Appendix A1

Model description

A general ontogenetic growth model for plants

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

$$B_p = B_r + B_s = B_r + E_s dm/dt \tag{A1}$$

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, B_s (Fig. A1). 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. A1): maintenance of biomass (B_{maint}), ion transport (B_{tran}) and biosynthesis (B_{syn}), which can be summarized as (Lambers et al. 2008):

$$B_r = B_{maint} + B_{tran} + B_{syn} = \sum B_m m_{living} + B_{tran} + E_c dm/dt \tag{A2}$$

where B_m denotes average mass-specific maintenance metabolic rate, m_{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 plant cells (tissue) are taken as a fundamental unit here, and possible differences between tissues are ignored (West et al. 2001). Note that the terms $B_s = E_s dm / dt$ in Eq. A1 and $B_{syn} = E_c dm / dt$ in Eq. A2 are quite different: S stands for the rate of

cumulative energy content of new biomass, whereas B_{syn} refers to the metabolic energy expended

on biosynthesis which is dissipated as heat instead of obtained as stored biomass (Hou et al. 2008).

Combining Eq. A1 and A2, we get

$$B_p = B_{maint} + B_{tran} + B_{syn} + B_s = \sum B_m m_{living} + B_{tran} + E_0 dm/dt \qquad (A3)$$

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 A3 is quite general, but B_{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_{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

$$B_{maint} = \sum B_m m_{living} = B_m m_L + B_m m_C = B_L + B_C \qquad (A4)$$

for woody plants, where B_L and B_C specify the metabolic rate for maintaining photosynthetic and

conducting tissues, respectively (Fig. A1). Combining Eq. A3 and A4 we can get the energy

conservation equation for woody plants:

$$B_p = B_m m_L + B_m m_C + B_{tran} + E_0 \, dm/dt \qquad (A5)$$

Based on empirical measurements and theoretical assumptions linking biomass and metabolism,

MST (West et al. 1999, 2009, Enquist 2002, Price et al. 2007, Enquist et al. 2009) predicts that

whole-plant, or gross, photosynthesis rate, B_p, and ion transport metabolic rate B_{tran} allometrically

scale with the total biomass of a plant, m, as $B_p \propto B_{tran} \propto m^{\theta}$, where $\theta \equiv 1 / (2\alpha + \beta)$ and α and β

representing the geometry and biomechanics of the vascular network. Their values may vary

across different taxa (Price et al. 2007).

Although the Eq. A5 can be easily recast by using empirical values of α and β, we use $\alpha =$

1/2 and $\beta = 1/3$ as common and idealized cases here (Price et al. 2007, West et al. 2009), so that θ

= 3/4. Models based on these scaling relationships predict that the standing leaf biomass, m_L, scales with respect to total biomass as $m_L \propto m^{\sim 3/4}$ across woody plants which was confirmed by empirical data (Sack et al. 2002; Niklas 2005).

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 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 $A_S \propto m^{3/4}$ and $h \propto m^{1/4}$ (Enquist 2002, Savage et al. 2010), we therefore derive the allometric relationship $m_C = d_C v_C \propto A_S h \propto m^{3/4} m^{1/4} \propto m$ for woody plants. Substituting the allometric relationship on biomass for all related terms in Eq. A5 gives

$$B_0 m^{3/4} = B_m a_L m^{3/4} + B_m a_S m + a_{tran} m^{3/4} + E_0 \, dm/dt \tag{A6}$$

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_{tran} are normalization constants. Equation A6 can therefore be rewritten as

$$dm/dt = a_1 m^{3/4} - b_1 m = a_1 m^{3/4} [\, 1 - (\, m \, / \, M_1 \,)^{1/4} \,] \tag{A7}$$

with $a_1 = (B_0 - B_m a_L - a_{tran}) / E_0$ and $b_1 = B_m a_S / E_0$. The value $M_1 = (a_1 / b_1)^4$ is 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 Eq. A7 dominates while plants grow to a moderate size, which has been shown to be a good quantitative description of plant growth (Niklas and 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, $m_{living} = m_L + m_S + m_R \approx m$ (Enquist 2002). Combining Eq. A3 with those scaling relationship leads to

$$B_0 m^{3/4} = B_m m + a_{tran} m + E_0 \, dm/dt \tag{A8}$$

for non-woody plants.

Taking the parameters in Eq. A8 in the same sense as before, Eq. A8 can be re-expressed as

$$dm/dt = a_2 m^{3/4} - b_2 m = a_2 m^{3/4} [\ 1 - (\ m\ /\ M_2)^{1/4}\ ] \tag{A9}$$

with $a_2 = B_0/E_0$, $b_2 = (B_m + a_{tran})/E$, and $M_2 = (a_2/b_2)^4$, which is the asymptotic maximum body size of a non-woody plant.

Equation A7 and A9 have same form, and we use a general form of the growth function for both woody and non-woody plants:

$$dm/dt = a m^{3/4} - bm = a m^{3/4} [\ 1 - (\ m\ /\ M_0)^{1/4}\ ] \tag{A10}$$

where a is a general constant and M_0 is the generally asymptotic maximum body size of plant. Although Eq. A7, A9 and A10 are similar to the 'von Bertalanffy growth function' and other phenomenological functions (Weiner et al. 2001; Chu et al. 2009, 2010), but the derivation is based on fundamental principles of MST and with all parameters determining plant growth are directly linked to physical and biological principles.
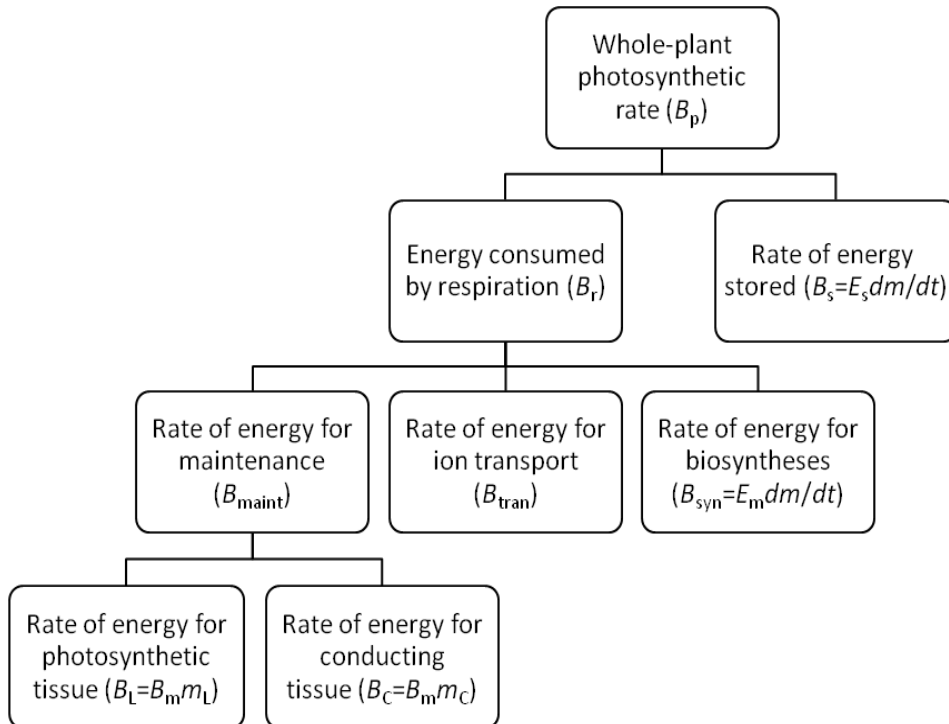

Figure A1. Assimilated energy partition of plants during ontogenetic growth.

Individual-based model (IBM) considering different modes of competition and resource limitation for above- and belowground compartment during 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, 2010),

Purpose

The aim of this model is to evaluate the multiple effects of the mode of competition (above- and belowground part) and resource limitation on regulating plant population dynamics, specifically on mass–density relationships (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 log mass–log density relationship under different environmental conditions. 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 (both shoot and root) and their position, i.e. coordinates of the stem. Each individual plant has its own circular zone-of-influence (ZOI) for both above- and belowground compartment. The pair of ZOIs stand for the physical space occupied by a plant's shoot and root respectively, and represents the energy and resources potentially available to this plant for above- and belowground part, which ZOIs are allometrically related to its shoot and root mass separately. Neighboring plants only compete for the resources when their above- or belowground 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 200×200

patches (Grimm and Railsback 2005), and each patch represents 0.25 cm^2 in reality. 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 for both above- and

belowground part. One time step in the model represents approximately one week for simulated

plants.

Table A1. 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]
Plants		
C	initial growth rate	1 ± 0.1 [mg cm^{-2} time step^{-1}]
m_0	initial total body mass	2 ± 0.2 [mg]
$m_{0, \text{shoot}}$	initial shoot mass	*50% of m_0* [mg]
$m_{0, \text{root}}$	initial root mass	*50% of m_0* [mg]
M_0	maximal biomass	$2\times10^6 \pm 2\times10^5$ [mg]
M	current total body mass	[mg]
m_{shoot}	current shoot mass	[mg]
m_{root}	current root mass	[mg]
A_a	aboveground zone of influence	[cm^{-2}]
A_b	belowground zone of influence	[cm^{-2}]
Patches		
RL_a	aboveground resource limitation	$0, RL_a \in [0, 1)$
RL_b	belowground resource limitation	$0, 0.4, 0.8, RL_b \in [0, 1)$

Initialization

Mortality	threshold of death	3% of $m^{3/4}$
Density	number of plants	3163 and 10 000 / total area
Random seed	generation of random number	1, 2, 3, 4, 5

Process overview and scheduling

After initialization, all individual plants with a given density are randomly distributed in the world. The processes of above- and belowground resource competition, growth and mortality of each plant are fulfilled within each time step. In each step, individual plants first sense the above- and belowground resource qualities of environment (levels of resource limitation of patches) within their shoot and root ZOIs, the areas (radius) of an individual plant's ZOIs are determined from its current shoot and root biomass correspondingly. When the above- or belowground ZOIs of neighboring plants are overlapping, plants compete only within the overlapping area. Thus, the overlapping area is divided according to the competition mode which reflecting the way of resource division. The growth rate of plant is determined by the outcome of above- and belowground process, which is restricted by the compartment with minimum resource uptake rate according to growth function. The synthesized biomass is allocated to shoot and root optimally which follows the rule of functional balanced growth (Niklas 2005, May et al. 2009). Plants with growth rates falling below a threshold die and are removed immediately. We also tested a model version were death was less abrupt but plants more gradually decomposed, but found no differences in the main results (data not shown). 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), which seems to be the more natural and realistic approach here because time steps are small and competition is a continuous process.

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 for both above- and belowground compartment and resource limitation.

Emergence

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

Interaction

Individual plants interact via shoot and root competition for resources in the overlapping area of their ZOIs.

Stochasticity

Initial growth rate, initial biomass (for shoot and root respectively), 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, shoot and root 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 (We also used regular and clustered distribution as initial distribution, which do not change our main findings). Resources are spatially and temporally constant. Each plant has an initial biomass (m_0), initial shoot and root biomass ($m_{0, \text{shoot}}$ and $m_{0, \text{root}}$), maximal biomass (M) and initial growth rate (c) 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

One layer model – plant growth, resource limitation and competition

In our individual-based model the plant's ZOI, A, stands for the physical space occupied by the 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 $c_0 A = m^{3/4}$ (Enquist and Niklas 2001), where c_0 is a normalization constant. Since plant growth in our simulation is discrete, therefore Eq. 10 can be rewritten as

$$\Delta m / \Delta t = cA[\ 1 - (\ m\ /\ M_0)^{1/4}\ ] \tag{A11}$$

where $c = ac_0$, is the initial growth rates in units of mass per area and time interval. For simplicity, we choose 1 ± 0.1 in our model.

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

$$\Delta m / \Delta t = f_R f_p cA[\ 1 - (\ m\ /\ M)^{1/4}\ ] \tag{A12}$$

where $M = (f_R f_p)^4 M_0$ is the maximum body size with resource limitation and competition.

9

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).

As for competition, the modes 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 and Weiner 1998). To represent different modes of competition explicitly, we describe the competitive index f_p as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{m_i^p}{\sum_{j=1}^{n_j} m_j^p} \cdot A_{o,k}) / A \qquad (A13)$$

This factor thus refers to the fraction of resources available in the area which plant i could obtain after a loss of potential resources due to areas overlapped by neighbors of sizes m_j (Schwinning and Weiner 1998). A_{no} is the area not overlapping with neighbors, $A_{o,k}$ denotes the n_o areas overlapping with n_j different 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 Fig. A2).
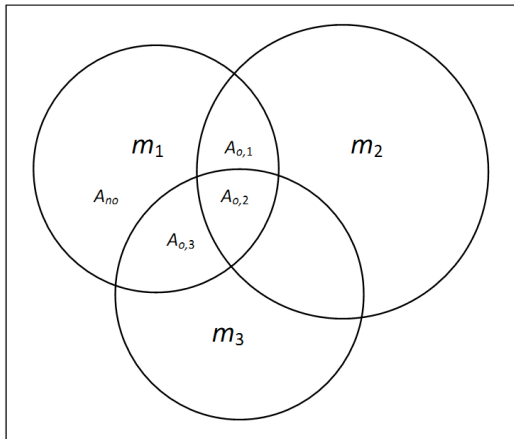

Figure A2. An example of calculating the interactive indexes (Eq. A13) with different modes of competition and facilitation in an individual-based model as a way of

dividing plants' ZOI (zone-of-influence). Three plants with sizes m_1, m_2 and m_3 are interacting 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, f_p, 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 $A = m_1^{3/4} / c$.

Two layer model – shoot versus root competition, biomass allocation and mortality

Because competition among plants can occurs at both above- and belowground simultaneously, the relative importance of shoot versus root competition and their ZOI can varies depending on the environmental factors (Deng et al. 2006, May et al. 2009). Therefore, the one layer model however cannot properly represent this property. We developed the two layer individual-based model to represent the plant's shoot and root competition. In our two layer model, a plant has two ZOIs stand for the above- and belowground physical space occupied by the plant, which ZOIs represent the corresponding levels of energy and resources (e.g. light, water and nutrient) potentially available to this plant.

We assume that 1) under optimal conditions without resource limitation and competition, the

abilities of above- and belowground resource uptake are balanced, with relationships between

metabolic rate, B, and biomass, m, being $B = c_{shoot} m_{shoot}^{3/4} = c_{root} m_{root}^{3/4}$ (Niklas 2005, Cheng and

Niklas 2007), where c_{shoot} and c_{root} are normalization constants (to simplify, we assume $c_{shoot} = c_{root}$

= 1), and 'shoot' and 'root' refer to the above- and belowground compartment, respectively; 2) the

plant's above- and belowground ZOIs are proportional to the plant metabolic rate, B, and then

allometrically related to the plant's shoot and root biomass (Enquist and Niklas 2001, May et al.

2009), $A_a = c_a m_{shoot}^{3/4}$ and $A_b = c_b m_{root}^{3/4}$, where c_a and c_b are normalization constants (to simplify,

we use $c_a = c_b = 1$); 3) growth of the entire plant is limited by the compartment with smaller

resource uptake rate (May et al. 2009). In a view of comparability with one-layer model, the real

growth rate of whole plant in two-layer model has been doubled. Accordingly, Eq. A12 can be

applied to above- and belowground compartment, and then we get the whole plant growth rate as

$$
\frac{\Delta m}{\Delta t} = \begin{cases} 2 \times \Delta AGR = 2 \times f_{R,a} f_{p,a} c_a A_a [1 - (m/M_a)^{1/4}], & \Delta AGR < \Delta BGR \\ 2 \times \Delta BGR = 2 \times f_{R,b} f_{p,b} c_b A_b [1 - (m/M_b)^{1/4}], & \Delta AGR > \Delta BGR \\ \Delta AGR + \Delta BGR, & \Delta AGR = \Delta BGR \end{cases} \quad (14)
$$

where ΔAGR and ΔBGR are above- and belowground determined growth rate. The factor of

resource availability (f_R), competitive index (f_p) and ZOI (A) were applied to both two layers

independently, with the corresponding subscript a and b indicate the above- and belowground

compartment respectively (Fig. A3). The above- and belowground ZOIs can vary along the

resource gradient and also can be changed according to the specific scenario of parameter setting.

  Adjustability of root/shoot allocation as the morphological plasticity allows plants to adapt

to changing biotic and abiotic environmental conditions (Berger et al. 2008). We adopt the optimal

allocation theory, functional balance growth hypothesis and metabolic scaling theory to quantify

the partition of growth between the shoots and roots (Weiner 2004, Niklas 2005, May et al. 2009):

$$
\frac{\Delta m_{shoot}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta BGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} \quad (15a)
$$

$$
\frac{\Delta m_{root}}{\Delta t} = \frac{\Delta m}{\Delta t} \frac{\Delta AGR^{3/4}}{\Delta AGR^{3/4} + \Delta BGR^{3/4}} \quad (15b)
$$

which means plant allocates more biomass to the compartment that is most limiting growth for increasing its uptake of resource. An allometric form (3/4) of resources allocation was used here as metabolic balance, we also tested the original allocation of linearity which only lead to a small difference on root/shoot ratio but do not change our general findings.

An individual's mortality rate is proportional to its mass-specific metabolism (as current total metabolic rate divide by body mass; Brown et al. 2004). Based on this, we assume that individuals die if their actual growth rate ($\Delta m / \Delta t$, represent actual metabolic rate) falls below a threshold of their basal metabolic rate (allometrically scaled with body mass), i.e. 3% of $m^{3/4}$. Therefore, individual plants may die due to metabolic inactivation driven by above- or/and belowground resource limitation, competition, senescence (when m approaches M) or combinations thereof. This provides a more realistic representation of relevant ecological process than in previous models (Stoll et al. 2002, Chu et al. 2009, 2010). In addition, we are able to ascribe the mortality of individual plants to above- or belowground process explicitly.

In total, Eq. 14, 15a and 15b clearly showed how a plant's growth, biomass allocation and mortality are jointly determined by above- and belowground resource level and local competition.
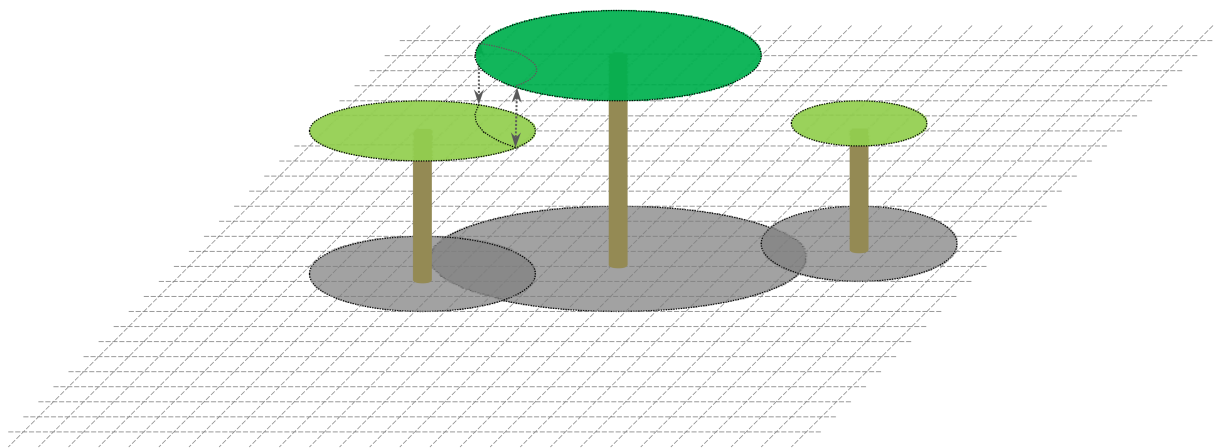

Figure A3. A visual illustration of the two-layer zone-of-influence (ZOI) approach including both above- and belowground competition. The above- and belowground

ZOIs (green: aboveground, gray: belowground) are allometrically related to the plant shoot and root biomass, respectively. Plants only compete for the resources in overlapped areas with their neighbors which can occur independently at above- and belowground compartment (arrows indicate the overlapped area of aboveground competition).

References

Berger, U. et al. 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. – Perspect. Plant Ecol. 9: 121–135.

Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Chu, C. J. et al. 2009. Positive interactions can increase size inequality in plant populations. – J. Ecol. 97: 1401–1407.

Chu, C. J. et al. 2010. Effects of positive interactions, size symmetry of competition and abiotic stress on self-thinning in simulated plant populations. – Ann. Bot. 106: 647–652.

Deng, J. M. et al. 2006. Plant mass-density relationship along a moisture gradient in northwest China. – J. Ecol. 94: 953–958.

Enquist, B. J. 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. – Tree Physiol. 22: 1045–1064.

Enquist, B. J. and Niklas, K. J. 2001. Invariant scaling relations across tree-dominated communities. – Nature 410: 655–660.

Enquist, B. J. et al. 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. – Proc. Natl Acad. Sci. USA 106: 7046–7051.

Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.

Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based

models. – Ecol. Modell. 198: 115–126.

Grimm, V. et al. 2010. The ODD protocol: a review and first update. – Ecol. Modell. 221: 2760–2768.

Hou, C., Zuo, W., Moses, M.E., Woodruff, W.H., Brown, J.H. & West, G.B. (2008). Energy uptake and allocation during ontogeny. Science, 322, 736-739.

Lambers, H. et al. 2008. Plant physiological ecology, 2nd edn. – Springer, pp. 134–143.

Maestre, F. T. et al. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. – J. Ecol. 97: 199–205.

May, F. et al. 2009. Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. – Oikos 118: 1830–1843.

Molofsky, J. and Bever, J. D. 2002. A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. – Proc. R. Soc. B 269: 2389–2393.

Molofsky, J. et al. 2001. Coexistence under positive frequency dependence. – Proc. R. Soc. B 2001: 268–277.

Niklas, K. J. 2005. Modelling below-and above-ground biomass for non-woody and woody plants. – Ann. Bot. 95: 315–321.

Niklas, K. J. and Enquist, B. J. 2001. Invariant scaling relationships for interspecific plant biomass production rates and body size. – Proc. Natl Acad. Sci. USA. 98: 2922–2927.

Price, C. A. et al. 2007. A general model for allometric covariation in botanical form and function. – Proc. Natl Acad. Sci. USA. 104: 13204–13209.

Sack, L. et al. 2002. Global allocation rules for patterns of biomass partitioning. – Science 296: 1923a.

Schwinning, S. and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. – Oecologia 113: 447–455.

Stoll, P. et al. 2002. Size symmetry of competition alters biomass–density relationships. – Proc. R. Soc. B 269: 2191–2195.

Travis, J. M. J. et al. 2006. The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. – J. Theor. Biol. 241: 896–902.

Weiner, J. et al. 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. – Am. Nat. 158: 438–450.

Weiner, J. 2004. Allocation, plasticity and allometry in plants. – Persp. Plant Ecol. Evol. Syst. 6: 207–215.

West, G. B. et al. 1999. A general model for the structure and allometry of plant vascular systems. – Nature 400: 664–667.

West, G. B. et al. 2001. A general model for ontogenetic growth. – Nature 413: 628–631.

West, G. B. et al. 2009. A general quantitative theory of forest structure and dynamics. – Proc. Natl Acad. Sci. USA 106: 7040–7045.

Figure A4. Mass–density relationships between the mean total, above- and belowground biomass in simulated plant populations (log–log transformed). The gray dotted lines have a slope of –4/3. RL_b defined the level of below-ground resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). C with superscript and subscript indicated the mode of competition for above- and below-ground part correspondingly (AA: allometric asymmetry, $p = 10$; SS: size symmetry, $p = 1$).
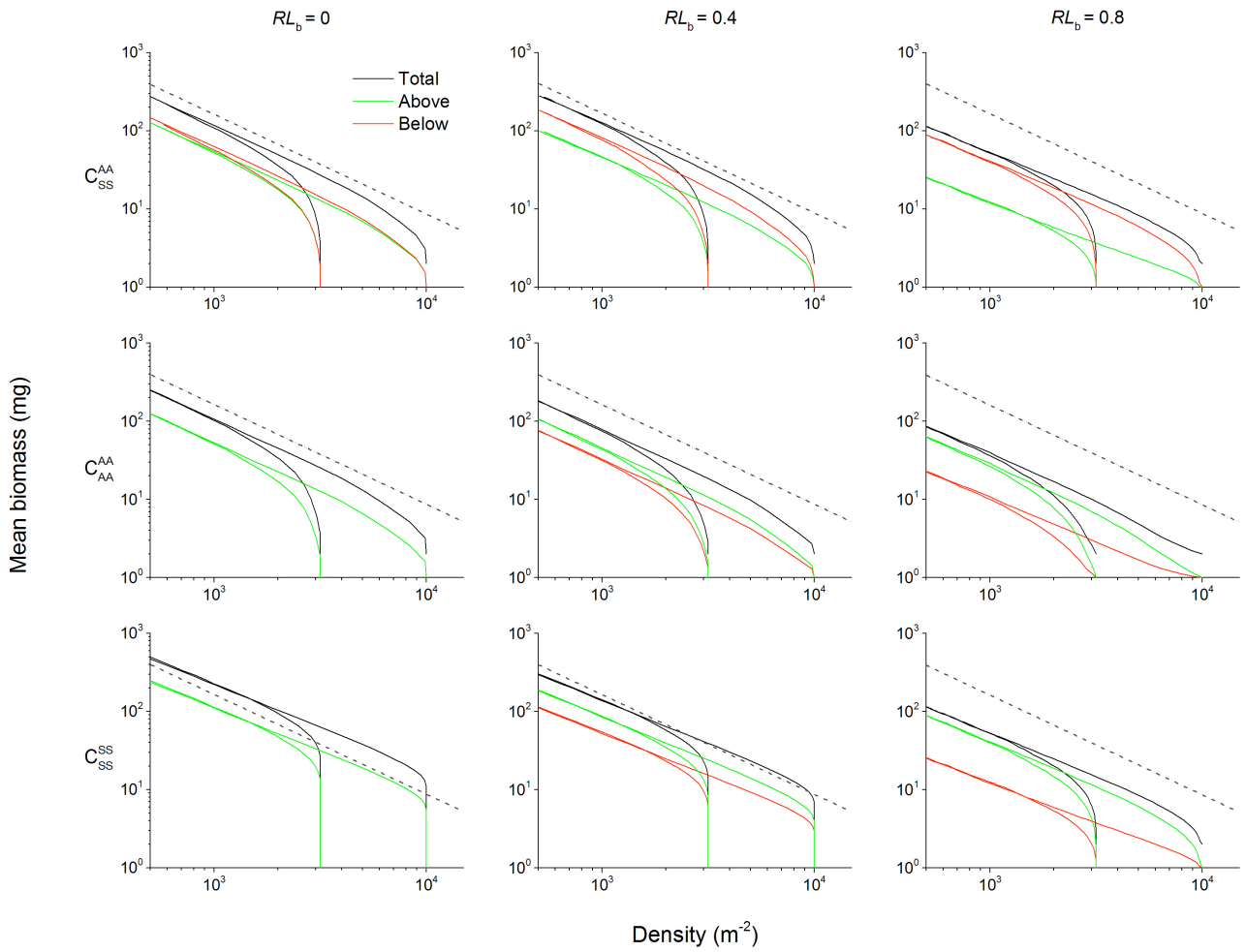
Table A1. Slopes and intercepts of mass–density relationships between the mean total, above- and belowground biomass in simulated plant populations (log–log transformed; as estimated by standard major axis). RL_b defined the level of belowground resource limitation, with its value ranging from 0 (no resource limitation) to 1 (maximum resource limitation). CA: complete asymmetry, $p = \infty$; AA: allometric asymmetry, $p = 10$; SS: size symmetry, $p = 1$; CS: complete symmetry, $p = 0$.

Resource limitation	Mode of Competition		Mean total biomass					Mean aboveground biomass					Mean belowground biomass				
RL_b	Above ground	Below ground	Slope	95% CI	Intercept	95% CI	R^2	Slope	95% CI	Intercept	95% CI	R^2	Slope	95% CI	Intercept	95% CI	R^2
0	CA	CA	-1.450	-1.509, -1.399	6.423	6.243, 6.616	0.990	-1.450	-1.507, -1.396	6.122	5.932, 6.310	0.990	-1.450	-1.508, -1.395	6.122	5.933, 6.317	0.990
0	CA	AA	-1.475	-1.537, -1.416	6.502	6.290, 6.707	0.988	-1.477	-1.543, -1.417	6.204	5.991, 6.423	0.988	-1.474	-1.534, -1.415	6.198	5.996, 6.399	0.988
0	CA	SS	-1.417	-1.461, -1.377	6.333	6.196, 6.479	0.993	-1.387	-1.432, -1.348	5.907	5.775, 6.054	0.993	-1.443	-1.491, -1.401	6.145	5.999, 6.293	0.993
0	CA	CS	-1.439	-1.482, -1.401	6.420	6.289, 6.563	0.993	-1.392	-1.432, -1.353	5.922	5.790, 6.063	0.993	-1.471	-1.514, -1.429	6.293	6.154, 6.436	0.993
0	AA	CA	-1.475	-1.538, -1.413	6.502	6.288, 6.718	0.988	-1.474	-1.533, -1.414	6.198	5.995, 6.399	0.988	-1.475	-1.541, -1.419	6.204	5.999, 6.421	0.988
0	AA	AA	-1.351	-1.391, -1.316	6.109	5.987, 6.242	0.996	-1.351	-1.392, -1.315	5.807	5.685, 5.943	0.996	-1.351	-1.389, -1.314	5.807	5.681, 5.946	0.996
0	AA	SS	-1.359	-1.394, -1.329	6.174	6.068, 6.286	0.996	-1.333	-1.367, -1.303	5.758	5.658, 5.870	0.996	-1.384	-1.419, -1.350	5.977	5.862, 6.092	0.996
0	AA	CS	-1.401	-1.426, -1.379	6.348	6.273, 6.430	0.998	-1.359	-1.382, -1.338	5.869	5.800, 6.094	0.997	-1.438	-1.464, -1.414	6.203	6.124, 6.289	0.997
0	SS	CA	-1.417	-1.462, -1.376	6.333	6.195, 6.480	0.993	-1.443	-1.491, -1.401	6.145	5.999, 6.293	0.993	-1.387	-1.432, -1.348	5.907	5.775, 6.054	0.993
0	SS	AA	-1.359	-1.394, -1.329	6.174	6.068, 6.286	0.996	-1.384	-1.420, -1.350	5.977	5.861, 6.091	0.996	-1.333	-1.367, -1.303	5.758	5.658, 5.870	0.996
0	SS	SS	-1.100	-1.110, -1.092	5.647	5.618, 5.678	0.999	-1.100	-1.110, -1.109	5.346	5.315, 5.377	0.999	-1.100	-1.109, -1.092	5.346	5.315, 5.376	0.999
0	SS	CS	-1.351	-1.365, -1.342	6.764	6.728, 6.805	0.994	-1.308	-1.321, -1.299	6.282	6.241, 6.321	0.995	-1.390	-1.405, -1.378	6.623	6.581, 6.667	0.993
0	CS	CA	-1.439	-1.482, -1.401	6.420	6.289, 6.563	0.993	-1.471	-1.516, -1.430	6.293	6.154, 6.436	0.993	-1.392	-1.432, -1.352	5.922	5.791, 6.052	0.993
0	CS	AA	-1.401	-1.425, -1.380	6.348	6.273, 6.429	0.999	-1.438	-1.464, -1.414	6.203	6.124, 6.290	0.997	-1.359	-1.380, -1.339	5.869	5.790, 5.945	0.997
0	CS	SS	-1.351	-1.363, -1.340	6.764	6.727, 6.803	0.994	-1.390	-1.404, -1.378	6.623	6.583, 6.667	0.993	-1.308	-1.319, -1.297	6.282	6.240, 6.326	0.995
0	CS	CS	-1.060	-1.060, -1.059	5.868	5.866, 5.870	1.000	-1.060	-1.060, -1.059	5.567	5.565, 5.569	1.000	-1.060	-1.060, -1.059	5.567	5.565, 5.569	1.000
0.4	CA	CA	-1.319	-1.344, -1.298	5.845	5.776, 5.921	0.997	-1.300	-1.324, -1.280	5.414	5.349, 5.486	0.997	-1.333	-1.361, -1.308	5.650	5.577, 5.731	0.996
0.4	CA	AA	-1.319	-1.345, -1.294	5.849	5.776, 5.921	0.996	-1.299	-1.322, -1.278	5.409	5.343, 5.478	0.997	-1.334	-1.364, -1.308	5.660	5.575, 5.726	0.996
0.4	CA	SS	-1.391	-1.421, -1.363	6.261	6.170, 6.352	0.992	-1.314	-1.340, -1.290	5.586	5.510, 5.667	0.994	-1.440	-1.473, -1.407	6.213	6.110, 6.315	0.992
0.4	CA	CS	-1.425	-1.448, -1.403	6.405	6.337, 6.474	0.999	-1.318	-1.339, -1.298	5.616	5.557, 5.681	0.999	-1.487	-1.514, -1.462	6.411	6.334, 6.489	0.993
0.4	AA	CA	-1.315	-1.340, -1.293	5.834	5.762, 5.901	0.997	-1.294	-1.316, -1.274	5.396	5.333, 5.462	0.998	-1.331	-1.359, -1.306	5.643	5.564, 5.728	0.996
0.4	AA	AA	-1.288	-1.309, -1.269	5.758	5.697, 5.822	0.998	-1.271	-1.289, -1.253	5.327	5.273, 5.383	0.999	-1.312	-1.335, -1.289	5.563	5.489, 5.633	0.998
0.4	AA	SS	-1.292	-1.313, -1.273	5.980	5.921, 6.044	0.996	-1.227	-1.242, -1.212	5.340	5.292, 5.389	0.997	-1.332	-1.355, -1.312	5.908	5.842, 5.977	0.995
0.4	AA	CS	-1.311	-1.345, -1.279	6.286	6.190, 6.387	0.995	-1.138	-1.170, -1.107	5.232	5.137, 5.330	0.995	-1.395	-1.430, -1.364	6.387	6.291, 6.481	0.995
0.4	SS	CA	-1.325	-1.352, -1.301	5.884	5.810, 5.976	0.996	-1.313	-1.338, -1.291	5.496	5.423, 5.573	0.997	-1.334	-1.361, -1.309	5.657	5.575, 5.709	0.996
0.4	SS	AA	-1.281	-1.298, -1.267	5.758	5.707, 5.809	0.999	-1.272	-1.287, -1.258	5.368	5.325, 5.419	0.999	-1.289	-1.307, -1.274	5.525	5.475, 5.578	0.998
0.4	SS	SS	-1.096	-1.101, -1.093	5.428	5.416, 5.441	1.000	-1.070	-1.073, -1.067	4.929	4.920, 4.938	1.000	-1.114	-1.119, -1.108	5.271	5.255, 5.288	1.000
0.4	SS	CS	-1.017	-1.017, -1.016	5.391	5.390, 5.393	1.000	-0.888	-0.889, -0.886	4.434	4.431, 4.438	1.000	-1.072	-1.072, -1.071	5.418	5.415, 5.421	1.000
0.4	CS	CA	-1.333	-1.361, -1.308	5.919	5.841, 6.001	0.996	-1.333	-1.359, -1.309	5.583	5.506, 5.666	0.996	-1.332	-1.360, -1.308	5.650	5.572, 5.735	0.996
0.4	CS	AA	-1.285	-1.303, -1.268	5.775	5.722, 5.831	0.998	-1.286	-1.303, -1.270	5.436	5.385, 5.488	0.998	-1.284	-1.302, -1.269	5.510	5.462, 5.563	0.998
0.4	CS	SS	-1.102	-1.108, -1.097	5.483	5.466, 5.501	0.999	-1.100	-1.105, -1.095	5.089	5.073, 5.107	1.000	-1.104	-1.110, -1.099	5.258	5.242, 5.277	0.999
0.4	CS	CS	-1.021	-1.021, -1.020	5.398	5.397, 5.400	1.000	-0.899	-0.900, -0.897	4.450	4.444, 4.456	0.999	-1.070	-1.071, -1.069	5.414	5.411, 5.417	1.000

0.8	CA	CA	-1.286	-1.303	-1.271	5.436	5.387	5.489	0.996	-1.152	-1.155	-1.149	4.477	4.467	4.488	1.000	-1.340	-1.365	-1.320	5.485	5.417	5.559	0.993
0.8	CA	AA	-1.263	-1.274	-1.251	5.373	5.336	5.409	0.998	-1.138	-1.114	-1.136	4.438	4.432	4.444	1.000	-1.320	-1.341	-1.301	5.404	5.352	5.463	0.995
0.8	CA	SS	-1.143	-1.151	-1.135	5.155	5.131	5.179	0.999	-1.020	-1.022	-1.018	4.138	4.132	4.144	1.000	-1.185	-1.197	-1.174	5.171	5.137	5.207	0.997
0.8	CA	CS	-1.038	-1.041	-1.035	4.889	4.880	4.898	1.000	-0.911	-0.917	-0.905	3.792	3.773	3.811	0.996	-1.075	-1.080	-1.070	4.905	4.889	4.920	0.999
0.8	AA	CA	-1.285	-1.301	-1.270	5.433	5.387	5.484	0.996	-1.149	-1.152	-1.146	4.469	4.459	4.479	1.000	-1.350	-1.373	-1.328	5.486	5.417	5.558	0.993
0.8	AA	AA	-1.256	-1.267	-1.244	5.350	5.318	5.387	0.998	-1.134	-1.136	-1.133	4.428	4.422	4.434	1.000	-1.319	-1.337	-1.303	5.374	5.323	5.430	0.996
0.8	AA	SS	-1.132	-1.137	-1.127	5.118	5.102	5.134	0.999	-1.021	-1.024	-1.018	4.144	4.135	4.152	1.000	-1.169	-1.177	-1.161	5.118	5.094	5.144	0.998
0.8	AA	CS	-1.034	-1.035	-1.032	4.874	4.870	4.878	1.000	-0.921	-0.927	-0.915	3.821	3.802	3.840	0.996	-1.065	-1.068	-1.062	4.876	4.877	4.884	1.000
0.8	SS	CA	-1.284	-1.301	-1.269	5.434	5.385	5.482	0.996	-1.147	-1.151	-1.143	4.469	4.457	4.481	1.000	-1.341	-1.365	-1.318	5.491	5.420	5.565	0.993
0.8	SS	AA	-1.257	-1.258	-1.237	5.329	5.297	5.361	0.998	-1.129	-1.129	-1.128	4.418	4.411	4.427	1.000	-1.321	-1.337	-1.298	5.347	5.299	5.398	0.997
0.8	SS	SS	-1.127	-1.132	-1.123	5.106	5.092	5.111	0.999	-1.013	-1.015	-1.010	4.125	4.116	4.133	1.000	-1.167	-1.175	-1.159	5.111	5.088	5.136	0.999
0.8	SS	CS	-1.033	-1.034	-1.032	4.870	4.867	4.873	1.000	-0.917	-0.923	-0.911	3.808	3.788	3.828	0.996	-1.065	-1.067	-1.062	4.874	4.866	4.888	1.000
0.8	CS	CA	-1.285	-1.302	-1.269	5.436	5.387	5.487	0.996	-1.147	-1.152	-1.143	4.473	4.461	4.487	1.000	-1.351	-1.375	-1.329	5.492	5.422	5.565	0.993
0.8	CS	AA	-1.248	-1.259	-1.238	5.331	5.300	5.365	0.998	-1.129	-1.131	-1.127	4.420	4.414	4.426	1.000	-1.301	-1.317	-1.285	5.350	5.301	5.400	0.997
0.8	CS	SS	-1.122	-1.127	-1.118	5.092	5.079	5.109	0.996	-1.011	-1.013	-1.009	4.121	4.116	4.129	1.000	-1.161	-1.168	-1.154	5.093	5.079	5.118	0.996
0.8	CS	CS	-1.033	-1.034	-1.032	4.871	4.867	4.874	1.000	-0.918	-0.924	-0.911	3.808	3.789	3.830	0.996	-1.065	-1.067	-1.062	4.874	4.866	4.882	1.000

Table A2. Slopes and intercepts of mass–density relationships between the mean total, above- and belowground biomass of *Betula pendula* seedlings in greenhouse experiment with different nutrient treatments (log-log transformed; as estimated by standard major axis). F: fertilization, NF: non-fertilization.

Treatment	Biomass	Slope	95% CI	Intercept	95% CI	R^2
F	total	−1.031	−1.428 to −0.745	5.967	5.145 to 7.288	0.609
	above	−1.047	−1.450 to −0.756	5.943	5.168 to 7.327	0.609
	below	−1.066	−1.489 to −0.738	5.330	4.447 to 6.685	0.498
NF	total	−0.901	−1.146 to −0.709	5.081	4.389 to 5.771	0.760
	above	−0.895	−1.145 to −0.701	4.961	4.255 to 5.617	0.748
	below	−0.954	−1.209 to −0.753	4.575	3.882 to 5.338	0.767

Supplement

Model implementation and source code of pi model v2.0 in platform NetLogo 4.1.3 (.nlogo file).