

# LAND PLANTS: NEW THEORETICAL DIRECTIONS AND EMPIRICAL PROSPECTS

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### SUMMARY

**1** Scaling relationships are observed at multiple levels of plant biology. Metabolic scaling theory, which integrates the West, Brown, and Enquist network model (WBE), the metabolic theory of ecology (MTE), other existing network theories, and empirical knowledge, offers a unified framework to mechanistically connect scaling phenomena.

**2** Over the last decade, metabolic theory has rapidly developed, matured, and evolved. Several critiques have raised important questions, some of which have been incorporated into new versions of the theory and some of which have been addressed and shown to be incorrect. Some critiques have suggested metabolic theory is incomplete or perhaps wrong; others have noted variation in scaling exponents and have questioned the ability of the theory to account for this variation. These critiques have mainly focused on quantifying scaling exponents but not the hypothesized underlying mechanisms generating scaling.

**3** A review of the foundations of metabolic theory as applied to botany shows how it is not a completely new theory as presumed by several of its critics. Instead, it builds upon and unites several long-standing lines of botanical investigation.

**4** We show that the theory can address several criticisms and become more predictive by relaxing many of the secondary or optimizing assumptions presented in the original WBE model (West et al. 1997).

**5** An important insight is that extensions of the theory make quantitative predictions for botanical scaling exponents and scaling normalizations. The origin of their values is shown to be due to a handful of quantifiable functional traits. These traits appear to be central in regulating the scaling of whole-plant metabolism and growth and are key for connecting variation in the environment with coexisting phenotypes and for developing a more quantitative plant ecology.

**6** We show that a mechanistic understanding of the allometric exponent and normalization lays the foundation by which to scale from plant cells to ecosystems. Elaboration of the original theory now encompasses three aspects of plant form and function: branching geometry/architecture, variation in functional traits, and how differential selection can act on these traits to optimize plant performance in differing environments.

## 14.1 INTRODUCTION

Since the pioneering work of Julian Huxley (Huxley 1932), questions concerning how natural selection influences specific traits within integrated phenotypes have been a prominent focus in comparative biology (Coleman et al. 1994; Murren 2002). The phenotype is a constellation of traits that often covary with each other during ontogeny. Further, organism size is a central trait that influences how most biological structures, processes, and dynamics covary with each other.

Being able to scale from specific traits of organisms to whole-organismal performance is a central question not only in plant physiological ecology but also in population biology, and community and ecosystem ecology (Suding and Goldstein 2008; Lavorel et al. 2011). For example, plants dominate the flux of carbon on the planet (Field et al. 1998; Beer et al. 2010). This flux ultimately reflects spatial and temporal variation in the traits that govern plant metabolism. Nonetheless, our ability to accurately predict spatial and temporal variation in autotrophic carbon flux remains a continuing challenge (Moorcroft 2006). In order to begin to predict and “scale up” spatial and temporal variation in the autotrophic metabolism – from individuals up to ecosystems – one must link the diversity of botanical form with variation in plant function (Moorcroft et al. 2001).

This chapter outlines how, over the last decade, metabolic scaling theory, as applied to plants, has rapidly developed and matured. The original assumptions and predictions of this theory for the scaling of plant metabolic rate with plant size were given by West, Brown, and Enquist (1999b; the WBE2 model), and for how the scaling of plant metabolism ramifies to ecology were given by the metabolic theory of ecology (Enquist et al. 1998; Brown et al. 2004). It is now becoming clear that several parts of the theory appear to be useful while other parts have needed revision. There is a need to provide a more biologically realistic theory capable of more fully incorporating a diversity of form and function. Here we argue that metabolic scaling theory provides a rich framework and a quantitative roadmap to then scale up from anatomy and physiology cells to ecosystems. Further, elaboration of WBE2 in plants has shown that it is unique in being able to explicitly identify the key traits necessary to measure in order to make explicit quantitative scaling predictions.

Here we focus on the foundations of metabolic scaling theory (WBE2 and MTE) as applied to plants. Specifically, our goal is to clarify the road forward for

developing a more predictive plant ecology but based on a trait-based metabolic theory. While we briefly touch on the role of temperature, we mainly focus on the key plant traits (which may have temperature dependencies). In doing so this chapter has five specific goals. First, we show that metabolic scaling theory as applied to plants actually has its basis in several seemingly disparate but related theoretical developments and empirical findings. Together, these lines of research form the foundation for a predictive trait-based framework for the scaling of botanical phenotypes and enable one to scale up to ecology. Second, we review development and debates of botanical scaling since the original formulations of WBE and MTE. Third, we provide a framework for a botanical scaling synthesis. This framework focuses on the origin of botanical scaling exponents and normalizations and allows one to account for ecological variation. Fourth, we show how this framework provides a framework for scaling from plant cells to populations and ecosystems. Lastly, we present several questions and challenges for moving forward.

## 14.2 PLANT SCALING: HISTORICAL OVERVIEW

Perhaps the most important achievement of metabolic scaling theory is the integration of disparate lines of botanical investigation under a common mechanistic framework. However, several critics of application of MTE to plants have assessed it as a completely separate theory (Coomes 2006; Petit and Anfodillo 2009). It needs to be emphasized that the WBE2 model or even its application to ecology (e.g., the metabolic theory of ecology, MTE) does not “come out of the blue.” Both start with and are grounded in several foundational insights that arguably have formed a theoretical foundation for botanical scaling. This foundation can be traced to several separate lines of investigation that are the basis for much comparative botany and plant ecology (Westoby 1984; Niklas 1994a; Westoby and Wright 2006; Falster et al. 2011).

### 14.2.1 Allometric scaling

How organismal shape and function changes as size increases – allometry – has a substantial research history, and the similarity of many allometric scaling

relationships across diverse taxa has suggested to many the promise of a unified scaling framework for biology (e.g., Huxley 1932; Thompson 1942; see also Peters 1983; Schmidt-Nielsen 1984; Niklas 1994b, 2004). In particular, organismal size appears to be a central organismal trait. Size influences nearly all aspects of structural and functional diversity by influencing how several other traits and whole-organism properties scale. Most size-related variation can be characterized by allometric scaling relationships of the form

$$Y = Y_0 M^\alpha \quad (14.1)$$

where  $Y$  is the variable or trait of interest and  $Y_0$  is a normalization constant that may vary across taxa and environments. An allometric approach has been a part of the botanical literature since 1927 with the foundational studies of Pearsall and Murray (Murray 1927; Pearsall 1927). As is discussed below, the central contribution of the WBE model was to offer a mechanistic theory for the origin of *both*  $\alpha$  and  $Y_0$ .

#### 14.2.2 Relative growth rate and trait-based literature

Plant ecologists have been notably successful in predicting variation in plant relative growth rate or RGR (Hunt 1978; Lambers et al. 1989; Poorter 1989). This theory sought to identify and link together fundamental traits, building on a long line of research going back to Blackman (Blackman 1919). Blackman detailed a “law of plant growth” based on the central assumption that it is directly proportional to leaf area, assuming that carbon assimilation per unit leaf mass is constant. Consequently, whole-plant net biomass growth rate,  $dM/dt$ , should be directly proportional to total plant photosynthetic leaf area or leaf biomass,  $M_L$  (see also Niklas and Enquist 2001; Koyama and Kikuzawa 2009), where

$$\frac{dM}{dt} = \dot{M} = \beta_A M_L \quad (14.2)$$

where  $\beta_A$  is an allometric normalization and  $M_L$  is the net biomass produced per unit leaf mass. Plant relative growth rate has traditionally been shown (Hunt 1978; Lambers et al. 1989; Poorter 1989) to be influenced by three key traits: (1) leaf net carbon assimilation rate

(NAR, the carbon gain per unit area of leaf,  $\text{g cm}^{-2} \text{t}^{-1}$ ); (2) specific leaf area (SLA, the leaf area per unit mass,  $a_L/m_L$ ,  $\text{cm}^2 \text{g}^{-1}$ ); and (3) leaf weight ratio (LWR, the ratio of total leaf mass to total plant mass,  $M/M_L$ ). Dividing  $dM/dt$  by total mass gives the relative growth rate  $\text{RGR} = (dM/dt)/M = \text{NAR} \times \text{SLA} \times \text{LWR}$  (Hunt 1978). Thus, the allometric normalization for equation 14.2 can be shown to originate in two key plant traits as  $\beta_A = \text{NAR} \times \text{SLA}$ . Below (section 14.5) we show that this decomposition of RGR is consistent with the WBE model but still is incomplete in terms of the critical traits that influence growth.

#### 14.2.3 Pipe model

In two novel papers, Shinozaki et al. (1964a, 1964b) proposed a theory for the origin of several plant allometric scaling relationships. The pipe model is unique as it provided, for the first time, a hypothesis for how changes in plant size will govern scaling the total number of leaves and total plant biomass. The pipe model implicitly assumes, as point (2) above, that growth dynamics are driven by the total number of leaves. Each leaf is supplied by a given number of xylem “tubes” that extend from the leaf down to the trunk (see Brown and Sibby, Chapter 2, Fig. 2.2). As these “tubes” or “pipes” diverge at branching junctions the dimensions of the distal branches must change in proportion to the number of leaves. As the tree grows, some branches and twigs are shed so some pipes then turn into disused pipes that lose their connection to the foliage, stop growing, and become embedded in the woody structure, creating heartwood or non-conducting tissue. This basic model predicts the total number of leaves,  $n_L$ , distal to a branch of a given radius  $r$ , as  $n_L \sim r^2$ . Thus, the pipe model predicts that the cross-sectional area of the branching network is “area preserving” so that the total number of branches,  $N$ , distal to a given branch of radius  $r$ , scales inversely as  $N \sim r^{-2}$ . Further, the total above-ground biomass,  $M$ , will scale as  $M \sim r^{8/3}$ . The pipe model can be seen as providing perhaps the most simple model of the allometry of plant form and function that makes a number of predictions for whole-plant scaling relationships (see Table 14.1). The WBE model builds upon the pipe model but importantly adds several further assumptions for how selection has shaped the scaling of the external and internal vascular branching networks (Savage et al. 2010; Sperry et al. in preparation; von

**Table 14.1** Predicted scaling exponents for physiological and anatomical variables of plant internal networks as a function of branch radius ( $r_{ext,k}$ ) for the pipe model, the 1999 WBE model, and the Savage et al. (2010) model. Observed values for average cross-species scaling exponents (mean, 95% confidence intervals using standardized major axis (SMA) regression) are shown for literature data and measurements for oak, maple, and pine.

Internal network property	Pipe model (1964)	WBE model (1999) exponent for $r_{ext,k}$	Savage et al. (2010) model exponent for $r_{ext,k}$	Observed average interspecific exponent from the literature for $r_{ext,k}$	Observed average intraspecific exponent for all measured trees for $r_{ext,k}$
Packing (conduit frequency versus conduit radius, $r_{int,k}$ , NOT branch radius)	0	0	-2	-2.04 (-2.74, -1.34)	-2.16 (-3.35, -0.97)
Conduit radius taper ( $r_{int,k}$ )	0	$1/6 \approx 0.17$	$1/3 \approx 0.33$	0.27 (0.20, 0.34)	0.29 (0.08, 0.50)
Number of conduits in branch segment ( $N_{int,k}^{seg}$ )	2	2	$4/3 \approx 1.33$	n.d.	1.19 (0.86, 1.52)
Fluid velocity ( $u_k$ )	0	-1/3	0	n.s.	n.m.
Conducting-to-non-conducting ratio	0	1/3	0	n.d.	0.00 (-0.88, 0.88)
Network conductance ( $\kappa_k$ )	1/2	2	<b>1.84 (finite)</b> <b>2 (infinite)</b>	1.44 (Meinzer et al. 2005)	n.m.
Branch segment conductivity ( $K_k$ )	0	$8/3 \approx 2.67$	$8/3 \approx 2.67$	2.78 (Meinzer et al. 2005)	n.m.
Leaf-specific conductivity ( $K_k/N_{leaves}$ )	0	$2/3 \approx 0.67$	$2/3 \approx 0.67$	2.12 (-1.38, 5.62)	n.m.
Volume flow rate ( $Q_k$ )	1/2	2	2	1.77 (1.38, 2.16)	n.m.
Total number of branches	-2	-2	-2	-2.14 (-2.34, -1.95) (West et al. 2009)	
Pressure gradient along branch segment ( $\Delta P_k/l_k$ )	0	-2/3	-2/3	n.d.	n.m.
Total biomass, $M$	8/3	8/3	8/3	2.62 (Enquist 2002)	2.64 (Pilli et al. 2006)

n.d., no data found; n.s., non-significant; n.m., not measured.

Allmen et al. in preparation). Indeed, these recent elaborations and rephrasing of the theory go beyond resolving problems with WBE and WBE2.

The MTE model appears to accurately predict many attributes of vascular plants and provides a more realistic characterization of plant structure and function than previous models such as the pipe model. A com-

parison between allometric predictions with the original pipe model (Shinozaki et al. 1964a, 1964b) reveals several important differences between the more recent scaling models. The pipe model does not explicitly include biomechanical constraints, nor allow for the presence of non-conducting tissue. More critically, it does not incorporate the paramount problem of total

hydrodynamic resistance increasing with increasing path length from root to leaf. Both WBE and Savage et al. build upon certain aspects of the pipe model (as reflected in similar scaling exponents for some plant traits) but importantly these models invoke additional selective drivers on whole-plant form and function not included in the pipe model. For hydraulic conductance Savage et al. calculated the predicted exponent based on a finite size network (a network with realistic range of branching generations) and infinite network (a network with an infinite number of branching levels).

#### 14.2.4 Exchange surfaces and the classification of plants based on branching architecture

There has been a long tradition in botany of searching for general principles of plant form and function through the way selection has operated on the surface areas where resources are exchanged with the environment. For example, in 1930, Bower concluded that those who search for general principles shaping plant evolution will find that “the size-factor, and its relation to the proportion and behavior of the surfaces of transit will take a leading place” (Bower 1930, p. 225). Bower hypothesized that understanding how natural selection has shaped the scaling of resource exchange surfaces as plant size increased would lead to an understanding of size-related scaling relationships in botany. This hypothesis has been extended in the more recent work of Karl Niklas who has shown that a few branching traits can form the basis for the diverse architectures of plants (Niklas 1982, 1997). The search for general principles that have shaped plant branching architecture and vascular networks has been fundamental to understanding the integration of the plant phenotype (Horn 1971). Interestingly, only a few branching “network” or architectural designs exist in all vascular plants (Hallé et al. 1978; Niklas 1982). This surprising fact suggests that perhaps similar equations, but with different parameter values, have governed the evolution of botanical form and diversity (see Niklas 1997). As is argued in WBE and MTE, the principles of space-filling and area-preserving branching appear to characterize plant branching geometries and the way organisms fill space and compete for limiting resources. Further, a focus on a few similar branching traits also provides a central component of the development of WBE2.

#### 14.2.5 Models on plant hydraulics

A long-standing central question in plant functional biology focuses on how plants are able to transport water and nutrients to such impressive heights (see Zimmermann 1983; Ryan and Yoder 1997). The focus has been to understand how physical and selective processes govern fluid flow within the vascular system and how they influence the evolution of xylem anatomy (e.g., Huber 1932; Huber and Schmidt 1936; Zimmermann and Brown 1971; Zimmermann 1978; Tyree et al. 1983; Tyree and Sperry 1988; Tyree and Ewers 1991; Sperry et al. 1993; Comstock and Sperry 2000). These “resistance-capacitance” models use Ohm’s Law to show how anatomical and physiological attributes of plants and their environment influence the water potential gradient from root tips to leaves and the rate of fluid transport throughout the individual (Van den Honert 1948; Jones 1978; Smith et al. 1987; Tyree and Sperry 1988; see also Jones 1992; Schulte and Costa 1996). These models link how differences in the local environment (e.g., drought) can influence xylem flow resistance and vulnerability to cavitation through differences in tissue (wood) density and xylem conduit size (Hacke et al. 2001). As we show below, many of these hydraulic traits are central to the WBE model. Further, differential selection across differing environments, as reflected by variation in hydraulic traits (tissue density and xylem conduit size), will ramify to constrain the scaling of plant productivity and ecological dynamics within MTE.

#### 14.2.6 Models of plant geometry, competition, demography, and the thinning law

In 1963 Yoda et al. showed that most plant populations and forest stands exhibit a negative relationship between size and number of plants. The self-thinning rule describes how this relationship is generated by plant mortality due to competition in crowded, even-aged (sized) stands (Yoda et al. 1963). Self-thinning is the label applied to density-dependent mortality due to competition (Harper 1977). Yoda et al. argue that three basic principles shape many dynamics in plant population and community ecology (Yoda et al. 1963): (1) there is an upper limit or “constraint” on the total leaf area or biomass that can be supported given a certain number of plants; (2) under this constraint, mortality



(self-thinning) is caused by the growth rates of competing individuals; (3) the inverse relationship between size and density is general and originates from an equally general rule of how plant morphology scales with plant size. Similarly, “demographic theory” (Holsinger and Roughgarden 1985; Kohyama 1993 and references therein) has shown how the distribution of sizes in a plant population or community must ultimately reflect the outcome of size-dependent growth and mortality rates. As shown below, MTE applied to plant populations and communities builds upon these arguments. It shows how the scaling of size and number of individuals within populations and ecological communities is constrained by the geometry of fractal-like branching architectures. Further, it argues that, under resource steady state, the allometric scaling of resources use (metabolism) then constrains the scaling of turnover and mortality of individuals.

As shown below, metabolic scaling makes a modest number of additional assumptions in order to integrate each of these theories and insights into a common theoretical framework capable of making detailed quantitative predictions. In doing so it provides unique insight into how natural selection has guided the evolution and diversity of plant form and function (e.g., see Niklas 1997; Shipley 2010). As we discuss below, a mechanistic understanding of the allometric exponent  $\alpha$  and normalization  $Y_0$  lays the foundation by which to scale from plant cells to ecosystems. Specifically, the origin of both  $\alpha$  and  $Y_0$  encompass how selection has acted on these traits to optimize plant performance in differing environments (e.g., Norberg et al. 2001). Applying additional assumptions at the ecological scale then forms the basis for the metabolic theory of ecology (MTE, Brown et al. 2004) which then enables a series of additional predictions for the ramification of the scaling of metabolism and metabolic traits.

### 14.3 EXAMPLES OF BOTANICAL SCALING: FROM ANATOMY AND PHYSIOLOGY TO ECOSYSTEMS

Since the publication of the original WBE2 model for plants (West et al. 1999b) numerous papers have documented scaling relationships associated with metabolism. Other papers have elaborated metabolic theory. Scaling relationships are observed at multiple botanical levels. The similarities in scaling exponents (often

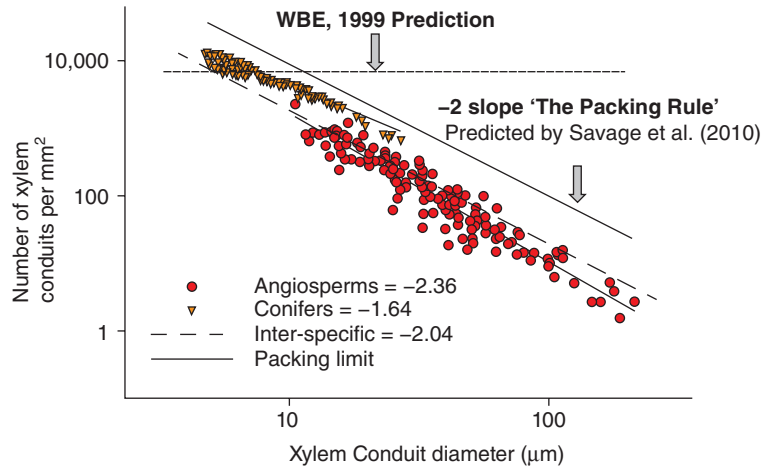
quarter-powers, so  $3/4$ ,  $-3/4$ ,  $1/4$ ,  $3/8$ , etc. when expressed as a function of size or  $-2$ ,  $2$ ,  $2/3$ , and  $8/3$  when expressed as a function of stem radius). Remarkably, scaling relationships are observed from the cellular to the ecosystem level. In the interest of space we focus on a few examples to give a sense of the breadth of patterns found.

#### 14.3.1 Within-plant scaling relationships

Many allometric scaling relationships are observed in plants (Niklas 1994b). Robust scaling relationships within the internal vascular network of plants ultimately control the scaling of whole-plant water use and carbon flux. Figure 14.1 shows an inverse relationship between the total number and size (diameter) of the xylem conduits in a branch. This relationship holds within plants as well as across diverse taxa. It is known as the “packing rule” (Sperry et al. 2006). In general the number decreases as the inverse square of diameter. Several other scaling relationships are associated with variation in the dimensions of internal vascular (xylem) anatomy and external branching architecture. Several of these relationships are reported in Table 14.1 (see also West et al. 1999b; Savage et al. 2010).

#### 14.3.2 Whole-plant scaling relationships and the partitioning of biomass and production

Papers by Niklas and Enquist (2002a) and Enquist et al. (2007c) have shown that interspecifically, whole-plant rates of production scale with exponents indistinguishable from  $3/4$  across Angiosperms and Gymnosperms (Fig. 14.2; see also Ernest et al. 2003). Similarly, total leaf area scales as the square of branch diameter (Fig. 14.3A). Until relatively recently, the general principles underlying how plant metabolic production is allocated between above- and below-ground compartments was unclear (Bazzaz and Grace 1997). As shown in Figure 14.3, biomass allocation is a size-dependent phenomenon ultimately controlled by the scaling of metabolism and growth rate. Enquist and Niklas derived the inter- and intraspecific scaling exponents for leaf, stem, and root biomass at the level of the individual plant (Enquist and Niklas 2002a; Niklas and Enquist 2002b).



**Figure 14.1** A plot showing the “packing rule” in Angiosperm and Gymnosperm plants. The relationship is measured by counting the frequency of xylem conduits and the conduit radius within and across branches. The relationship across each group varies approximately inversely with the square of conduit radius. This packing rule contradicts the WBE model’s assumption (horizontal dotted line) that conduit frequency remains unchanged as conduit radii taper, decreasing in size from trunk to terminal twig. Selection for hydraulic safety and efficiency considerations have been proposed to underlie the packing rule, suggesting new theory is needed to accurately describe vascular architecture. Data from Sperry et al. (2008) by permission of John Wiley & Sons, Ltd.

### 14.3.3 Scaling relationships in plant ecology

Several authors have reported scaling relationships at the level of plant populations or forest stands. Several of these relationships appear to be remarkably general across diverse environments and taxa. For example, Figure 14.4 shows community size distributions for two forests – one a tropical forest with about 100 species and the other a temperate forest with 15 species. Despite the difference in physiognomy and species composition, scaling of number of stems with size is similar. Further, Figure 14.5 shows that the rate of mortality or turnover of individuals scales inversely with size. A global sample of forest plots suggests that these ecological relationships may be general (Enquist and Niklas 2001; Enquist et al. 2009).

### 14.3.4 Scaling relationships at the level of the ecosystem

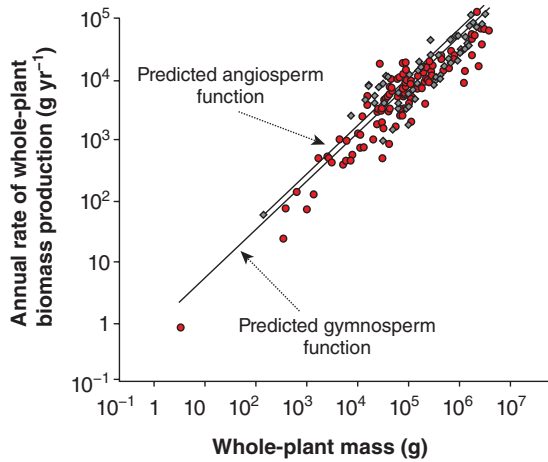
A recent novel empirical insight is the documentation of ecosystem-level scaling relationships. Two examples are given in Figure 14.6. First, plotting whole-ecosystem biomass of plants (autotrophic biomass) versus the annual net primary production reveals a

scaling exponent significantly less than  $3/4$  (Kerkhoff and Enquist 2006). The shallow slope indicates that the NPP per unit biomass across ecosystems actually decreases as phytomass increases.

Below we discuss how recent developments in metabolic scaling theory not only can make sense of these relationships but also show how they are interconnected with each other and are influenced by a handful of functional traits at the organismal level.

## 14.4 ORIGIN OF BOTANICAL SCALING EXPONENTS: WEST, BROWN, AND ENQUIST MODEL

MTE rests upon the original network theory proposed by West, Brown, and Enquist in 1997 (but note that the temperature part of MTE does not). This model (WBE for short) was presented as a general framework for understanding the origin of allometric scaling laws in biology. Similarity in metabolic scaling relationships and allometric relationships within and across taxa are used in MTE to scale up from organisms to ecological and ecosystem attributes. In order to properly test and assess metabolic theory it is important to distinguish core predictions and assumptions from secondary predictions and assumptions. Much of the confusion in



**Figure 14.2** Allometric scaling of total plant biomass (roots, stems, and leaves),  $M$ , versus annual biomass production,  $dM/dt$  for both Angiosperms (red circles) and Gymnosperms (gray diamonds). Figure from Enquist et al. (2007c) by permission of Nature Publishing Group. The allometric scaling relationship for each group is indistinguishable from 0.75. The shown allometric functions (solid lines) are not the fitted function but instead the predicted allometric scaling function where the exponent (slope) and normalization (intercept) are predicted from metabolic theory. The normalization of the scaling function was calculated for each taxon based on re-sampling global values of taxon-specific mean trait values as specified by equations 14.7 and 14.8. As shown by empirical data for these same plants, we used the value of  $\theta = 3/4$ . The predicted allometric functions for whole-plant growth, based on trait data, provide good allometric approximations of annualized plant growth.

the literature in interpreting the various predictions of the metabolic theory stems from a lack of understanding of the differences between the core and secondary aspects of the theory. These distinctions were not clearly made in any of the original WBE papers but have been delineated subsequently (Price et al. 2007).

#### 14.4.1 Core assumptions and hypotheses of the WBE model

Building on several of the above botanical theories and insights, there are three core assumptions of the WBE network model. First, at the heart of the model is the hypothesis that the scaling of metabolism is primarily influenced by the geometry of vascular networks that

control the scaling of effective surface areas where resources are exchanged with the environment. These surface areas control the transport of resources to metabolizing tissue (West et al. 1997). This then implies that the value of *several additional* allometric scaling exponents also arises from the geometry of branching networks. The second assumption is that normalization ( $Y_0$  in equation 14.1) is driven by traits that define the metabolic demand of “terminal metabolic units” (i.e., leaves). The third assumption is that natural selection can act to shape the scaling of metabolism and several associated allometric relationships via selection for the scaling of resource uptake and the cost of resource uptake (West et al. 1999a). In sum, the core hypothesis of the WBE model is that the scaling of many organismal, anatomical, and physiological traits (e.g., whole-plant carbon assimilation, vascular fluid flow rate, and the number and mass of leaves) is mechanistically determined by natural selection, which has shaped the geometry of the external branching network (see West et al. 1997).

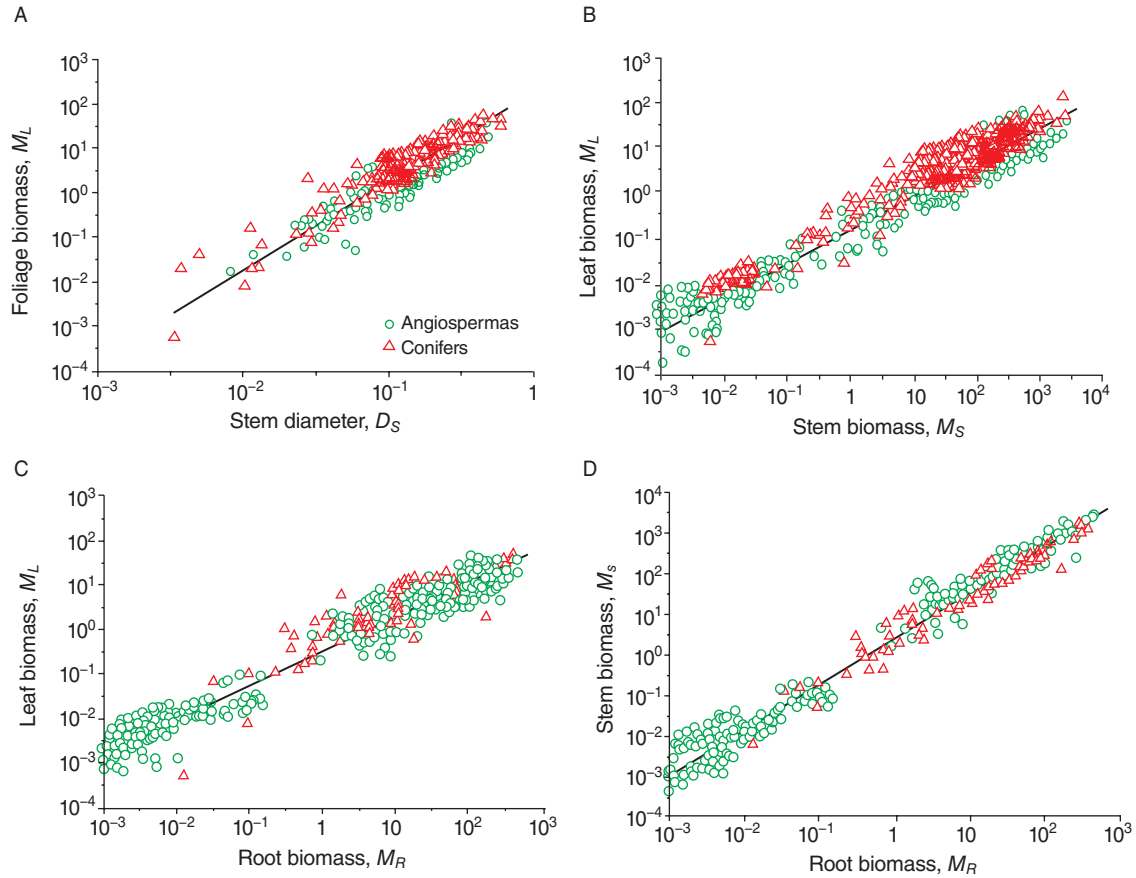
#### 14.4.2 Secondary assumptions of the WBE model

On top of the three core assumptions, WBE then also invoked several additional secondary assumptions for an “allometrically ideal plant.” For simplicity, they assumed that the plant’s external branching network is a hierarchical, symmetrically branching network (see Brown and Sibly, Chapter 2, Fig. 2.2). Therefore, the radii ( $r$ ) and the lengths ( $l$ ) of all branches within branching level  $k$  are assumed to be approximately the same. At each branching node, a parent branch (at level  $k$ ) splits into  $n$  daughter branches (level  $k + 1$ ). All parent branches,  $N_k$ , are assumed to give rise to the same number of daughter branches,  $N_{k+1}$ , across the tree, so that the branching ratio  $n_k$  is a constant as  $n_k = N_{k+1}/N_k$ . Under this framework, there are two branching traits that govern the allometric scaling within a tree. The scaling of the branch length ratio,  $\gamma$ , is defined by the exponent  $b$ , and the scaling of branch radii ratio,  $\beta$ , is defined by the exponent  $a$ ,

$$\gamma = \frac{l_{k+1}}{l_k} \equiv n_k^{-b}; \beta = \frac{r_{k+1}}{r_k} \equiv n_k^{-a} \quad (14.3)$$

As we discuss next, the above core assumptions when combined with these secondary assumptions, lead to a





**Figure 14.3** Global allometric relationships in biomass partitioning across Angiosperms and Gymnosperms. Here we plot basal stem diameter,  $D_S$ , leaf mass,  $M_L$ , stem mass,  $M_S$ , and root mass  $M_R$ . Data are from worldwide datasets as reported in Enquist and Niklas 2002a. Solid lines are reduced major axis regression curves of log-transformed data. Angiosperm and conifer species are denoted by circles and triangles, respectively. (A)  $M_L$  versus  $D_S$  (trunk diameter at breast height). (B)  $M_L$  versus  $M_S$ . (C)  $M_L$  versus  $M_R$ . (D)  $M_S$  versus  $M_R$ . See Enquist and Niklas 2002a for additional statistics. Note, the relatively larger spread in (B) and (C) is due to differences between Angiosperms and Gymnosperms. Extension of the WBE model for plants predicts the scaling exponents for each of these relationships. Predicted  $M_L$  versus  $M_S$  slope = 0.75, observed = -0.75, 95% CI = 0.73–0.76; predicted  $M_L$  versus  $M_R$  slope = 0.75, observed = 0.79, 95% CI = 0.76–0.82; predicted  $M_S$  versus  $M_R$  slope = 1.00, observed = 1.09, 95% CI = 1.05–1.13.

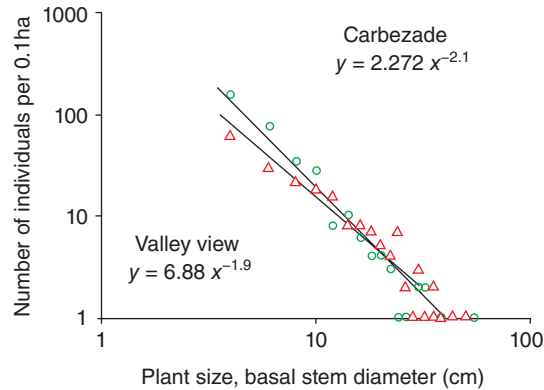
different set of predictions depending on how selection has shaped the branching traits  $a$  and  $b$ .

#### 14.4.3 Core predictions of the West, Brown, and Enquist model: scaling exponents driven by branching traits

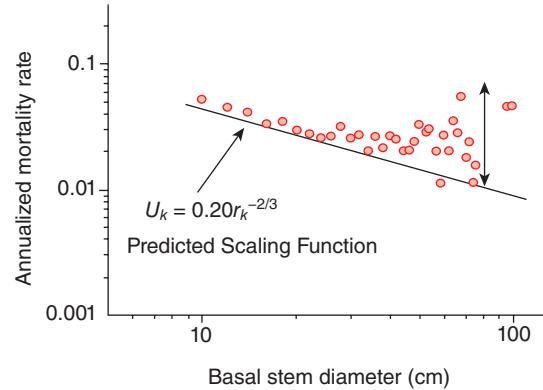
An important implication of the core assumption of the WBE model is that the values of  $a$  and  $b$  deter-

mine numerous scaling relationships within and between plants. The total metabolic rate,  $B$ , or flow through the plant network,  $\dot{Q}$ , scales as  $\dot{Q} \propto B = b_v V^\theta$  where the allometric constant or normalization,  $b_v$ , indexes the intensity of metabolism per unit canopy or rooting volume,  $V_{plant}$ . Here, the allometric scaling exponent is

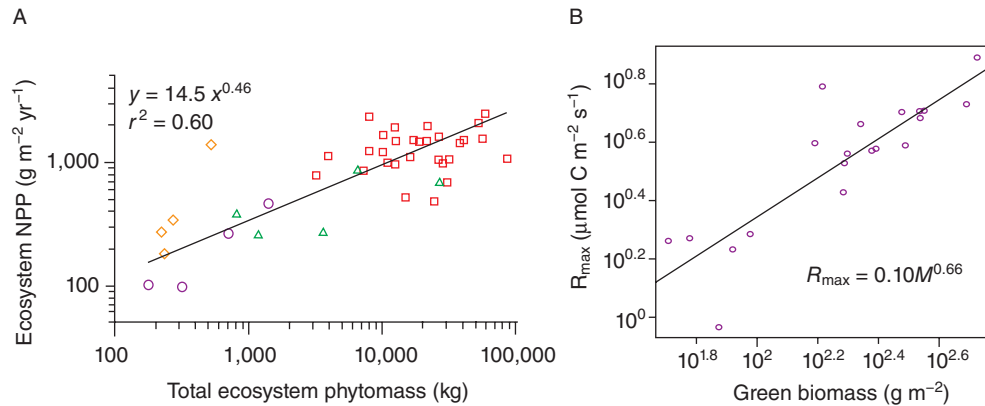
$$\theta = \frac{1}{(2a + b)} \quad (14.4)$$



**Figure 14.4** Community-level scaling relationships. Here, an inverse relationship exists between tree size and abundance within 0.1 ha forest communities. These inverse “size frequency” distributions tend to show approximate power-function scaling with a slope of  $-2$ . The 95% CI of the exponent for each distribution includes the predicted value of  $-2.0$  based on model type I or II regression analyses. The two overlapping size/frequency distributions of a 0.1 ha sample of the South American tropical forest community located at Carbezade ( $-10.2^\circ$  latitude; data shown as open circles) and a 0.1 ha sample of a North American community located at Valley View Glades, Missouri ( $38.15^\circ$  latitude; data shown as open triangles).



**Figure 14.5** Relationship between tree size (measured as basal stem diameter,  $D_k$ , where  $D_k = 2r_k$ ) and annualized mortality rate,  $\mu_k$ , for tagged trees within a dry tropical forest, the San Emilio forest (see Enquist et al. 1999). Size-classes are binned at 1 cm resolution. The shown line is not a fitted line but instead is the predicted mortality function based on scaling of growth and the allometric relationship between stem diameter and total biomass for individual trees in this forest. Whereas the observed data are generally close to the predicted curve, there is increasing variation and deviation for the largest trees, likely because of noncompetitive sources of mortality not included in the model (see Enquist et al. 2009 for additional detail).



**Figure 14.6** Whole-ecosystem allometries. (A) Whole-ecosystem scaling of net primary productivity across grasslands (diamonds), tundras (circles), shrublands (up triangles), and forests (squares). Figure from Kerkhoff and Enquist (2006) by permission of John Wiley & Sons, Ltd. These data show that above-ground NPP scales with total plant mass to the 0.46 power. (B) Similarly, the total above-ground plant respiration scales as a function of the total phytomass (excluding dead woody material) to the 0.66 power. Data from a study of several temperate montane meadow communities near Gothic, Colorado (Kerkhoff and Enquist, in preparation). As discussed in the main text, these ecosystem-level scaling relationships can be predicted from the metabolic theory of ecology that scales up metabolism from cells to ecosystems.

Thus, WBE predicts how various allometric relationships ultimately originate in just two branching traits,  $a$  and  $b$ , so that

$$N_N \propto V^\theta = V^{\frac{1}{2a+b}} \quad (14.5)$$

where  $N_N$  is the total number of terminal twigs or leaves on a plant, and  $V$  is the volume of all branches of the whole tree (a proxy for mass). Similarly, the scaling of the total number of leaves is related to stem radius and length as  $N_N \propto r_0^{1/a}$  and  $N_N \propto l_0^{1/b}$ , where  $r_0$  is the radius at ground level, and  $l_0$  is the tree's maximum path length from base to the most distant terminal twig (West et al. 1999b).

Importantly, the values  $a$  and  $b$  also directly determine numerous other scaling relationships, such as whole-plant respiration rate,  $\dot{R}$ , carbon assimilation rate  $\dot{P}$ , xylem flow rate  $\dot{Q}_0$ , and total number of leaves ( $n_L$ ). Converting to plant mass we have  $M = V\rho$  where  $\rho$  is the tissue density. If  $\rho$  does not vary with plant size,  $V$ , and if the water flux per unit leaf area as well as photosynthesis and respiration per unit leaf area are independent of plant size then a central prediction of the WBE model is

$$\dot{R} \propto \dot{P} \propto \dot{Q}_0 \propto n_L \propto M^\theta \quad (14.6)$$

As we discuss below, equation 14.6 is an approximation (Savage et al. 2008) for allometric scaling for plants with a large number of branching generations (West et al. 1999b; Savage et al. 2008). So, these predictions are expected to hold for plants larger than seedlings (Reich et al. 2006; Enquist et al. 2007a, 2007b). An important question is: what sets the value of  $\theta$  in any given taxon or environment?

If the branching traits,  $a$  and  $b$ , are constant within a tree and do not vary with the size of the branching network,  $V$ , then the network is self-similar. A self-similar network predicts that (1) allometric relationships will be best fit by a power function; (2) branching architecture will be fractal-like within and across trees; and (3) branching architecture will play a crucial role in shaping analogous scaling relationships for the internal vascular network (Savage et al. 2010). This leads to extensions of the WBE plant model and extensions to new models that predict similar patterns across plants, plant communities, and forest ecosystems (Enquist 2002; Enquist et al. 2009; West et al.

2009; but see Coomes 2006; Muller-Landau et al. 2006a; Russo et al. 2007; Coomes and Allen 2009).

#### 14.4.4 Additional secondary assumptions: selection to optimize external branching network geometry and the origin of quarter-power scaling relationships

Many of the initial papers by West, Brown, and Enquist focused on the origin of the well-known relationship where  $\theta = 3/4$  (see Brown and Sibly, Chapter 2). This allometric scaling rule, between whole-organism metabolic rate and body mass, has been documented across taxa for decades (Kleiber 1932; Hemmingen 1950; Peters and Wassenberg 1983; Schmidt-Nielsen 1984; Niklas 1994c). Within the framework of the WBE model, the  $3/4$  rule originates from four secondary optimizing assumptions (West et al. 1999b): (1) selection has maximized the scaling of total whole-plant leaf surface area with plant size, resulting in a branching network that is space-filling. This assumption builds upon a long-held notion in botany (discussed above) that selection for increased surface areas where resources are exchanged with the environment has likely been a central organizational principle (Bower 1930; Küppers 1989; Farnsworth and Niklas 1995); (2) selection has also acted to maximize water conductance and minimize the scaling of hydrodynamic resistance through the vascular network with plant size (see below); (3) the dimensions and physiology of leaves and petioles do not systematically vary with plant size; and (4) biomechanical constraints to elastic buckling (McMahon and Kronauer 1976; King and Louks 1978) are uniform. This assumption enforces biomechanical stability across branching levels and leads to eventual  $2/3$  scaling between tree height and diameter and  $3/8$  scaling between tree mass and diameter. Because WBE also assume that plant metabolic rate,  $B$ , is directly proportional to the number of petioles (or leaves, see equation 14.6), and using assumption #3 and assuming large number of branching levels,  $N$ , this dictates the scaling of whole-plant resource use and metabolic rate. Furthermore, assumption #1 leads to  $b = 1/3$ , and assumptions #2 and #4 leads to "area-preserving branching" where the sum of cross-sectional areas of daughter branches equals the cross-sectional area of the mother branch (Richter 1970; Horn 2000). Thus,  $a = 1/2$ . Together, the principles of space-filling and area-preserving

branching set the values of  $a$  and  $b$  and then govern a suite of different allometric scaling relationships within an “allometrically ideal” plant (see Table 14.1). Using equations 14.5 and 14.6 then leads to the prediction  $\theta = 3/4$ .

In general the  $3/4$  scaling of metabolism (Niklas and Enquist 2001) appears to hold across a broad sampling of plants. Building on these arguments, Enquist and Niklas used the “allometrically ideal” predictions of the WBE model to show how the total amount of stem, root, and leaf biomass – as well as the total above- and below-ground biomass – should scale with each other (Enquist and Niklas 2002b; Niklas and Enquist 2002a, 2002b). Global data are in general agreement with predictions from the WBE model (Fig. 14.3).

#### 14.4.5 Evolution by natural selection on the hydraulics of internal vascular network geometry

How selection has shaped the scaling of whole-plant hydraulics appears to have been central to the evolution of plant form and function. Evolutionary increases in the range of plant sizes over macroevolutionary scales (Knoll and Niklas 1985) necessitate a hydraulic cost. Selection for increase in sizes also necessitates an increase in the transport distance over which resources must be transported (Enquist 2003). As a result the hydrodynamic resistance of transport must also increase (Zimmermann 1983). This linear increase in resistance would constrain any diversification of plant size (Raven and Handley 1987; Ryan and Yoder 1997). The WBE model demands that selection has acted to minimize the scaling of resistance with increased plant size (or transport distance). The WBE model predicts that if selection has shaped internal xylem networks so that radius of xylem tubes ( $r_{\text{xylem}}$ ) must taper from the base of the tree to the leaf (see Fig. 14.9), then the total xylem resistance along a given path length from leaf to trunk is minimized (see Table 14.1). If  $r_{\text{xylem}}$  scaled positively with the size of a branch,  $r_k$ , then the total resistance, which is the sum of the resistances through all branches, could be minimized and approximately independent of the number of branchings,  $N$ , and the total xylem transport length,  $l_T$  (West et al. 1999b). Thus, a volume-filling, area-preserving external network, that contains an internal vascular network that minimizes the scaling of resistance with path length, will result in a  $3/4$  scaling of

whole-plant water flux and conductance with plant mass, or a square law for the scaling with stem diameter (see Table 14.1).

#### 14.4.6 Intra- or interspecific?

It is critical to point out that, although it was not emphasized in the original papers, WBE2 is primarily an *intra*-specific model. However, its predictions should also hold *inter*-specifically if (and only if) terminal branch, leaf, xylem, and physiological traits do not vary systematically across species. This has led to some confusion and discussion regarding how to best test the predictions and the scope of inference of WBE, as well as the specific assumptions that need to be assessed (see Mencuccini 2002).

The assumptions and optimization principles stated above straightforwardly lead to quantitative predictions of how, within an “allometrically ideal plant,” numerous aspects of physiology and anatomy scale with plant size (see Table 14.1). Allometric exponents are predicted to be “quarter-powers” when plotted in terms of plant mass,  $M$  (see West et al. 1999a). These predictions can be straightforwardly converted to allometric predictions based on stem diameter,  $D$ , or stem radius  $r_k$  (Table 14.1).

### 14.5 ORIGIN OF BOTANICAL SCALING NORMALIZATIONS: MERGING OF WBE2 WITH TRAIT-BASED PLANT ECOLOGY

An important aspect of metabolic theory is that it is also capable of predicting the allometric normalization (and not just the allometric exponent). Several papers have taken the original WBE and expanded to derive the value of the allometric normalization (Enquist et al. 1999; Economo et al. 2005; Gillooly et al. 2005a; Enquist et al. 2007c). Here we show how two key plant allometric scaling normalizations originate in a handful of plant traits. A core assumption of the WBE model is that the normalization of metabolic allometry is driven by metabolic demand of “terminal metabolic units” (see also section 14.2.2 on RGR theory above). In the case of plants, the terminal “unit” is the leaf and metabolic rate depends on the properties of the leaf and how the total number of leaves scales with plant size (Eqn. 5).

### 14.5.1 Normalization of leaf allometry

The net carbon assimilation rate of a plant, NAR, can be rewritten as  $NAR = c\dot{A}_L/\omega$ , where  $\dot{A}_L$  ( $\text{g C} \cdot \text{cm}^{-2} \cdot \text{t}^{-1}$ ) is leaf-area-specific photosynthetic rate,  $c$  is the net proportion of fixed carbon converted into biomass (Gifford 2003) or the carbon assimilation use efficiency (dimensionless), and  $\omega$  is the fraction of whole-plant mass that is carbon (Enquist et al. 2007c). Thus, using this expression (see also Hunt 1978; Lambers et al. 1989; Poorter 1989) for NAR, the equation for whole-plant growth (see equation 14.2) becomes

$$\dot{M} = \beta_A M_L = NAR \cdot SLA \cdot M_L = \left( \frac{c}{\omega} \dot{A}_L \right) \left( \frac{a_L}{m_L} \right) M_L \quad (14.7)$$

where  $\beta_A$  is an allometric normalization in equation 14.2 and is the net biomass produced per unit leaf. Its value represents several leaf level traits. An example is SLA, the specific leaf area (leaf area/leaf mass). In principle, the plant traits listed in equation 14.7 can vary. Equation 14.8 can be expanded by incorporating the importance of whole-plant size and biomass allocation into the equation for growth rate (i.e., equation 14.3).

### 14.5.2 Normalization of growth rate

The WBE model states that  $M_L$  scales with whole-plant mass as  $M_L = \beta_L M^\theta$  (this is essentially a version of equation 14.5). Elaborations of the WBE model (Enquist et al. 1999) show that the term  $\beta_L$  is governed by additional functional traits and plant size. Specifically,  $\beta_L = M_L M^{-\theta} = M_L (\rho V)^{-\theta}$  where again,  $\rho$  is the tissue density. The allometric constant,  $\phi_L \rho^{-\theta}$ , measures the mass of leaves per allometric volume of the plant body. Therefore, substituting for the  $M_L$  term in equation 14.7 yields a growth law dependent on several traits including the branching that define  $\theta$ :

$$\dot{M} = \left( \frac{c}{\omega} \dot{A}_L \right) \left( \frac{a_L}{m_L} \right) \beta_L M^\theta = \left( \frac{c}{\omega} \dot{A}_L \right) \left( \frac{a_L}{m_L} \right) (\phi_L \rho^{-\theta}) M^\theta \quad (14.8)$$

Extensions of metabolic scaling theory shows that it is possible to predict plant growth from knowledge of a handful of traits. From above, we predict the normalization constant for the scaling relationship between

plant size and growth  $b_0 \approx \beta_G \approx (a_L/m_L)([c/\omega]\dot{A}_L)\beta_L$ , where each of the variables corresponds to a critical trait. To predict growth rate one must first measure these traits as specified by the model. Enquist et al. (2007c) analyzed a global data compilation for the traits listed in equations 14.7 and 14.8, for a wide sampling of Angiosperm and Gymnosperm trees. Figure 14.2 shows that predictions successfully approximate, *with no free parameters*, the empirical scaling of plant growth. The lines that pass through the allometric relationship comprise the predicted scaling function based on plant traits. Interestingly, as supported by data, our model predicts that Gymnosperms have a higher value of  $\beta_A$  (see equation 14.3) than Angiosperms, but that both taxa have similar values of  $\beta_G$  due to opposing mean trait differences:  $(a_L/m_L)$  and  $\dot{A}_L$ .

### 14.5.3 Temperature

Here, due to space limits, we have not focused on the role of temperature in plant metabolism (see Anderson-Teixeira and Vitousek, Chapter 9, for more detail). However, temperature is critically important and its influence is also expressed in the scaling normalizations of equations 14.7 and 14.8 via temperature influences on traits – most notably the net carbon assimilation  $\dot{A}_L$  (which includes respiration) as well as  $c$ , the carbon use efficiency (see Enquist et al. 2007c). While the Arrhenius equation appears to hold within plants (Gillooly et al. 2001; Enquist et al. 2003; Anderson et al. 2006) in our opinion an open question focuses on the relative importance of temperature acclimation, adaptation, and the replacement of taxa with different metabolic traits (as defined by equations 14.7 and 14.8) across communities (assembly) observed broad-scale temperature gradients (Kerkhoff et al. 2005; Enquist et al. 2007a; Enquist 2011). Specifically, how important are these biotic responses (what we call the three As: acclimation, adaptation, and assembly) across broad-scale temperature gradients in influencing observed variation in plant growth and physiology (Enquist et al. 2007a)? Another open question is whether the activation energy for photosynthesis is 0.6 eV or, instead, 0.3 eV (see discussion in Allen et al. 2005, Kerkhoff et al. 2005, and Marba et al. 2007). These two points may have important implications for temperature-correcting biological rates across broad gradients (Kerkhoff et al. 2005).



The theoretical framework that we have outlined here will also ultimately provide a basis for similar predictions for how variation in plant traits influences the scaling of whole-plant performance. Variation in the traits specified in equations 14.7 and 14.8 will influence the normalization (i.e., the residual scatter about the allometric function). As we discuss below (section 14.6.1.4), a trait-based elaboration of metabolic scaling theory now enables one to assess how selection for different trait values in differing environments (such as specific leaf area or allocation to leaves or roots) then must influence the scaling of whole-plant growth and resource use. This is an exciting development, as a trait-based elaboration of the WBE model then effectively integrates a long line of research in trait-based ecology (Wright et al. 2004; Westoby and Wright 2006) with MTE.

#### 14.6 WHAT HAVE WE LEARNED SINCE 1997 AND 1999?

The publication of the WBE in 1997 and WBE2 in 1999 (West et al. 1997; West et al. 1999b) has led to numerous and multifaceted studies testing its predictions and implications in plants. On the one hand, several studies, outside of our scaling collaborators, have found general support for many of the predictions. For example, (1) xylem conduits taper as predicted, from the roots to the leaves, so as the scaling of hydraulic resistance is minimized (Anfodillo et al. 2006); (2) the scaling of branch dimensions and plant biomass generally scale as predicted (Pilli et al. 2006); (3) analysis of whole-plant physiology shows convergence in the  $3/4$  scaling of plant water use and growth across diverse species (Meinzer 2003; Meinzer et al. 2005); (4) plant birth and death rates also scale with quarter-powers (Marba et al. 2007); and (5) several novel methodological approaches using remote sensing have largely confirmed many of the predictions for the scaling of leaf area and partitioning of biomass within and across numerous trees and biomes (Wolf et al. 2010). On the other hand, there have been several criticisms that question its basic framework, assumptions, generality, and applicability (Harte 2004; Tilman et al. 2004; Kozłowski and Konarzewski 2005; Makarieva et al. 2005b). Further, several additional studies, as we discuss below (section 14.6.1), have highlighted seeming deviations from the model predictions and problems with the model assumptions.

Several prominent critics have argued that the WBE model cannot explicitly account for the range and origin of inter- and intraspecific variability in allometric exponents (Bokma 2004; Glazier 2005). Here we focus on the nature of these criticisms and show how revisiting the secondary assumptions of WBE and WBE2 not only provides a way to integrate these concerns but also provides additional quantitative predictions for plant scaling.

Several studies have identified a number of issues and questions with the original WBE2 1999 plant model, as follows. (1) Several authors have suggested that selection for hydraulic safety and efficiency, instead of space filling and minimization of resistance as assumed by WBE, has shaped the evolution of vascular networks (Mencuccini 2002; Sperry et al. 2008). (2) Others have questioned whether vascular safety and efficiency (McCulloh and Sperry 2005; Zaehle 2005; Petit and Anfodillo 2009) or the carbon costs associated with the scaling of plant hydraulic networks (Mencuccini et al. 2007) are adequately described by WBE. (3) Several additional studies have revealed empirical patterns that contradict some of the predictions (McCulloh et al. 2003, 2004, 2010; Mencuccini et al. 2007; Petit et al. 2009). (4) Reich et al. (2006) have questioned whether the scaling exponent for whole-plant metabolism (respiration) actually scaled with an exponent closer to 1.0 rather than  $3/4$  (see also Mencuccini 2002). (5) Lastly, several studies have pointed out that not all species follow the  $3/4$  scaling prediction. They have emphasized that there is variation in metabolic scaling relationships within and between species (Mäkelä and Valentine 2006; Russo et al. 2007) – especially in trees that grow in light- or resource-limited environments (Muller-Landau et al. 2006b) – as well as changes in leaf traits during plant ontogeny that would influence metabolic scaling (Sack et al. 2002).

Perhaps the most significant criticism of the 1999 WBE2 model is that it makes several incorrect assumptions about plant anatomy. For example, building on earlier work (Van den Oever et al. 1981), Sperry and colleagues compiled data for the xylem conduits that transport water in plants, and documented the general inverse square “packing rule” discussed above (Fig. 14.1). This “packing rule” contradicts the assumption of the WBE model that number of conduits remains unchanged as conduit radii taper, decreasing from trunk to terminal twig. Natural selection for safety and efficiency considerations have been proposed to

underlie the packing rule (Sperry et al. 2008), suggesting that a new or revised theory is needed to more accurately describe the observed scaling (Weitz et al. 2006; Price and Enquist 2007; Sperry et al. 2008; Petit and Anfodillo 2009).

#### 14.6.1 Proposed ways to advance metabolic scaling theory

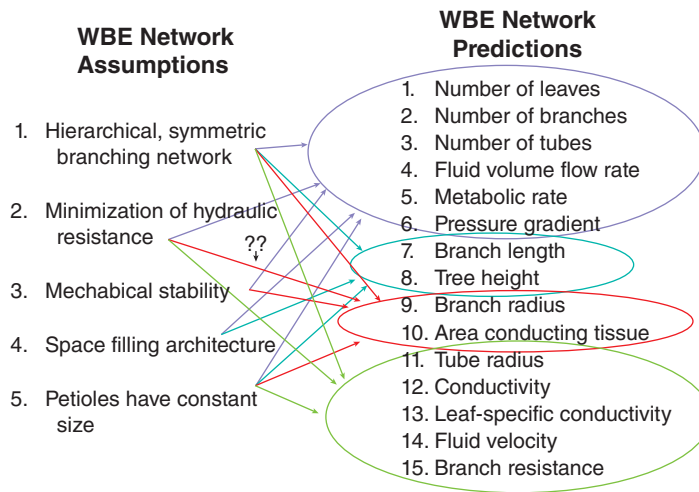
Several recent papers have proposed a way forward in order to develop a more predictive metabolic scaling theory applied to plants (Price and Enquist 2006; Price et al. 2007; Savage et al. 2010). This framework can be summarized in the diagrams in Figures 14.7 and 14.8. Figure 14.7 is a schematic that shows which assumptions are necessary for which predictions of the WBE model. Specifically, these authors proposed to expand the scope of metabolic scaling theory by: (1) deriving more realistic predictions for botanical scaling exponents based on more detailed models of plant architecture and hydrodynamics; (2) deriving the nor-

malization constants for all of the scaling relationships listed in Table 14.1 by relaxing some of the secondary assumptions of the WBE model; and (3) elaborating on the network model by incorporating additional plant traits and differences in resource availability and limitation.

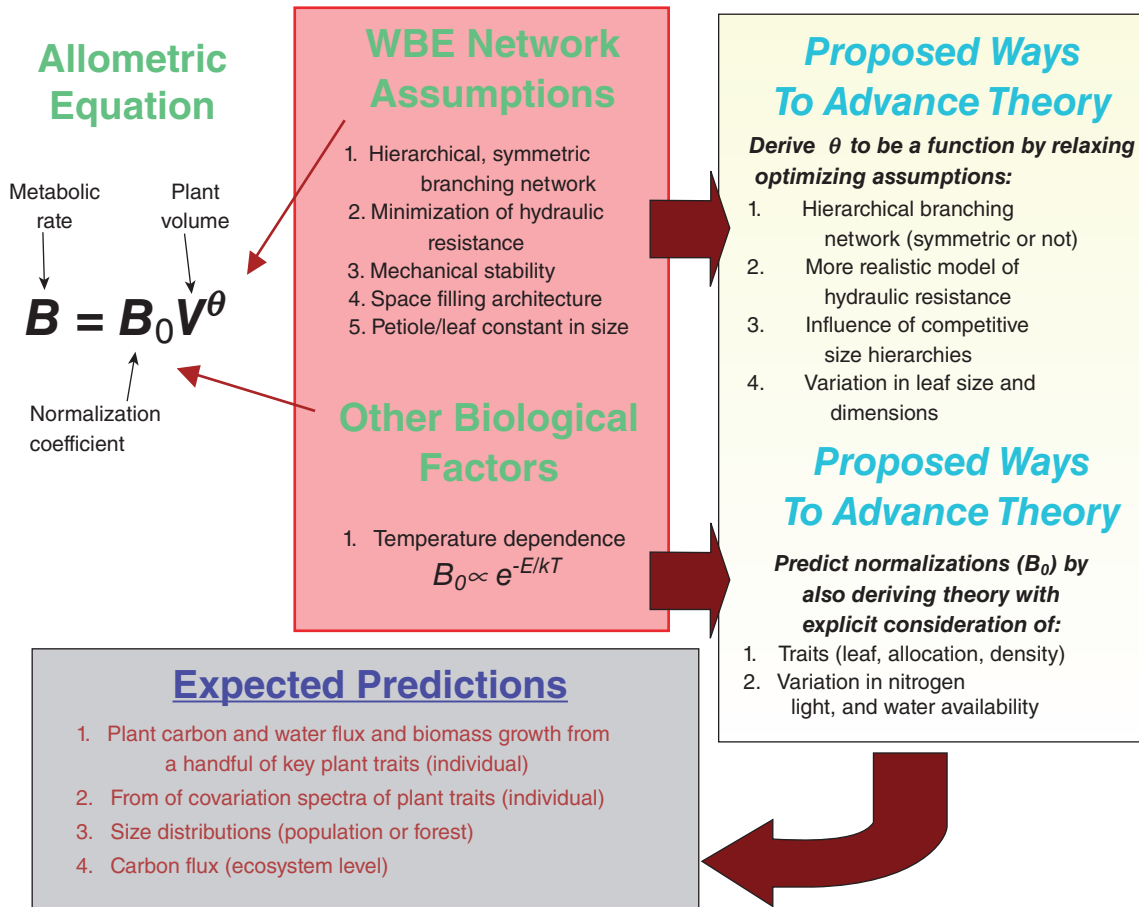
There appear to be four specific points that will enable the original WBE model to address several of the above criticisms. As we discuss below (sections 14.6.1.1 to 14.6.1.4), these approaches collectively will allow for a more integrative metabolic theory of ecology able to “scale up” from traits characteristic of different environments to the ecological implications of this variation. Already, several studies have begun to address these points and thus to point the way forward to a more integrative metabolic scaling theory.

##### 14.6.1.1 Addition of further selection drivers on plant metabolism

Recently, Savage et al. 2010 proposed a unified framework to integrate divergent views on the applicability



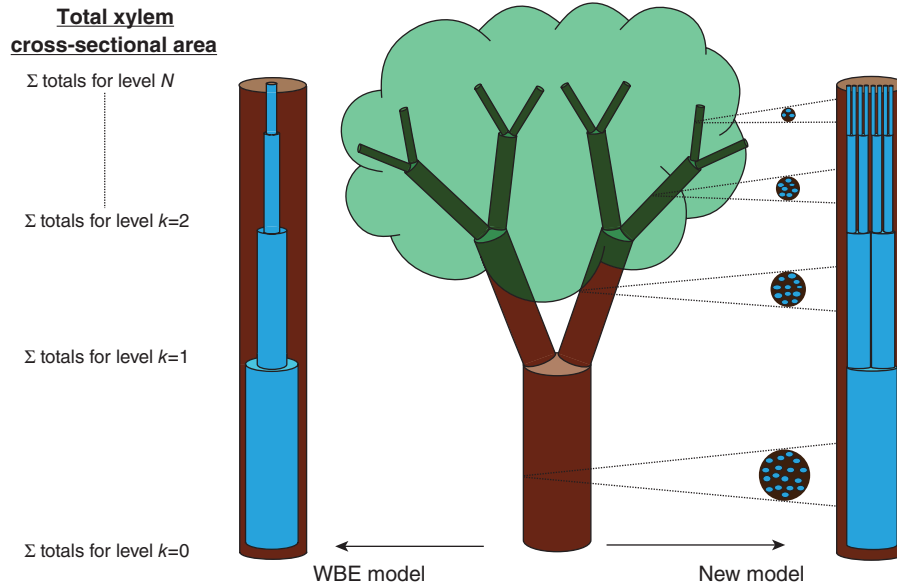
**Figure 14.7** Summary of which of the secondary assumptions of the WBE network model influence which scaling predictions for several plant traits. This schematic shows which assumptions are necessary for which predictions in the WBE model. Therefore, it links how certain violations of any of the *secondary* optimizing assumptions will influence specific predicted scaling relationships. It is important to emphasize that violations of *any* of these secondary assumptions yield different values of  $a$  and/or  $b$ , and hence deviations from  $\theta = 3/4$ . All of these will influence plant-scaling relationships including growth and flux. As an example, for small plants, including plants early in ontogeny such as seedlings and saplings, area-preserving branching may not hold. Indeed, empirical data shows that  $a \sim 1/3$  and  $\theta \approx 1$ . Further, in plants with unusual architectures and growth forms (such as palms, lianas, ground spreading herbs, succulents), where volume filling is absent and/or the biomechanical constraints are minimal,  $\theta$  will likely deviate from the canonical  $3/4$  predicted by the secondary assumptions of the WBE model.



**Figure 14.8** Proposed framework for incorporating additional biological and evolutionary processes into MTE. This involves relaxing the secondary assumptions of the WBE model (see Fig. 14.7). This framework will allow for a more predictive botanical scaling theory that will: (1) derive more detailed predictions for botanical scaling exponents by basing theory on more realistic models of plant architecture and hydrodynamics (Fig. 14.9); and (2) derive the scaling normalizations for all of the scaling relationships listed in Table 14.1. This is done by relaxing some assumptions of the WBE model (Fig. 14.7) as well as further elaboration of the WBE theory by incorporating key plant traits and resource acquisition. The foundations of this proposed theoretical development have recently been published (see text for details).

of the metabolic scaling theory to understanding the scaling of plant hydraulics (Fig. 14.9). In a revision to the West, Brown, and Enquist model, Savage et al. argued that the evolution of plant branching and vascular networks can be better understood to be guided by five general selection drivers (see Table 14.2). These selection drivers are hypothesized to be the central principles that have shaped the integration and scaling of botanical phenotypes: Principles #2 and #3 in Table

14.2 are more central in a more generalized botanical metabolic scaling than in the original theory (Shinozaki et al. 1964a; West et al. 1999b). Furthermore, Savage et al. elevate the importance of the principle of space filling not only to the external network but *also* to the internal vascular network, allowing one to relate conduit radius to conduit frequency (Fig. 14.1). These principles together enable metabolic scaling theory to now predict and incorporate this vascular “packing



**Figure 14.9** Progress in integrating criticisms of the 1999 WBE model in constructing a more flexible and realistic botanical scaling theory. Branching structures depicting the difference in internal network structure for the Savage et al. (2010) model compared with the 1999 WBE model. Trees are labeled from the base (level  $k = 0$ ) to the terminal twigs (level  $k = N$ ). The left and right columns represent simplified versions of the models. Both models predict conduit taper, but the Savage et al. (2010) model also allows additional section drivers on plant hydraulics so that the numbers of conduits increase and potentially fill a constant fraction of available wood area (shown to the right).

rule" (Fig. 14.1) and other vital plant properties that better match real plant networks and empirical data (Table 14.1). Table 14.1 also shows the progress in the development of plant scaling models (ranging from the pipe model, to the West, Brown, and Enquist 1999 model, and the more recent Savage et al. (2010) model) that better predicts observed plant scaling relationships (see also Fig. 14.9). One insight from the Savage et al. (2010) model is that the principle of space filling appears to apply at all scales of botanical organization – from anatomy, to canopies, to ecology – indicating that this principle is behind the patterns in Figures 14.1–14.6 and so is perhaps the most important principle shaping the range of variation in traits and sizes across scales in botany.

#### 14.6.1.2 Incorporation of finite size effects

There appear to be two types of finite size effects that can influence plant scaling predictions. Both necessitate relaxing some of the secondary assumptions of the original theory. First, equation 14.5 is an approximation that will only hold for plants with several or

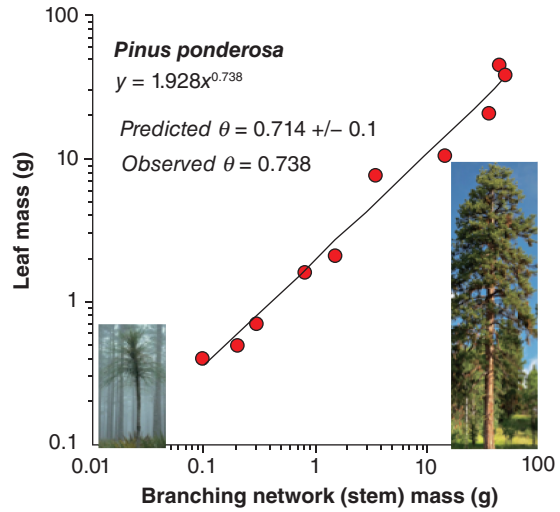
more branching generations, if not infinite, number. Savage et al. (2008) estimate that  $\sim 20$  branching generations (from roots to above ground) is required for these equations to begin to approximately hold. So, the WBE and WBE2 predicted scaling relationships will change if the number of branching generations is small. So, during ontogeny, or from very small plants to large plants, the scaling exponent should actually change with  $N$ , the total number of branchings, and result in a curvilinear scaling function when viewed across all plant sizes. The curvilinearity is constant across all sizes but is subtle enough that a large range of data must be analyzed to observe it. As a result, fitting a power function to very small plants will produce deviations between the metabolic scaling predictions based on a large number ("infinite networks") or branches and data collected from networks that have just a few branches ("finite networks").

Another type of finite size effect is if the values of the branching traits  $a$  and  $b$  are not constant during ontogeny but instead change during growth. There is indication that ontogenetic changes in  $a$  and  $b$  occur within very small plants as they grow. For plants early

**Table 14.2** Savage et al. (2010) proposed that the scaling of plant form and function within integrated botanical phenotypes can be better understood and predicted by a handful of general principles. Specifically, the evolution of plant branching and vascular networks has been primarily guided by five general selection drivers. Note, these build upon and detail the original WBE selective drivers but these are more specific to the way selection has shaped plant hydraulic architecture.

- 1 Selection for space-filling branching geometries in order to maximize carbon uptake by leaves and sap flow through xylem conduits
- 2 Selection to minimize the scaling of hydraulic resistance which is equivalent to maximizing the scaling of hydraulic conductance and resource supply to leaves
- 3 Selection to protect against embolism and associated decreases in vascular conductance
- 4 Selection to enforce biomechanical stability constraints uniformly across the plant branching network
- 5 Within plants during ontogeny and across species, terminal leaf size, physiological rates, and internal architecture are independent of increases in plant size.

in ontogeny such as seedlings and saplings, gravity is relatively unimportant, so the  $2/3$  law is relaxed so that branch radius might then scale isometrically with branch length so  $r_k \approx l_k$  and  $a \approx 1/3$  rather than  $a = 1/2$  (Fig. 14.10). Additionally, there are few branching levels so branches do not completely fill space and  $b > 1/3$ . Thus, relaxing the secondary assumptions of WBE so that  $a$  and  $b$  can vary then predicts that in the case of very small plants  $\theta \approx 1.0$ . However, as plants grow, gravity becomes increasingly important and volume-filling architecture develops (West et al. 1999b), so a relaxed version of the theory predicts a shift in  $\theta$  from  $\theta \approx 1.0$  to  $\approx 3/4$  (Fig. 14.11). Indeed, empirical data (Niklas 2004) shows that  $r_k \sim l_k$ , leading naturally to  $a \sim 1/3$  and  $\theta \approx 1$ , consistent with a predicted shift to isometry of  $R$ ,  $P$ , and  $n_L$ . Indeed, *intra- and interspecific* scaling of total leaf mass,  $M_L$ , shows (Enquist and Niklas 2002a) a transition from  $\theta \approx 1.0$  in seedlings to  $\theta \approx 3/4$  in larger plants (Enquist et al. 2007b; Fig. 14.10). Further, a recent study by Mori et al. (2010) measured whole-tree respiration rate as a function of size. As expected, the scaling of metabolism was steep for small plants with an exponent close to 1.0



**Figure 14.10** (A) Metabolic scaling theory (MST) predicts a coordinated shift in allometric exponents. Interspecific scaling for branch diameters ( $2 \times r$ ) and lengths ( $l$ ) from seedlings to trees (from Enquist et al. 2007c). As predicted, the scaling exponent changes from  $\geq 1$  for small plants and seedlings (green squares, above-ground biomass  $< 1$  g, reduced major axis (RMA) fit,  $b/a = 1.8 \pm 0.12$ ; see text) to  $b/a = 0.97 \pm 0.048$  for all the larger plants (red and brown diamonds; RMA fit not shown) to  $\sim 2/3$  (RMA fit,  $b/a = 0.65 \pm 0.02$ ) for the maximum interspecific heights achieved (brown diamonds). (B) As the scaling of branch lengths and radii changes, the scaling of total leaf biomass,  $M_L$ , as well as  $R$  and  $P$ , are then all predicted to change. Indeed,  $\theta = 1.01 \pm 0.7$  ( $n = 95$ ,  $r^2 = 0.88$ ) for plants with a mass of  $< 1$  g and  $\theta = 0.77 \pm 0.2$  for plants with a mass of  $> 1$  g ( $n = 563$ ,  $r^2 = 0.959$ ), which is consistent with the MST-predicted shift from  $\theta = 1$  to  $\theta = 3/4$  and the scaling relationships observed in Fig. 14.11A.

but then settled to a shallower exponent close to  $3/4$  (see Brown and Sibly, Chapter 2, Fig. 2.3; Mori et al. 2010). Further, in plants with unusual architectures and growth forms (such as palms, lianas, ground spreading herbs, succulents), where volume filling is absent and/or the biomechanical constraints are minimal,  $\theta$  will likely deviate from the idealized  $3/4$ .

#### 14.6.1.3 Variation in branching architecture (scaling exponents)

First, as discussed above, plants exhibit a plethora of branching architectures – ranging from palm trees, to



grasses and succulents, to vines and lianas, to ground spreading forbs. Each of these different growth forms clearly violates the general principles of space filling and perhaps area preserving invoked by the secondary assumptions of WBE (Price et al. 2007; Dietze et al. 2008; Koontz et al. 2009). Second, unlike the network model (see Brown and Sibly, Chapter 2, Fig. 2.2, and Fig. 14.9), many plants exhibit architectures in which the branching is asymmetric such that the daughter vessels/branches are very different sizes. Indeed, plants show a wide range of apical dominance where the main stem or branch is larger and grows preferentially over the side branches (see also Price and Enquist 2006). Strongly apically dominant trees, such as conifers, thus reflect strong branching asymmetry.

Recent work by Price et al. has shown that a relaxed version of the WBE model begins to capture a diversity of morphologies and architectures. Doing so shows that the WBE model is capable of matching observed variation in metabolic scaling exponents that range within 0.5 to 1.0. This captures the range of variation in observed scaling exponents (Price et al. 2007; see also Glazier 2010) and runs counter to the criticism that generalizations and extensions of WBE or MTE can only predict 0.75 (or quarter-power scaling). This range of values will then be reflected by shifts in branching geometry. As of yet we are unaware of any study that has started to incorporate branching asymmetries into metabolic theory (although see Turcotte et al. 1998). An exciting implication of a relaxed version of WBE (and hence MTE) is that it shows that variation in scaling exponents must be ultimately due to variation in branching geometry (see equations 14.6 and 14.7) or size-related variation in the functional traits that underlie the allometric normalization (see equations 14.8 and 14.9). Relaxing the secondary assumptions allows for a unique test of the core predictions of the WBE model (Price and Enquist 2007). Specifically, the core prediction states that if you measure the two network branching traits ( $a$  and  $b$ ) then one should be able to predict exactly the scaling exponent.

As a test of the core prediction of MTE we compiled *intraspecific* data showing the allometric relationship between the mass of the above-ground branching network and leaf mass. We collected data from 10 individual *Pinus ponderosa* trees (Driscoll, Bentley, and Enquist, unpublished data). The observed reduced major axis scaling slope for total leaf mass and plant network biomass (or exponent  $\theta$ ) is  $0.714 \pm 0.2$  (Fig. 14.11). We then calculated the predicted value  $\theta$  based

on the branching traits,  $a$  and  $b$ , measured within the branching network of each of these trees. Our predicted scaling slope from equations 14.5 and 14.6 is 0.738, which is strikingly close to the observed exponent.

#### 14.6.1.4 Variation in environment and traits (scaling normalizations)

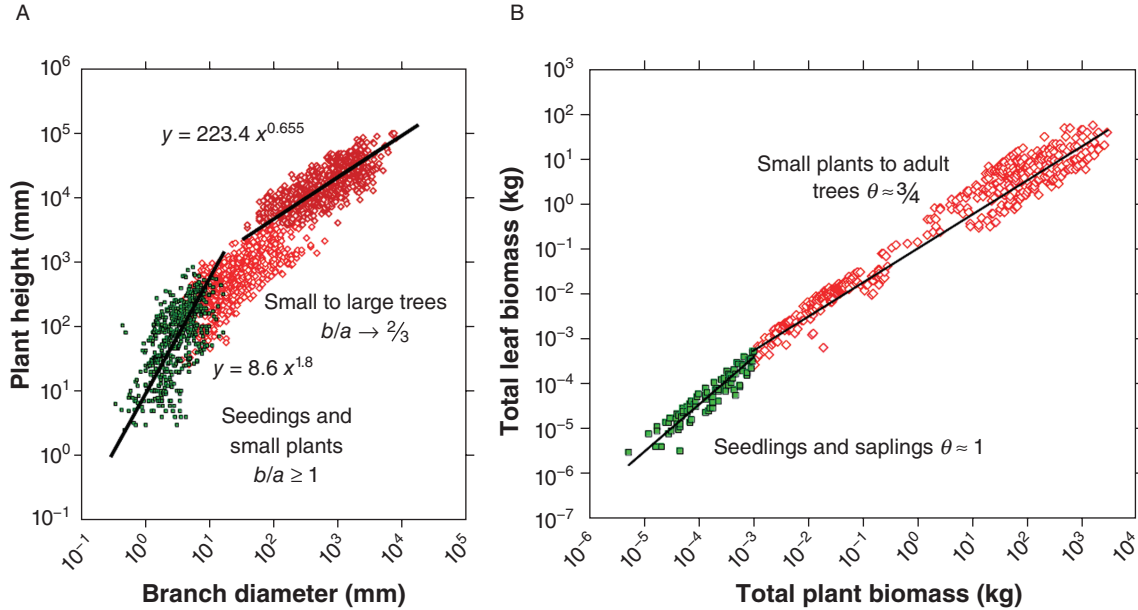
Plant functional traits vary across environmental gradients (Westoby and Wright 2006). Given their importance to plant transport and construction, variation in traits must affect whole-plant growth,  $dM/dt$  (equations 14.7 and 14.8), and plant energetics. Additional studies have argued that size-dependent variation in resource availability can also influence scaling relationships. For example, light limitation should be an important component of our understanding of variation in growth rate and the scaling of whole-plant form and function (Muller-Landau et al. 2006b). Elaborations of WBE can incorporate this environmentally driven variation in traits via variation in the scaling normalizations (see equations 14.7 and 14.8; see also Kaitaniemi and Lintunen 2008). Specifically, variation in the environment will be reflected in specific trait values. Nonetheless, a still open question is: how strong is this influence and what is its form? The effect of variation in these variables will certainly shift normalization constants among taxa and environment, but it is still unclear whether leaf size and tissue stoichiometry vary systematically with plant size and thus also affect the scaling exponents.

### 14.7 SCALING UP TO POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

The WBE model provides the basis to “scale up” from individual plants and their specific traits to populations, communities, and ecosystems. The metabolic theory of ecology or MTE extends the WBE model to ecology by invoking four additional principles or assumptions (Enquist et al. 1998). Intriguingly, these assumptions appear to have identified important organizational principles that are shared across ecological systems.

#### 14.7.1 Resource steady state

MTE assumes that within a given plant community or population, ultimately biomass production is limited by



**Figure 14.11** A test of the core predictions of the WBE model by measuring the branching traits ( $a$  and  $b$ ) in order to predict the scaling exponent. Preliminary *intraspecific* data showing the allometric relationship between the mass of the above-ground branching network and leaf mass from 10 individual *Pinus ponderosa* trees (Driscoll and Enquist, unpublished). The scaling slope (or exponent  $\theta$ ) is 0.714. For each of these trees we calculated the predicted value  $\theta$  based on the branching ratios measured within the branching network of each of these trees. Our predicted scaling slope from the branching ratios of the network is 0.738 which is strikingly close to the observed. Note, our theory indicates that a more detailed measure of leaf size allometry and the asymmetry of branching will provide an even more accurate prediction of  $\theta$ . Further, measures of the specific traits listed in equation 14.7 will then yield the value of the  $y$ -intercept or normalization of this function. Thus, in principle, we can predict the entire function with no fitted parameters.

the rate of resource supply,  $\dot{R}_{Tot}$  (Enquist et al. 1998). Consequently, plants tend to grow until they are limited by resources. This then leads to a trade-off between plant size and abundance. The maximum number of individuals that can be supported per unit area ( $N_{max}$ ) is related to the rate of resource supply,  $\dot{R}_{Tot}$ , per unit area and the average rate of resource use per individual,  $\dot{Q}$ , so that  $\dot{R}_{Tot} = N\dot{Q} \propto NM^{3/4}$ , and so  $N \propto (1/\dot{R}_{Tot})M^{-3/4}$ . Thus, population density is predicted to scale inversely with plant size. This is the idea sometimes referred to as energy equivalence (Damuth 1981; but see also White et al. 2007).

#### 14.7.2 Demographic steady state

Resource steady state essentially demands that the plant population or community also be in demographic

steady state. Understanding the origin and maintenance of demographic steady state requires an understanding of population transitions between size-classes as individuals grow from seedlings to the canopy. In steady state, the number of individuals within a given  $k$ th size-class,  $\Delta n_k$ , does not change with time so growth and death rates are not independent but inextricably linked (Clark 1990). Thus, as individuals grow then individuals must also die. The steady-state assumption is consistent with dynamical data and canopy gap size distribution data from several old-growth forests (Hubbell and Foster 1990; Lieberman et al. 1990; Kellner and Asner 2009).

#### 14.7.3 Ecological space-filling

Metabolic ecology invokes the principle of ecological space-filling. Space-filling is assumed to be a necessary

outcome of all plants competing for similar limiting resources and the resource steady-state assumption. Space-filling is the end result of individuals filling in space so as to use all available resource. It is assumed to imply that the total area of leaves of all individuals within any size-class  $k$ ,  $\Delta n_k a_k^L$ , equally fills the same amount of area, across all of the size-classes. Specifically  $\Delta n_k a_k^L = \Delta n_{k+1} a_{k+1}^L$  where  $k$  is a given size-class,  $a_k^L$  is the average leaf area per plant in size-class  $k$  and  $\Delta n_k$  is the number of plants whose age is between  $t$  and  $t + \Delta t$  and whose size is between  $r_k$  and  $r_k + \Delta r_k$  where  $\Delta r_k$  is the size of the bin used to visualize the size distribution.

#### 14.7.4 Allometric similarity across taxa

The MTE has often made the simplifying assumption that all individuals follow the same (specifically, quarter-power) scaling relationships. For example, in applying MTE to populations and whole communities, the scaling of plant canopy and rooting dimensions as well as the scaling of growth rate and resource use is assumed to be similar across taxa. This explicitly assumes that the scaling of plant form and function (as reflected by the branching traits  $a$  and  $b$ ) and the metabolic demands and traits reflected in the scaling normalization of whole-plant growth and metabolism (in equations 14.7 and 14.8) are similar within individuals and across organisms.

#### 14.7.5 MTE predictions

As a result of the above ecological assumptions, several predictions emerge. However, as shown by the examples below, violations of any of these assumptions will lead to deviations from MTE predictions. One important prediction is the scaling of number of individuals and their size. MTE predicts that there should be an inverse relationship between size and number (West et al. 2009). Specifically,  $\Delta n_k \propto 1/a_k^L \propto 1/r_k^2$ . The steady-state size distribution then approximates an inverse square law with many small individuals and few large ones. This prediction appears to be largely supported by empirical data sampled across different biomes as well as following a given forest through time (Enquist and Niklas 2001; Enquist et al. 2009; see also Anderson-Teixeira and Vitousek, Chapter 9, Fig. 9.3A; see also Coomes et al. 2003; Muller-Landau et al.

2006a). It is convenient to translate the above discrete formulation into a continuum notation. The distribution function representing the number of individuals per unit trunk radius,  $\Delta n_k / \Delta r_k$ , becomes  $f(r) \equiv dn/dr$  (see West et al. 2009 for details). When size-classes are characterized by linear binning of radii, corresponding to a constant infinitesimal  $\Delta r_k$ , independent of  $k$ , we now have the more general statement

$$N_k \approx \frac{\dot{R}}{(K+1)b_0} r_k^{-2} \text{ or } f(r) = \frac{dn}{dr} = \frac{\dot{R}}{r_m b_0} r^{-2} \quad (14.9)$$

where  $r_m$  is the stem radius of the largest tree sampled. Since  $r \propto m^{3/8}$ , equation 14.9 is equivalent to  $f(r) \propto m^{-3/4}$  reflecting the “allometrically ideal” 3/4-power scaling of metabolism and growth (see also discussion regarding transformation of size variables within discrete and continuous size distributions, in supplemental material in West et al. 2009). Note, relaxing the secondary assumptions of the WBE model (see Figs 14.7 and 14.8) would yield different scaling exponents than the canonical  $-2$ . An important implication of a metabolic theory of ecology is that the predicted scaling function of number and size explicitly predicts that the normalization of the size distribution should increase with increasing rates of limiting resource supply,  $\dot{R}$  (as was recently shown by Deng et al. 2006) and decrease with increasing rates of mass-corrected metabolism,  $b_0$ . Here the value of  $b_0$  can again be seen to be linked to fundamental plant traits detailed in equations 14.7 and 14.8 where  $b_0 \approx \beta_0 \approx (a_L/m_L)([c/\omega]\dot{A}_L)\beta_L$ . Thus, equation 14.10 provides a basis to integrate variation in functional traits and resource supply with variation in the relationship between plant size and number. Lastly, we note that if climatic or biophysical limits constrain the maximum size of a tree so that  $r_m$  has an upper limit in equation 14.9, then this would induce another “finite-size” effect but at ecological scales. This would be expressed as a “curvy” size–frequency relationship that is “bent down” at large sizes (see truncated Pareto fit to power functions in White et al. 2008).

Another prediction from MTE applied to forests stems from the resource steady-state assumption is that the mortality rate of a population,  $\mu$ , or stand should scale inversely with stem radius,  $r$ , as  $\mu = A r^{-2/3}$  (see Fig. 14.5). Broad support for this prediction at the population scale is reported in Marba et al. (2007). However, this prediction should also hold within diverse communities if the central assumptions of MTE

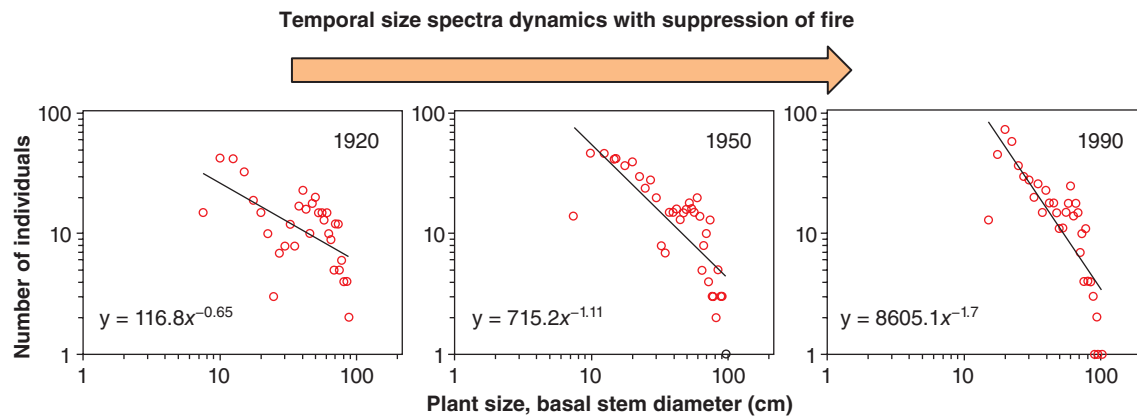
hold. Further, the normalization of the mortality scaling relationship,  $A$ , can be shown to relate directly to the scaling of plant growth rate (see equations 14.7 and 14.8; Enquist et al. 2009).

### 14.7.6 Scaling up MTE to ecosystem scaling and dynamics

#### 14.7.6.1 Disturbance and succession

A central prediction of MTE is that *even* when disturbed from steady state, the successional trajectory of a community or stand is governed by the allometry of growth and mortality but is constrained ultimately by the central assumptions of MTE. An important implication is that a forest that conspicuously violates the assumption of steady state due to a major recent disturbance should deviate substantially from theoretical predic-

tions. Over time, however, as new seedlings are recruited, grow, and fill space to reestablish a steady-state mature forest (Odum 1969), the size distribution should converge asymptotically on the canonical form,  $f(r) \propto r^{-2}$  (Kerkhoff and Enquist 2007). Enquist et al. (2009) show a series of Costa Rican forests in various stages of recovery from disturbance, with steady state reached in approximately 50–100 years. Early in succession the scaling exponent is steeper than  $-2$ , while later in succession the size distribution exponent begins to approximate the resource steady-state distribution (see Anderson-Teixeira and Vitousek, Chapter 9, Fig. 9.3B). These data and previously published data on forest recovery from fire (Fig. 14.12) and other disturbances (Kerkhoff and Enquist 2007) predicted return to the inverse square law. These results support the assumption that resource steady state is a strong “attractor” that significantly guides and constrains ecological dynamics.



**Figure 14.12** A unique prediction of MTE is that the shape of the size distribution (i.e., its exponent) can provide a general indicator of time since disturbance. Changes in the size distribution for a *Pinus ponderosa* forest in northern Arizona, from 1920 (at the dawn of active fire suppression) to 1990. With the suppression of fire, the size distribution exponent becomes steeper, approaching the energetic equivalence rule prediction of  $-2$ . Furthermore, the distribution shifts from clearly bimodal to more continuous, perhaps reflecting the relaxation of cohort dynamics that results from the typical fire return interval (data from Biondi et al. 1994). This scenario leads naturally to the hypothesis that if the processes limiting recruitment are somehow removed from the system, the forest size structure will converge toward the EER expectation. Before European settlement, this vegetation type was controlled by high-frequency, low-intensity ground fires, and stands were characterized by an open mosaic structure dominated by mature, fire-resistant trees, with little understory vegetation. With the introduction of grazing and active fire suppression in the early part of the twenty-first century, recruitment of *P. ponderosa* has been less sporadic, and the increased fuel load has led to a more catastrophic, crown-fire disturbance regime (Savage and Swetnam 1990). In accordance with our hypothesis, with the elimination of recruitment limitation by fire, the size structure of the forest appears to become steeper over time. Thus, systematic departures from scaling (both the shallow exponent and the structural size gap observed in 1920) appear to be the signature of a natural structuring process (ground fire), which in this case limits recruitment (ecological space-filling and resource steady state).

#### 14.7.6.2 What is the size of the terrestrial carbon sink? How much organic carbon is below ground?

Recent re-evaluations of global change models used to understand how ecosystems respond to climate change as well as to calculate the amount of carbon stored in terrestrial ecosystems show that they do not sufficiently incorporate the observed plant scaling relationships (e.g., Figs 14.2 and 14.3; Wolf et al. 2011). Understanding of the role of metabolic scaling will likely greatly inform global change models. For example, in a series of papers David Robinson (2004, 2007) used allometrically informed scaling relationships between above- and below-ground biomass components (as shown in Fig. 14.3; Enquist and Niklas 2002a) to calculate how much root biomass and carbon there was in the soil. He then revised the estimates for the global root carbon pool and the results are striking. He found that, given the above-ground biomass within a site, the amount of carbon stored in plant roots could be almost 70% more than previously estimated. His work then also provides a theoretical basis to argue for a significant revision of the global root carbon pool that influences estimates of global carbon sources and sinks. Robinson predicted a global pool of at least 268 petagrams (1 Pg = 1 gigatonne), which compares with previous estimates of about 160 Pg. Based on these metabolic scaling predictions Robinson concluded that the land-based carbon sink is larger than previously thought. He estimated the sink could be 2.7 Pg per year – 0.1 Pg per year greater than current estimates, indicating a stronger role of the terrestrial environment in regulating the Earth's carbon cycle (see also Allen et al. 2005).

#### 14.7.6.3 Ecosystem allometry

An exciting recent development in MTE is the ability to begin to predict whole-ecosystem scaling relationships. For example, given the metabolic rate of an individual,  $B = b_0 r^2$ , where  $b_0$  is a normalization constant, and the size distribution function,  $f(r) = c_n r^{-2}$ , where  $c_n$  is another normalization constant, the total energy use of the stand, per unit area, extension of metabolic theory (see Enquist et al. 2009) shows that the total flux of energy,  $\dot{B}_{Tot}$ , (as well as total autotrophic net primary production) is predicted to scale non-isometrically with total stand biomass:

$$\dot{B}_{Tot} = b_0 c_n (5c_m / 3c_n M^{Tot})^{3/5} \quad (14.10)$$

where  $c_m$  is from the allometry of stem radius and plant biomass,  $m$  where  $m = c_m r^{3/8}$ . Thus, variation in whole-ecosystem autotrophic metabolism scales with phyto-mass,  $M_{Tot}$  to the 3/5 or 0.6 power. Comparison of two datasets potting NPP and autotrophic respiration (Kerkhoff and Enquist, unpublished) bracket the predicted scaling exponent and are indeed close to the predicted value (see Fig. 14.6). Note also that the scaling normalization is given by several key plant functional traits and other scaling normalizations (see equation 14.9) and thus provides a way to link plant traits with ecosystem processes.

#### 14.7.7 Proposed ways to advance the metabolic theory of ecology

In order for MTE to reach its potential as a quantitative foundation of plant ecology it is important to integrate several new insights and criticisms. While the above studies highlight several empirical patterns that support MTE, as we discuss below, several studies have identified some limitations and failings of MTE applied to plant ecology (Coomes 2006; Muller-Landau et al. 2006b). In order to develop a more predictive and quantitative plant ecology, it is important to cast WBE – as applied to plants – and its extension to ecology (MTE) in a proper light. We make three specific points.

First, the WBE model and the metabolic theory of ecology (MTE) is a “Fermi approach” or “zeroth-order” model (Harte 2002). It is a deliberately simplified theory in that it starts with the fewest number of assumptions and principles to make the most number of predictions. Scaling predictions from MTE builds on a rich theoretical foundation of plant ecology (Yoda et al. 1963; Shinozaki et al. 1964a) by starting from a trait-based view of the organism and the general principles of metabolism and allometry that are shared across most plants. Consequently, the theory requires no additional fitted parameter values to predict many scaling functions including: (1) the allometry of plant growth (Enquist et al. 2007c); (2) the allometry of whole-plant water flow and conductance (Savage et al. 2010; von Allmen et al., in preparation); (3) the steady-state distribution of tree sizes (Enquist et al. 2009); and (4) the scaling of mortality (Enquist et al. 2009). The above predictions run counter to arguments made by Tilman et al. (2004) who argued that MTE was sufficiently removed from more pressing questions asked by most researchers in community



ecology. Predictions from MTE have strong implications for both population and community ecology because metabolism fuels growth and powerfully constrains plant form, which in turn constrains abundances, sizes, and rates of competitively driven mortality (see also Clark 1990, 1992).

Second, a zero-order framework can reveal the influence of factors in addition to metabolism and allometry, because these will appear as deviations from MTE predictions of a deliberately simplified model. So, for example, deviations from the predicted scaling function of growth or metabolism will reveal which traits are affected and hence how selection has shaped variation in growth rate in differing environments, and will also let us quantify the magnitude of effect of this variation on whole-plant performance. Similarly, deviation from the predicted mortality scaling function (Fig. 14.5) and hence the predicted  $-2$  scaling of individuals will allow mortality to be partitioned between competitive density-dependent and non-competitive density-independent sources (see Clark (1992) and Fig. S3 in Enquist et al. (2009)).

Third, metabolic theory provides a conceptual foundation, which can be fleshed out with additional idiosyncratic detail as needed to account for site- or taxon-specific variation. For example, deviations in the scaling of plant growth potentially associated with plants growing in light-limiting environments (Coomes 2006), or forests experiencing herbivory or disturbance such as fire so as to deviate from MTE predictions (Coomes et al. 2003; Muller-Landau et al. 2006a), etc., rather than providing evidence against metabolic theory, instead illustrate the value and promise of a general theory based on fundamental mechanistic features of an idealized population or community. For example, quantifying the degree of variation from metabolic theory then provides a measure of the degree to which these processes are important.

## 14.8 CONCLUSIONS

Metabolic scaling theory applied to plants perhaps offers some of the better examples of how the theory can integrate scaling phenomena observed at multiple biological scales. A central component of a metabolic theory is the origin of allometric relationships. The WBE model is unique in that it provides a framework for deriving the traits that not only underlie scaling exponents (most of the traditional focus of metabolic

studies) but also scaling normalizations. This work builds on the core hypothesis originated by the WBE model that branching networks are fundamentally connected to the flux of matter and energy (West et al. 1997). The geometry of branching networks then governs the scaling of energy, carbon, and water flux within branches and trees, as well as across size-classes, taxa, and whole forests (Enquist et al. 2009). These scaling relationships form a baseline for integrating how plant traits influence physiological processes and life histories. Network geometry partly controls abundance, leaf area, and ultimately ecosystem fluxes through complex feedback mechanisms. By understanding how key functional traits and network geometry relate to variation in environments, we can understand how plants interact with their environment, especially light, water, and temperature, and how networks and their traits ramify to influence ecology and how they will potentially react to future climate change.

Many recent studies are integrating metabolic theory and modifying it in order to account for much more of the rich variation in the diversity of plants and ecosystem processes that influence whole ecosystem flux. While several authors have been critical of the approach, we know of no other theoretical framework that offers the ability to predict from first principles the range of scaling functions observed as well as to mechanistically connect how variations in traits then combine to influence plant form and function as well as ecology and ecosystem dynamics. Our approach is pragmatic. It builds on the successes and failures of the original WBE and MTE approaches. By continuing to evaluate the original and secondary assumptions as well as pushing to discover the limits of the predictive ability of the theory, we are optimistic that MTE will increasingly reveal a powerful and predictive framework for plant ecology and global change biology.

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