

## Appendix A

### Plant interactions alter the predictions of metabolic scaling theory

Yue Lin\*, Uta Berger, Volker Grimm, Franka Huth and Jacob Weiner

\* Institute of Forest Growth and Computer Science, Dresden University of Technology, P.O. 1117, 01735 Tharandt, Germany  
yue.lin.tud@googlemail.com

### Model description<sup>1</sup>

#### A GENERAL ONTOGENETIC GROWTH MODEL FOR PLANTS

The essential basis for modeling the ontogeny of individual plants starts with an energy conservation equation (Enquist & Niklas 2001; West *et al.* 2001; Hou *et al.* 2008):

$$B_p = B_r + S = B_r + E_s dm/dt \quad (1)$$

where  $B_p$  is defined as total energy intake rate (i.e. gross photosynthetic rate). A fraction of this assimilated energy is consumed by respiration,  $B_r$ , the remainder is stored as reserves and used for synthesizing new tissues,  $S$  (Fig. S1).  $E_s$  is the metabolic energy stored in one unit of biomass and  $dm/dt$  is the change in biomass ( $m$ ) per unit time ( $t$ ).

The rate of energy consumed by respiration,  $B_r$ , depends on three major processes that require energy (Fig. S1): maintenance of biomass ( $B_{\text{maint}}$ ), ion transport ( $B_{\text{tran}}$ ) and biosynthesis ( $B_{\text{syn}}$ ), which can be summarized as (Lambers *et al.* 2008):

$$B_r = B_{\text{maint}} + B_{\text{tran}} + B_{\text{syn}} = \sum B_m m_{\text{living}} + B_{\text{tran}} + E_c dm/dt \quad (2)$$

where  $B_m$  denotes average mass-specific maintenance metabolic rate,  $m_{\text{living}}$  stands for the biomass of living tissues, and  $E_c$  designates the energy required to synthesize a unit of biomass.

Typical average biological parameters of cells (tissue) are taken as a fundamental unit here, and possible differences between tissues are ignored (West *et al.* 2001). Note that the terms  $S=E_s dm/dt$  in Eqn (1) and  $B_{\text{syn}}=E_c dm/dt$  in Eqn (2) are quite different:  $S$  stands for the rate of cumulative energy content of new biomass, whereas  $B_{\text{syn}}$  refers to the metabolic energy expended on biosynthesis which is

---

<sup>1</sup> References: see article.

dissipated as heat instead of obtained as stored biomass (Hou *et al.* 2008).  
Combining Eqns (1) and (2), we get

$$B_p = B_{\text{maint}} + B_{\text{tran}} + B_{\text{syn}} + S = \sum B_m m_{\text{living}} + B_{\text{tran}} + E_0 dm/dt \quad (3)$$

where  $E_0 = E_c + E_s$ , is constant for a given taxon and stands for the sum of energy stored in a unit of biomass plus the energy used to synthesize this biomass, i.e. the synthesis costs of a unit of biomass.

Equation (3) is quite general, but  $B_{\text{maint}}$  may vary between woody and non-woody plants, as woody plants contain nonliving tissues (e.g. heartwood in stem and root) which do not need energy for their maintenance (Enquist *et al.* 2009). Also large trees with a large amount of heartwood, contain much less living tissues ( $m_{\text{living}}$ ) in comparison to the total biomass ( $m$ ). We assume that during ontogeny, woody plants mainly expend energy for maintaining their photosynthetic tissues (leaves),  $m_L$ , and conducting tissues (standing sapwood of stem and root),  $m_C$ , and suppose

$$B_{\text{maint}} = \sum B_m m_{\text{living}} = B_m m_L + B_m m_C = B_L + B_C \quad (4)$$

for woody plants, where  $B_L$  and  $B_C$  specify the metabolic rate for maintaining photosynthetic and conducting tissues, respectively (Fig. S1). Combining Eqns (3) and (4) we can get the energy conservation equation for woody plants:

$$B_p = B_m m_L + B_m m_C + B_{\text{tran}} + E_0 dm/dt \quad (5)$$

Based on empirical measurements and theoretical assumptions linking biomass and metabolism, MST (West *et al.* 1999; Enquist 2002; Price *et al.* 2007<sup>2</sup>; Enquist *et al.* 2009) predicts that whole-plant, or gross, photosynthesis rate,  $B_p$ , and ion transport metabolic rate  $B_{\text{tran}}$  allometrically scale with the total biomass of a plant,  $m$ , as  $B_p \propto B_{\text{tran}} \propto m^\theta$ , where  $\theta \equiv 1/(2\alpha + \beta)$  and  $\alpha$  and  $\beta$  representing the geometry and biomechanics of the vascular network. Their values may vary across different taxa (Price *et al.* 2007).

Although the Eqn (5) can be easily recast by using empirical values of  $\alpha$  and  $\beta$ , we use  $\alpha = 1/2$  and  $\beta = 1/3$  as common and idealized cases here (Price *et al.* 2007), so that  $\theta = 3/4$ . Models based on these scaling relationships predict that the standing leaf biomass,  $m_L$ , scales with respect to total biomass as  $m_L \propto m^{-3/4}$  across woody plants, which was confirmed by empirical data (Sack *et al.* 2002<sup>3</sup>; Niklas 2005<sup>4</sup>).

The relationship between standing sapwood biomass ( $m_C$ ) and total biomass  $m$  is largely unknown, therefore here we assume that the tissue- or species-specific wood density of conducting tissues,  $d_C$ , is constant for a given plant. Its total volume of

<sup>2</sup> Price, C.A., Enquist, B.J. & Savage, V.M. (2007). A general model for allometric covariation in botanical form and function. *Proc. Natl Acad. Sci. USA.*, 104, 13204-13209.

<sup>3</sup> Sack, L., Maranon, T., Grubb, P.J., Enquist, B.J. & Niklas, K.J. (2002). Global allocation rules for patterns of biomass partitioning. *Science*, 296, 1923a.

<sup>4</sup> Niklas, K.J. (2005). Modelling below-and above-ground biomass for non-woody and woody plants. *Ann. Bot.*, 95, 315-321.

conducting tissues,  $v_C$ , can be formulated as  $v_C \propto A_S h$ , where  $A_S$  is the mean cross-sectional area of sapwood and  $h$  is the height of plant. Because we can assume that  $A_S \propto m^{7/8}$  and  $h \propto m^{1/4}$  (West *et al.* 1999; Enquist 2002), we derive the allometric relationship  $m_C = d_C v_C \propto A_S h \propto m^{7/8} m^{1/4} \propto m^{9/8}$  for woody plants. Substituting the allometric relationship on biomass for all related terms in Eqn (5) gives

$$B_0 m^{3/4} = B_m a_L m^{3/4} + B_m a_S m^{9/8} + a_{\text{tran}} m^{3/4} + E_0 dm/dt \quad (6)$$

where  $B_p = B_0 m^{3/4}$  reflects the total energy intake rate (i.e. gross photosynthetic rate) under optimal situation,  $B_0$  is constant for a given taxon (West *et al.* 1999),  $a_L$ ,  $a_S$  and  $a_{\text{tran}}$  are normalization constants. Eqn (6) can therefore be rewritten as

$$dm/dt = a_1 m^{3/4} - b_1 m^{9/8} = a_1 m^{3/4} [1 - (m/M)^{3/8}] \quad (7)$$

with  $a_1 = (B_0 - B_m a_L - a_{\text{tran}})/E_0$  and  $b_1 = B_m a_S/E_0$ . The value  $M = (a_1/b_1)^{8/3}$  is the asymptotic maximum body size of the woody plant (calculated for  $dm/dt = 0$ ), which depends on species-specific traits and is determined by the systematic variation of the *in vivo* metabolic rate within different taxa (West *et al.* 2001). The gain term ( $a_1 m^{3/4}$ ) in Eqn (7) dominates while plants grow to a moderate size, which has been shown to be a good quantitative description of plant growth (Niklas & Enquist 2001; Enquist *et al.* 2009).

Across non-woody plants which lack secondary tissues (or juveniles of woody plant which have not accumulated much secondary tissue), the total biomass of living tissues (as leaves,  $m_L$ , stem,  $m_S$ , and roots,  $m_R$  is approximately equal to the whole plant mass,  $m_{\text{living}} = m_L + m_S + m_R \approx m$  (Enquist 2002). Combining Eqn (3) with those scaling relationship leads to

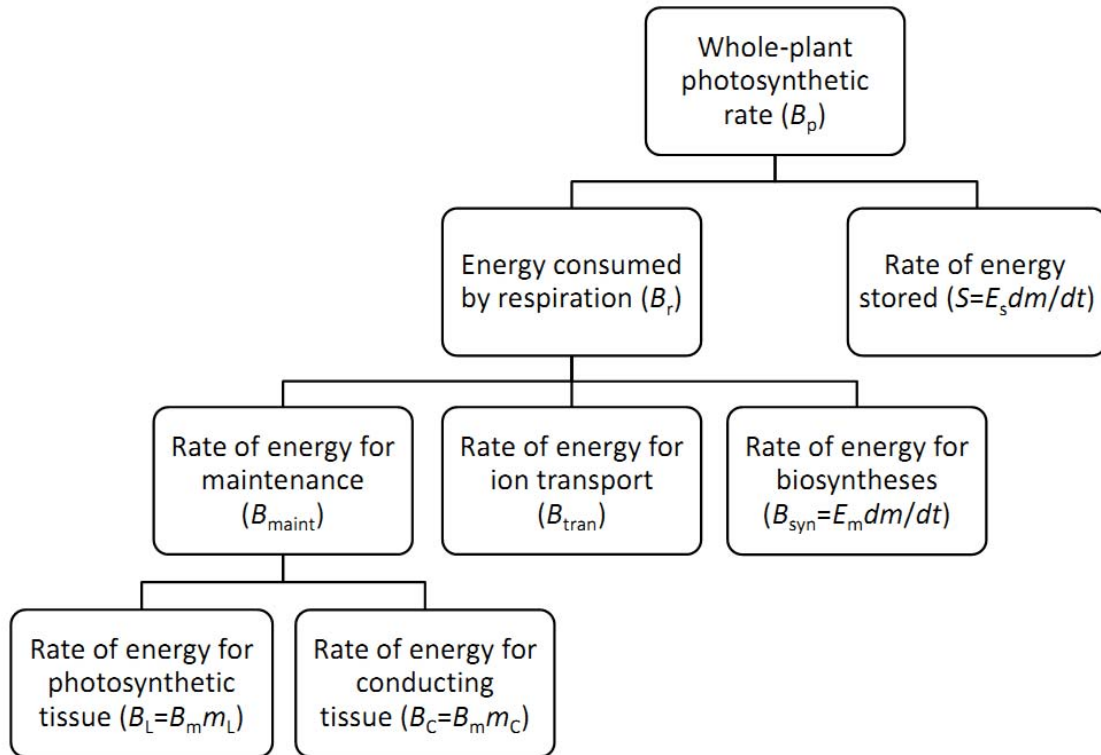
$$B_0 m^{3/4} = B_m m + a_{\text{tran}} m + E_0 dm/dt \quad (8)$$

for non-woody plants.

Taking the parameters in Eqn (8) in the same sense as before, Eqn (8) can be re-expressed as

$$dm/dt = a_2 m^{3/4} - b_2 m = a_2 m^{3/4} [1 - (m/M)^{1/4}] \quad (9)$$

with  $a_2 = B_0/E_0$ ,  $b_2 = (B_m + a_{\text{tran}})/E_0$ , and  $M = (a_2/b_2)^4$ , which is the asymptotic maximum body size of a non-woody plant.



**Figure S1** Assimilated energy partition of plants during ontogenetic growth.

## INDIVIDUAL-BASED MODEL (IBM) CONSIDERING MODE OF COMPETITION, RESOURCE LIMITATION AND ONTOGENETIC GROWTH

The following model description follows the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010),

### *Purpose*

The aim of this model is to evaluate the multiple effects of the mode of competition and resource limitation on regulating plant population dynamics, specifically on self-thinning trajectories and density-dependent mortality. In particular, we test whether interactions on individual plant level can alter the slope and intercept of the self-thinning line. The model does not represent specific species, but generic ones.

### *Entities, state variables, and scales*

The entities in the model are plants and square habitat units, or patches (Table A1). Plants are characterized by the following state variables: initial growth rate, initial biomass, maximum biomass (asymptotic biomass), current biomass and their position, i.e. coordinates of the stem. Each individual plant has its own circular zone-of-influence (ZOI). The ZOI stands for the physical space occupied by a plant, and represents the energy and resources potentially available to this plant, which is

allometrically related to its body mass. Neighboring plants only compete for the resources when their ZOIs are overlapping.

In order to make the spatial calculations of resource competition easier, ZOIs are projected onto a grid of patches. To avoid edge effects, we use a torus world with a size of  $200 \times 200$  patches (Grimm & Railsback 2005<sup>5</sup>). Each patch represents  $0.25 \text{ m}^2$  or  $0.25 \text{ cm}^2$  for woody- and non-woody plants, respectively. The state of each patch is characterized by its resource availability. We use a homogeneous environment here as all patches have the same, and constant, degree of resource limitation. One time step in the model represents approximately one year for woody plants and one day for non-woody plants.

**Table A.1** State variables and initialization in the individual-based model. Actual values are drawn from the given intervals to introduce a certain degree of heterogeneity among individuals.

Variable	Description	Initial Value [unit] (woody/non-woody)
Plants		
$c_1$ or $c_2$	Initial growth rate	$1 \pm 0.1 \text{ [kg m}^{-2} \text{ time step}^{-1}] / \text{[mg cm}^{-2} \text{ time step}^{-1}]$
$m_0$	Initial body mass	$2 \pm 0.2 \text{ [kg]} / \text{[mg]}$
$M$	Maximal biomass	$2 \times 10^6 \pm 2 \times 10^5 \text{ [kg]} / \text{[mg]}$
$m$	Current biomass	$\text{[kg]} / \text{[mg]}$
$A$	Zone of influence	$\text{[m}^{-2}] / \text{[cm}^{-2}]$
Patches		
$RL$	Level of resource limitation	$[0, 1]$
Initialization		
Mortality	Threshold of death	$2\% \text{ of } m^{3/4}$
Density	Number of plants	$8100 \text{ ha}^{-1} / \text{m}^{-2}$

### *Process overview and scheduling*

After initialization, all individual plants with a given density are randomly distributed in the world. The processes of resource competition, growth and mortality of each plant are fulfilled within each time step. In each step, individual plants first sense the resource qualities of patches within their ZOIs, the area (radius) of an individual plant's ZOI is determined by its current biomass. When their ZOIs are overlapping, individuals compete within the overlapping area. Thus, the overlapping area reflecting resources is divided according to the competition mode. Considering the outcome of the competition process, all individual plants grow according to the growth function. Plants with growth rates falling below a threshold die and are

<sup>5</sup> Grimm, V. & Railsback, S.F. (2005). *Individual-based modeling and ecology*. Princeton University Press, Princeton and Oxford.

removed immediately. The state variables of the plants are synchronously updated within the subroutines, i.e. changes to state variables are updated only after all individuals have been processed (Grimm and Railsback 2005).

### *Design concepts*

*Basic principles:* From “Metabolic Scaling Theory”, we derived a general ontogenetic growth model for individual plants. We combine this model, via the ZOI approach, with the effects of different modes of competition and resource limitation.

*Emergence:* All features observed at the population level, e.g. mass-density relationship or self-thinning trajectories (i.e. size distribution and spatial distribution, respectively), emerge from the interaction of individual plants with their neighbors and the resource level of their abiotic environment.

*Interaction:* Individual plants interact via competition for resources in the overlapping area of their ZOIs.

*Stochasticity:* Initial growth rate, initial biomass, maximum biomass and initial position of plants are randomly taken from the intervals given in Table 1. This introduces a certain level of heterogeneity among individual characteristics to take into account that real plants are never exactly identical.

*Observation:* Population size, biomass of each plant, and mean biomass of all living plants are the main observations.

### *Initialization*

Initially, individual plants are randomly distributed according to the chosen initial density. Resources are spatially and temporally constant. Each plant has an initial biomass ( $m_0$ ), maximal biomass ( $M$ ) and initial growth rate ( $a$ ) drawn from truncated normal distributions with average and intervals given in Table 1.

### *Input*

After initialization, the model does not include any external inputs, i.e. the abiotic environment is constant.

### *Submodels*

#### *Plant growth*

In our individual-based model the plant’s ZOI stands for the physical space occupied by a plant and represents the energy and resources potentially available to this plant. This space is allometrically related to the plant’s body mass,  $m$ , as  $cA=m^{3/4}$  (Enquist & Niklas 2001), where  $c$  is a normalization constant. Accordingly, Eqns (7) and (9) can be rewritten as

$$dm/dt = c_1 A [ 1 - ( m / M )^{3/8} ] \quad (10a)$$

for woody plants and

$$dm/dt = c_2 A [ 1 - ( m / M )^{1/4} ] \quad (10b)$$

for non-woody plants, where  $c_1 = a_1c$  and  $c_2 = a_2c$ , are initial growth rates in units of mass per area and time interval. For simplicity, we choose  $1 \pm 0.1$  in our model. We also simulate the model with different  $c_1$  and  $c_2$  values. As expected, the results from different values were qualitatively similar (the slopes didn't change).

### *Resource competition and limitation*

Resource limitation and competition usually cause a reduction of resource availability for plants. We therefore represent resource limitation via a dimensionless efficiency factor or index,  $f_R$ , for different levels of resource availability. Resource competition is incorporated by using a dimensionless competition factor or index,  $f_p$ , leading to

$$dm/dt = f_R f_p c_1 A [1 - (m / M_1)^{3/8}] \quad (11 \text{ a})$$

for woody plants and

$$dm/dt = f_R f_p c_2 A [1 - (m / M_2)^{1/4}] \quad (11 \text{ b})$$

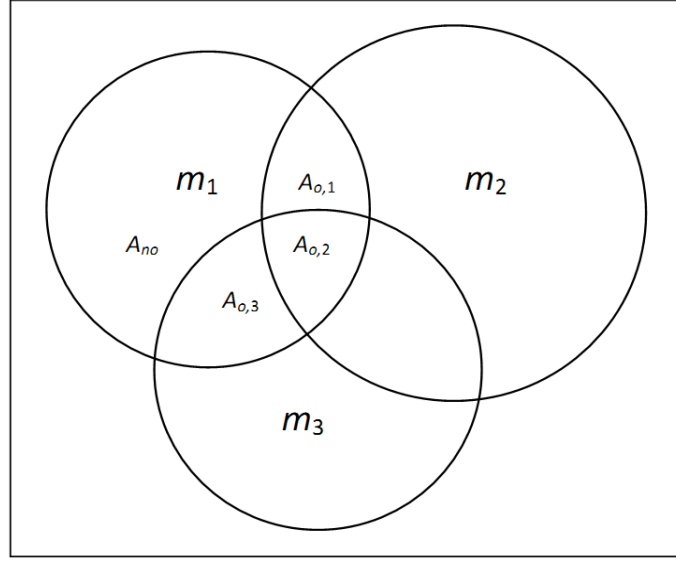
for non-woody plants, where  $M_1 = (f_R f_p)^{8/3} M$  and  $M_2 = (f_R f_p)^4 M$ , are maximum body size with resource limitation and competition.

The efficiency factor  $f_R$ , can take different forms depending on the characteristics and level of the limiting resource. For simplification, we use a linear form here, i.e.  $f_R = 1 - RL$ , where  $RL$  indicates the level of resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation; Table 1).

As for competition, the mode of resource-mediated competition among plants can be located somewhere along a continuum between completely asymmetric competition (largest plants obtain all the contested resources) and completely symmetric competition (resource uptake is equal for all plants, independent of their relative sizes; Schwinning & Weiner 1998). To represent different modes of competition explicitly, we describe the competitive factor  $f_p$  as

$$f_p = (A_{no} + \sum_{i=1}^x A_{o,i} \frac{m^p}{\sum_{j=1}^y m_j^p}) / A \quad (12)$$

This factor thus refers to the percentage of realized resource uptake from the amount of resources available (the entire resource that plant could potentially occupy) among competitors with sizes  $m_j$  (Schwinning & Weiner 1998).  $A_{no}$  is the area not overlapping with neighbors,  $A_{o,i}$  denotes the area overlapping with neighbors. Parameter  $p$  determines the mode of competition, ranging from complete symmetry ( $p = 0$ ) to complete asymmetry ( $p$  approaching infinity; for details and examples see Figure S2).



**Figure S2.** An example of calculating the competitive index (Eq. 12) with different modes of resource competition in an individual-based model as a way of dividing plants' ZOI (zone-of-influence). Three plants with sizes  $m_1$ ,  $m_2$  and  $m_3$  are competing in this example. For plant 1, its ZOI ( $A$ ) was divided into four parts:  $A_{no}$ , the area not overlapping with the other two plants;  $A_{o,1}$ , the area overlapping with plant 2;  $A_{o,2}$ , the area overlapping with plants 2 and 3;  $A_{o,3}$ , the area overlapping with plant 3.

Then the actual area that plant 1 can take from  $A_{o,1}$  is

$$A_{o,1} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,1} \frac{m_1^p}{m_1^p + m_2^p}$$

For  $A_{o,2}$ ,

$$A_{o,2} \frac{m_1^p}{\sum_{j=1}^3 m_j^p} = A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p}$$

And for  $A_{o,3}$ ,

$$A_{o,3} \frac{m_1^p}{\sum_{j=1}^2 m_j^p} = A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}$$

Therefore, the competitive index for plant 1 is:

$$f_p = (A_{no} + A_{o,1} \frac{m_1^p}{m_1^p + m_2^p} + A_{o,2} \frac{m_1^p}{m_1^p + m_2^p + m_3^p} + A_{o,3} \frac{m_1^p}{m_1^p + m_3^p}) / A$$

Where  $A = m_1^{3/4} / c$

In total, Eqns (11 a) and (11 b) clearly show how a plant's growth rate is jointly determined by resource availability,  $f_R$ , and competition,  $f_p$ . This also implies that a plant's final size is usually smaller than its asymptotic maximum size ( $M$ ) during resource limitation and local competition.

### Mortality

An individual's mortality rate is proportional to its mass-specific metabolism (Brown *et al.* 2004). Based on this, we assume that individuals die if their actual growth rate



1  $(dm/dt)$  falls below a threshold of their current scaled body mass, i.e. 2% of  $m^{3/4}$ .  
2 Therefore, individual plants may die due to metabolic inactivation driven by resource  
3 limitation, competition, senescence (when  $m$  approaches  $M$ ) or combinations thereof.  
4 This provides a more realistic representation of relevant ecological process than in  
5 previous models (Stoll *et al.* 2002; Chu *et al.* 2010).  
6

# SLOPES AND INTERCEPTS OF SELF-THINNING TRAJECTORIES PRODUCED BY THE MODEL

**Table S1.** Slope and intercept (log-log transformed) of self-thinning trajectories for woody plants under different levels of resource limitation and modes of competition\*.

<i>RL</i>	<i>P</i>	Slope			Intercept			<i>r</i> <sup>2</sup>
		Mean	95% CI		Mean	95% CI		
0	∞	-1.478	-1.525	-1.429	6.258	6.096	6.424	0.994
0	10	-1.342	-1.361	-1.322	5.848	5.808	5.898	0.999
0	1	-1.140	-1.156	-1.125	5.714	5.664	5.769	0.997
0	0	-1.083	-1.085	-1.082	6.208	6.204	6.212	0.999
0.1	∞	-1.478	-1.526	-1.427	6.217	6.074	6.377	0.994
0.1	10	-1.354	-1.374	-1.333	5.848	5.778	5.918	0.998
0.1	1	-1.144	-1.158	-1.130	5.697	5.650	5.744	0.997
0.1	0	-1.094	-1.098	-1.091	6.185	6.180	6.190	0.999
0.5	∞	-1.480	-1.516	-1.445	6.176	6.060	6.297	0.995
0.5	10	-1.385	-1.402	-1.365	5.805	5.736	5.875	0.997
0.5	1	-1.188	-1.198	-1.179	5.554	5.519	5.585	0.998
0.5	0	-1.124	-1.126	-1.122	5.978	5.972	5.984	0.999
0.9	∞	-1.486	-1.499	-1.472	5.918	5.873	5.963	0.996
0.9	10	-1.395	-1.401	-1.389	5.637	5.619	5.657	0.999
0.9	1	-1.201	-1.209	-1.194	5.370	5.345	5.395	0.998
0.9	0	-1.130	-1.139	-1.122	5.474	5.446	5.502	0.997

\**RL* indicates the level of resource limitation (0–1), *p* indicates the modes of competition (with ∞: completely asymmetric; 10: highly size-asymmetric; 1: perfectly size-symmetric; 0: completely symmetric). CI is confidence intervals.

**Table S2.** Slope and intercept (log-log transformed) of self-thinning trajectories for non-woody plants under different levels of resource limitation and modes of competition\*.

<i>RL</i>	<i>P</i>	Slope			Intercept			<i>r</i> <sup>2</sup>
		Mean	95% CI		Mean	95% CI		
0	∞	-1.476	-1.523	-1.424	6.223	6.055	6.388	0.992
0	10	-1.393	-1.420	-1.357	6.039	5.919	6.166	0.995
0	1	-1.084	-1.091	-1.076	5.451	5.427	5.475	0.999
0	0	-1.061	-1.062	-1.061	5.905	5.903	5.907	0.999
0.1	∞	-1.466	-1.512	-1.419	6.173	6.021	6.331	0.992
0.1	10	-1.385	-1.417	-1.353	5.995	5.886	6.109	0.995
0.1	1	-1.091	-1.098	-1.083	5.446	5.420	5.470	0.999
0.1	0	-1.063	-1.063	-1.062	5.860	5.858	5.862	0.999
0.5	∞	-1.452	-1.483	-1.419	6.049	5.942	6.151	0.994
0.5	10	-1.377	-1.395	-1.358	5.877	5.812	5.940	0.997
0.5	1	-1.108	-1.114	-1.102	5.331	5.312	5.351	0.999
0.5	0	-1.084	-1.085	-1.083	5.616	5.614	5.618	0.999
0.9	∞	-1.408	-1.431	-1.381	5.580	5.542	5.615	0.997
0.9	10	-1.356	-1.362	-1.350	5.436	5.417	5.456	0.999
0.9	1	-1.145	-1.152	-1.138	4.916	4.894	4.937	0.996
0.9	0	-1.091	-1.097	-1.086	4.790	4.755	4.806	0.997

\**RL* indicates the level of resource limitation (0–1), *p* indicates the modes of competition (with ∞: completely asymmetric; 10: highly size-asymmetric; 1: perfectly size-symmetric; 0: completely symmetric). CI is confidence intervals.