

Opinion

Toward a general theory of plant carbon economics

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Plant life-history variation reflects different outcomes of natural selection given the strictures of resource allocation trade-offs. However, there is limited theory of selection predicting how leaves, stems, roots, and reproductive organs should evolve in concert across environments. Here, we synthesize two optimality theories to offer a general theory of plant carbon economics, named as Gmax theory, that shows how life-history variation is limited to phenotypes that have an approximately similar lifetime net carbon gain per body mass. In consequence, fast-slow economics spectra are the result of trait combinations obtaining similar lifetime net carbon gains from leaves and similar net carbon investment costs in stems, roots, and reproductive organs. Gmax theory also helps explain ecosystem and crop productivity and even helps guide carbon conservation strategies.

Leaf optimal lifespan theory as the first cornerstone

A persistent challenge in ecology has been to produce a general theory to link species life-history variation with patterns of trait covariation. Particularly fruitful efforts have documented a worldwide pattern of plant trait covariation known as the **leaf economics spectrum (LES)** (see [Glossary](#)) [1]. The LES shows that even though leaves span a vast range in form and function, worldwide leaf diversity is bounded by covariation between tissue density, metabolism, and lifespan. Along the LES, species vary from light flimsy leaves with short lifespans and high metabolic rates ('fast' leaves) to heavy, tough leaves with long lifespans and low metabolic rates ('slow' leaves). This global pattern in leaf diversity is explained by a body of theory based on economics referred to here as **leaf optimal lifespan theory (LOLT)** [2–13].

LOLT explains the LES as different ways of producing a leaf that maximizes lifetime net carbon gain. Introduced by Chabot and Hicks [2], LOLT hypothesizes that evolution by natural selection favors individuals with leaves that assimilate more carbon during their lifespans than the carbon they invested in their construction and maintenance. As a result, some trait combinations should be rare or never observed. For example, tough leaves with short lifespans do not have enough photosynthetic time to pay off their high carbon investment in tissue construction. Instead, selection favors tough leaves with longer lifespans [8,10]. It might seem that inexpensive, lightweight leaves with long lifespans are favored by selection over lightweight leaves with short lifespans. However, in pioneering work by Kikuzawa, LOLT shows that species with lightweight leaves with long lifespans are not favored because leaf carbon gains decrease with age logistically [3] ([Box 1](#)). As a result, it is more profitable for a plant to replace a leaf whose carbon **marginal gain** (instantaneous gain) starts to decrease with age for a new vigorous leaf with higher marginal gains. Therefore, lightweight leaves with short lifespans are more profitable than lightweight leaves with long lifespans. Building on the foundational work of Chabot and Hicks [2] and Kikuzawa [3], LOLT represents a significant step toward the goal of a selection-based theory explaining **plant economics** spectra. Nonetheless, although LOLT is a basis to understand the LES, it is unclear how LOLT can explain other plant economics spectra and link them at the

Highlights

A key element of functional ecology is understanding why some combinations of organismal traits are observed whereas others are rare or absent.

Compelling hypotheses explain why certain traits associate with one another into fast-slow economics spectra. Yet, biologists would also like to have a general theory explaining how these trait combinations connect with individual fitness.

Merging existing leaf optimal lifespan theory and metabolic scaling theory yields Gmax theory as an example of formalizing a metabolic definition of fitness that explain how life-history variation and economics trait correlation patterns emerge from natural selection favoring individuals with the highest lifetime net carbon gain per body mass.

Gmax theory shows that life-history diversity is the manifestation of a myriad of evolutionary ways to obtain a similar individual lifetime net resource gain per body mass across and within species living in a given environment.

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whole-plant level. But because it focuses on leaves, LOLT does not explicitly cover organs such as roots, stems, reproductive parts, and consequently, the whole-plant [14].

Metabolic scaling theory as the second cornerstone

Another body of theory known as **metabolic scaling theory (MST)** [15–20] provides a framework for scaling up the conceptual core of LOLT to the whole-plant level. MST predicts plant carbon economics from small to large individuals with the fundamental premise that body mass influences how traits covary with one another via **allometry**. MST predicts that many physiological processes scale on average to the $\frac{3}{4}$ and $\frac{1}{4}$ power of body mass (Box 2) [15–17,20–22]. Physiological rates, such as respiration rate, photosynthetic rate, or growth rate, scale to the $\frac{3}{4}$ power of body mass, whereas biological times, such as lifespan, reproductive maturity, or physiological cycles, have $\frac{1}{4}$ power scaling relationships with body mass. Like rates and times, individual lifetime net carbon gain and lifetime net carbon cost are plant traits that are also mainly a matter of body mass [23]. Both traits are the products of individual photosynthetic rate (carbon gain) and individual respiration rate (carbon cost) with lifespan, combining $\frac{3}{4}$ and $\frac{1}{4}$ power-law allometric relationships. As a result, both traits are directly proportional to body mass (Box 3) and invariant when correcting them by body mass (Figure 1C). Therefore, mass-corrected lifetime net carbon gain in leaves and net carbon investment cost in **heterotrophic organs** (stems, roots, and reproductive organs) should be similar for small to large individuals (Figure 1D,G). In MST, size-corrected plant carbon economics is expressed as the lifetime net carbon gain of all

Box 1. Extending LOLT predictions to heterotrophic organs

LOLT states that replacing old leaves with new ones maintains high marginal carbon gains for the whole-plant individual. We can extend this statement by modifying Kikuzawa's cost-benefit model for leaves [3] to define a general carbon economic allocation framework. First, we define leaf carbon marginal gain g_l [mol C · s⁻¹] as:

$$g_l = \frac{1}{t_l} \left[\int_0^{t_l} i_l(t) dt - \int_0^{t_l} r_l(t) dt - \int_0^{t_l} s_l(t) dt \right] \quad [I]$$

where t_l [s] is leaf lifespan, i_l [mol C] is leaf gross photosynthetic rate (carbon income), r_l [mol C] is leaf respiration rate (carbon maintenance cost), and s_l [mol C] is leaf carbon construction cost, which, contrary to Kikuzawa's model, we assume to vary with time to reflect growth. Integrating $i_l(t)$ reflects leaf lifetime gross photosynthetic activity. Integrating $r_l(t)$ reflects leaf lifetime respiratory activity. Integrating $s_l(t)$ reflects the net amount of carbon allocated to leaf cellular structure (organelles, cell wall, genetic material, enzymes, etc.). Leaf net carbon gains have a logistic relationship with lifespan, but Kikuzawa shows that they can validly be assumed as linear if it is assumed that natural selection favors leaves with lifespans that maximize g_l [3]. LOLT predicts that fast leaves have lower lifetime net carbon gains per unit mass (or area) than slow leaves, but they have time-discounting benefits [10] that are expressed by having higher g_l during their lifespans than slow leaves.

Second, we extend Equation I to predict that natural selection should also favor individuals with heterotrophic organs with lifespans that minimize their marginal carbon investment costs k_h [mol C · s⁻¹] as:

$$k_h = \frac{1}{t_h} \left[\int_0^{t_h} i_h(t) dt - \int_0^{t_h} r_h(t) dt - \int_0^{t_h} s_h(t) dt \right] \quad [II]$$

where t_h [s] is the lifespan of a discrete developmental unit such as a ring of sapwood, a fine-root, or an annual shoot, i_h [mol C] is the amount of carbon that a heterotrophic organ gains via photosynthates, carbon recycling, and sometimes via photosynthesis in green heterotrophic organs, r_h [mol C] is carbon lost to respiration, and s_h [mol C] is carbon construction cost of a given heterotrophic unit h . Long lifespans and high lifetime metabolic activities mean high capacity of minimizing k_h via i_h . Therefore, slow heterotrophic organs are more expensive than fast heterotrophic organs, but they have higher lifetime metabolic activities and higher i_h . By contrast, fast heterotrophic organs are favored because of time-discounting benefits by having higher k_h during their lifespans than slow heterotrophic organs (Figure I).

Glossary

Allometry: the study of how organismal traits change or scale with changes in body size and the impact of this relationship on ecology and evolution. The term originally referred to the scaling relationship between the size of a body part and the size of the body. However, the term allometry has been expanded to refer to biological scaling relationships in general.

Ecosystem gross primary productivity: is the rate of the absolute amount of CO₂ that is photosynthesized through the foliage from a given landscape area. Ecosystem respiration is the rate of the absolute amount of CO₂ coming out to the atmosphere from a given landscape area. The difference ecosystem gross primary productivity and ecosystem respiration is termed ecosystem net primary productivity.

Gmax theory: a body of theory coming from the synthesis between LOLT and MST. Gmax theory explains that natural selection favors intrapopulation variants with the highest lifetime net carbon gain per body mass because they have more surplus resources for growth, survival, and reproduction as compared to conspecifics with low lifetime net carbon gain per body mass.

Heterotrophic organs: any plant organ that is not a leaf, that is, stems, roots, and reproductive organs. Even when photosynthetic, we consider stems, roots, and reproductive organs as heterotrophic organs that, in this case, use RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) in minimizing marginal carbon costs (i.e., increasing i_h ; see Equation II in Box 1).

Leaf economics spectrum (LES): a worldwide leaf trait correlation pattern across species that describes a fast-slow spectrum of growth and life-history strategies. The core of the LES is a positive relationship between leaf tissue density and leaf lifespan and a negative relationship between leaf net photosynthesis rate per unit mass (or area) and leaf lifespan.

Leaf optimal lifespan theory (LOLT): a body of cost-benefit theory showing that natural selection favors individuals with leaves with lifespans that maximize marginal carbon gains. LOLT states that it is more profitable to replace old leaves with low marginal carbon gains for new leaves with high gains.

Marginal gain or cost: in economics, the marginal gain marginal or cost of

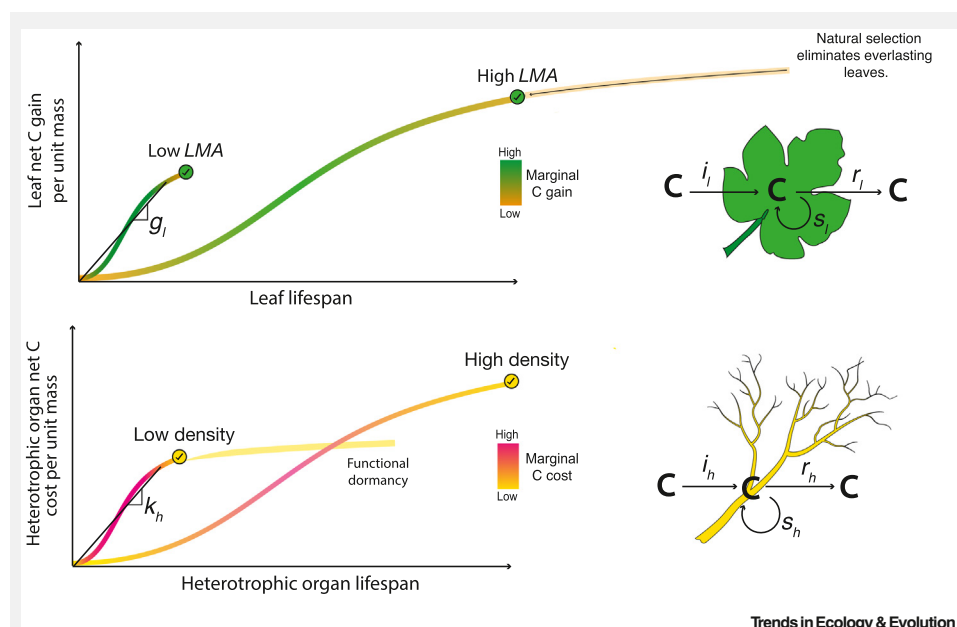


Figure 1. Size-corrected net carbon gains and net carbon investment costs have a logistic function with lifespan. Natural selection favors individuals that replace their leaves or heterotrophic organs before their carbon marginal gain or marginal investment costs decrease with age. According to LOLT, slow leaves with high leaf mass per area (*LMA*) have higher lifetime net carbon gains per unit mass (or area) than fast leaves with low *LMA*. By contrast, fast leaves have time-discounting benefits (e.g., acquiring canopy space quickly) reflected in higher marginal carbon gains. As for heterotrophic organs, slow ones with high tissue density have higher metabolic activities and higher i_h . However, fast heterotrophic organs of low tissue density have time-discounting benefits reflected in low lifetime net carbon investment costs and high marginal carbon investment cost. In contrast to leaves, functional dormancy for low-density stems and roots might be a favorable alternative to senescence, maintaining water and carbon resources for subsequent growing seasons.

production is the rate of change of net production gain or cost that comes from producing one additional unit or one additional production time unit. Marginal cost analysis determines when a given entity can achieve a positive balance in economies of scale to optimize production and overall performance.

Metabolic activity: the net amount of energy (joules) consumed in metabolism in a given time. Lifetime metabolic activity refers to the net amount of energy consumed during the lifespan of a given individual.

Metabolic scaling theory (MST): a body of theory showing that natural selection favors resource distribution networks that maximize resource exchange areas and minimize transport distances within the network. The result is $3/4$ -scaling relationships between individual physiological rates and body mass and a $1/4$ -scaling relationship between individual lifespan and body mass.

Plant economics: a concept used in plant functional ecology referring to certain plant trait combinations that are 'economic' because they are thought to reflect different ways in which plants can assign their finite reserves of resource 'currency'.

Time-discounting effects: a concept used in economics that refers to the economic benefits of strategies involving high marginal gains and short lifespans.

the leaves in a plant canopy, contributing to individual gross carbon gain that is invested in the production and maintenance of heterotrophic organs (see the supplemental information online). MST provides a standard language of plant carbon economics, but by itself, it does not predict the ways that fast-slow life-history variation should be associated with lifetime net carbon gains and net carbon costs per body mass. We now show that LOLT predictions involving the maximization of carbon marginal gains in leaves can be extended to heterotrophic organs to assume that individual lifespan maximizes carbon marginal gains.

Extending LOLT predictions to heterotrophic organs

MST predicts that the scaling normalization factors in the allometric relationships of lifetime net carbon gains and lifetime net investment costs per body mass (i.e., y-intercepts; Box 3) show variation that is independent of size and potentially associated with life-history variation [24]. However, additional theory is needed to understand how fast-slow spectra align with these scaling normalization factors. As part of LOLT, Falster *et al.* [10] showed that fast leaves have lower lifetime net carbon gains per unit mass (or area) than slow leaves. They suggest that this difference between fast and slow leaves is a matter of **time-discounting effects**. Although fast leaves have lower lifetime net carbon gains per unit mass than slow leaves, they can be favored because of time-discounting benefits [25] that produce higher marginal carbon gains [1] (Box 1 and Figure 1F).

Box 2. Why does MST predict $\frac{3}{4}$ and $\frac{1}{4}$ power allometric scaling relationships?

A core prediction of MST is that individual body mass is a central biological trait governing virtually every biological trait or process. The role of body mass is represented in allometric scaling relationships as:

$$y = cM^\alpha \quad [I]$$

where y is any trait of interest, c is the scaling normalization factor, M is body mass, and α is the scaling exponent, which reflects the proportionality between y and M . Over a century of empirical studies establish the ubiquity of $\frac{3}{4}$ and $\frac{1}{4}$ scaling exponents in multiple traits [21] showing that, as body mass increases, multiple traits covary with body mass disproportionately. For example, biological rates (e.g., metabolism, photosynthesis, excretion, circulation) scale with $\alpha \sim \frac{3}{4}$ whereas biological times (e.g., lifespan, time to maturity, gestation duration, population doubling time) scale with $\alpha \sim \frac{1}{4}$. It was not until 1997 that West *et al.* [15] showed formally how these and other values for α could originate from selection shaping resource distribution networks. They showed that $\alpha = \frac{3}{4}$ characterizes resource distribution networks that maximize resource exchange areas and minimize transport distances. In turn, $\alpha = \frac{1}{4}$ characterizes life cycles that minimize the necessary time to be completed within metabolic costs [37,50,51].

We can extend MST to predict the total metabolic activity per lifespan of an organism. First, we note that an important prediction of MST is the $\frac{1}{4}$ power scaling of the pace and timing of growth, allocation, and life-history events [18,50]. Different selective contexts favor different timings of life-history events such that individuals can complete their life cycles. Across differing selective contexts, we would then expect a concomitant response in body mass and the normalization factors associated with the scaling of biological rates or times or both. MST predicts that lifetime metabolic activity combines the $\frac{3}{4}$ and $\frac{1}{4}$ scaling exponents as:

$$x \cdot z = c_x M^{3/4} \cdot c_z M^{1/4} = c_x c_z M^1 \quad [II]$$

where x is a biological rate, z is a biological time, and c_x and c_z are scaling normalization factors. Here, we define the life cycle of an organism as rate of production x (the metabolic activity needed to grow, survive, and leave viable descendants) during lifespan z (i.e., $x \cdot z$) [36,37]. Importantly, MST predicts that the scaling of any lifetime metabolic activity will be directly proportional to body mass. Therefore, lifetime metabolic activity per body mass (xz/M) is invariant across small to large individuals (see Figure 1C in main text) where:

$$\frac{xz}{M} = \frac{c_x c_z M^1}{M} = c_x c_z M^0 = c_x c_z \quad [III]$$

With Equation III, MST offers the way to test for additional factors that are independent of size evolution driving variation in mass-corrected lifetime metabolic activities by determining correlations with $c_x c_z$. The product of both scaling normalization factors defines the amount of metabolic activity that a given body mass performs during lifespan. In Box 3, we show how Equations II and III are required for a formal language of whole-plant carbon economics.

Extending LOLT to heterotrophic organs means that life-history is associated with variation in how much carbon a gram of heterotrophic organ costs in terms of its production and maintenance during its lifespan, which, as in leaves, is also subject to time-discounting effects. This extension predicts that fast heterotrophic organs have time-discounting benefits with low lifetime net carbon investment costs at the expense of low lifetime **metabolic activity**, meaning that they have less energy resources to perform physiological processes such as maintaining foliage, transporting photosynthates through the phloem, or recycling carbon via PEPCase activity [26–28]. Because they are not as disposable as leaves, fast stems and roots (e.g., wood in a low-density tree like a baobab, or parenchyma in a tuber) tend to go dormant or quiescent shortly after growing, potentially as an adaptation involved in water and starch storage associated with low lifetime metabolic activities (see Figure I in Box 1). By contrast, slow heterotrophic organs have high lifetime net carbon investment costs per unit mass, but they have high lifetime metabolic activities. For example, high-wood density trees store more starch in their sapwood [29], in general, they maintain leaves longer in seasonal environments [30], recuperate faster from injuries [31], tend to be pioneers in dryland environments [32], and perhaps even live longer [33] than low-wood density trees. Slow stems and roots tend to produce visible, metabolite-laden heartwood rather than producing wide regions of dormant sapwood the way that fast heterotrophic

Box 3. How do we estimate the normalization coefficients of the allometric scaling relationships of lifetime net carbon gain and lifetime net carbon cost per body mass?

According to MST, one must first control for the allometric influence of body size and then focus on studying the residual variation to compare the diversity of life histories. MST shows how to test for size-independent drivers of lifetime net carbon gain and net investment cost per body mass via testing correlations with the scaling normalization factors. As in Equation II in Box 2, $\frac{3}{4}$ and $\frac{1}{4}$ scaling exponents of biological rates and times also apply to allometric scaling relationships of plant photosynthesis, respiration rate, and lifespan. Individual lifetime net carbon gain combines the effects of $\frac{3}{4}$ and $\frac{1}{4}$ scaling exponents; thus, it is directly proportional to body mass as:

$$\bar{P} \cdot T = c_P M^{3/4} \cdot c_T M^{1/4} = c_P c_T M^1 \quad [I]$$

where $\bar{P}$ is mean foliage net photosynthetic rate [$\text{mol C} \cdot \text{s}^{-1}$], T is individual lifespan [s], and c_P [$\text{mol C} \cdot \text{s}^{-1} \cdot \text{g}^{-3/4}$] and c_T [$\text{s} \cdot \text{g}^{-1/4}$] are scaling normalization factors. Likewise, individual lifetime net carbon cost should also be directly proportional to body mass as:

$$\bar{R} \cdot T = c_R M^{3/4} \cdot c_T M^{1/4} = c_R c_T M^1 \quad [II]$$

where $\bar{R}$ is mean individual respiration rate [$\text{mol C} \cdot \text{s}^{-1}$] and c_R [$\text{mol C} \cdot \text{s}^{-1} \cdot \text{g}^{-3/4}$] is another scaling normalization factor. As in Equation III in Box 2, lifetime net carbon gain per body mass should be invariant across small to large plant individuals:

$$\frac{\bar{P}T}{M} = \frac{c_P c_T M^1}{M} = c_P c_T M^0 = c_P c_T \quad [III]$$

Likewise, lifetime net carbon cost per body mass should also be invariant across small to large plant individuals:

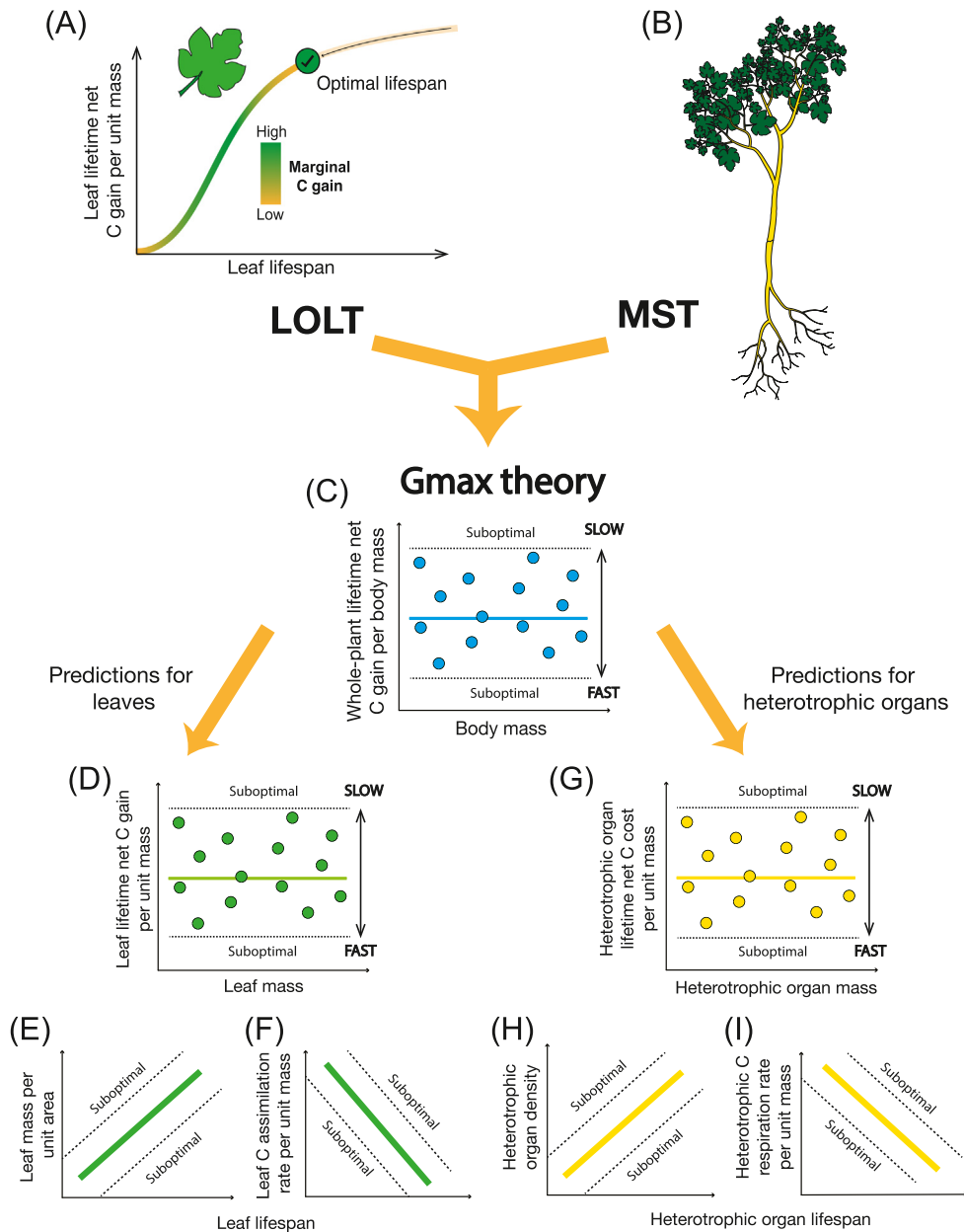
$$\frac{\bar{R}T}{M} = \frac{c_R c_T M^1}{M} = c_R c_T M^0 = c_R c_T \quad [IV]$$

Equations III and IV show that the scaling normalization factors c_P , c_R , and c_T are each independent of size evolution and underlie variation in lifetime net carbon gain and net carbon cost per body mass. The scaling normalization factor c_P is the net photosynthetic rate of $\frac{3}{4}$ of a gram of leaf. Similarly, c_R is the respiration rate of $\frac{3}{4}$ of a gram of heterotrophic organ. Lastly, c_T is how long $\frac{1}{4}$ of a gram of tissue lives. The product of $c_P c_T$ shows how much carbon is photosynthesized by a gram of leaf during its lifespan, and $c_R c_T$ shows how much carbon is respired by a gram of heterotrophic organ during its lifespan. The terms $c_P c_T$ and $c_R c_T$ can be correlated to size-independent factors that potentially drive lifetime net carbon gain. For example, Gmax theory predicts that fast species have low $c_P c_T$ and $c_R c_T$ whereas slow species have high $c_P c_T$ and $c_R c_T$. Other factors such as temperature, vapor pressure deficit, C3/C4 photosynthesis, or experimental treatments can also drive these scaling normalization factors. These and other scaling normalization factors are important in biology to test for size-independent factors driving variation in any trait of interest [19,24].

species do. As a result, even when slow stems and roots have lower sapwood fractions and do not have the time-discounting benefits of acquiring space quickly, low fractions of slow sapwood are ultimately performing more in terms of lifetime metabolic activity than fast stems and roots. In sum, extending LOLT to heterotrophic organs provides a foundation for formalizing the linkage between trait variation in leaves and heterotrophic organs for a whole-plant perspective.

LOLT and MST give rise to Gmax theory

Given MST and extending LOLT predictions to heterotrophic organs (Box 1), here we build what we call ‘**Gmax theory**’ as a theory of whole-plant carbon economics (Figure 1). The central hypothesis of Gmax theory is that, within a population, individual plants with the highest lifetime net carbon gain per body mass (thus ‘Gmax’ as in maximum gain) have more surplus carbon to allocate in growth, survival, and reproduction. As a result, they outcompete conspecifics with lower surpluses. If correct, then natural selection favors individuals that maximize lifetime net carbon gains in leaves and minimize lifetime net carbon investment costs in heterotrophic organs. Importantly, Gmax theory suggests that at least 430 million years of evolution has pushed plants to similar values of lifetime net carbon gain per body mass (Figure 1C). In other words, plants in general, regardless of their size, gain on average during their lifespans a similar amount



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Figure 1. Combining leaf optimal lifespan theory (LOLT) and metabolic scaling theory (MST) to forge Gmax theory. (A) LOLT shows that leaf net carbon gain per unit mass (or area) scales logarithmically with lifespan. As a result, natural selection favors individuals with leaves of 'optimal' lifespans that maximize marginal lifetime carbon gains (Box 1). 'Suboptimal' then means variants that live too long or too little to either maximize their marginal carbon gains or minimize their marginal carbon investment costs in heterotrophic organs (stems, roots, and reproductive organs). (B) MST offers a standard language of whole-plant carbon economics across and within species (Box 2) (C) We synthesized LOLT and MST to offer Gmax theory as a general theory of optimal plant carbon economics. The central hypothesis of Gmax theory is that natural selection favors individuals with the highest lifetime net carbon gain per body mass by maximizing leaf lifetime net carbon gains and minimizing lifetime net carbon investment costs in heterotrophic organs (see the supplemental information online). Life-history diversity emerges as additional variation in the scaling normalization factors (i.e., y-intercept; Box 3). Gmax theory shows plant life-history diversity as a myriad of viable ways of maximizing individual (Figure legend continued at the bottom of the next page.)

of carbon per body mass [8,13,34–37]. This similarity implies that natural selection maximizes leaf lifetime net carbon gain per unit mass and minimizes heterotrophic organ lifetime net carbon investment costs per unit mass in similar ways across species (Figure 1D,G). If correct, then the evolution of plant diversity is the result of natural selection favoring myriad different ways of attaining similar maximal lifetime net carbon gain per body mass. Given LOLT and MST, Gmax theory provides a basis for understanding fast–slow plant economics spectra which currently lack formal theoretical treatment [38], explaining variation in life-history across species from the same community. Gmax theory fills this role by explaining that fast species have time-discounting benefits that are ultimately as viable as slow species with higher lifetime net carbon gains per body mass and higher lifetime metabolic activities. Before concluding, we show how Gmax theory has impacts beyond plant functional ecology.

Gmax theory for the study and management of ecosystem carbon fluxes and pools

By defining the net amount of carbon that a given individual fixes during its lifespan depending on its phenotype and life-history, Gmax theory suggests that ecosystem carbon gain and storage is influenced by the range of fast–slow strategies found in a given landscape. First, estimating community-weighted means of traits linked to leaf lifetime net carbon gain per unit mass and heterotrophic lifetime net carbon investment costs per unit mass can help estimate ecosystem carbon fluxes and pools across landscapes [39]. Communities with trait means tending to the fast end of the spectrum, low C_{PCT} and C_{RCT} (Box 3), should have high **ecosystem gross primary productivity**, high ecosystem respiration, and low carbon pools because of the dominance of fast plant organs that rapidly metabolize carbon and decompose. Therefore, a practical example to accelerate ecosystem carbon fluxes in a given landscape could be planting fast growing species with low C_{PCT} and C_{RCT} values. The opposite tendencies should be found in plant communities with trait means tending to the slow end of the spectrum, high C_{PCT} and C_{RCT} . A practical example for this case would be prioritizing the conservation of large trees with high-density tissues (with high C_{PCT} and C_{RCT} values) to increase ecosystem carbon pools. As a result, Gmax theory can help ecosystem carbon conservation strategies to balance ecosystem carbon fluxes and pools via managing species by their body size and life-history. Second, community-weighted trait variances are also significant because they reflect life-history diversity correlated with environmental factors. For example, warm drylands tend to have high trait variances, whereas cool and moist environments have lower trait variances with few extremes [40]. In sum, Gmax theory suggests that plant phenotypic diversity reflects variation in traits that drive growth, survival, and reproduction across resource gradients, thus influencing the distribution of species at any given site. Plant trait variation should scale-up to the ecosystem level with fast traits being associated with landscapes with fast ecosystem carbon fluxes and small carbon pools and slow traits being associated with slow ecosystem carbon fluxes and large carbon pools [38].

Gmax theory for the study of crop productivity

One goal for meeting global food demand is to increase the productivity of key crop species [41–45]. Gmax theory helps this agricultural goal by providing tools to predict which trait combinations

lifetime net carbon gain, with slow species having higher lifetime net carbon gains per body mass than fast species. Fast species are viable because of having time-discounting benefits that are expressed in high marginal carbon gains during lifespan. (D) Gmax theory predicts that leaves have approximately similar lifetime net carbon gains per unit mass, with fast leaves having lower gains than slow leaves for the time-discount benefit of having higher lifetime marginal carbon gains during lifetime. (E,F) Gmax theory aligns with leaf economics spectrum (LES) core predictions. (G) By extending LOLT predictions to heterotrophic organs, Gmax theory also predicts that heterotrophic organs have similar lifetime net carbon costs per unit mass. Fast heterotrophic organs are cheaper but have lower lifetime metabolic activities than slow heterotrophic organs. (H,I) Gmax theory aligns with empirical research showing analogous patterns to the LES across heterotrophic organs.

or environmental conditions may limit crop productivity. According to Gmax theory, efforts to increase the current range of productivity in key crop species must focus on how to maximize lifetime net carbon gain per body mass. This maximization is translated into increases in the scaling normalization factors for leaf net lifetime carbon gain c_{PC_T} (Box 3). As for heterotrophic organs, aiming toward increasing or decreasing the scaling normalization factors for lifetime net carbon investment cost c_{RC_T} (Box 3) implies minimizing or maximizing costs in either stems, roots, or reproductive organs. Examples of these sorts of agricultural adjustments include artificially selecting variants with high leaf area indices or low self-shading architecture or both, finding the specific microenvironment that maximizes leaf CO_2 intercellular conductance and minimizes leaf photorespiration, and preferring crop species with C4 photosynthesis.

Concluding remarks

This work represents the synthesis of two optimality theories, LOLT and MST, to predict how plant life-history variation emerges in the context of selection favoring similar lifetime net carbon gains per body mass (Figure 1). From the point of view of Gmax theory, plant life-history diversity can be seen as myriad ways of achieving viable plant carbon economics [46]. Gmax theory provides a lynchpin around which optimality theory regarding the functions of leaves, stems, roots, and reproductive organs can be constructed, addressing essential questions (see Outstanding questions) regarding why natural selection should favor certain combinations of traits, resulting in covariation patterns such as the leaf [1], the wood [47], the root [48], the flower [49], and even the whole-plant economics spectra [38]. Moreover, Gmax theory implies the remarkable notion that all plants gain approximately the same amount of carbon per body mass during their lifespans regardless of their size. Most notable of all, it reveals that the vast diversity of plant form and function is a subset of possible trait combinations due to natural selection mercilessly holding all plants to account in the starkest terms of their carbon economy.

Acknowledgments

M.C. thanks CONACYT (Mexico) Becas al Extranjero fellowship award 472328 and University Fellows Award 2017 (University of Arizona). M.E.O. thanks CONACYT (Mexico) project grant A1-S-26934 and PAPIIT (UNAM) project grant IN210719. B.J. E. thanks NSF awards HDR-1934790, DEB-1457812, and DEB-1457812 (USA). A.F. thanks ANID/FONDECYT (Chile) project grant 1190900. The authors thank four anonymous reviewers for their valuable comments and the Enquist Lab for feedback on early discussions of these ideas.

Declaration of interests

No interests are declared.

Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2022.05.007>.

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Outstanding questions

What are the global means and variances for c_P , c_T , and c_R across plants? Thanks to a vast amount of evidence underlying the LES, there is more potential to answer this question for c_{PC_T} than there is for c_{RC_T} .

What are the main drivers for c_P , c_T , and c_R across plants?

Are there outliers in trait spectra 'suboptimal' spaces? Are these spaces empty because they are impossible for plants to produce developmentally? Alternatively, finding that plants can occupy these empty spaces but that these variants only occur in unusual ecological situations (including artificial selection) is consistent with the empty spaces being the result of selection.

Does 'senescence' of whole-plant individuals truly occur? Gmax theory suggests that individual plant body units have finite optimal lifespans, but these units can be constantly replaced until the individual dies. It is still unclear whether selection also favors species-characteristic lifespans, and if so, why?

Does Gmax theory 'scale-up' to the ecosystem level? Is seasonal net productivity approximately similar across ecosystems?

What is the best study system to experimentally test Gmax theory? Gmax theory assumes that natural selection has favored maximal lifetime net carbon gains per body mass across and within species for hundreds of millions of years, resulting in species falling within narrow ranges of mass-corrected lifetime net productivity (Figure 1C). Is there a way to recreate this in experiments?

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