Australian sabbatical, in which he worked on comparative photosynthesis patterns among *Eucalyptus* sp. The key aspect of the breakthrough was the recognition of a direct relationship between leaf photosynthetic capacity and leaf nitrogen concentration (see Mooney et al. 1978; see Fig. 2). Recognition of this relationship was a key to understanding why long-lived leaves were constrained in their maximum photosynthetic capacity, what we now refer to as A_{max}. Extending the relationship across the lifetime of a leaf, Mooney and Gulmon (1979; hereafter MG79) developed a theory that the level of investment of N in the carboxylation capacity of photosynthesis (through the enzyme Rubisco) is directly tied to fitness and is under selection to maximize photosynthetic rate concordant with the potential for an investment return (as growth) given habitat resource availability. In MG79, the economic term 'net marginal gain' (G) was developed as the difference between photosynthetic gain and the cost of enzyme synthesis per unit of enzyme added to a leaf. At the leaf Rubisco content where $G = 0$, further investment in leaf photosynthetic capacity would have a negative impact on fitness and thus be disfavored by selection. In dry habitats (with xerophytic leaves), the $G = 0$ limit would be reached at a lower Rubisco concentration and thus lower photosynthetic capacity, than in plants native to moist habitats (with mesophytic leaves). Accordingly, by principles of resource-use optimization, selection would favor lower photosynthetic capacities in longer-lived leaves from resource-limited habitats and higher photosynthetic capacities in shorter-lived leaves from resource-replete habitats. The economic theories of MG79 were included in the book chapter published at the Cornell

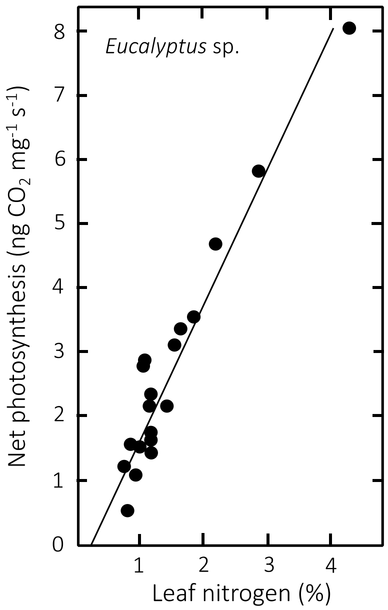

Fig. 2 The linear dependence of mass-based net photosynthesis rate on leaf nitrogen content among several species of *Eucalyptus*. Redrawn from Mooney et al. (1978)

1977 conference and extended in a later paper that developed the cost–benefit framework to explain optimal patterns in the allocational tradeoffs among growth, stress-tolerance, and herbivore defense traits (Mooney and Gulmon 1982; hereafter MG82).

In 1985, Bloom, Chapin, and Mooney (Bloom et al. 1985; hereafter BCM85) published a formal treatment of plant resource allocation patterns within the context of financial economic theory. Here, concepts, such as profit maximization, marginal product ratio, cost–benefit difference, and optimal resource allocation, as applied to successful financial strategies were used as analogs to understand patterns of trait association, reproductive fitness, and evolutionary optimization within plant species. The economic theories developed in BCM85 are summarized in the following quote:

> “Our survey of the literature suggests that at least the vegetative growth of plants conforms closely to those theorems of economics that predict how profit should be maximized and resources optimally allocated.”

Publication of this treatment enabled the ease with which economic analogies have been used in subsequent studies of plant adaptation, including the development of the WLES, in which cost–benefit relations are used as justification for the coordinated assembly of trait clusters (e.g., Wright et al. 2004).

The emergence of a framework for understanding traits within the context of ecological strategies

To explain the evolution of trait spectrum patterns, economic theories rely on a direct relationship between resource use and reproductive fitness. While economic theories matured as the foundation for understanding trait expression, an independent line of thought emerged on the relationships between traits and ecological pressures—what is often referred to as trait strategies—rather than a direct linkage between traits and fitness—which is better described by trait economics. In the case of plants, trait strategy theories emerged, once again, from the animal literature, especially that based on life-history traits in relation to population density. The relationships among traits in populations subjected to density-dependent selection, where competition for resources is strong, were predicted to be fundamentally different than in populations with density-independent selection (MacArthur 1962; MacArthur and Pianka 1966; Gadgil and Bossert 1970). Theories on ecological trait strategies included some economic concepts, such as optimality in the use of resources. However, the focus was on how resource patches in an animal’s habitat are optimally used, rather than on how limiting resources are optimally allocated to produce an animal’s phenotype. In some cases, efforts were extended to bring animal allocation theory (especially regarding maximization of fecundity) in line with patch-use theory (e.g., Cody 1966). Generally, in trait-strategy theories, traits were recognized as favoring the persistence of certain animal phenotypes in the face of density-dependent selection, referred to as *K*-selection, or the fecundity of certain phenotypes in the face of density-independent selection, referred to as *r*-selection.

The early plant literature in trait strategies descended from these studies on animal habitat use and was developed in parallel to the resource assimilation and allocation discussions that followed M72. One influential line of research concerning plant ecological strategies was developed by Philip Grime, initially in 1974 and in a fuller format in 1977 (Grime 1974, 1977; hereafter G77). In G77, Grime proposed that selection has shaped the ecological strategies of species depending on three fundamental habitat constraints, i.e., competition, stress, and disturbance. In productive, but undisturbed habitats, traits supporting competitive success, such as the rapid production of leaf and root surface area, will maximize above- and below-ground resource acquisition, sustain the exclusive occupation of space within the habitat, and therefore enhance persistence (like the traits produced by *K*-selection in animals). In resource-poor habitats, wherein the productive potential of a plant is strained, traits promoting persistence through stress tolerance will be most favored, resulting in growth strategies such as sclerophyllous leaves, resource storage, and slow growth rates (not truly analogous to traits produced by either *K*- or *r*-selection in animals). In resource-rich, but disturbed habitats, potential production rates will be high, and density-dependent constraints will be low, favoring phenotypes with rapid growth and maximum fecundity (like *r*-selection in animals).

The triangular theory for understanding the relative roles of competition, stress, and disturbance in generating selection for plant strategies, which was described in G77, has generated considerable debate within the ecological research community (Grime 1979; Tilman 1982; Grace 1991; Brooker et al. 2005). It is beyond the scope of this essay to rehash the multiple dimensions and axes of this debate, which are tangential to the points we make about trait economics. In fact, mention of M72, and any of the other early-70 s papers on the costs and benefits of traits, were missing from the citations in G77, demonstrating differences from the outset in the foci of these two lines of theory. However, since its initial introduction in G77, trait-strategy theory has moved closer to trait-economic theory, and by the early 2000s the two lines of thought had, at least in part, settled into a combined integrative framework including economics, optimality, and ecology.

The forging of this intersection centered on the stress- and disturbance-legs of the G77 strategy triangle. In G77, the resource-limited condition of stress was hypothesized to favor phenotypes with slow growth, slow turnover of acquired resources, long-lived organs, evergreen leaves, and the opportunistic behavior of accumulating resources when supply exceeds demand. G77 offered the first explicit statement on the general increase in plant defense for species native to resource-poor habitats. Even deeper within G77, the resource-rich nature and frequent opportunities for recruitment in disturbance-associated habitats were hypothesized to favor phenotypes with fast growth rates, rapid turnover of organs and plants, and maximum allocation of resources to propagules. From these lines of thought, a perspective emerged within G77 of parallel ecological axes, one for gradients of resource availability (from high to low) and one for spectra of traits (supporting fast-to-slow plant-growth rates). The link ensuring parallel tracks between these axes was natural selection, which shaped plant trait combinations and established possible points of intersection between theories of ecological strategy and the economics of trait cost–benefit differences (though not explicitly recognized in G77).

A synthesis between trait-strategy theory and trait-economic theory began, shortly after G77, with the publication of Chapin (1980; hereafter C80). In C80, the concepts concerning carbon allocation and trait tradeoffs from M72 were broadened to include the ecological relations of high- and low-resource habitats from G77. Furthermore in C80, Chapin developed a clear extension of the relationships among leaf longevity, rates of carbon and nitrogen acquisition (fast versus slow), relative plant growth rates, and adaptation to fertile versus infertile habitats. He did not delve deeply into economic analogies, and the theoretical aspects of cost and benefit were discussed mostly through an a priori assumption of evolutionary optimization. The concepts developed in C80 explained why certain combinations of traits are repeated across nutrient availability gradients. This paper offered the most explicit explanation to that point on the advantages of slow growth rates in plants native to infertile soils and, by inference, the *raison d'etre* for selection favoring plants with positive trait correlations among longer leaf longevity, reduced photosynthesis rates, slower growth rates and conservative activation of growth meristems in resource-limited habitats. Early in C80, Chapin relies on M72 and OS77 to justify the trait correlations of longer leaf longevity, lower leaf N concentrations, and lower photosynthetic rates in the sclerophyllous leaves of infertile habitats. In the Summary section of C80, Chapin openly discusses G77 and its presentation of ecological strategies as forming the basis for his development of theory concerning the generality of trait associations in plants native to fertile or infertile habitats.

In 1985, Coley, Bryant, and Chapin (Coley et al. 1985; hereafter as CBC85) continued the development of the concepts presented in G77, MG79, MG82 and C80, and specifically those associated with the economic basis for growth-defense tradeoffs. In CBC85, a general theory was proposed whereby habitat resource availability determines patterns of selection that favor the type and amount of defense deployed by species, and the association of defense, as a trait, with other traits such as relative growth rate and leaf longevity. The theory underlying growth-defense tradeoffs in CBC85 is often cited as the authoritative treatment of cost–benefit theory, evolutionary optimization, and trait economics in the discussion of plant defense strategies.

Cost–benefit tradeoffs and the worldwide leaf economic spectrum (WLES)

The legacy of M72 is seen in the establishment and acceptance of the general paradigm of carbon as the fundamental currency in discussions of plant adaptation. What has emerged in plant ecology across scales from molecular to whole plant is that the energy contained within the bonds of organic compounds provides a clear approach for assessing the costs and benefits of tradeoffs in adaptation, life history, competition, and plant-animal interactions. As plant physiological ecology and related disciplines have matured over the last half-century, it is often easy to forget the remarkable unifying contributions of M72 to studies and concepts that followed. Anticipation of the broader importance of carbon balance theory toward understanding global patterns of trait function can be found in the second sentence of M72:

> "It is likely that through a quantitative understanding of how different plants gain and allocate their resources it will be possible to make predictions as to their success in any given physical environment in combination with any competitor and predator."

This statement strikes a broad and obvious note in today's discussions of economic trait spectra and global optimization models of carbon and water cycling. However, fifty years ago, scientists were still struggling to formulate even the simplest of general theories concerning plant function.

By 1985, thirteen years after M72, the concepts presented in OS77 and BCM85 had described clear economic frameworks for evaluating plant trait associations. Furthermore, G77 and CBC85 had developed a theoretical foundation connecting traits with ecological strategies, including those involving growth pressures due to competition and herbivory. Shortly thereafter, ecologists began to study the generality of these emerging frameworks. In 1986, Field and Mooney presented evidence of a first-order correlation between N concentration (on a leaf dry mass basis) and $A_{\max}$ that is similar across a broad range of species and life forms, thus validating the universal importance of N as a resource governing observed patterns in photosynthetic adaptation (Field and Mooney 1986; hereafter FM86). Five years later, Reich et al. (1991; hereafter RUWE91) explored many of the trait correlations described in the previous economic frameworks of M72, MG79, CBC85, and FM86 using 23 Amazonian tree species, with a focus on leaf life span (Fig. 3). RUWE91 was among the earliest studies detecting multiple, similar trait correlations, which followed the predictions of optimization theory. They found that leaf life span was inversely correlated with $A_{\max}$ (expressed on a leaf mass basis), leaf N concentration, stomatal conductance (g_s), and leaf-specific area (the inverse of LMA) (Fig. 3). During the following decade, these types of correlations would be frequently observed among studies of plants in diverse ecosystems and biomes, and of different life forms (e.g., Reich et al. 1992, 1995, 1997; Reich 1993; Reich and Walters 1994). The empirical correlations that emerged from these studies provided global validation of the cost–benefit trait theories that had been developed earlier.

The piece of theory that was becoming most obvious in explaining global trait correlations was that species are arrayed along a spectrum stretching from slow-to-fast growth rates, which are respectively correlated with slow-to-fast metabolic rates (e.g., photosynthesis and respiration), low-to-high leaf N concentrations, long-to-short leaf turnover rates, and high-to-low levels of plant defense (Reich et al. 1997; Díaz et al. 2004). From these observations, the global convergence of traits toward specific correlations was formalized in 2004 as the WLES. The initial form of the WLES included the traits of over 2,500 plant species from 175 habitats (Wright et al. 2004; hereafter W04). The common thread tying the WLES to past economic theories is captured in the following statement from the Conclusions section in W04:

> “But, surely, the broad generality of the relationships we describe suggests that natural selection eventually eradicates leaf investment strategies that are not economically competitive. The leaf economics spectrum reflects a mixture of direct and indirect causal relationships between traits.”

In the second paragraph of W04, the economic theories in OS77, BCM85, and Givinish (1986) are cited to establish the economic nature of plant allocation strategies. Optimization theory was applied to the WLES as an integrated part of the slow-to-fast spectrum, invoking slower growth returns on resource investments to conservative (slow) plant strategies, relative to acquisitive (fast) strategies. Deeper connections to the early trait economics literature, including to MD70a, MD70b, M72, MG79, and MG82, were, unfortunately, not cited.

The roots of W04 in the earliest trait literature can be seen in the fact that they share the first three defining attributes of the modern field of ‘trait-based ecology’, according to Shipley et al. (2016). (1) A description of organisms that emphasizes ‘the values of their phenotypic traits over phylogenetic or taxonomic affinities’. (2) The ‘explicit comparison of trait values’ across a large and varied set of species and phylogenies to discover general trends in trait distributions. (3) A ‘comparison of these trait values’ across environmental gradients to discover how traits affect the environment and how selection favors specific trait combinations. The promise of W04 to catalyze a new type of ecology is recognized in the fourth defining attribute of trait-based ecology,

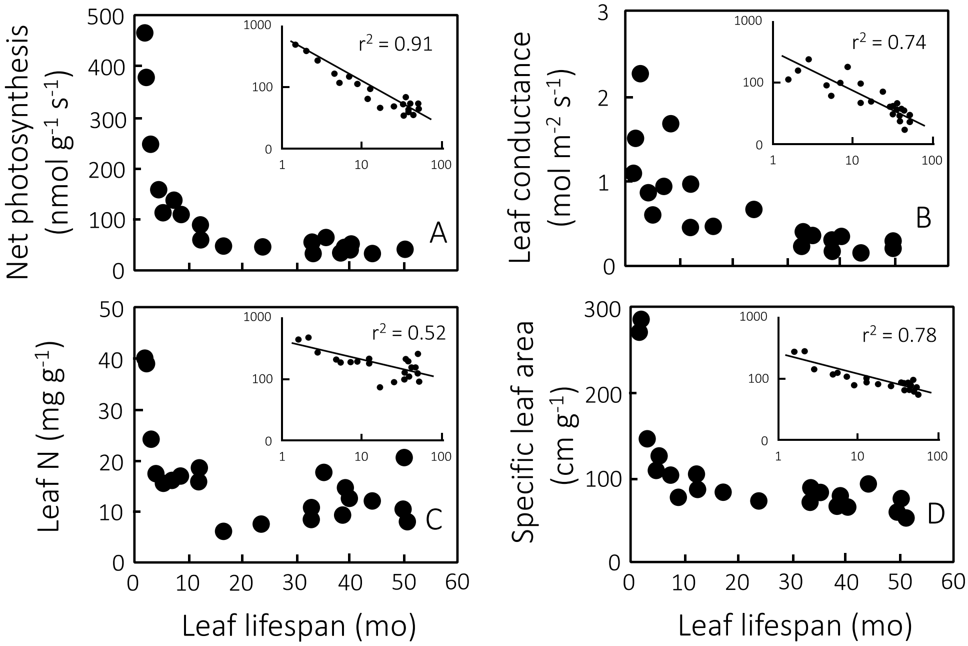

Fig. 3 Correlations between leaf lifespan and several leaf traits for sun leaves in 21 species of Amazonian trees. The insets provide linear correlations scaled to log–log axes. This study represents one of the earliest efforts to expand the scope of trait associations to multiple species, and ultimately global gradients. Redrawn from Reich et al. (1991)

which reflects a clear expansion from the earlier trait literature. (4) An ‘explicit scaling of traits, or composites of these,’ from plants to ecosystems (and ultimately the globe), under the assumption that traits underlie causative linkages across broad spatiotemporal scales. The latter attribute has provided the basis for a predictive form of economic trait-based ecology.

The WLES and the expansion of predictive ecology (albeit in limited directions)

The publication of W04 catalyzed a fundamental shift in the way that ecologists view traits. After 2004, the focus within the discipline shifted from the cost–benefit reconciliation of trait evolution to the distribution of traits across habitat gradients (moving closer to the plant strategy theories of G77). There remained a residual interest in the economic underpinnings of trait correlations. For example, Reich (2014) used the economic trade-off theory to extend the slow-to-fast trait spectrum from carbon and nutrient resources to include water acquisition and utilization. Diaz et al. (2016) used a WLES database (the TRY database; see Kattge et al. 2019) to demonstrate that plant and organ size, in addition to cost–benefit constraints, has a large effect on patterns within the slow-to-fast spectrum. Onoda et al. (2018) isolated carbon allocation to leaf cell walls as a primary cost influencing the evolution of tradeoffs between leaf longevity and photosynthetic capacity. However, most studies in trait-based ecology over the past two decades have looked in the direction of environmental influences on trait correlations (e.g., gradients and selection) or trait influences on ecosystem function (e.g., traits and biogeochemical cycles; see Pierce et al. 2014; Bai et al. 2015; Kleyer et al. 2019).

By the numbers, the field of trait-based ecology has exploded during the past two decades. For example, for the 19-year period between January 2004 and 2023, 9,172 papers were published on the general topic of ‘plant trait correlation’, compared to only 1,434 papers for the 19-year period between January 1985 and 2004 (Clarivate, Web of Science). That represents a 540% increase for the topic of trait correlations versus a 212% increase for all listed scientific papers. While some of this increase may be due to changes in indexing practices, the number is still quite large The rapid expansion of trait-based research has been especially effective in broadening the ecological context within which traits, rather than species, serve as predictive ecological variables (Reichstein et al. 2014; Sakschewski et al. 2015; Verheijen et al. 2015), providing a means to condense two or more variables into ratios and scaling parameters that, in turn, act as conveniences in generating predictions across multiple scales. Beyond the use of two-trait correlations, the constraint of evolutionary optimality provides even greater opportunities for model simplification (Prentice et al. 2014; Franklin et al. 2020; Harrison et al. 2021). For example, assumptions of stomatal optimality in the diffusive tradeoffs linking transpiration and photosynthesis provide the basis for constraining biospheric and atmospheric exchanges of CO_2 and H_2O across scales from the leaf-to-globe and partitioning those controls according to climate and soil resource gradients (Smith et al. 2019).

In several ways, the expansion of trait-based ecology has fulfilled the optimistic predictions that were made shortly following W04, especially with respect to advancing the perspectives of ‘Schimper World’—a scientific view embedded in physical geography and focused on species distributions and ecological roles across resource gradients, landscapes and latitudes (Westoby and Wright 2006). These advances have served ecology well regarding improvement in our ability to assess ecological services and their susceptibility to the threats of future global change (Lavorel and Grigulis 2012). In other ways, however, the discipline has failed to establish expected linkages to a broader ecological perspective. In the area of community ecology, while there have been some studies demonstrating links between functional traits and life-history traits (e.g., Adler et al. 2014), there has been a general failure to translate those linkages into a framework capable of predicting community dynamics (Funk et al. 2017; Bruelheide et al. 2018; McWilliam et al. 2022). Furthermore, much of the early motivation to explain the underlying functional interactions that guide fitness margins and cost–benefit differences during trait selection has dissipated (Shipley et al. 2016). In two of the most explicit evaluations of the promise and progress of trait-based ecology (published 10 years apart following W04), an emphasis was placed on: (1) the need to develop ‘a strong grasp of trait costs and benefits, in the context of a competitive environment and expressed as quantitative models’ (Westoby and Wright 2006), and (2) the failure to adequately evaluate how ‘traits are functional to the degree that they determine individual fitness’ (Shipley et al. 2016).

Beyond trait correlations: Trait economics and the emerging synthesis between cellular biology and trait ecology

The slow progress in integrating functional trait ecology with the determinants of fitness is unfortunate given the breakthroughs that have occurred during the past two decades in understanding the cellular and molecular controls over adaptive gene expression and associated patterns in positive and negative trait correlations (Schuman and Baldwin 2016; Züst and Agrawal 2017; Monson et al. 2022). Those breakthroughs include traits contributing to plant growth rate, maximum photosynthesis rate, leaf longevity, plant defenses against herbivores and pathogens, and plant nutrient acquisition and utilization – the same traits dominating the WLES. It is likely that the extension of trait economics into the cellular realm will create opportunities for not only understanding the cost–benefit basis for observed trait correlations but also the development of new quantitative models for linking trait expression patterns to global gradients in climate and resource availability (Monson et al. 2022; Walker et al. 2022).

Trait relations at the cellular scale are coordinated through protein-based signaling hubs that facilitate crosstalk and feedbacks among multiple biochemical pathways and ensure tight linkages of gene expression to external environmental cues and internal resource states. In model plant systems, direct connections between cellular carbohydrate status and the expression of traits are coordinated through sugar signaling, which has been recognized in general terms for at least the last 25 years (Sheen et al. 1999; Smith and Stitt 2007). In the past decade, details of the primary sugar-signaling networks have been described and include three primary signal hubs (Fig. 4) – the TOR and SnRK1 kinase networks, which have been described in greater detail than relationships involving the third hub, that are associated with trehalose-6-phosphate (Tre6P) (Dobrenel et al. 2016; Wingler 2018; Meng et al. 2022). Together, the three hubs can be thought of as carbon budget 'fuel gauges' that accelerate or decelerate the rate of cellular growth and modulate the channeling of resource substrates through alternative metabolic and developmental pathways by controlling patterns of trait gene expression. The signal networks that lie downstream from the sugar-sensing hubs include a series of additional pathways that are specialized for specific sets of traits (Fig. 4). These include the auxin, cytokinin, and brassinosteroid pathways that promote growth and the ethylene and abscisic acid pathways that promote stress tolerance.

In response to high cellular sugar concentrations (the positive side of the carbon balance ledger), the Target of Rapamycin (TOR) is activated and initiates pathways that lead to increased rates of cellular expansion, increased allocation of resources to the synthesis of Rubisco and nitrate reductase enzymes for C and N acquisition, and the activation of shoot and root meristems in ways that affect the growth of leaves and roots. In other words, TOR acts as a positive influence on the expression of *acquisitive* cellular traits. Sucrose-non-fermenting-1-Related Kinase-1 (SnRK1) is a plant kinase that serves as an antagonist to TOR (thereby controlling the downside of the carbon balance ledger). SnRK1 kinases are activated in the low resource state of cells for both carbohydrate and other nutrient resources (Baena-González and Sheen 2008; Baena-González et al. 2007). At low resource

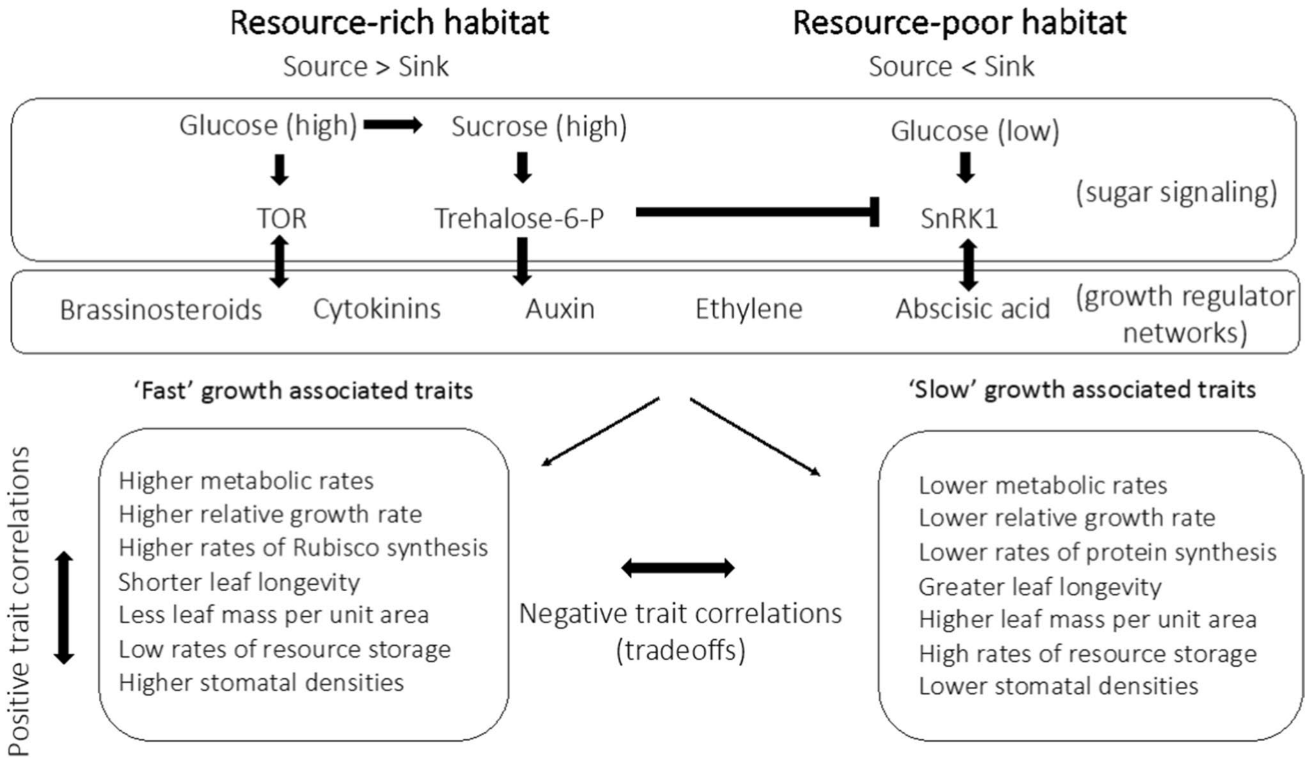

Fig. 4 Alignment of traits at the 'fast' and 'slow' poles of the WLES with cellular signaling networks controlling the genetic expression of traits. The proposed association of different trait syndromes with resource-rich versus resource-poor habitats is also shown, whereby resource limitations resulting in sugar source-sink imbalances trigger sugar signaling pathways that ultimately control trait expression

availability, activation of SnRK1 protein complexes leads to the downregulation of growth-associated pathways, and the upregulation of pathways that promote nutrient recycling (e.g., cellular autophagy), the formation of carbohydrate reserves (e.g., starch formation), and slower rates of cellular expansion. In other words, SnRK1 acts as a positive influence on the expression of *conservative* traits. TOR likely functions as a default sensor, which is negatively regulated in the low-resource state by activated SnRK1 complexes operating upstream from TOR (Crepin and Rolland 2019). Conversely, in the high resource state, SnRK1 is deactivated by specific sugars, including glucose-1-P, glucose-6-P, and trehalose-6-P (Tre6P), which therefore permit the default signaling by TOR to proceed. The regulatory role of Tre6P in plants has apparently evolved as a means of fine-tuning the broader sugar-signaling system of TOR-SnRK1 interactions, thereby establishing a sensitive link of plant carbon balance to the expression of a broad spectrum of functional traits (Wingler 2018).

From optimality to traits to biogeochemistry

In addition to the above-mentioned progress in downscaling a trait-based perspective on plant function, we have seen huge advances in scaling upward to ecosystems and biogeochemical cycles thanks to links developed between the ideas put forward in M72 and theoretical advances in ecosystem ecology that occurred just a few years later. In 1975, a key paper was published linking nutrient availability with plant growth at the ecosystem scale and noting that mismatches between the supply and demand side of plant function lay at the heart of both growth and successional change (Vitousek and Reiners 1975; Vitousek 1977). These ideas became the basis for the development and application of stoichiometric thinking as a basis to explain ecological and evolutionary change (Reiners 1986; Sterner and Elser 2002). In this framework, the stoichiometric balance of essential elements becomes the target of an optimality strategy, rather than maximization. Evolutionary change in the form of new stoichiometries then changes the optimization target and can thus be evaluated in the context of selection.

These ideas had, of course, an impact long before they were revitalized by Reiners, Sterner, and others. Hutchinson (1944) and Redfield (1958) took advantage of stoichiometric ratios in their efforts to understand global-scale biogeochemical patterns. Now, with our understanding of trait distributions and patterns of optimization in resource use, we are in a position to integrate the ecological constraint on elemental stoichiometry with that of selection for maximum fitness. By considering stoichiometry as a constraint on the range of trait expression and patterns of trait covariance, it might be possible to connect the selection-based physiological ecology of M72 to continental and global scale efforts to understand Earth system functioning. Like the opportunities available at the cellular scale, we are now within reach of expanding functional trait ecology upward, beyond its use as a tool for earth-system model simplification, and into the realm of explaining the processes that regulate the most meaningful connections of ecological scale.

Conclusions

The resource-balance perspective laid out by Mooney over 50 years ago offers a theoretical framework for connecting the molecular biology of plants to understanding their impacts on scales as large as the globe. Much of the early research into plant carbon balance focused on the patterns by which traits controlled the costs and gains of the plant carbon budget. Later, that focus on traits served as the foundation for understanding trait distributions across life forms and resource gradients, what is now known as functional trait ecology, providing a global perspective of plant and trait distributions. To this point in time, functional trait ecology has been dominated by a focus on individual organisms, the core of plant physiological ecology. Several disciplines outside the traditional core of the discipline are now within reach for integrative efforts. These include 'big data' biology within the realms of multi-omics, cellular biology, and the sensor networks of biogeochemistry and earth-systems biology. For some of us who have lived the journey, hindsight seems like a long trek—basically the length of an entire generation. Yet, when viewed more objectively it is hard to deny that the conceptual progress made in five decades is a testament to the catalytic role of creativity during scientific discovery.

Acknowledgements This paper is intended to celebrate the 200th Volume of Oecologia, and the role that the journal has played in the development of the discipline of plant physiological ecology, and more specifically functional trait ecology. The authors thank the journal for the opportunity to assemble the historical perspectives presented herein. ML thanks his seminar class on 'Plant Function in a Changing World' for helpful insights during manuscript preparation. RKM and JRE declare that they are Editorial Board members of this journal, and ML is a former Editorial Board member.

Author contributions statement MTL, RKM, and JRE jointly developed the concept, framework, and ideas for the manuscript and all authors participated in writing the paper.

Funding ML acknowledges the support of NSF-IOS 2005574 ('The coordinated structural and physiological responses of trees to water stress: an organismal approach') during manuscript preparation.

Availability of data and material Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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