



## Tansley review

# The metabolic theory of ecology: prospects and challenges for plant biology

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## Summary

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The metabolic theory of ecology (MTE) as applied to the plant sciences aims to provide a general synthesis for the structure and functioning of plants from organelles to ecosystems. MTE builds from simple assumptions of individual metabolism to make predictions about phenomena across a wide range of scales, from individual plant structure and function to community dynamics and global nutrient cycles. The scope of its predictions include morphological allometry, biomass partitioning, vascular network design, and life history phenomena at the individual level; size-frequency distributions, population growth rates, and energetic equivalence at the community level; and the flux, turnover and storage of nutrients at the ecosystem

level. Here, we provide an overview of MTE, by considering its assumptions and predictions at these different levels of organization and explaining how the model integrates phenomena among all of these scales. We highlight the model's many successes in predicting novel patterns and draw attention to areas in which gaps remain between observations and MTE's assumptions and predictions. Considering the theory as a whole, we argue that MTE has made a significant contribution in furthering our understanding of those unifying aspects of the structure and function of plants, populations, communities, and ecosystems.

## I. Introduction

Plant ecology encompasses a vast array of factors and processes. The survival and reproduction of the individual depend on its ability to acquire resources through photosynthesis and nutrient uptake, and to transform those resources into biomass for growth, survival, and reproduction, all the while maintaining a homeostatic environment that differs markedly from its surroundings. Add to this the combined dynamics of intra- and interspecific interactions, and spatial and temporal heterogeneity in environmental variables, and the high dimensional nature of ecology soon confounds most attempts at synthesis. Any theoretical effort that begins to distill this vast array of factors into a unifying framework would help ecology to become a more predictive science.

The metabolic theory of ecology (MTE) is an attempt to provide a general, synthetic theory for the structure and function of plants and animals that integrates across scales from cells to ecosystems (Brown *et al.*, 2004). MTE is grounded in the premise that the flux of energy at the organismal level can be predicted using basic biophysical principles of mass balance, hydrodynamics, biomechanics, and thermodynamics (West *et al.*, 1997; Gillooly *et al.*, 2001). Also central to the theory is the principle that organisms have evolved via natural selection to use resources efficiently. Applications of MTE to the plant sciences have been used to predict individual-level biological rates (e.g. primary production) and states (i.e. leaf mass, nutrient content), and the consequences of such phenomena at lower and higher levels of biological organization (Brown *et al.*, 2004). The scope of the theory continues to expand and now encompasses a large array of biological phenomena – from the dynamics of cellular organelles to global patterns in biodiversity – and subdisciplines, including plant physiology, community ecology, and ecosystem science.

Since its inception, MTE has generated considerable enthusiasm and controversy in the form of elaborations, extensions, and challenges to its theoretical precepts and empirical predictions. Theoretical and empirical evaluations point to both successes and failures of the assumptions and

predictions of the many interrelated models that comprise the theory. Consequently, there has been a vigorous debate about its merits and limitations (Dodds *et al.*, 2001; Agutter & Wheatley, 2004; Harte, 2004; Tilman *et al.*, 2004; Sousa *et al.*, 2008), a debate filled with claims and counter-claims that have served to both obfuscate and clarify what MTE is and what it is not (Kozłowski & Konarzewski, 2004, 2005; Brown *et al.*, 2005).

Here, we aim to provide a condensed review of those aspects of MTE that are most relevant to plant biologists, one that focuses on current applications of the theory, and the prospects and challenges for future applications. In doing so, we do not argue that the theory as a whole is entirely 'correct' or 'incorrect', but rather, we identify ways in which the theory is useful and areas in need of further refinement. Like all general theories, MTE is an imperfect representation of reality. As such, we evaluate the utility of MTE for both the questions it answers and the questions it raises, and show multiple examples in which MTE has provoked new empirical tests of plant biology, an undoubtedly useful outcome. In this way, we hope to emphasize that MTE offers a coarse-grained view of the world that is insightful for understanding relationships between plant form and function, and relationships between individuals, populations, communities and ecosystems.

With this objective in mind, we begin by reviewing the conceptual framework of MTE to clarify its major assumptions and mechanistic underpinnings with respect to plants. Next, we address what we perceive to be the strengths and weaknesses of MTE and of its key foundational predecessor, namely the model of West, Brown, and Enquist (WBE) (West *et al.*, 1997, 1999), which offers a derivation for the body-mass scaling of metabolic rate and related traits in plants. Following this, we discuss some of the major predictions and applications of MTE regarding the structure and function of plants at different levels of biological organization, from individuals to populations to ecosystems. In doing so, we examine the utility of this framework for explaining particular biological phenomena and discuss promising new applications of MTE, as well as prospects and challenges for extending the theory.

## II. Background and theoretical foundations: assumptions of WBE

Max Kleiber's seminal work on mammal metabolism (Kleiber, 1932) inspired many scientists to investigate if and why biological scaling relationships had exponents that were integer multiples of 1/4 (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). In particular, the whole-organism metabolic rate,  $B$ , which is equal to the gross rate of photosynthesis for a plant and the respiration rate for an animal, is often approximated by a power function of the form

$$B = B_0 M^{3/4}, \quad \text{Eqn 1}$$

where  $B_0$  is a normalization constant independent of body mass,  $M$ . This 'mystery of 1/4 power scaling in biology' (Brown & West, 2000) motivated the development of the WBE model (West *et al.*, 1997), which built conceptually on several earlier theoretical efforts (Murray, 1926; Shinozaki *et al.*, 1964; McMahon & Kronauer, 1976; Blum, 1977). The original WBE model proposes an explanation for the supposed 3/4-scaling of metabolic rate with body mass for mammals, the scaling of other rates and times related to metabolism (e.g. heart rate, blood circulation time), and the dependence of these biological rates and times on attributes of mammalian distribution networks (e.g. number of capillaries, blood volume, aorta radius) (West *et al.*, 1997).

Following this initial effort, the WBE model was adapted to the distinct physiological attributes of plants in an effort to predict the scaling of metabolic rate in relation to plant mass, and the structure and function of plant traits related to metabolism (West *et al.*, 1999). The plant model was meant to represent an average idealized vascular plant based on the idea that sublinear scaling of metabolic rates with size can be explained by the physical nature of distribution networks (Shinozaki *et al.*, 1964), namely vascular networks that deliver water and nutrients to the organelles and organs responsible for fixing reduced carbon compounds through photosynthesis (i.e. chloroplasts, leaves).

The model invokes the following simplifying assumptions with regard to geometric and mechanical constraints:

WBE1: The network is strictly hierarchical and self-similar, meaning that each segment of the vascular network branches into a fixed number of daughter branches, from trunk to petiole, with no side-branching.

WBE2: The plant has a large number of orders of branching.

WBE3: The network is 'volume-filling' such that each branch has an associated service volume.

WBE4: Branches are elastically self-similar, meaning that the ratio of a branch's length to its deflection under its own weight is constant.

WBE5: Bulk-tissue density is constant for all tissues, including those tissues composing branches and petioles.

WBE6: Branches are terete cylinders, and thus do not taper within any specific order of branching level, but may differ in diameter among different orders of branching.

WBE7: The structure (e.g. length and radius) and function (e.g. water flux, photosynthetic rate) of the terminal units of the network (e.g. petioles, leaves) do not vary with plant size.

WBE8: Vascular architecture has evolved to minimize hydrodynamic resistance along flow paths.

Many of these assumptions build upon previous work. For example, WBE1–WBE3 imply that the architecture of a vascular plant can be characterized as having a self-similar, fractal-like geometry, as proposed by Mandelbrot (1977); WBE4 was first proposed by McMahon & Kronauer (1976); C.D. Murray (1926) and D'Arcy Thompson (1942) considered WBE8. The novel and insightful contribution of the WBE model was to integrate these simplifying assumptions into a mathematical framework in an attempt simultaneously to account for physiological, biomechanical, and hydrodynamic constraints on plant form and function. Moreover, given the conceptual links to the previous model for mammalian circulation (West *et al.*, 1997), these combined models provided a potential unifying explanation for the scaling of metabolism across a broad sampling of organismal diversity.

Provided that assumptions WBE1–WBE8 are upheld, the WBE model demonstrates that the numbers of petioles, and hence total leaf mass,  $M_L$ , will scale as the 3/4 power of plant mass (see Supporting Information, Fig. S1);

$$M_L = l_0 M^{3/4}, \quad \text{Eqn 2}$$

where  $l_0$  is a normalization constant independent of plant size. Since fluxes of water, nutrients, and hence metabolic energy at the level of the petiole and leaf are assumed to be independent of plant size, the overall rate of plant metabolism will scale as predicted by Eqn 1,

$$B = M_L P_L = P_L l_0 M^{3/4}, \quad \text{Eqn 3}$$

where,  $P_L$  is the photosynthetic rate per unit leaf tissue. In Eqn 3, the 3/4-power scaling of metabolic rate reflects the fact that leaf-level photosynthesis,  $P_L$ , is independent of plant size, owing to assumptions WBE7 and WBE8, and that the quantity of photosynthetic tissue scales as  $M^{3/4}$ , owing to assumptions WBE1–WBE6. Thus, for plants, the normalization constant  $B_0$  from Eqn 1 is equal to the product  $P_L l_0$ , reflecting the combined effects of plant form, characterized by  $l_0$  in Eqn 2, and plant function, characterized by  $P_L$ , on the metabolic rate of a plant.

In practice, evaluations of the WBE model have focused largely on interspecific comparisons of phylogenetically diverse taxa that encompass a broad size range (e.g. from seedlings to sequoias) which entails the implicit assumption

(hereafter referred to as WBE9) that the core aspects of plant metabolism, vascular structure, and gas exchange are highly conserved across the higher land plants, because of a shared evolutionary history and, in some cases, evolutionary convergence (Niklas, 1994; Lambers *et al.*, 1998).

### III. Background and theoretical foundations: assumptions of MTE

The basis of the WBE model as applied to plants can be found in two foundational papers (West *et al.*, 1997, 1999). MTE grew out of these models applied to both mammals and plants, but the logic and underlying assumptions of MTE are distinct from those of the WBE model in a number of ways. Specifically, the underlying premise of MTE is that the interrelated currencies of energy and matter are linked through body size and thus provide an integrative framework with which to understand ecological processes across different scales (Brown *et al.*, 2004). The importance of energy as a biological currency has been known since at least the time of Lotka (1925), and the primary roles of body size and temperature in constraining fluxes of this currency at the individual level were established by a series of seminal works in comparative physiology (Huxley, 1932; Kleiber, 1932; Thompson, 1942; Hemmingsen, 1960).

The MTE builds on this foundational work to derive predictions based on six assumptions, which we denote as MTE1–MTE6:

MTE1: The metabolic rate of an individual, which is assumed to exhibit 3/4-power scaling, is predictably constrained by temperature through its effects on biochemical reaction rates at the level of organelles.

MTE2: The fluxes of energy and matter at the level of the individual are equal to the sums of the fluxes by the organelles (e.g. chloroplasts) and organs (e.g. leaf) that control metabolism.

MTE3: The scaling of individual demographic rates is predictable based on the constraints on the flux, storage, and turnover of energy and matter, as dictated by metabolic rate.

MTE4: The metabolic rate of an individual is independent of resource availability in the environment.

MTE5: Metabolic rate links an individual to its environment (including other organisms) by determining the rates of energy and mass exchange and transformation.

MTE6: The flux, storage, and turnover of energy and matter attributable to biota at the levels of population, community, and ecosystem are equal to the sum of the contributions of constituent individuals.

MTE1, as applied to plants, requires that the functional properties of metabolically active organelles (e.g. temperature-dependence of photosynthesis in chloroplasts) are essentially invariant with respect to body size, taxonomy, and environment. Thus, MTE1 can be viewed as an

extension of assumption WBE7. However, this first assumption does not, in fact, require a particular theoretical explanation for the scaling relationships. To date, MTE has considered 3/4-power scaling to be an empirical fact. However, MTE is robust to changes in the underlying power law relationship. MTE2, MTE5 and MTE6 all follow directly from mass and energy balance, and should not evoke controversy for that reason. However, in order to yield quantitative predictions, these three assumptions must be combined with MTE1 and MTE2.

Following MTE1, plant metabolic rate is assumed to have a fixed dependence on body size and temperature. With respect to size, MTE1 assumes that the metabolic rate of a plant,  $B$ , is proportional to leaf mass,  $M_L$ , and therefore exhibits 3/4-power scaling, as in Eqn 3. With respect to temperature, MTE assumes that plant metabolic rate exhibits the same temperature dependence at the level of both the chloroplast and the individual,  $f_c(T)$ . The importance of temperature as a determinant of metabolic rate is well established for plants and animals (Rosenzweig, 1968; Lieth, 1973; Berry & Bjorkman, 1980; Farquhar *et al.*, 1980; Raven & Geider, 1988). Thus far, MTE models have approximated the effects of temperature on photosynthesis using a Boltzmann–Arrhenius function of the form  $f_c(T) \propto \exp(-E_p/kT)$ , where  $k$  is Boltzmann's constant ( $= 8.62 \times 10^{-5}$  eV K<sup>-1</sup>),  $T$  is the inverse of absolute temperature, and  $E_p$  is a parameter that characterizes the overall magnitude of the temperature dependence (Allen *et al.*, 2005). This expression, which is a one-parameter approximation of the model of Farquhar *et al.* (1980), was obtained by imposing specific assumptions for the temperature kinetics of photosynthesis and the concentrations of CO<sub>2</sub> and O<sub>2</sub> in the chloroplast stroma (Allen *et al.*, 2005). After accounting for the effects of photorespiration on C3 photosynthesis, the calculated value for  $E_p$  ( $\approx 0.32$  eV) corresponds to only a fourfold increase in rates from 0 to 30°C. Following Eqn 3, the combined effects of size and temperature on metabolic rate (i.e. the gross rate of photosynthesis) can then be characterized as

$$B = M_L P_L = \sigma_C p_o e^{-E_p/kT} l_o M^{3/4}, \quad \text{Eqn 4}$$

where  $v_p = p_o e^{-E_p/kT}$  is the temperature-dependent rate of photosynthesis per chloroplast and  $\sigma_C$  is the number of chloroplasts per unit leaf tissue (Allen & Gillooly, 2009).

### IV. MTE at the individual plant level: metabolism, architecture and demography

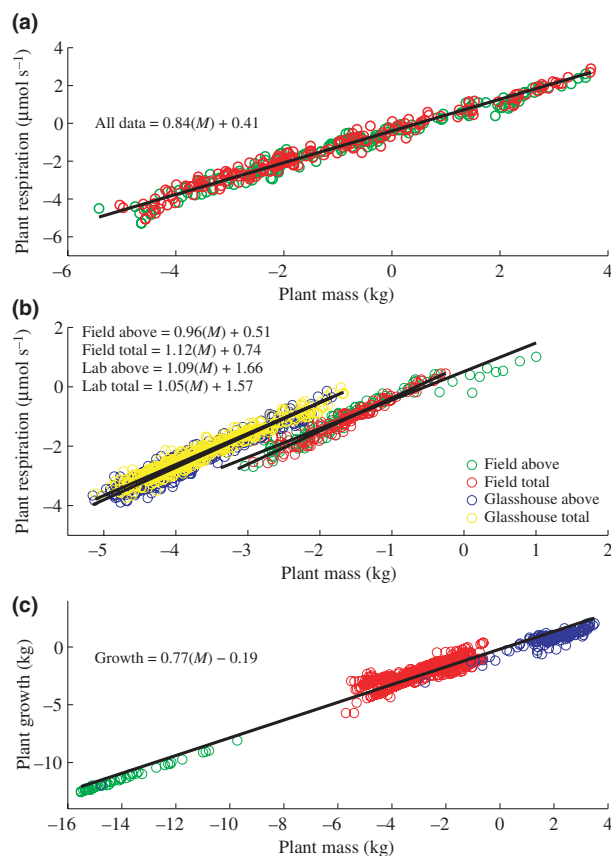
Individual plant species span over 21 orders of magnitude in mass and exhibit a dizzying array of morphological diversity. Some of the variability in morphology is itself a function of size, and the applicability of WBE2–WBE4 all increase with plant size. This is because small plants often

lack many branching generations (WBE2), often depart from volume-filling (WBE3) and are less subject to the effects of gravity than larger plants (WBE4). These departures were, to some extent, anticipated by West *et al.* (1999). Specifically, WBE anticipated that real plants may deviate from idealized assumptions by noting that ‘not all branches are subject to the same ‘biomechanical constraint’ and that there may be, ‘departures from precise volume-filling in plants such as palms, vines, ferns, grasses and saplings with few branches’. These departures have implications for intra- and interspecific tests of the theory, and several recent efforts have explored these implications for diverse plant taxa (Enquist *et al.*, 2007a; Price *et al.*, 2007), including those lacking many branching orders (Price & Enquist, 2006) and leaves (Price & Enquist, 2007). In the sections on metabolism and morphology that follow (Sections V and VI), we discuss the ramifications of some of these changes with respect to the expectations from interspecific analyses.

## V. Metabolism

At the individual level, MTE and WBE yield predictions on the gross rate of photosynthesis,  $B$ , which is equal to the sum of fluxes in respiration and biomass production. Owing to a number of technical challenges involved in measuring this quantity directly, components or proxies of plant metabolism are usually measured instead. Typically, the scaling of whole-plant metabolic rate with mass has been evaluated in one of three ways. The first method involves quantifying the amount of water fluxed per unit time in plants of varying size, usually based on stem diameter or height (Wullschlegel *et al.*, 1998; Meinzer *et al.*, 2005). Empirical tests using this first method concluded that  $B$  scaled approximately as  $M^{0.73}$  (Enquist *et al.*, 1998), a finding that was generally consistent with subsequent evaluations of whole-tree water use (Meinzer *et al.*, 2001, 2005). The second method involves measuring the amount of carbon released during dark respiration via gas exchange methods (Reich *et al.*, 2006; Mori *et al.*, 2010). These studies found that metabolism scales isometrically with mass at small sizes, perhaps as a result of isometric relationships between nitrogen and metabolism (Reich *et al.*, 2006), and converges to power-law behavior at large sizes with an exponent of 0.81, close to the proposed  $3/4$  (Mori *et al.*, 2010) (Fig. 1a,b). A third method, which used individual net growth (rather than biomass production) as a surrogate for metabolic rate (Fig. 1c) concluded that annual growth scales roughly as the  $3/4$  power of body mass for a broad diversity of species, including unicellular algae (e.g. diatoms and chlorophytes), aquatic ferns, and a variety of nonwoody and woody plants (Niklas, 1994; Niklas & Enquist, 2001).

Collectively, this empirical work suggests that plant metabolism may scale isometrically with size for small seedlings and saplings and converge to slopes at or slightly above



**Fig. 1** Scaling of whole-plant metabolism with mass. (a) and (b) are based on dark respiration, (c) is based on plant growth. Note that based on the respiration data, the scaling of metabolism is isometric for small plants, converging to negative allometry (slope < 1) for larger plants. Lines in all panels correspond to standardized major axis (SMA) regression fits. (a) Plant respiration vs fresh mass for whole plants (green circles) and above-ground mass (red circles). Data graciously provided by Mori *et al.* (2010). As reported in the text, Mori *et al.* (2010) fitted a mixed-power model to their data, which is a better fit to data. For illustrative purposes only, we fitted a simple SMA regression line to the combined above-ground and whole-plant data. (b) Respiration vs dry mass for field- and laboratory-grown plants, including measurements for whole plants (total) and above-ground components alone (above). Data graciously provided by Reich *et al.* (2006). Note original data in g converted to kg for comparison with (a). (c) Whole-plant growth (kg dry mass per plant) vs whole-plant mass (kg) including over 19 orders of magnitude in mass (data from Niklas, 2004): algae (green circles), herbs and young woody (red circles), woody (blue circles). Note the SMA regression slope 0.768 is only slightly higher than the predicted slope of 0.75.

$3/4$  for larger plants. Hence, the scaling of metabolic rates with respect to body mass exhibits some curvilinearity, particularly at the small end of the size spectrum. As mentioned earlier, one could argue that departures from  $3/4$ -power scaling towards isometry for smaller plants are not unexpected in the WBE model because datasets including seedlings and saplings are less likely to conform to WBE2–WBE4 (Enquist *et al.*, 2007a; Price *et al.*, 2007).

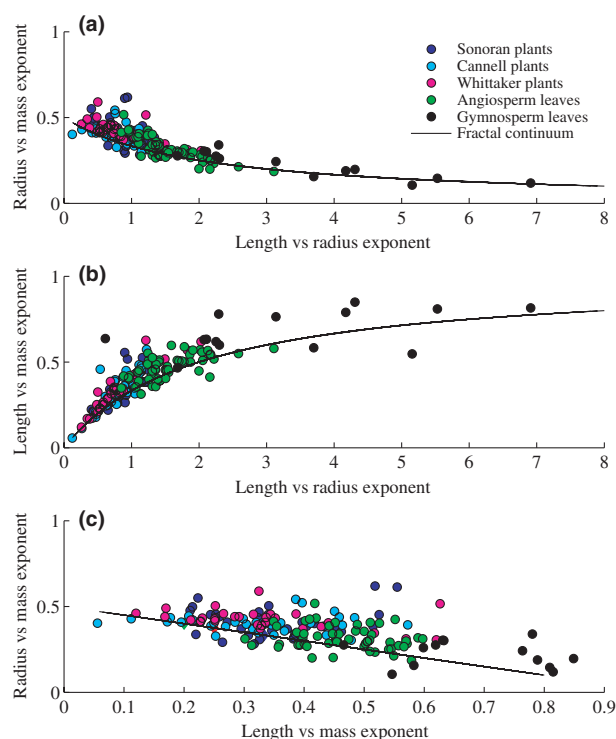
Technically, the  $3/4$ -power scaling exponent only holds in the limit of infinitely sized networks (Fig. S1; Savage *et al.*, 2008). While the authors of the WBE model recognized this fact (West *et al.*, 1999), the importance of ‘finite size’ effects in inducing deviations from power-law scaling in the WBE framework is only recently becoming fully appreciated (Savage *et al.*, 2008).

While it has long been known that temperature influences metabolism in plants, and different approaches toward correcting for temperature have been utilized (Atkin & Tjoelker, 2003), the influence of temperature specifically on the allometry of plant metabolism is an area in need of further attention (Gillooly *et al.*, 2001; Clarke & Fraser, 2004; Allen *et al.*, 2005; White *et al.*, 2006; Enquist *et al.*, 2007b). Thus far MTE has utilized the activation energy of metabolism ( $E_p$ ), referred to as an ‘effective’ activation energy, rather than a ‘true’ activation energy, because the overall effect of temperature on the rate of photosynthesis is neither predicted nor observed to be exponential (Farquhar *et al.*, 1980). Within this framework the Boltzmann–Arrhenius relationship for temperature dependence of Eqn 4 has been proposed because the effective activation energy  $E_p = 0.32$  eV provides a useful benchmark for comparison with the activation energy of respiration,  $E_R$ , which is predicted and observed to be of greater magnitude ( $E_R \approx 0.65$  eV) and similar for plants and animals (Gillooly *et al.*, 2001; Allen *et al.*, 2005).

## VI. Morphology

Building upon the aforementioned departures from WBE3–WBE4, Price *et al.* (2007) relaxed the volume-filling and area-preserving assumptions in the model and found that they could describe considerable allometric covariation between the exponents governing intraspecific plant morphology and biomass partitioning (Fig. 2a–c). This finding suggests that plant morphology is well approximated by fractal-like geometries even in instances where the elastic self-similarity and volume-filling assumptions do not hold: for example, see the work of Turcotte *et al.* (1998) for similar research on side-branching networks in biology. Consistent with this assertion, Price *et al.* (2009) found that this new, more flexible model provided a better statistical fit to data than the original WBE model, and several other general models.

These new findings serve as an illustration of how general models and WBE in particular can help to inform our biological understanding through an iterative process of model formulation and empirical observation that focuses on refining biological assumptions and quantitative predictions. Future elaborations based on a more flexible network design, biomechanical constraints, or both, might provide still further insights into the general nature of plant morphology (Niklas, 2007).



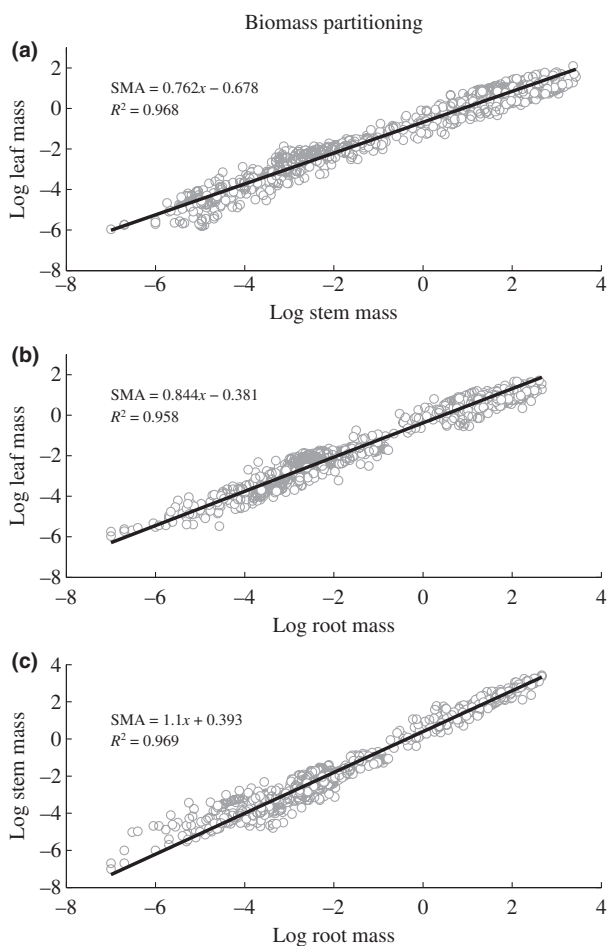
**Fig. 2** Allometric covariation of intraspecific morphology (a–c). Data from Price *et al.* (2007) and Price *et al.* (2009). The black line on each panel represents a continuum of all hierarchical fractals obtained by letting  $\alpha$  and  $\beta$  from Eqns 2 and 3 vary (Supporting Information, Fig. S1) (see Price *et al.*, 2007 for details). Note that the left end of the continuum corresponds to fractal networks that are volume-filling and area-preserving (e.g. trees). The right end of the continuum corresponds to networks with area-increasing branching that approach being one-dimensional (e.g. conifer needles). Relative agreement between model and data could be the result of changes in network structure, plant or leaf shape, or both (see Price *et al.*, 2007 for full treatment).

## VII. Biomass partitioning

In an extension of the WBE model, Enquist & Niklas (2002) derived general predictions on the partitioning of biomass within an individual among leaves ( $M_L$ ), stems ( $M_S$ ), and roots ( $M_R$ ), specifically, that  $M_L \propto M_S^{3/4}$ ,  $M_L \propto M_R^{3/4}$ , and  $M_S \propto M_R$ . These predictions were derived by combining the assumptions and predictions of WBE with the additional assumptions that hydraulic cross-sectional areas of stems and roots are equivalent (owing to the conservation of water mass flowing through a plant), and that root length and stem length are isometric. These predictions provide a basis for understanding fundamental aspects of biomass partitioning in plants, which are important for understanding how plants allocate available energy for survival, growth and reproduction.

At present, the predictions are well supported based on interspecific analysis of several compendia of biomass partitioning data (Enquist & Niklas, 2002; Niklas, 2004). For

example, as shown in Fig. 3(a)–(c), allometric relationships for biomass partitioning within a broad array of plant species, including angiosperms and conifers, herbaceous and woody species, annual and perennial taxa are generally consistent with these predictions. While these results are compelling, recent work has indicated that these relationships may be more variable under more natural conditions, with many communities exhibiting scaling relationships statistically different than  $M_L \propto M_S^{3/4}$  (Deng *et al.*, 2008). Interestingly, the mean exponent reported in Deng *et al.* is 0.80, and the exponents range from 0.47 to 1.06, the mid-point of which is 0.76. Thus, while indicative of variability in scaling exponents, these data could be interpreted as supportive of a central tendency which is close to the predicted  $3/4$ . Clearly, further studies conducted on plants growing under natural conditions would be a welcome addition to this literature.



**Fig. 3** The allometry of plant biomass partitioning (a–c). Data from K. J. Niklas (2004), plus some unpublished data also courtesy of K. J. Niklas. The biomass partitioning data are well fitted by power laws, and in reasonable agreement with theoretical predictions,  $M_L \propto M_S^{3/4}$ ,  $M_L \propto M_R^{3/4}$  and  $M_S \propto M_R$ .

## VIII. Hydraulics

The WBE model also makes specific predictions with respect to the tapering of vascular elements such that the radii of tracheids or vessel members increase in a power-law form with increasing distance from the petiole (West *et al.*, 1999). The specific profile should be one that minimizes resistance to flow, such that the total resistance along the path length is nearly invariant with respect to changes in tree height. Such tapering would permit tracheids or vessel members near the tops of trees to minimize water stress resulting from increasingly negative water potentials with increasing path length. The prediction of power-law tapering has enjoyed support even if the specific tapering exponent predicted cannot be considered universal (Anfodillo *et al.*, 2006; Weitz *et al.*, 2006; Coomes *et al.*, 2007). A recent and thorough review by Petit & Anfodillo (2009) has highlighted that while the tapering model cannot capture all of the variability observed over vascular ontogeny, it has been of significant value in focusing research in this important area of plant physiology, and providing intuitive and insightful ideas for the optimization of xylem tapering in plants.

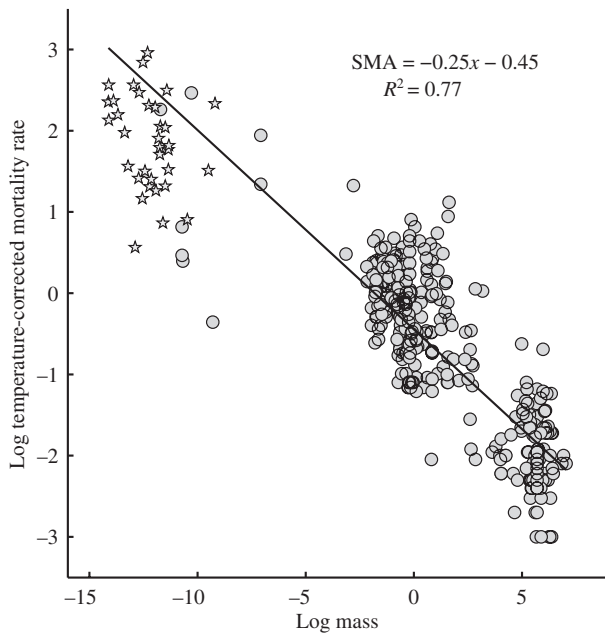
## IX. Demography

Understanding the factors that govern biological rates and times, including individual life span, birth and death rates, and rates of seed production (Shiple & Dion, 1992; Niklas, 1994; Nielsen *et al.*, 1996), have long been central questions in plant biology because of their importance for predicting a broad range of ecological and evolutionary phenomena, including population growth, competition, and natural selection.

Following MTE3, MTE assumes that life history is driven by metabolic rate, since metabolic rate fuels key biological rate processes (Gillooly *et al.*, 2002; Savage *et al.*, 2004). For example, regardless of the mechanisms responsible for the scaling of metabolic rate and its underlying functional form, MTE predicts that death and birth rates ( $D$ ) are proportional to mass specific metabolic rate,  $D \propto B/M$ . Consequently, if individual metabolic rate scales as  $M^{3/4}$ , the rates of birth and death are predicted to scale with  $M$  and  $T$  as

$$D \propto B/M \propto M^{-1/4} f_c(T). \quad \text{Eqn 5}$$

A recent empirical analysis considered the mortality rate of single-celled phytoplankton and allometrically derived mass of terrestrial plants (Marba *et al.*, 2007) (Fig. 4). The authors reported a combined scaling of approx.  $-0.25$ , consistent with the MTE and WBE models. These findings suggest that the dynamics of birth and death of highly disparate organisms adhere to the same or similar rules that are



**Fig. 4** Temperature-corrected mortality rates as a function of mass for phytoplankton (stars) and terrestrial plants (circles). Data originally from Marba *et al.* (2007). Note the observed slope for both groups, standardized major axis (SMA) is close to the predicted value of  $-1/4$  and that mass of plants was estimated based on size measurements using an allometric model.

both explicable and predictable based on the scaling of metabolic processes. The good fit of models to field mortality rate data is perhaps surprising given that the proximate mechanisms responsible for mortality may be extrinsic factors such as disease, drought, or herbivory.

## X. MTE at population, community, and ecosystem scales

Building on patterns described at the individual level, MTE has also been successful at predicting patterns at higher levels of organization. In Sections XI through XV, we consider MTE's predictions for plant population density, both generally and within a given site, and its predictions for population growth rates, and ecosystem dynamics.

## XI. Plant population density

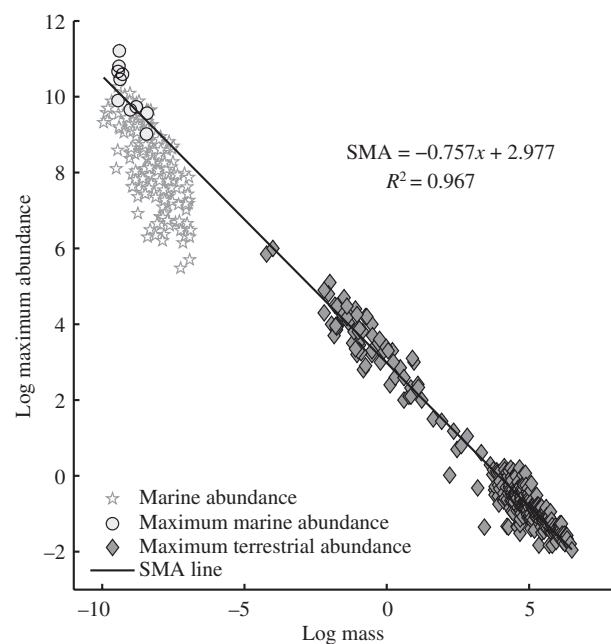
One of ecology's long-standing goals is a mechanistic understanding of the forces responsible for structuring communities (Skellam, 1951; Janzen, 1970; Connell, 1971; Tilman, 1982; Pacala, 1997; Chesson, 2000; Hubbell, 2001). Toward this goal, MTE has been modified and developed to yield models at the level of populations and communities. A significant focus of research, as applied to populations, has involved understanding the controls on population abundance (Enquist *et al.*, 1998, 2003; Brown

*et al.*, 2004; Savage *et al.*, 2004; Allen *et al.*, 2005). As currently formulated, MTE assumes that resource availability affects total biomass and abundance, but not metabolic rate, following MTE4. This simplifying assumption implies that population abundance per unit area,  $J/A$ , should exhibit the following scaling relationship to the supply rate of limiting resources in the environment (e.g. water),  $R$ , when population abundance is at equilibrium with an environment's carrying capacity (Enquist *et al.*, 1998; Savage *et al.*, 2004)

$$J/A \propto 1/B \propto M^{-3/4} f_C^{-1}(T) \propto R. \quad \text{Eqn 6}$$

This equation is useful for making comparisons among plant populations and communities comprised of individuals of identical size. It yields three potentially important predictions regarding plant abundance.

First, holding variables other than size constant, this equation predicts that population abundance per unit area should scale as  $M^{-3/4}$ . There exist broad interspecific comparisons that demonstrate that maximum phytoplankton and terrestrial plant populations are well fitted by a power function with an exponent of  $c. -0.75$  (Fig. 5). In instances where plant metabolic rate scales as  $M^{3/4}$ , the existence of  $M^{-3/4}$  power scaling for population density implies that total energy flux per unit area is independent of plant size and standing biomass, that is  $Q_{\text{Tot}} \propto B(J/A) \propto M^0$ . Hence, following MTE4–MTE6, populations comprising



**Fig. 5** Log maximum abundance as a function of log mass for marine and terrestrial plants. Simple moving average regression line fit to terrestrial data after Belgrano *et al.* (2002). Note the observed slope is very close to the predicted value of  $-3/4$ .



organisms of different sizes should be 'energetically equivalent' with respect to total energy and mass flux provided that resource availability,  $R$ , is independent of size (Damuth, 1981; Enquist *et al.*, 1998). This formulation makes the surprising prediction that a population of grasses and a population of similarly aged trees can exhibit similar rates of net primary production despite substantial differences in standing biomass. Interestingly, other recent analyses have found that the exponents describing the dependence of population density and metabolism (using leaf mass as a proxy) on plant mass may differ from 1/4-power scaling, but have roughly opposite signs, and thus covary across ecological communities as one would expect under energetic equivalence (Deng *et al.*, 2008). Thus, these findings are consistent with the hypothesis that individual metabolism is a primary determinant of population and community abundance.

Second, Eqn 6 predicts a decrease in plant abundance with increasing temperature based on assumptions MTE4 and MTE5, based on the temperature kinetics of photosynthesis in chloroplasts,  $f_C(T)$ . Finally, third, with respect to resource availability, after controlling for size and temperature, abundance is predicted to increase linearly with  $R$ . This prediction follows directly from the MTE assumption that the gross rate of photosynthesis per plant,  $B$ , is independent of resource availability (MTE4), and the assumption in Eqn 6 that abundance is at equilibrium with the supply rate of limiting resources. Recent work of Allen *et al.* (2008) provides some support for this prediction, at least qualitatively, by showing that the size-corrected population abundances of water-limited desert shrubs are positively correlated with mean annual precipitation. Evaluating this prediction is more challenging in instances where it is difficult to identify the limiting resource or where there may be co-limitation of multiple resources.

## XII. Plant population density within a site

An extension of the WBE model yields predictions on the scaling of abundance within uneven-aged forest stands at demographic equilibrium (Enquist *et al.*, 2009; West *et al.*, 2009), meaning that the overall birth and death rates are equal in every size class, and therefore that the size–frequency distribution is unchanging through time. Interestingly, this forest model predicts that declines in abundance with increasing size and canopy height adhere to a function identical in form to Eqn 6, even though the mechanistic basis differs. Specifically, in the forest model, this size distribution arises as a consequence of geometric constraints on how plants of different size are packed in an 'idealized' closed-canopy forest at steady state.

While the model has proven useful in capturing broad-scale trends in the data, deviations from  $M^{-3/4}$ -power law scaling have been found in several studies of closed-canopy

tropical forests (Coomes *et al.*, 2003; Muller-Landau *et al.*, 2006a,b), which may reflect violations of one or more assumptions in the WBE model. For example, the WBE model assumes that the only sources of mortality in a forest are size-selective competitive thinning and senescence at a fixed asymptotic adult size. In reality, large, but still growing, individuals may be particularly susceptible to other extrinsic sources of mortality owing to their greater age and higher canopy position (e.g. wind and disease) (Muller-Landau *et al.*, 2006a,b). Second, the WBE forest model makes the simplifying assumption that individuals of all size have potential access to space and that other resources are not limiting. In reality, light availability may limit plant metabolism and abundance, giving larger individuals higher in the canopy an advantage (Muller-Landau *et al.*, 2006a,b). Self-shading by larger individuals may also be important, and incidentally has been invoked to explain deviations from predicted size–metabolism scaling relationships in marine phytoplankton (Finkel, 2001).

Taken together, the first-order predictions generated by MTE models with respect to abundance are at times sufficient to describe general patterns and at times too simplistic in their current form. In the latter case, the MTE models have proven useful for providing a theoretical baseline for quantifying the relative importance of additional factors in structuring plant communities. It remains a challenge to incorporate heterogeneous resource distributions, such as light availability, into the MTE models.

## XIII. Population growth rates

Thus far, we have considered abundance predictions of MTE and WBE for populations and communities at steady state, which is a common assumption in theoretical ecology. However, MTE also yields at least some predictions regarding the properties of populations and communities that are not in steady state, as for example when populations or communities are disturbed. Perhaps the simplest of these predictions is that maximum plant population growth rates,  $r$ , should show the same size and temperature dependencies as individual metabolic rate (Savage, 2004).

$$r \propto M^{-1/4} f_C(T). \quad \text{Eqn 7}$$

This prediction arises from the assumption that a fixed percentage of total metabolic energy is devoted to growth and reproduction, irrespective of size and temperature.

From an applied perspective, predicting  $r$  may be useful for better understanding how quickly populations can respond to disturbance. Toward this goal, Anderson *et al.* (2006) found that the rate of community succession, as indexed by biomass accumulation, increased with temperature along a latitudinal gradient as expected based on the overall temperature dependence of C3 photosynthesis in

chloroplasts,  $f_c(T)$ , even after controlling for the length of the growing season, consistent with predictions arising from Eqn 7. When and whether or not body mass and temperature alone are the primary determinants of population growth rates depend highly on intra- and interspecific variability in demographic rates. Increased empirical and theoretical attention in this area will certainly help to resolve these issues.

#### XIV. Ecosystem dynamics

Ecologists have long recognized that plants play important roles in the biogeochemical cycling of key elements, including carbon, nitrogen, and phosphorus (Lotka, 1925; Redfield, 1958), but quantifying their contributions has proved challenging (Reiners, 1986; Jones & Lawton, 1995). By applying assumption MTE5, the theory provides an estimate of the flux, storage, and turnover of energy and mass at the level of ecosystems by summing across individuals comprising the biota. For example, as a result of mass and energy balance, the carbon flux per unit area,  $Q_{\text{Tot}}$ , for a plant community is predicted to equal the sum of the individual fluxes,  $Q_i$ , which are proportional to  $B$  (Eqn 4), according to assumption MTE4:

$$Q_{\text{Tot}} = (1/A) \sum_{i=1}^J Q_i \propto (J/A) \langle M^{3/4} \rangle_J f_{\text{chlor}}(T) \\ \propto M_{\text{Tot}} \langle M^{-1/4} \rangle_M f_{\text{chlor}}(T) \propto R. \quad \text{Eqn 8}$$

Here  $\langle M^{3/4} \rangle$  is the average of  $M_i^{3/4}$  for individuals (i.e.  $\langle M^{3/4} \rangle_J = (1/J) \sum_{i=1}^J M_i^{3/4}$ ), and  $\langle M^{-1/4} \rangle_M$  is the average of  $M_i^{-1/4}$  for biomass in the pool (i.e.  $\langle M^{-1/4} \rangle_M = (1/AM_{\text{Tot}}) \sum_{i=1}^J M_i^{3/4} = \langle M^{3/4} \rangle_J / \langle M \rangle_J$ ).

Finally, Eqn 8 can be rearranged to yield an expression for biomass turnover in an ecosystem:

$$q/M_{\text{Tot}} = q_0 \left( \frac{\langle M^{3/4} \rangle_J}{\langle M \rangle_J} \right) e^{-E/kT} \\ = q_0 \langle M^{-1/4} \rangle_M f_{\text{chlor}}(T). \quad \text{Eqn 9}$$

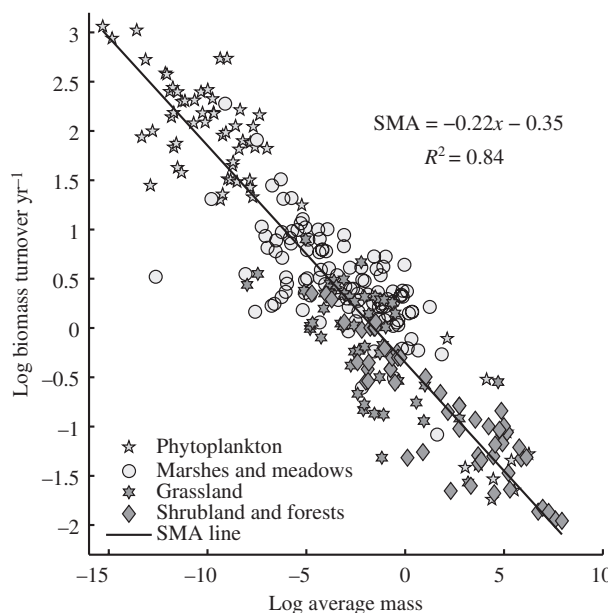
Three aspects of Eqn 8 are noteworthy. First, in order to take the sums, the size distribution of individuals is required as an input. This distribution is only predicted by MTE and WBE under certain idealized circumstances (e.g. idealized closed-canopy forests at demographic equilibrium), which can make the application of these equations challenging. Second, the average  $\langle M^{-1/4} \rangle$  is not calculated at the level of the individual; rather, it is calculated as the biomass-weighted average of  $M^{-1/4}$ , which implies that larger individuals make a proportionally greater contribution to

the overall turnover rate, and hence residence time, of elements in an ecosystem.

Eqn 9 yields two nonintuitive predictions. First, it predicts that turnover is essentially independent of resource availability, based on MTE4. Second, it predicts that the rate of carbon turnover at the level of the ecosystem exhibits a size and temperature dependence identical to that of an individual plant (Fig. 6). Consequently, differences in carbon turnover rates among biomes, which are broadly defined based on plant size, can be estimated based on differences in the sizes of constituent plants (Allen *et al.*, 2005).

Eqns 7–9 are examples of how MTE can be used to make *a priori* predictions about the flux, storage, and turnover of organic carbon in diverse plant communities by using individual-level scaling relationships and summing across individuals. Moreover, these equations show how ecosystem-level fluxes can ultimately be related to plant abundance,  $J/A$ , and biomass,  $M_{\text{Tot}}$ , the size distribution of individuals,  $\langle M^{-1/4} \rangle_M$ , and chloroplast-level fluxes ( $\propto f_{\text{chlor}}(T)$ ). As such, the mathematical formulation of ecosystem-level MTE models provides a starting point for linking ecosystem-level processes to the basic biochemistry of individual plants and thus provides a basic theoretical foundation for comparative ecosystem ecology. Moreover this approach is robust to changes in the particular values of power law exponents.

The metabolic theory of ecology has been successfully utilized in investigating ecosystem-level processes in the



**Fig. 6** Biomass turnover rates as a function of mass across various plant communities, including phytoplankton, marshes and meadows, grasslands, and shrublands and forests. Data are originally from Cebrian (1999). Note the observed slope for simple moving average regression fit,  $-0.22$ , is close to the predicted  $-0.25$ .

marine realm (Duarte, 2007; Jennings *et al.*, 2008). For example, Lopez-Urrutia *et al.* (2006) used MTE to predict how the ocean carbon balance will change in response to global warming. This change was quantitatively predicted by MTE models based on differences in the temperature dependence of photosynthesis in chloroplasts vs respiration in mitochondria (Allen *et al.*, 2005). These differences in temperature dependency have also been used to explain why algal blooms are far more prevalent in colder environments (Lopez-Urrutia, 2008) and to predict changes in aquatic producer–consumer biomass ratios in response to warming (O'Connor *et al.*, 2009).

## XV. Discussion

As shown here, the MTE seeks to integrate processes operating at the level of subcellular metabolic machinery to those acting on global resource dynamics – an ambitious goal. As a consequence, it potentially provides a theoretical framework for linking disparate subdisciplines in biology, from cell biology and physiology to ecology and evolution. In recent years, the domain of the theory has been extended considerably by combining MTE and WBE models with other theoretical frameworks designed to address questions outside the domain of MTE. For example, MTE has recently been combined with the neutral theory of biodiversity (O'Dwyer *et al.*, 2009), information theory (Harte *et al.*, 2008), life history theory (Charnov & Gillooly, 2004; Brown & Sibly, 2006), Kimura's neutral theory (Kimura, 1968; Allen *et al.*, 2006; Stegen *et al.*, 2009), food web theory (Gillooly *et al.*, 2006), resource limitation models (Niklas *et al.*, 2005; Lichstein *et al.*, 2007; Allen & Gillooly, 2009; Elser *et al.*, 2010) and predator–prey models (Vasseur & McCann, 2005; Brose *et al.*, 2006; Weitz & Levin, 2006) to yield predictions on a suite of additional processes ranging from molecular evolution to food web structure.

In many instances, the models of MTE and WBE have proven successful in yielding first-order predictions on a range of phenomena, particularly when examined over 'macro' scales, and overall, we find many of the basic premises of MTE and WBE to be grounded in well-established principles of plant biology or physiology. At the most general level, one can hardly dispute the central role of metabolism in governing plant function, the links between form and function, and the importance of considering the fundamental importance of size, temperature, and resource availability. It is also clear that the boundary conditions that govern to what extent a plant can take up and use energy for life's processes at the cellular level are constrained by the geometry and shape of its exchange surfaces and internal transport system.

However, we also see that some of the more specific assumptions and predictions of the WBE and MTE models are in need of further study, modification or replacement

(Table 1). We have pointed to a number of cases where the assumptions and predictions are not well supported. In moving forward, it is important to continue to test these for both MTE and WBE. With respect to the assumptions, further testing and evaluation are needed for WBE1–WBE7 and MTE1, MTE3–MTE4 (Table 1). For example, while a power law is clearly a reasonable first approximation to data for the scaling of metabolic rate with mass (Fig 1a,b), departures at the small end of the size spectrum require further validation and understanding (Reich *et al.*, 2006; Kolokotronis *et al.*, 2010; Mori *et al.*, 2010). With respect to the predictions, ideally it would be best to test their performance against similarly broad theories. But we are unaware of any current or past theoretical efforts that are of similar scope. Less ideal, but still valuable, are tests of the individual WBE and MTE models against alternative models that are equally general in nature and scope. To date, most tests of MTE, and particularly WBE, have evaluated model predictions, and only relatively few have evaluated model assumptions (but see McCulloh *et al.*, 2003; Meinzer *et al.*, 2005; Anfodillo *et al.*, 2006). Progress can also be made by considering approaches, such as hierarchical Bayesian methods, that allow multiple predictions to be evaluated simultaneously and that explicitly account for uncertainty in measured traits (Clark, 2005; Latimer, 2007; Dietze *et al.*, 2008; Hillebrand *et al.*, 2009; Price *et al.*, 2009). The value of this iterative process in developing the theory can already be seen both for the theory and for plant biology. In many instances, the original authors have revised or corrected aspects of their theory in response to new empirical evidence and tests of assumptions or predictions (Enquist *et al.*, 2009; West *et al.*, 2009). In other cases, critiques of the WBE and MTE models have led other groups to construct and test alternative hypotheses of plant form at the individual to ecological scales (Muller-Landau *et al.*, 2006a).

Significant progress can be made in the future by incorporating additional factors into the models of WBE and MTE. In particular, further consideration of the size-dependent nature of morphological scaling and an explicit consideration of the space individual plants occupy would be a welcome addition. Moreover, MTE has not explicitly incorporated dynamic resource availability into the models in any general form (see reviews by Allen & Gillooly, 2009; Elser *et al.*, 2010). To a large degree, this will entail integrating MTE with theories that deal with the elemental stoichiometry of biomass and of resource in the environment. In recent years, we have seen significant progress in this regard (Niklas *et al.*, 2005; Lichstein *et al.*, 2007). These recent studies combine resource-based models of plant form and function with energetic-based models. The result is models that have much greater predictive power, particularly for addressing important environmental challenges faced by society.

**Table 1** A list of some research priorities toward a fully integrative model of plant form and function across scales

Research priority	Area	Literature resources
Thorough descriptions of xylem and branching architecture across branching generations in plants	Network architecture	Honda (1971); Horn (1971, 2000); Leopold (1971); West <i>et al.</i> (1997, 1999); Koontz <i>et al.</i> (2009)
Incorporation of phloem network into models of vascular architecture	Network architecture	Lough & Lucas (2006); Mencuccini & Holttla (2010)
Incorporating root network structure and function in whole-plant models	Network architecture	Ennos (1997); Doussan <i>et al.</i> (1998); Jackson <i>et al.</i> (2000); Pages <i>et al.</i> (2004)
Further empirical and theoretical understanding of the space-filling nature of plant growth and its dependence on environmental factors such as light or water limitation	Network architecture	Mandelbrot (1978); Morse <i>et al.</i> (1985); Tatsumi <i>et al.</i> (1989); Zeide & Pfeifer (1991); Fitter & Strickland (1992); Neilson <i>et al.</i> (1997); Eshel (1998); McLellan & Endler (1998); Ozier-Lafontaine <i>et al.</i> (1999); Bailey <i>et al.</i> (2004a); Muller-Landau <i>et al.</i> (2006a,b); Adams <i>et al.</i> (2008); Purves <i>et al.</i> (2008)
Evaluation of the utility of branching hierarchies (e.g. Tokunaga) for describing the side branching nature of real plants	Network architecture	Leopold (1971); Turcotte <i>et al.</i> (1998); McConnell & Gupta (2008)
Model refinement to incorporate plants with photosynthetic stems	Network architecture	Adams & Strain (1969); Niklas (2002); Price & Enquist (2006)
Incorporating network properties of leaves into models of whole-plant hydraulics	Hydrodynamics	McCulloh <i>et al.</i> (2004); McCulloh & Sperry (2005); Sack & Holbrook (2006); Price & Enquist (2007); Coomes <i>et al.</i> (2008); Noblin <i>et al.</i> (2008); Sack <i>et al.</i> (2008); Katifori <i>et al.</i> (2010)
Examining the tapering profile of plants growing under different hydrodynamic regimes	Hydrodynamics	Anfodillo <i>et al.</i> (2006); Weitz <i>et al.</i> (2006); Mencuccini & Holttla (2007); Petit & Anfodillo (2009)
Increased understanding of the dependence of metabolic organelle form, function and number on ecological and/or environmental factors	Leaf Traits	Walters & Horton (1995); Bailey <i>et al.</i> (2004b)
Characterization of the invariance (or lack thereof) of gross leaf traits (size, petiole dimensions) across a broad spectrum of plant taxa differing in whole-plant size	Leaf traits	Meinzer (2003); Niklas <i>et al.</i> (2007); Xiang <i>et al.</i> (2009); Liu <i>et al.</i> (2010)
Mechanistic understanding of the scaling of metabolism in unicellular phytoplankton	Individual metabolism	Patterson (1992); Beardall <i>et al.</i> (2009)
Increased understanding of the influence of temperature on whole-plant metabolic rate	Individual metabolism	Atkin <i>et al.</i> (2007); Enquist <i>et al.</i> (2007); Hogue <i>et al.</i> (2010)
Further work characterizing the body size scaling of whole-plant metabolic rate	Individual metabolism	Enquist <i>et al.</i> (1998); Meinzer <i>et al.</i> (2005); Reich <i>et al.</i> (2006); Hogue <i>et al.</i> (2010); Mori <i>et al.</i> (2010)
Further understanding of the allometry of seed production and allocation in plants and the relationship to plant metabolism	Individual metabolism	Shipley & Peters (1990); Shipley & Dion (1992); Sugiyama & Bazzaz (1998); Westoby <i>et al.</i> (2002); Niklas & Enquist (2003); Bonser & Aarssen (2009)
Analysis of stoichiometric relationships among N, P and C and their influence on plant growth rates	Resources/stoichiometry	Sterner & Elser (2002); Gusewell (2004); Matzek & Vitousek (2009); Elser <i>et al.</i> (2010)
Further understanding of element/biomass allocation in different plant parts	Resources/stoichiometry	Reekie & Bazzaz (1987); McConnaughay & Coleman (1999); Poorter & Nagel (2000); Enquist & Niklas (2002)
Further understanding of the different turnover rates of plant parts their stoichiometry and their size and/or temperature dependence.	Resources/stoichiometry	Shaver & Chapin (1991); Hobbie & Chapin (1998); Gill & Jackson (2000); Gusewell (2004); Elser <i>et al.</i> (2010)
Better understanding of relationship between short-term and long-term respiration in plants	Acclimation	Atkin & Tjoelker (2003); Allen <i>et al.</i> (2005); Atkin <i>et al.</i> (2007)
Better understanding of acclimatization response in plants with respect to temperature	Acclimation	Dewar <i>et al.</i> (1999); Tjoelker <i>et al.</i> (2001); Atkin & Tjoelker (2003); Atkin <i>et al.</i> (2007)
More characterizations of the dependence of plant demographic rates on size and temperature	Population/community dynamics	Gillooly <i>et al.</i> (2002); Savage <i>et al.</i> (2004); Marba <i>et al.</i> (2007)
Further characterizations of the relationship between size and abundance within and across communities	Population/community dynamics	Coomes <i>et al.</i> (2003); Muller-Landau <i>et al.</i> (2006); Enquist <i>et al.</i> (2009); West <i>et al.</i> (2009)
Better general understanding of how rates of survival, individual and population growth are controlled by the effects of plant size, temperature, and resource availability	Population/community dynamics	Gillooly (2002); Savage <i>et al.</i> (2004); Marba <i>et al.</i> (2007); Allen & Gillooly (2009); Elser <i>et al.</i> (2010)

The literature resources cited here represent only a sample of contributions toward each priority. The literature resources are available in Supporting Information, Table S1.

Thus, to close, we find MTE to be useful for investigating a broad range of phenomena in plant biology. But it should not be viewed as a 'theory of everything'. While its domain is clearly expanding, there are limitations in both its scope and predictive power. By design, it is intended to provide first-order predictions that identify the central tendencies of form and function in plants by using deliberately oversimplified models. This broad-scale theoretical approach will invariably lead to a healthy tension with those investigators addressing questions at finer scales. These alternative approaches represent different scales of inquiry and different scientific approaches that can inform one another. As George Bartholomew (1966) once stated:

...members of each specialty tend to feel their work is fundamental and that of others, although sometimes technically ingenious, is trivial or peripheral to understanding truly basic problems. The familiar resolution to this problem is sometimes difficult to accept emotionally. That is, there are a number of levels of biological integration and each level offers unique problems and insights; each level finds its mechanisms in the levels below, and its significances in the levels above.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Detailed derivation of WBE theory.

**Table S1** A list of some research priorities toward a fully integrative model of plant form and function across scales and the literature resources: the literature resources cited here represent only a sample of contributions toward each priority

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