

COMPUTER SIMULATIONS SUPPORT A CORE PREDICTION OF A CONTENTIOUS PLANT MODEL¹

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- *Premise of the study:* An overarching but vigorously debated plant model proposed by the West, Brown, Enquist (WBE) theory predicts the scaling relationships for numerous botanical phenomena. However, few studies have evaluated this model's basic assumptions, one of which is that natural selection has resulted in hierarchal networks that minimize the energy required to distribute nutrients internally and have thus produced highly efficient organisms.
- *Methods:* If these core assumptions are correct, an "idealized" plant complying with all of the scaling relationships emerging from the WBE plant model should rapidly outcompete other plants, even those that differ slightly from it. To test this reasoning, a computer model was used to simulate competition between an idealized WBE plant, a generic "average" angiosperm (GA), and one of seven variants of the idealized WBE plant, each being similar to the GA in one of the GA's scaling parameters.
- *Key results:* Replicate simulations show that the idealized WBE plant rapidly outcompetes all other plants under light-shade and open-field conditions. However, changing only one of the WBE's scaling parameters results in death or in the coexistence of WBE and GA plants.
- *Conclusions:* These simulations support a core assumption of the WBE plant model and suggest why this idealized plant has not evolved.

Key words: allometry; metabolic theory of ecology; plant competition; scaling theory; species competition; WBE plant model.

Numerous theories—including those of D'Arcy Thompson (1917), Cecil Murray (1926), and Julian Huxley (1932)—have been advanced to provide a mechanistic explanation for size-dependent (allometric) intra- and interspecific relationships observed across phylogenetically unrelated organisms. The most contentious among the recent theories for allometric relationships is the theory advanced by Geoffrey West, James Brown, and Brian Enquist (henceforth the WBE theory), which predicts the numerical values of the scaling exponents governing a remarkably broad spectrum of size-dependent relationships among plants, animals, and bacteria (West et al., 1997, 1999). The core of the WBE theory revolves around how resources are distributed within hierarchal nutrient-delivery networks consisting of tubular conduits, such as the arteries of mammals and the vessels of vascular plants (West et al., 1997, 1999, 2001, 2003). The numerical values of the scaling exponents predicted by the WBE theory emerge from constraints imposed by three assumptions: (1) the dimensions of the terminal conduits in hierarchal networks are size-invariant, (2) these networks fill the entire volume of each system, and (3) natural selection has optimized networks to minimize the energy required to distribute nutrients, thereby making idealized WBE organisms optimally efficient. Collectively, these three assumptions obtain relationships

that take the general form $Y_1 = \beta Y_2^\alpha$, where α is a scaling exponent predicted to have a numerical value of 1/4 or multiples of 1/4 (West et al., 1997, 1999, 2001, 2003). Among the best known of these relationships is Kleiber's curve, which describes the scaling of basal metabolic activity with respect to body mass (Kleiber, 1932, 1961; Brody, 1945; Hemmingsen, 1950; Niklas, 2004).

Since its introduction, numerous criticisms have been leveled against the WBE theory (e.g., Dodds et al., 2001; Kozłowski and Konarzewski, 2004, 2005; Makarieva et al., 2004, 2005). For example, Dodds et al. (2001) rigorously re-examined data sets purported to show 3/4-scaling relationships and found statistical inconsistencies and weaknesses in both the data and the WBE theory. Makarieva et al. (2005) demonstrated analytically that 1/4- and multiple 1/4-power rules emerge if, and only if, the spatial volume of hierarchal distribution networks scale as the 3/4 power of body mass and reported that this expectation is inconsistent with the available data. Meinzer et al. (2005) found different scaling exponents for the scaling of water transport among different plant groups, while Reich et al. (2006) reported differences in respiratory metabolism and plant size and nitrogen content. Likewise, whereas West et al. (1997, 1999) hypothesized that metabolic rates should scale as the 3/4 power of body mass, Reich et al. (2006) reported that metabolic rates scale isometrically for young and comparatively small plants, while Mori et al. (2010) reported a shift from isometric to a 3/4 scaling across nine orders of magnitude of body mass (i.e., mass $\sim 10^{-5}$ kg to 10^3 kg) based on 271 whole-plant measurements.

These and other empirical and theoretical criticisms have resulted in numerous clarifications and reformulations of the WBE theory and of its predictions (see Gillooly et al., 2001; Savage et al., 2004; West and Brown, 2005; Price et al., 2010). Indeed, the history of the WBE theory is so involved that, to quote a recent treatment of the history of the WBE theory, these

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“claims and counter-claims...have served to both obfuscate and clarify what [*the WBE theory and its recent elaboration, the metabolic theory of ecology*] is and what it is not” (italics added; Price et al., 2010, p. 697).

Nevertheless, despite its modifications and reformulations, the three core assumptions of the WBE theory remain unaltered (and, as far as we know, untested) (see Price et al., 2010), albeit sometimes hidden from view. For example, the minimum energy assumption is not mathematically explicit when the WBE theory was used to model plant allometry (West et al., 1999; Enquist et al., 2000, 2007b). Rather, it is found in the mathematics that specifies the geometry predicted to optimize the flow of nutrients in xylem and phloem. The predictions that emerge from this WBE plant model arise from the fractal-like geometry that optimizes the collection of resources such as light and the occupation of space. Testing the validity of this version of the WBE theory, therefore, poses a challenge. Although it is possible to measure the hierarchical dimensions of xylem and phloem in a plant (McCulloh et al., 2003; Meinzer et al., 2005; Anfodillo et al., 2006; Savage et al., 2010), it is nearly impossible to determine directly whether these fractal-like dimensions are the result of evolution by natural selection acting on the ability of a plant to capture light and occupy space.

The goal of this paper is not to explore in detail the mathematical pros and cons of the WBE plant model. Rather, our intent is to explore a fundamental logical consequence of the WBE core assumptions. Specifically, if these assumptions are valid, it is logical to surmise that an idealized WBE plant—a plant that obeys all of the scaling relationships predicted by the WBE plant model—will outcompete other plants, even those that differ from it slightly. No known living plant obeys all of these predicted scaling relationships. However, it is possible to simulate an idealized WBE plant with a computer and to examine the consequences when this plant competes with plants that obey different scaling relationships.

We explored this reasoning using a computer model called SERA (Hammond and Niklas, 2009, 2011a, b). Previous studies using this computer model have shown that it accurately mimics the behavior of real plants. For example, when an extensive data set accumulated over 95 years was used to parameterize an *Abies alba* plant, simulations predicted all of the allometric relationships observed for an entire *A. alba* population including the phenomenology of self-thinning (Hammond and Niklas, 2009). These simulations also predicted the age at which *A. alba* plants reached reproductive maturity, even though there is nothing in how plants are parameterized that directly affects when they are capable of reproduction. From the perspective of testing the consequences of the WBE plant model's assumptions, the use of SERA has the advantage that the numerical values used to parameterize a plant can be altered to observe the consequences on growth and competition. For example, SERA simulations show that a plant parameterized to obey strict 2/3-power (Euclidean) rules violates Euler's buckling law governing the elastic stability of stems. Another advantage is that the equations used by SERA to simulate plants neither mimic the mathematical structure nor the numerical predictions of the WBE theory. For example, the WBE theory predicts that annual plant growth will scale as the 3/4 power of total body mass, whereas SERA computes annual growth as a power function of the product of the projected canopy area and standing leaf mass (Table 1).

TABLE 1. Formulas and numerical values of variables used to parameterize a generic angiosperm (GA) and a WBE plant. The WBE plant differs numerically from the GA plant in seven scaling parameters (denoted by †). Seven WBE variants were simulated, each differing numerically from a GA plant in only one of these seven parameters (see Table 5).

Variable (formula in which it appears)	GA plant	WBE plant
1a. Growth exponent $\left[\alpha_1 \text{ in } G_T = \beta_1 (A_L M_L)^{\alpha_1}\right]$	0.448	0.448
1b. Growth constant $\left[\beta_1 \text{ in } G_T = \beta_1 (A_L M_L)^{\alpha_1}\right]$	1.506	1.506
2a. Young canopy mass exponent $\left(\alpha_2 \text{ in } M_L = \beta_2 M_S^{\alpha_2}\right)$	0.882	0.750†
2b. Young canopy mass constant $\left(\beta_2 \text{ in } M_L = \beta_2 M_S^{\alpha_2}\right)$	0.085	0.116†
3a. Mature canopy mass exponent $\left(\alpha_3 \text{ in } M_L = \beta_3 M_S^{\alpha_3}\right)$	0.772	0.750†
3b. Mature canopy mass constant $\left(\beta_3 \text{ in } M_L = \beta_3 M_S^{\alpha_3}\right)$	0.116	0.116
4a. Stem mass exponent $\left(\alpha_4 \text{ in } M_S = \beta_4 M_T^{\alpha_4}\right)$	1.022	1.000†
4b. Stem mass constant $\left(\beta_4 \text{ in } M_S = \beta_4 M_T^{\alpha_4}\right)$	0.864	0.864
5a. Stem diameter exponent $\left(\alpha_5 \text{ in } D = \beta_5 M_S^{\alpha_5}\right)$	0.383	0.375†
5b. Stem diameter constant $\left(\beta_5 \text{ in } D = \beta_5 M_S^{\alpha_5}\right)$	0.026	0.026
6a. Young stem height exponent $\left(\alpha_6 \text{ in } H = \beta_6 D^{\alpha_6} - \beta_7\right)$	1.096	0.667†
6b. Young stem height constant $\left(\beta_6 \text{ in } H = \beta_6 D^{\alpha_6} - \beta_7\right)$	161.812	65.000†
6c. Young stem height constant $\left(\beta_7 \text{ in } H = \beta_6 D^{\alpha_6} - \beta_7\right)$	0 ^a	0 ^a
7a. Mature stem height constant $\left(\beta_8 \text{ in } H = \beta_8 + \beta_9 \ln D\right)$	31.464	31.464
7b. Mature stem height exponent $\left(\beta_9 \text{ in } H = \beta_8 + \beta_9 \ln D\right)$	7.705	7.705

Notes: total annual growth, G_T (kg/yr); total plant mass, M_T (kg); growth in stem mass, G_S (kg/yr); growth in leaf mass, G_L (kg/yr); canopy projected area, A_L (m²); leaf mass, M_L (kg); stem mass, M_S (kg); stem diameter, D (m); and stem height, H (m). World-space dimensions = 100 m × 100 m.

^aThe allometric constant β_7 is embedded in the algorithm but its numerical value can equal zero in the case of a particular species, whether real or hypothetical.

For this study, we parameterized a plant that mimics all of the 1/4 (and multiples of 1/4) scaling relationships predicted by the WBE plant model, and we placed this idealized WBE plant in competition with a plant parameterized to mimic all of the allometric relationships observed across a broad spectrum of angiosperm shrub and tree species (Niklas, 2004). For convenience, we refer to this plant as a “generic angiosperm” (denoted as GA). We also constructed seven other plants. Each of these was a variant of the idealized WBE plant in that it differs from the WBE plant in only one numerical parameter, which was created by substituting one of the seven corresponding numerical values of the GA scaling parameters for the one characterizing an idealized WBE plant. The GA plant was used because it mimics many of the allometric properties of real plants (Hammond and Niklas, 2009, 2011a, b). It was also selected because each of its scaling exponents could be used as a parsimonious starting point from which to identify the numerical values of the exponents needed to parameterize the ideal WBE plant. Finally, the seven WBE variant plants were simulated to determine if, when, and how an ideal WBE plant fails, i.e., the seven variant WBE plants served in a sensitivity analysis of the ideal WBE plant model.

All plants were placed in competition in spatiotemporally homogenous and heterogeneous world-spaces to evaluate

whether habitat disturbance or patchiness altered their competitiveness. The ability of plants to compete with one another was evaluated by observing the degree to which plants sown from equal numbers of equally sized propagules successfully competed for light and space over the equivalent of 200 or 500 years under identical conditions. The tree growth-form was selected because it is long-lived, sedentary, and undergoes large changes in size as a result of indeterminate growth. It therefore has all of the biological attributes that make competitive exclusion experiments *in silico* relatively easy to design and measure. Also, the WBE theory (West et al., 1997, 1999, 2001, 2003) and its subsequent modifications relating to plants (Enquist et al., 2000, 2007a, b; Gillooly et al., 2001; Savage et al., 2004) stipulate all of the power rules characterizing the allometric behavior of an “idealized WBE tree”.

As noted, the equations required to parameterize a plant using SERA are not predicted by or mathematically embedded in the WBE plant model. The WBE model predicts the allometric behavior of plants. In contrast, SERA’s seven equation parameterize how an individual plant harvests light and occupies space (Table 1). Thus, it is the interactions among neighboring plants (and not the seven equations) that dictate the allometric relationships observed for the GA or the WBE plant. This mathematical disconnect is important because, without it, SERA simulations in the context of this study would be an exercise in circular logic.

We recognize that the results of our simulations do not *directly* test whether the core assumptions of the WBE model are valid. For example, a direct test of the minimal energy assumption would, by definition, require modeling and evaluating the efficiency of different nutrient-delivery systems within leaves, stems, and roots. Currently, SERA lacks this capability. However, even if it did, such simulations would shed no direct light on the biological consequences of possessing different internal hierarchical networks on plant–plant interactions, such as competition, which is a central venue for natural selection. In contrast, SERA does provide a direct quantitative method to assess the biological consequences on competition of a plant obeying different power rules, and, in particular, the consequences of those rules that mathematically emerge *a priori* if the assumptions of the WBE model are valid. In this manner, simulations directly address whether a key prediction emerges when the core assumptions of the WBE theory are correct.

MATERIALS AND METHODS

The basic model—The computer model used in this study is available at <https://github.com/seanth/SERA> in a format that permits downloading, running, and editing the code. The model is conceptually similar to other computer models, notably those of Chave (1999), Niklas (2000), and Enquist and Niklas (2001), in that each plant is simplified to consist of a single photosynthetic surface (canopy) elevated by a single stem (Hammond and Niklas, 2009). SERA differs from previously published models in three important ways: (1) it requires fewer input variables among which only six scaling exponents are required to initialize a plant (Table 1), (2) it is an individual-based model (i.e., species identification files define only the properties of plants belonging to a particular species), and (3), where some models represent the canopy as a flat disc (e.g., Chave, 1999; Enquist and Niklas, 2001), SERA’s default setting creates hemispherical canopies of uniform thickness. This last difference is important because a disk-shaped canopy casts a significantly larger projected area than a hemispherical canopy (with equivalent mass and thickness) and thus over-estimates the space that must be occupied to capture a fixed quantity of light.

The parameterization of plants requires 15 variables in seven equations (Table 1) that specify how the projected canopy area (A_L) of a plant captures light energy ($E = kA_L$), converts it into total annual growth in biomass (G_T), and

how G_T is partitioned into leaf, stem, and reproductive biomass (M_L , M_S , and M_R) (Fig. 1A). These seven equations are derived analytically from the premise that the size of the canopy and the extent to which it is shaded by neighboring plants dictate the ability of the individual plant to harvest light and grow annually, and on the premise that taller plants with larger canopies harvest more light than plants with smaller body sizes. The derivation of these equations, therefore, is not based on any of the three core assumptions of the WBE theory. Many of these equations also have a format that is mathematically unlike the basic predictions of the WBE theory. For example, the WBE theory predicts that G_T will scale as the 3/4 power of total body mass, M_T (i.e., $G_T \propto M_T^{3/4}$), whereas the equation for G_T in SERA is a power function of the product of A_L and M_L (Table 1: Eq. 1).

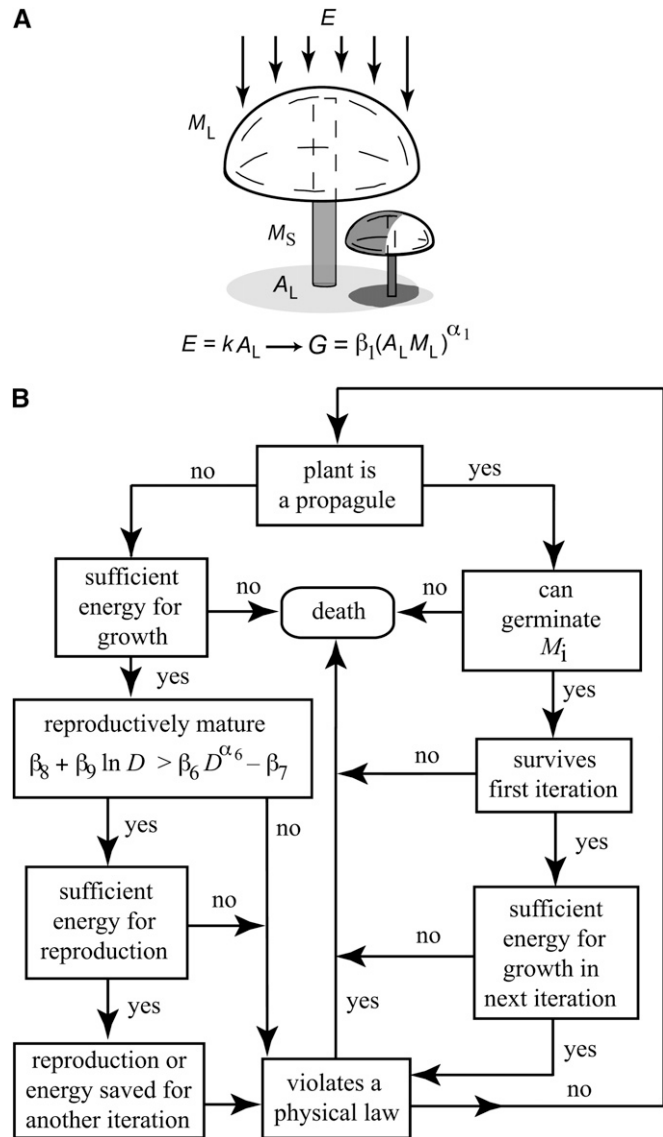


Fig. 1. The computational logic of SERA. (A) Canopy mass (M_L) and projected area (A_L) determine the light energy (E) captured that is converted into annual growth (G_T) and allotted to new M_L and stem mass (M_S). Shading reduces the effective A_L and thus G_T . (B) The propagule vs. plant status is assessed each iteration for each object. If a propagule germinates, its initial mass M_i is allocated to seedling M_L and M_S . If the object is a plant that has energy to grow, its vegetative vs. reproductive status is assessed. Reproductive maturity requires an inequality of an equation dictating how M_S is apportioned between growth in diameter and height, which depends on G_T . Adapted from Hammond and Niklas (2009).

TABLE 2. Transition to maturity for generic angiosperm (GA) and WBE plants. Values for height (H) with respect to stem diameter (D) use Eqs. 6 and 7 in Table 1 for each plant. The onset of reproductive maturity occurs when H in Eq. 7 is larger than H in Eq. 6 such that $H = \beta_6 D^{\alpha_6} - \beta_7$ is replaced by $H = \beta_8 + \beta_9 \ln D$ (shown in boldface).

Cycle	Generic angiosperm			WBE plant		
	Stem diameter (D)	$H_{\text{young}} (\beta_6 D^{\alpha_6} - \beta_7)$	$H_{\text{mature}} (\beta_8 + \beta_9 \ln D)$	Stem diameter (D)	$H_{\text{young}} (\beta_6 D^{\alpha_6} - \beta_7)$	$H_{\text{mature}} (\beta_8 + \beta_9 \ln D)$
0	0.00047199	0.03648266	-27.547543	0.0005013	0.40741536	-27.080942
1	0.00183278	0.16147399	-17.09419	0.00191678	0.99666143	-16.747025
2	0.00794853	0.80676325	-5.7892604	0.00949485	2.89772147	-4.4182289
3	0.0172582	1.8877126	0.18469393	0.01945001	4.67499905	1.10700966
4	0.02749565	3.14569309	3.77338065	0.02892335	6.09150926	4.16436889
5	0.0363629	4.27387052	5.927187	0.03759182	7.25536625	6.18413575
6	0.04467197	5.35574382	7.5129248	0.04558068	8.25047309	7.66886934
7	0.05250917	6.39428129	8.75842754	0.05302698	9.12665195	8.83476609
8	0.05995321	7.39474706	9.77997592	0.06003552	9.91448976	9.79123014
9	0.06706664	8.36208844	10.6439164	0.06668357	10.6339008	10.600426
10	0.07389816	9.30048617	11.3913431	0.07302882	11.2985505	11.3007765
11	0.08048597	10.213388	12.0493406	0.0791153	11.918231	11.9175784
12	0.08686049	11.1036342	12.6366444	0.08497737	12.5002112	12.4683219
13	0.09304629	11.9735804	13.1667244	0.09064238	13.0500461	12.9655789
14	0.09906353	12.8251984	13.649574	0.09613252	13.5720845	13.4186769
15	0.10492898	13.6601551	14.0928035	0.10146603	14.0698006	13.8347194
16	0.11065675	14.4798728	14.5023368	0.10665817	14.5460187	14.2192374
17	0.11625883	15.2855763	14.8828726	0.11172182	15.0030689	14.5766182
18	0.12174555	16.0783287	15.2381982	0.11666798	15.4428989	14.9103995

Notes: stem diameter D (m) and stem height, H (m). Each cycle equals one year.

In terms of annual allocations of mass and proportions, the allocation of M_S to stem diameter and height (D and H) involves two formulas that define (but do not require) a permanent transition from geometric self-similarity to nonself-similarity, i.e., a transition from the condition where $H = \beta_6 D^{\alpha_6} - \beta_7$ to the condition where $H = \beta_8 + \beta_9 \ln D$. Reproductive maturity occurs when $\beta_8 + \beta_9 \ln D > \beta_6 D^{\alpha_6} - \beta_7$ (Fig. 1B). Depending on G_T , a plant may produce n propagules with individual mass M_i , i.e., $M_P = nM_i$. All plants, regardless of size or species were parameterized to produce propagules of the same number and M_i , i.e., $M_P = nM_i = \text{constant}$. Propagules were randomly dispersed (using a Poisson distribution) around each parent up to a maximum distance proportional to H (following the logic of a simple wind dispersal model for seeds; see Okubo and Levin, 1989). The partitioning of M_i into M_L and M_S upon germination was the same for all plants, but species-specific after the first year of growth. Mortality resulted from the violation of a physical law (e.g., Euler's buckling law), light deprivation (due to the attenuation of light through over-topping canopies), or uniformly applied stochastic/age-dependent processes (Fig. 1B).

Parameterizing the generic angiosperm—The allometry of the GA was based on α - and β -values obtained from reduced major axis regression analyses of data tabulated from the primary literature for a total of 332 angiosperm managed populations and natural forested communities (Cannell, 1982). Values for the physical properties of wood that are required to estimate mechanical stability were taken from the literature (Lavers 1969; Niklas and Spatz, 2010). Analyses of the Cannell data set show that many allometric trends, particularly those involving plant height and stem and leaf biomass, are not log-log linear across the entire size-range of the data (Niklas, 2004; Niklas and Spatz, 2004). Rather, these data conformed to “broken-stick” statistical model in which the data were log-log linear within each of two size-ranges, a smaller (“young”) plant size-range ($5.93 \times 10^{-6} \text{ kg} \leq M_T \leq 6.41 \times 10^{-2} \text{ kg}$) and a larger (“mature”) plant size range ($6.41 \times 10^{-2} \text{ kg} < M_T \leq 3.18 \times 10^3 \text{ kg}$). This phenomenology is consistent with trends reported for metabolic rates and plant body size (Reich et al., 2006; Mori et al., 2010). Reduced major axis regression was applied to the data falling within each of these two empirically identifiable size-ranges to determine α - and β -values for small (young) and larger (mature) GA plants (Table 1; Eqs. 2 and 6 and Eqs. 3 and 7, respectively).

Parameterizing the idealized WBE plant—The parameterization of WBE plants was based on α - and β -values that produced trees obeying all of the scaling relationships predicted by the WBE plant model (West et al., 1997, 1999, 2001, 2003; Enquist et al., 2000, 2007b; Gillooly et al., 2001; West and Brown, 2005; Savage et al., 2004). These predicted scaling relationships are as follows: $M_L \propto M_S^{0.75}$, $M_L \propto D^{2.0}$, $M_L \propto M_T^{0.75}$, $H \propto M_T^{0.25}$, N (plant density) $\propto M_T^{-3/4}$, P_N

(total plant productivity) $\propto M_T^{0.0}$, $G_L \propto M_L^{1.0}$, $G_T \propto M_T^{0.75}$, $M_L \propto G_L^{1.0}$, and $G_L \propto G_T^{1.0}$ (Table 2). Notice that, with the exception of the $M_L \propto M_S$ relationship for mature plants (Table 1; Eq. 3a), none of these predicted scaling relationships is represented in the equations used to parameterize either the GA or the WBE plant. Therefore, the extent to which a simulated plant mimics the scaling relationships predicted by the WBE plant model could be used to determine whether the parameterization of such a plant was successful. We determined the numerical values for the scaling exponents required to parameterize an idealized WBE plant by trial-and-error using each of the α -values of the GA plant as a starting point. In excess of 200 simulations were required until the entire constellation of α -values was identified to produce a plant that conformed to the predicted behaviors of the WBE plant model.

In terms of the allometric constants (i.e., β -values), the WBE plant model can be used to predict β -values (e.g., see Enquist et al., 1999, 2000). However, this requires a large number of secondary and tertiary assumptions that made our analyses progressively more speculative and problematic. Additionally, our focus here was on the manner in which scaling exponents (rather than allometric constants) affect the competitive ability of plants. Therefore, with one exception (see below), the empirically determined β -values of GA plants were used to parameterize WBE plants.

The aforementioned exception relates to the age at which plants reach reproductive maturity about which the WBE model is moot. SERA-simulated plants become mature after the transition from juvenile to mature growth in height (Hammond and Niklas, 2009, 2011a, b), which also triggers a change in the M_L vs. M_S relationship. This is consistent with the findings of Enquist et al. (2007a) who also report a M_L vs. M_S transition from juvenile to mature growth. However, SERA predicts that this transition occurs when $M_S \geq 1 \text{ kg}$, whereas Enquist et al. (2007a) report that this transition occurs when $M_S < 1.0 \text{ g}$. Therefore, to be consistent with the WBE plant model, we parameterized WBE plants to manifest the M_L vs. M_S relationship of a mature plant upon germination and to maintain this scaling relationship over its lifetime, which had the consequence that WBE plants achieve reproductive maturity at roughly the same time as GA plants. This was achieved in SERA simulations by adjusting the equation relating stem height to diameter. In SERA simulations, the H vs. D relationship predicted by the WBE model is achieved using the equation $H = \beta_6 D^{\alpha_6} - \beta_7$, an equation that is consistent with empirical observations (Niklas and Spatz, 2004). However, for mature trees in SERA simulations, the H vs. D relationship is described by $H = \beta_8 + \beta_9 \ln D$, which results in mimicking a reduction in growth in H relative to D over time (Hammond and Niklas 2009). Therefore, as plants grew and $\beta_8 + \beta_9 \ln D$ exceeded $\beta_6 D^{\alpha_6} - \beta_7$, Eqs. 2 and 6 were replaced with Eqs. 3 and 7 (Tables 1, 2). This resulted in ontogenetic trends in plant height that are similar to those observed for real plants (Table 2; Fig. 2).

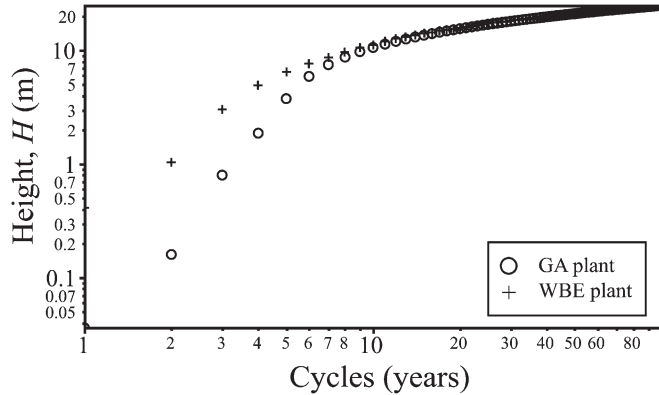


Fig. 2. Bivariate plots of plant height, H , vs. cycles (years). The data are from a simulation of an idealized WBE plant growing in isolation and a generic angiosperm (GA) plant growing in isolation. During the first 10 years, the WBE plant is taller. However, as it reaches maturity, the GA grows taller than the WBE plant (see Table 3).

WBE variant plants—After parameterization, the GA and WBE plants were observed to numerically differ in seven variables (Table 1). Substituting the corresponding numerical value of the WBE plant with one each of these variables from the GA plant resulted in seven variants of the WBE plant (see Table 5). Each of these variants was placed in competition with the GA plant using the same protocols described under the next heading (*World-spaces*). Our objective was to determine the extent to which the ideal WBE plant can be altered before its competitive behavior was quantifiably affected. Another objective was to determine which, if any, of the scaling exponents defining an ideal WBE plant are responsible for success or failure when competing with another species.

World-spaces—All simulations were run in triplicate for a total of 200 or 500 cycles (1 cycle = 1 yr) using a flat world-space measuring $100\text{ m} \times 100\text{ m}$. Data on the location and physical characteristics for each plant were saved for each cycle for subsequent regression analysis to determine the power rules governing the relationships among variables of interest. Plant competition and success were gauged by the number of plants surviving at the end of each simulation.

Details for simulating stable homogeneous and unstable heterogeneous world-spaces are given elsewhere (Hammond and Niklas, 2011a). Briefly, plants compete in homogeneous world-spaces for space and light energy under ambient light and soil conditions (Fig. 3A). Heterogeneous world-spaces are simulated with a hypothetical soil nutrient that limits growth in proportion to its concentration, e.g., G_T is reduced by 50% when the concentration is 50%. This protocol was successfully tested using *Abies alba* as a model tree species (Hammond and Niklas, 2009). The effects of environmental heterogeneity on competition were simulated in world-spaces divided into four patches with 100%, 75%, 50%, and 25% nutrient concentrations (Fig. 3B). Disturbance was mimicked by changing the locations of the patches every 5 or 20 yr (Fig. 3C, D).

RESULTS

Before reporting our results, it is important to reiterate three points: (1) the equations used to parameterize a species predetermine the behavior of an *individual* plant, (2) these equations differ substantively from the mathematics of the WBE theory, and (3) none of the seven SERA equations directly interrelates properties such as G_T , M_T , N , or plant productivity per plant density (P_N). Therefore, the scaling exponents reported for GA and the idealized WBE plant emerge as a consequence of how plants interact and compete with one another and not as a consequence of regurgitating the mathematics of the WBE plant model.

WBE plant-scaling relationships—Regression analyses of the data from simulations of idealized WBE plants gave the

numerical values for all of the scaling exponents predicted by the WBE model to describe the behavior of real plants (Table 3). Among these, three were particularly interesting. These were the scaling exponents for G_T vs. M_T , N vs. M_T , and P_N vs. M_T .

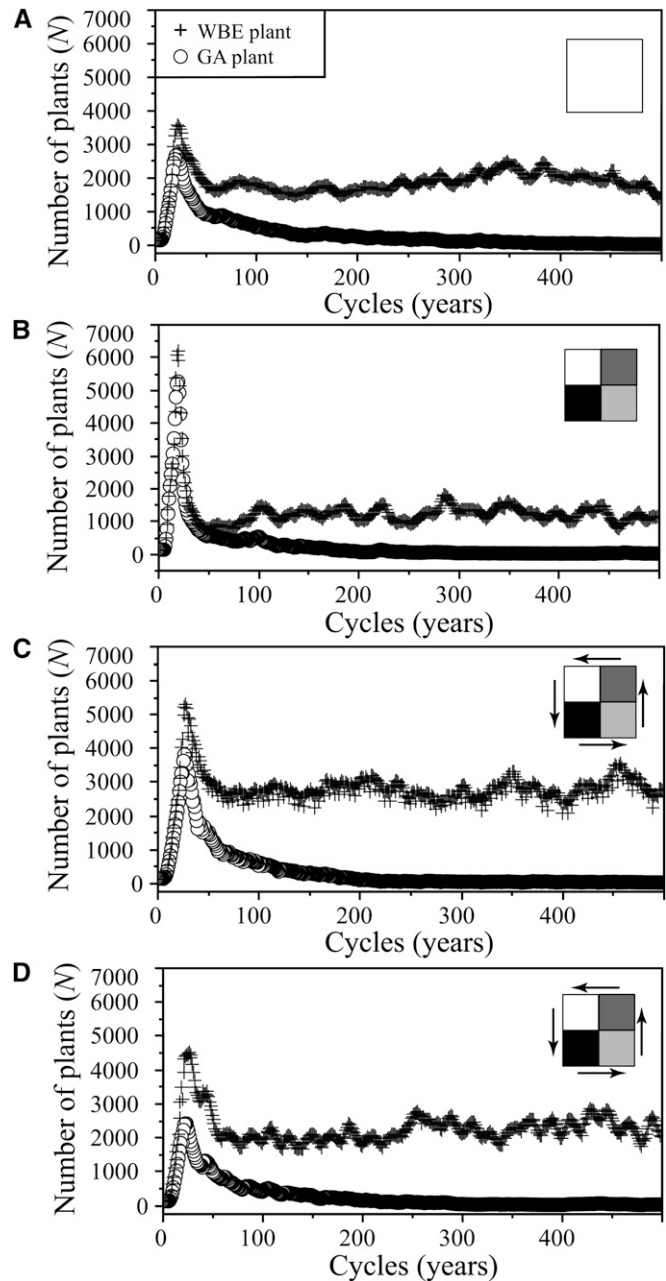


Fig. 3. Bivariate plots of plant number (N) vs. cycles (years) as idealized WBE plants and generic angiosperms (GA) compete for space and light under four world-space conditions. In each simulation, 50 propagules of each kind of plant were randomly distributed in a $100\text{ m} \times 100\text{ m}$ world-space. Homo- and heterogeneous world-spaces were simulated using different concentrations (%) of a hypothetical nutrient than limits growth (i.e., 100%, 75%, 50%, and 25%, respectively denoted by successively darker areas in the inserts). (A) A homogeneous world-space with a 100% ambient nutrient concentration. (B) A stable heterogeneous world-space (with four nutrient concentrations; see insert). (C, D) Heterogeneous world-spaces disturbed every 5 or 20 years by changing the locations of the nutrient (as indicated by arrows).

TABLE 3. Numerical values of scaling exponents predicted by the WBE model and those that were observed for simulations of an idealized WBE plant and a generic angiosperm (GA). All predicted values for the WBE plant are statistically indistinguishable from observed values. Values differing (at $\alpha = 0.05$) between the WBE plant and the GA plant are denoted by †.

Scaling relationship	WBE plant		GA plant
	Predicted by WBE model	Observed in simulations	Observed in simulations
$\log M_L$ vs. $\log M_S$	0.75	0.76	0.74
$\log M_L$ vs. $\log D$	2.00	2.01	1.98
$\log M_L$ vs. $\log M_T$	0.75	0.75	0.74
$\log G_T$ vs. $\log M_T$	0.75	0.76	0.75
$\log M_L$ vs. $\log G_L$	1.00	0.99	0.98
$\log G_L$ vs. $\log M_L$	1.00	1.01	0.99
$\log G_L$ vs. $\log G_S$	1.00	1.00	0.98†
$\log H$ vs. $\log M_T$	0.25	0.25	0.29†
$\log N$ vs. $\log M_T$	-0.75	-0.76	-0.70†
$\log P_N$ vs. $\log M_T$	0.00	0.00	0.05†

Notes: leaf mass, M_L (in kg); stem mass, M_S (in kg); stem diameter, D (in m); growth in leaf mass, G_L (kg/yr); growth in stem mass, G_S (kg/yr); tree height, H (m); total plant mass, M_T (kg); and total annual growth, G_T (kg/yr); number of plants per unit area (plant density, area⁻¹), N ; productivity per unit plant density, P_N (kg/yr/area).

The predicted WBE numerical values for these relationships are 0.75, -0.75, and zero, respectively. The observed values for idealized WBE plants are 0.76, -0.76, and zero (Table 3).

Additional scaling exponents of interest were those for M_L vs. D and M_L vs. M_S . The observed and predicted values for these relationships were statistically indistinguishable (Table 3), and it is worth noting that no parameterization equation relates M_L directly to D (Table 1). In addition, WBE plants differing in height and therefore shaded differently by neighboring WBE plants had different α -values for some scaling relationships. For example, the α -values for M_L vs. D for understory, mid-canopy, and top-canopy plants were 1.2, 1.8, and 2.2, respectively, although the exponent for plants of all sizes was 2.01 (Table 3).

Based on the similarities between the numerical values predicted by the WBE theory and those observed α -values for the simulated WBE plants grown in isolation or as populations, the parameterization of an ideal WBE plant was judged to accurately portray the WBE plant model.

Competition between idealized WBE and GA plants—When equal numbers of propagules grew sufficiently in size to compete with their neighbors, the WBE plant outcompeted the GA plant and, in most cases, drove it to near extinction in ~200 yr (Fig. 3). This behavior occurred under all simulated world-space conditions (Fig. 3). Plant–plant interactions were minimal during the first 20 years of growth because plants were too small to shade and compete with their neighbors. During this period, plants reached reproductive maturity, produced propagules, and the populations of both species increased in number. Subsequently, the canopies of neighboring plants reached sufficient size to overlap and shade one another, at which time the number of plants of both species declined but at the expense of GA plants as a result of light deprivation (Fig. 3).

World-space conditions did affect average plant size and number. Homogeneous world-spaces had fewer and larger plants than spatially heterogeneous, undisturbed world-spaces (Table 4; Fig. 3A, B). Average plant size also decreased as the frequency

TABLE 4. Mean \pm SE for body mass (kg) and height (m) of idealized WBE and GA plants at the end of simulations (Figs. 3, 4).

Simulation	WBE plant	GA plant
Homogeneous world-space (Fig. 3A)	203 \pm 23.6 kg 9.52 \pm 0.22 m	— —
Heterogeneous undisturbed (Fig. 3B)	108 \pm 11.5 kg 8.32 \pm 0.19 m	— —
Heterogeneous (5-yr disturbance; Fig. 3C)	54.5 \pm 5.50 kg	37.2 \pm 2.71 kg
Heterogeneous (20-yr disturbance; Fig. 3D)	33.5 \pm 3.48 kg 6.35 \pm 0.09 m	26.5 \pm 1.71 kg 4.43 \pm 1.15 m
WBE variant 1 vs. GA (Fig. 4A)	31.0 \pm 2.03 kg	52.0 \pm 2.22 kg
WBE variant 2 vs. GA (Fig. 4B)	27.9 \pm 2.17 kg 6.16 \pm 1.21 m	39.8 \pm 1.08 kg 7.68 \pm 0.15 m
WBE variant 3 vs. GA (Fig. 4C)	32.5 \pm 2.51 kg 6.10 \pm 2.00 m	42.0 \pm 1.49 kg 7.73 \pm 0.16 m
WBE variant 4 vs. GA (Fig. 4D)	29.4 \pm 1.99 kg 4.15 \pm 1.00 m	38.1 \pm 1.78 kg 6.65 \pm 0.09 m
WBE variant 5 vs. GA (Fig. 4E)	33.1 \pm 2.17 kg 4.78 \pm 1.78 m	50.3 \pm 1.09 kg 7.83 \pm 0.17 m
WBE variant 6 vs. GA (Fig. 4 F)	33.0 \pm 1.88 kg 5.32 \pm 1.78 m	50.1 \pm 1.99 kg 7.60 \pm 0.15 m

of disturbance increased (Fig. 3C, D). Habitat patchiness and disturbance decreased plant mass and height and increased density such that plants took on the characteristics of weedy shrubs.

Competition between WBE variants and GA plants—Altering the allometry of WBE plants even slightly reduced or eliminated their competitive advantage, or, in one case, resulted in death (Tables 4, 5). Among the six viable WBE variants, none completely or rapidly excluded GA plants, although some outnumbered GA plants at the end of simulations. These and additional simulations identified variables α_2 and β_2 in Eq. 2 as critical to the success of WBE plants (Table 1). The numerical values of α_2 and β_2 allow juvenile plants to allocate more biomass to stems (and to height, see Fig. 2) than to canopies compared to GA plants. Thus, young WBE plants harvest more light when young compared to GA plants. As a consequence, they grow faster and shade competitors earlier in their ontogeny. This competitive advantage is temporary, however, since, if they manage to reach maturity, GA plants reach heights in excess of mature WBE plants (Table 4).

Finally, simulations were run to determine whether randomly introduced WBE propagules could grow, compete with, and eventually outcompete a well-established population of GA plants. For this purpose, a population of GA plants was allowed to grow for 250 yr and subsequently randomly “seeded” with different numbers of WBE propagules. In these simulations, the majority of WBE propagules died immediately because they violated the physical law that no two objects can occupy the same location at the same time (most WBE propagules “landed” on or inside a GA tree). However, in simulations where one or more WBE propagules survived the first year, WBE plants outcompeted the GA plant, gaining numerical supremacy in 100 or more years (Fig. 4). Analyses of these simulations showed that WBE plants became established and gained in number as a consequence of the light gaps produced by the death of large GA plants. Once WBE plants established small populations, the WBE plants over grew and shaded out GA plants as in previously described simulations in which equal numbers of GA and WBE plants were randomly distributed in spatiotemporally homogeneous and heterogeneous world-spaces.

DISCUSSION

The representation of biological reality extends to the use of mathematical models to capture relationships in the form of hypotheses that can be manipulated with measurable variables. The validity of these models can be evaluated based on the extent to which predictions conform to reality. When different models obtain equivalent predictions, validation requires testing the core assumptions of the models rather than drawing potentially endless comparisons between observed and predicted results. However, the assumptions of some models are difficult, if not impossible to test experimentally using real organisms. In the case of the WBE model and its elaborations (West et al., 1997, 1999, 2001, 2003; Enquist et al., 2000, 2007a, b; Gillooly et al., 2001; Savage et al., 2004; West and Brown, 2005), it is extremely difficult to determine

experimentally whether 1/4 power rules are the result of natural selection operating on hierarchal networks to minimize energy because the number of competitive exclusion experiments required to validate this particular assumption would be astronomically large given the number and diversity of living plant species.

We therefore turned to computer simulations to evaluate a key consequence of the core WBE assumptions as reflected in how these assumptions affect plant–plant competition, which is a major focus of natural selection. The results of these simulations are consistent with the proposition that 1/4 (or multiples of 1/4) power rules confer a competitive advantage in a manner that supports the WBE plant model. An idealized WBE plant rapidly outcompetes all other simulated plants, a behavior that is all the more noteworthy because prior simulations have shown that one of its competitors (the generic angiosperm)

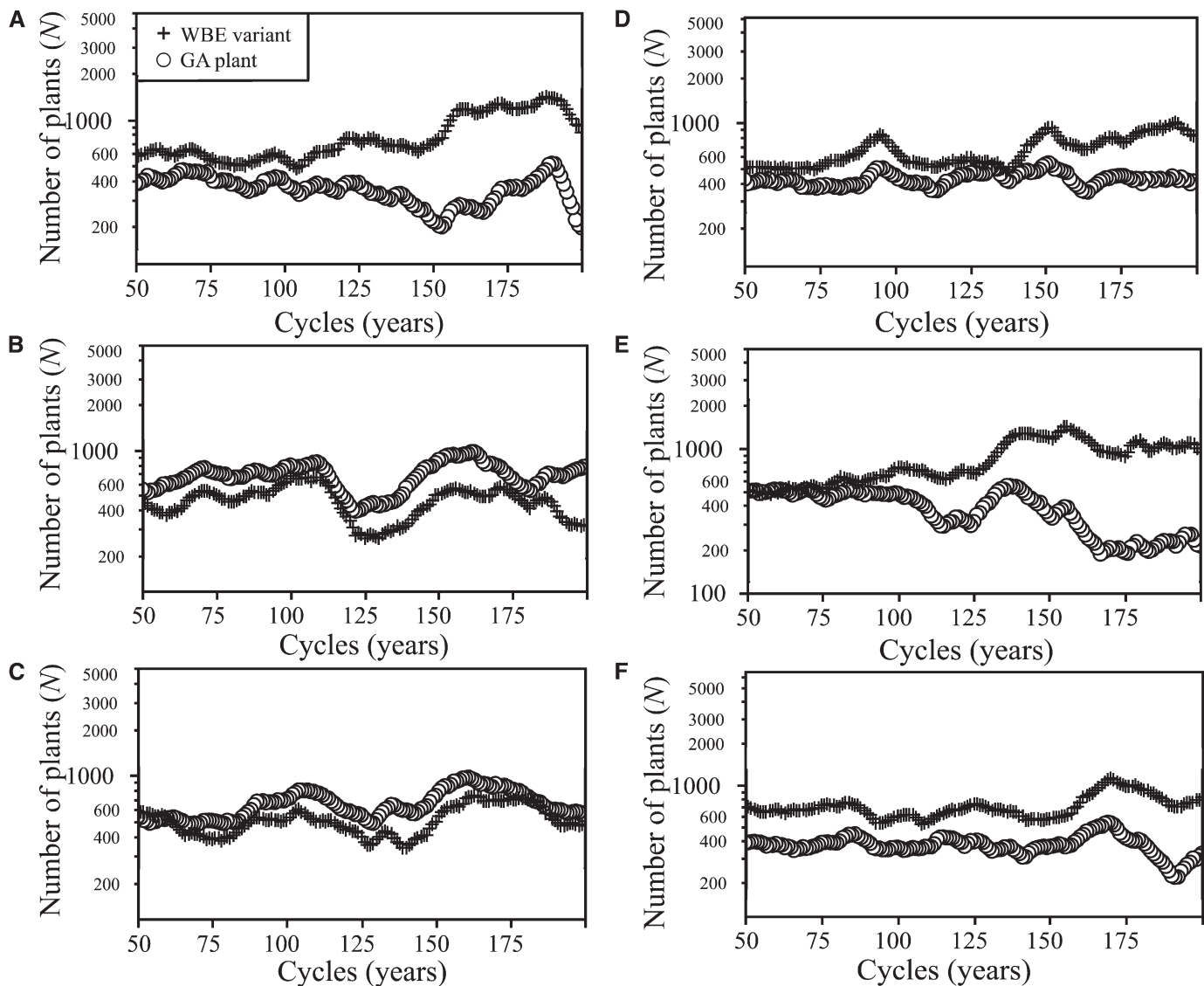


Fig. 4. Bivariate plots of plant number (N) vs. cycles (years) as generic angiosperms (GA) and six WBE variants (see Table 3) compete in a homogeneous $100 \text{ m} \times 100 \text{ m}$ world-space. Each simulation began with 125 randomly distributed propagules for each type of plant. (A) Competition between GA and WBE plants with $\alpha_2 = 0.882$ in Eq. 2a (see Table 1). (B) Competition between GA and WBE plants with $\beta_2 = 0.085$ in Eq. 2b. (C) Competition between GA and WBE plants with $\alpha_3 = 0.772$ in Eq. 3a. (D) Competition between GA and WBE plants with $\alpha_4 = 1.022$ in Eq. 4a. (E) Competition between GA and WBE plants with $\alpha_5 = 0.383$ in Eq. 5a. (F) Competition between GA and WBE plants with $\alpha_6 = 1.096$ in Eq. 6a.

TABLE 5. Results of changing the numerical values of seven variables used to parameterize GA and WBE plants. The numbers in parentheses are the respective numbers of GA and WBE plants that survive at the end of simulations.

GA value used to replace	The WBE value to create a variant	Results in
$\alpha_2 = 0.882$	$\alpha_2 = 0.750$	Coexistence (197 and 831)
$\beta_2 = 0.085$	$\beta_2 = 0.116$	Coexistence (784 and 314)
$\alpha_3 = 0.772$	$\alpha_3 = 0.750$	Coexistence (570 and 471)
$\alpha_4 = 1.022$	$\alpha_4 = 1.000$	Coexistence (409 and 823)
$\alpha_5 = 0.383$	$\alpha_5 = 0.375$	Coexistence (211 and 945)
$\alpha_6 = 1.096$	$\alpha_6 = 0.667$	Coexistence (325 and 814)
$\beta_6 = 161.8$	$\beta_6 = 65.00$	Violates Euler's law; dies

outcompetes all previously simulated plants (Hammond and Niklas, 2009, 2011a, b).

An additional finding is that altering only one of the numerical values of the idealized WBE plant dramatically alters its competitiveness, or results in its death. This idealized plant easily fails even if modified very slightly. It therefore is a highly integrated mathematical phenotype in terms of seven variables that distinguish WBE from GA plants. A numerical deviation of any one of these variables from its required numerical value without adjusting the remaining variables dramatically reduces the ability of WBE plants to compete. Such covariation among the variables that dictate scaling relationships has been demonstrated empirically and is thus the focus of considerable attention (Price et al., 2010; Savage et al., 2010). If these variables are analogous to genes or gene networks and if the formulas containing them are analogous to developmental processes, random mutation effects might prevent the evolution of idealized WBE plants. Under any circumstances, empirical studies show that different permutations of scaling relationships exist among real plants (e.g., McCulloh et al., 2003; Meinzer et al., 2005; Reich et al., 2006; Price et al., 2010). Indeed, if this were not the case, there would be little plant biodiversity.

Two other considerations must be entertained when considering the results reported here. First, we cannot exclude the possibility that the scaling properties of the WBE plant may result from other factors that coincidentally yield 1/4 power rules, and, second, real species undeniably compete in far more complex spatiotemporal world-spaces than simulated here. Natural selection operates at the level of differences in body size, and convergent solutions to increases in size are possible (Bonner and Horn, 2000; Price et al., 2010). Because size-dependent variables can scale to physical laws that obey 1/4 (or multiples of 1/4) power rules (e.g., the second moment of area and the Hagen-Poiseuille law), the predictions of the WBE model may be correct, but for mechanistically different reasons. Additionally, our simulations neglect the effects of water deprivation, temperature, herbivory, microbial attack, reproductive specialization to different ecological conditions, and a host of other biologically important phenomena that require metabolic energy or phenotypic specialization. This simplification was required to observe competition between different plants on an otherwise level playing field. Prior simulations do show that comparatively simple changes in the world-space that mimic severe ecological conditions (such as ice damage to xylem) can increase the mortality of one or more species and thus shift the balance in relative species abundance (Hammond and Niklas, 2009). Thus, the WBE plant may be “ideal” when competing against a generalist but not a specialist species. If true, empirically

observed α -values that deviate from 1/4 power rules may reflect the effects of localized environmental pressures that have selected away from the WBE ideal.

It is also important to emphasize that the simulations presented here deal with an “averaged” angiosperm rather than with a real flowering plant species. Angiosperm species are highly diverse and different allometries are known to exist among mature individuals and among juveniles, as noted by Sack et al. (2002) and others. It is possible therefore that one or more real angiosperm species exist that would outcompete the idealized WBE plant in one or more particular environmental settings or across the majority of settings. Our simulations mimic an open field (or open canopy) habitat in which the WBE allometry favoring early growth in height does particularly well. A population of WBE plants regenerating in very deep shade may suffer as a consequence of growth in height rather than growth in the spread of canopies. Simulations in which WBE plants are introduced at random into a well-established population of generic angiosperm plants (see Fig. 5) show that WBE plants gain numerical supremacy as a consequence of the death of large generic angiosperm plants (and thus under localized open canopy situations). This behavior is congruent in virtually every respect with the concept of Kohyama's “optimist” species, which has adaptive attributes under light shade or open field conditions (Kohyama, 1987, 1990, 1991). Additional simulations are required to establish with greater certainty the allometric features that confer advantages to WBE plants under different community densities.

In summary, many authors have emphasized that the assumptions of the WBE model need to be tested (e.g., Price et al., 2010). We believe that our simulations advance this agenda for the first time because they address a logical consequence of the WBE plant model, i.e., an idealized WBE plant is expected to outcompete species, even those that allometrically differ little from it. Perhaps equally intriguing is that the scaling properties of the average (generic) angiosperm do not differ all that much from those predicted by the WBE model (Niklas, 2004). This suggests to us that natural selection may have, on average, achieved the best results possible in a changing world occupied by real organisms competing for resources in complex ways. Future research

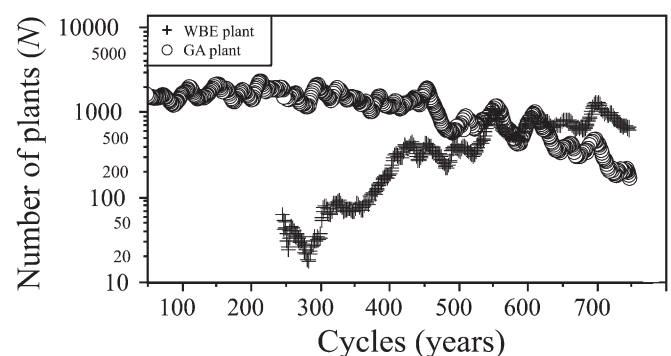


Fig. 5. A bivariate plot of plant number (N) vs. cycles (years) in a simulation of a generic angiosperm (GA) population growing for 250 years that is then “invaded” by WBE propagules. Sixty-five WBE plants survive in the first year (the majority of WBE propagules die because they land in the same location as a GA plant). After 16 cycles, the WBE population increases in number and eventually outnumbers the GA population. In all similar simulations, the WBE plant eventually drives the GA plant to extinction.

will focus on, among other things, whether it is possible to create a hypothetical plant with scaling relationships that confer competitive superiority over the idealized WBE plant.

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