ECOL586 Lecture 5
Scaling size and time;
Self-similarity
Brian J. Enquist
Dept. of Ecology and Evolutionary Biology,
University of Arizona, &
The Santa Fe Institute
Scaling in time and size dimensions:
Ontogenetic scaling

- Evolutionary allometry – Intraspecific variation and time
- Ontogenetic growth
- Fractals and self similarity
Evolutionary interpretations of allometric scaling relationships

Surprisingly there is little known about the evolution of scaling relationships!

Further, the field is somewhat split on the evolutionary interpretation of allometric relationships.
Evolutionary interpretations of allometric scaling relationships

Evolutionary constraint or a reflection of adaptive phenotypes?
Evolutionary interpretations of allometric scaling relationships

Two views

(1) Huxley (1932)

Allometric relationships should not be viewed as adaptive but instead reflect developmental constraints

Developmental or physical constraints on the correlation of traits
Example: Stem Biomechanics

Leonhard Euler

Stem will buckle if height exceeds diameter

\[ l_{\text{max}} = c \left( \frac{E}{\rho g} \right)^{1/3} 2r^{2/3} \]

\[ l_{\text{max}} \propto r^{2/3} \]

\( l_{\text{max}} \) = maximum height to which a vertical cylindrical stem can grow before it elastically buckles under its own weight

\( c \) = a constant

\( \rho \) = bulk tissue density of the tissue used to construct the stem

\( E \) = Young’s elastic modulus (think stiffness)

\( r \) = the stem radius

\( g \) = acceleration due to gravity

Height depends upon radius, stiffness, and the density of tissues
If selection has acted to increase plant height . . . .
(due to competition for light, increased reproductive output and dispersal)

. . . . what variables can selection operate on?

\[ l_{\text{max}} = c \left( \frac{E}{\rho g} \right)^{1/3} 2r^{2/3} \]

Water \( \rho = 1 \)
Conifer \( \rho \sim 0.5 \)
Angiosperm
\( \rho \sim 0.1 - \text{over 1 (!)} \)
$E$ has increased much over macroevolution and $\rho$ has decreased a little

\[ H_{\text{crit}} = C \left( \frac{E}{\rho} \right)^{1/3} D^{2/3} \]

<table>
<thead>
<tr>
<th>Tissue-Type</th>
<th>N</th>
<th>Young’s Elastic Modulus, $E$ (MN m$^{-2}$)</th>
<th>Bulk Tissue Density, $\rho$ (kN m$^{-3}$)</th>
<th>(Density-Specific Stiffness, $E/\rho$)$^{1/3}$ (m)$^{1/3}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>parenchyma</td>
<td>10</td>
<td>1.08 ± 0.058</td>
<td>7.87 ± 0.17</td>
<td>5.16</td>
</tr>
<tr>
<td>collenchyma</td>
<td>15</td>
<td>4.45 ± 0.547</td>
<td>7.20 ± 0.40</td>
<td>8.80</td>
</tr>
<tr>
<td>primary tracheids</td>
<td>14</td>
<td>742 ± 82.7</td>
<td>5.14 ± 0.27</td>
<td>52.8</td>
</tr>
<tr>
<td>sclerenchyma</td>
<td>10</td>
<td>1,900 ± 373</td>
<td>4.38 ± 0.21</td>
<td>75.9</td>
</tr>
<tr>
<td>wood</td>
<td>86</td>
<td>11,000 ± 282</td>
<td>5.54 ± 0.16</td>
<td>125</td>
</tr>
</tbody>
</table>

Ratio of $E/\rho$ has increased over evolutionary time this has allowed for increased diversification in plant height
Crude proxy for Evolutionary Time

Euler predicted max height based on values (changing!) of $E$ and $\rho$

$$l_{\text{max}} = c \left( \frac{E}{\rho g} \right)^{1/3} 2r^{2/3}$$

From Karl Niklas

Read more! http://www.accessexcellence.org/BF/bf04/niklas/
Evolutionary interpretations of allometric scaling relationships

**Two views**

Evolutionary constraint or a reflection of adaptive phenotypes?

(2) Allometric relations reflect adaptive phenotypes shaped by strong stabilizing selection on trait combinations

Maynard Smith et al. (1985)
Natural Selection and Developmental Constraints in the Evolution of Allometries

W. Anthony Frankino, Bas J. Zwaan, David L. Stern, Paul M. Brakefield

In animals, scaling relationships between appendages and body size exhibit high interspecific variation but low intraspecific variation. This pattern could result from natural selection for specific allometries or from developmental constraints on patterns of differential growth. We performed artificial selection on the allometry between forewing area and body size in a butterfly to test for developmental constraints, and then used the resultant increased range of phenotypic variation to quantify natural selection on the scaling relationship. Our results show that the short-term evolution of allometries is not limited by developmental constraints. Instead, scaling relationships are shaped by strong natural selection.
Interpretation of allometry requires careful consideration of the factors contributing to this variation.

Four important sources of allometric variation are usually recognized:

1) Ontogenetic variation due to differences in age and/or developmental rates;

2) Environmental variation due to differences in conditions influencing growth;

3) Genetic variation in heritable factors that influence the traits under consideration; and

4) Developmental noise or experimental error unexplained by other sources.
Intraspecific allometry - thought to reflect adaptive evolution and developmental constraints operating within populations;

reflects patterns of phenotypic integration and multivariate evolution

May be treated as an evolving character (slopes and intercepts) compared among species to test for evolutionary shifts in functional relationships between traits.
Two Types of Intraspecific Allometry

Ontogenetic allometry

- How two traits within an individual are correlated with changes in size (time)
- Describes the joint developmental trajectory of correlated traits

Static allometry

- Based on individuals measured at a common developmental stage with and/or across population(s)

Both types of intraspecific allometric analysis will likely help understand how selection will act on correlated traits

Sometimes ontogenetic and static allometries are different!
Interspecific allometry

Reflects the outcome of evolutionary divergence (or convergence) between taxa
Ontogenetic Growth – and trait based growth

• ‘Allometry over time’ . . . .

• Scaling in both time and mass dimensions

• Can we use metabolic scaling theory to derive a general model for ontogenetic growth?
Core Assumption - (#1) Scaling of metabolism, physiology, life history etc. determined by the size and geometry of hierarchical networks that control scaling of ‘metabolic units’ (leaves)

\[
\frac{dM}{dt} = b_0 M^\theta \propto N_L
\]

Production

Exponent governed by branching geometry (branching traits)

Size # of Leaves

West, Brown, Enquist 1997 Science
West, Brown, Enquist 1999 Nature
Can we use metabolic scaling theory to derive a ‘trait based’ growth function?
In biology there are two “Types” of Ontogenetic Growth Curves

<table>
<thead>
<tr>
<th>Time Parameter</th>
<th>Determinate Growth</th>
<th>Indeterminate Growth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative Time</td>
<td>Birth</td>
<td>Death</td>
</tr>
<tr>
<td>% Adult Size</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Graph A:**
- Sexual Maturity: ~3 months
- **Determinate** Danio rerio

**Graph B:**
- Sexual Maturity: ~4-5 months
- **Indeterminate** Devario aequipinnatus

**Relative Time**

**Notes:**
- $T_m = maturity$
History of growth models in Biology – a long history . . .

- Pütter (1920) developed a growth model often considered the base of most other growth models including the individual growth model by von Bertalanffy (1934) who’s name is most linked with growth models.


- These models often used in work on life history evolution, management (fisheries in particular), and ecology (see Charnov 1994).

  In plants – growth models have a similar line of development . . . .
In plants – similar theoretical development (balances between energy input and loss mainly from a carbon perspective). But the work has developed largely independent of animal ontogenetic growth work

• A common thread of theoretical work on plants can be traced to Blackman 1919 and a line of work summarized nicely in Evans 1972 and further elaborated in Thornley, 1970; Penning de Vries, 1975; Amthor, 1984.

• A strong foundation of theoretical work in plant biology and ecology! - often missed and under appreciated!

• This above work is canonized, in part, in the work on relative growth rate (RGR) in Grime and Hunt 1975 etc. which is more well known in ecology  

\[
RGR = \frac{\text{(Growth Rate)}}{\text{Plant Mass}}
\]
Karl Ludwig von Bertalanffy
(September 19, 1901 – June 12, 1972)
Also, early systems biology thinking similar to Odum
Individual growth model published by Ludwig von Bertalanffy in 1934

The Bertalanffy equation is the equation that describes the growth of a biological organism. The equation was offered by Ludwig von Bertalanffy in 1969

\[
\frac{dW}{dt} = \eta S - kV
\]

$W$ is organism weight, $t$ is the time, $S$ is the area of organism surface, $V$ is a physical volume of the organism. The two coefficients are (by Bertalanffy's definition) the "coefficient of anabolism" and "coefficient of catabolism" respectively.

Can we formalize early growth theory and integrate this work into allometric and metabolic scaling theory?
Incoming rate of energy flow, $B = \text{average metabolic demand of the entire organism at some time } t$

\[ B = \sum_c \left[ N_c B_c + E_c \frac{dN_c}{dt} \right] \]

Assume $E_c, B_c$ and $m_c$ are constant throughout ontogeny

At any time $t$, the total body mass, $m$, is given by

$$m = m_c N_c$$

The rate of change of body mass is

$$\frac{dm}{dt} \left( \frac{m_c}{E_c} \right) B - \left( \frac{B_c}{E_c} \right) m$$

(from constraints of vascular network)

$$B = B_0 m^{3/4}$$

At any time $t$, the total body mass,

$$m = m_c N_c$$

$$\frac{dm}{dt} \left( \frac{m_c}{E_c} \right) B - \left( \frac{B_c}{E_c} \right) m$$

(from constraints of vascular network)

$$B = B_0 m^{3/4}$$

General growth equation

$$\frac{dm}{dt} = am^{3/4} - bm$$

$$a = \frac{B_0 m_c}{E_c}$$

$$b = \frac{B_c}{E_c}$$
Network constrains the total number of supply units (capillaries, vessels/tracheids) to scale differently than the total number of cells supplied. Maximum size, $M$, is reached when the second term $bm$ begins to reach the magnitude of the first term $am^{3/4}$.

It is the imbalance between supply and demand that ultimately limits growth.
BUT! The scaling of the demand function may not be isometric.

\[ \frac{dm}{dt} = a m^{3/4} - bm \]

- Started by assuming that $bm$ is isometric (where $bm^4$) and scales isometrically with organismal size (number of living cells is directly proportional to its volume or size). But in some organisms not all mass is ‘living’.

- In plants, we can relax that assumption as either:
  - (i) dead mass and living mass may scale differently. In that case, if dead mass is proportional to leaf area then $bm^{3/4}$. Thus, there is no asymptotic size and growth is not limited by demand so then $\frac{dm}{dt} \approx am^{3/4}$.
  - (ii) OR it could be that $bm$, during the life span of a plant, is very small compared to $am^{3/4}$ so then also $\frac{dm}{dt} \approx am^{3/4}$.

See discussions in Enquist et al. 2007 (Nature) and 2009 (PNAS).
For all organisms (determinant and indeterminate), this equation predicts an asymptotic body size where

\[ \frac{dm}{dt} = 0 \quad m = M \]

\[
\left( \frac{m}{M} \right) = 1 - \left[ 1 - \left( \frac{m_0}{M} \right)^{1/4} \right] e^{-\frac{at}{4M^{1/4}}}
\]

\( M_0 = \text{birth mass} \quad M = \text{asymptotic size} \)

Fit model to empirical data -> estimate of a
From basic parameters of the cell predict value of $a$

For mammals

$E_c \approx 2.1 \times 10^{-5} \text{ J}$  \hspace{1cm} $m_c \approx 3 \times 10^{-9} \text{ g}$

$B_0 = 1.9 \times 10^{-2} \text{ watts}$

We predict that ->

$$a = \frac{B_0 m_c}{E_c} \approx 0.25 \frac{1}{\text{ g}^4/\text{day}}$$

- In principle, can also predict the asymptotic mass $M$, or $b$, or $B_0$ if one knew $B_c$

$$b = \frac{B_c}{E_c}$$

Fitted growth curves for mammals seem to support this prediction
• In principle, can also predict the asymptotic mass $M$, or $b$, if one knew $B_c$
\[ b = \frac{B_c}{E_c} \]

• According to model - variation in $M$ (adult animal size) is due to variation in $B_c$ (which does not change over ontogeny)

• Cells ‘know’ they are going to be in an organism of size $M$ when born!

• From network constraints, in all(?) metazoan cellular metabolism decreases with mass in order to match supply of the network $B_c \propto M^{1/4}$
Universal growth curve?

All organisms (determinant and indeterminate), when expressed as a function of

\[ r = \text{dimensionless mass ratio} \]

\[ \tau = \text{dimensionless time} \]

will fall on the same universal growth curve

\[ r = 1 - e^{-\tau} \]
Universal growth curve?

Figure 2: Universal growth curve. A plot of the dimensionless mass ratio, \( r = 1 - R = (m/M)^{1/2} \), versus the dimensionless time variable, \( \tau = (at/M^{1/2}) \) – \( \ln[1 - (m_t/M)^{1/2}] \), for a wide variety of determinate and indeterminate species. When plotted in this way, our model predicts that growth curves for all organisms should fall on the same universal parameterless curve \( 1 - e^{-\tau} \) (shown as a solid line). The model identifies \( r \) as the proportion of total lifetime metabolic power used for maintenance and other activities.
Predicts the scaling of the time to maturity, $t_m$ or any other time during development

$$t_m \propto M^{1/4}$$

(Peters 1983, Charnov 1993)
 partition coefficient of H₂O between wadsleyite and olivine is at least 5:1 (II). We can expect at least 5% partial melt in a bulk 1 wt % H₂O peridotite system where the partition coefficient between ringwoodite and silicate perovskite is 15:1 (II). Thus, production of up to 1% melt by dehydration melting of hydrous ringwoodite viscously entrained into the lower mantle is feasible.

The density of hydrous melt near the top of the lower mantle is uncertain, but it is likely buoyant with respect to the top of the lower mantle (28). Hence, we expect that the velocity decreases imaged beneath the 660 are transient features resulting from ongoing downward flow through the 660 that is driven by sinking slabs in the lower mantle. Eventually, the slightly buoyant hydrous melt would percolate upward, returning H₂O to the transition zone (4). Dehydration melting has also been suggested to occur where hydrous wadsleyite upwells across the 410 and into the olivine stability field (3, 27). Experiments indicate that hydrous melt is gravitationally stable atop the 410 (28), so once melt is generated, it may remain or spread laterally rather than maintaining a clear correlation with ongoing vertical flow patterns. Seismic detections of a lowvelocity layer atop the 410 are common but laterally sporadic beneath North America and globally (29, 30). The combination of dehydration melting driven by downwelling across the 660 and upwelling across the 410 could create a long-term H₂O trap in the transition zone (4).

DINOSAUR PHYSIOLOGY

Evidence for mesothermy in dinosaurs

John M. Grady,1,2 Brian J. Enquist,2,3 Eva Dettweiler-Robinson,1 Natalie A. Wright,1 Felisa A. Smith1

Were dinosaurs ectotherms or fast-metabolizing endotherms whose activities were unconstrained by temperature? To date, some of the strongest evidence for endothermy comes from the rapid growth rates derived from the analysis of fossil bones. However, these studies are constrained by a lack of comparative data and an appropriate energetic framework. Here we compile data on ontogenetic growth for extant and fossil vertebrates, including all major dinosaur clades. Using a metabolic scaling approach, we find that growth and metabolic rates follow theoretical predictions across clades, although some groups deviate. Moreover, when the effects of size and temperature are considered, dinosaur metabolic rates were intermediate to those of endotherms and ectotherms and closest to those of extant mesotherms. Our results suggest that the modern dichotomy of endothermic versus ectothermic is overly simplistic.

Over the past few decades, the original characterization of dinosaurs by early paleontologists as lumbering, slow-metabolizing ectotherms has been challenged. Recent studies propose that dinosaurs were capable of an active lifestyle and were metabolically similar to endothermic mammals and birds (1–3). This debate is of more than heuristic interest; energy consumption is closely linked to life history, demographic, and ecological traits (4). Extant endothermic mammals and birds possess metabolic rates ~5 to 10 times higher than
Variation in growth rates (biological times) reflect variation in metabolism

\[
\frac{dm}{dt} = am^{3/4} - bm
\]

\[
a = \frac{B_0 m_c}{E_c}
\]

\[
b = \frac{B_c}{E_c}
\]

\[
B = B_0 m^{3/4}
\]

\[
\frac{B}{m^{3/4}} = B_0
\]
Growth ~ Metabolism

Maximum growth rate \( \equiv G_{\text{max}} \)

Empirical observations indicates that \( G_{\text{max}} \) scales similarly to \( B \) where

\[
G_{\text{max}} = G_0 M^\alpha
\]

If so, then \( B \propto G_{\text{max}} \)

According to MST, the relationship between \( B \) (W) and \( G_{\text{max}} \) (g day\(^{-1}\)) at final adult mass \( M \) is

\[
B_M = c \, G_{\text{max}}^{\frac{1}{\alpha}}
\]

\( c \approx 0.66 \) (W g\(^{-1}\) day)

To observe the mass-independent relationship and compare energetic groups, we divide both sides by \( M^\alpha \), yielding

\[
B_0 = cG_0
\]

With substitution, the metabolic rate at any mass, \( m \), during ontogeny is

\[
B_m = cG_0 m^{3/4}
\]
(1) Gmax scales as $Ma$, where $a \sim 3/4$

(2) B scales isometrically with Gmax if masses are standardized. Regression of B against Gmax yields a slope of 1 and an intercept of $\approx 0.66$.

(3) Plotting G0 against B0 will reveal distinct energetic clusters corresponding to endotherms and ectotherms. High-power endotherms will exhibit an elevated G0 and B0, and ectothermic organisms the converse. Thermally intermediate taxa, termed mesotherms, such as tuna and lamnid sharks, should fall between the upper and lower quadrats.

(4) $B_{predicted} = B_{observed}$ in extant animals, where $B_{predicted}$ is calculated
Implications

- Parameters of growth equation have defined interpretation in terms of fundamental cellular properties (traits!) are quantitatively predicted independent of growth data.

- Variation in rates of physiological processing then leads to differences in the rate of biomass accumulation over time and maximum adult size, M.

- Differences in timing of reproduction and the allometry of scaling of reproductive output can modify and complicate growth curves.
Variation plant growth rate?
Whole-plant growth rates are hard to measure but we can measure stem growth rates.

**Letters to Nature**

**Allometric scaling of production and life-history variation in vascular plants**

Brian J. Enquist†, Geoffrey B. West‡, Eric L. Charnov§
& James H. Brown‡

† National Center for Ecological Analysis and Synthesis, 715 State Street, Suite 300, Santa Barbara, California 93101-3504, USA
‡ Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA
§ The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA

A prominent feature of comparative life histories is the well-documented negative correlation between growth rate and life span. Patterns of resource allocation during growth and reproduction reflect life-history differences between species. This is particularly striking in tropical forests, where tree species can differ greatly in their rates of growth and ages of maturity but still attain similar canopy sizes. Here we provide a theoretical framework for relating life-history variables to rates of production, $dM/dt$, where $M$ is above-ground mass and $t$ is time. As metabolic rate limits production as an individual grows, $dM/dt \propto M^{3/4}$. Incorporating interspecific variation in resource allocation to wood density, we derive a universal growth law that quantitatively fits data for a large sample of tropical tree species with diverse life histories. Combined with evolutionary life-history theory, the

---

**Box 1**

**The growth law**

As trees continue to increase in size throughout life, and this growth must be fuelled by metabolism, it is reasonable to assume that the growth rate (the rate at which its mass, $M$, increases over time), is directly proportional to metabolic rate, $B$, (the rate of gross photosynthesis). Thus, at any time $t$,

$$\frac{dM}{dt} = C_B B$$

where $C_B$ is a proportionality constant that can be time dependent. It has been shown that $B$ is proportional to $V^{3/4}$, and stem diameter, $D$, is proportional to $V^{2/3}$, where $V$ is the total volume of the plant. If $\rho = (MV)$ is the tissue- or species-specific wood density, then, at any time $t$, these can be expressed as

$$B = C_B \left(\frac{M}{\rho}\right)^{3/4} \quad D = C_D \left(\frac{M}{\rho}\right)^{2/3}$$

where $C_B$ and $C_D$ are corresponding proportionality constants. Implicit in these results is the assumption that the ratio $E/\rho$, where $E$ is the Young’s modulus of elasticity, is constant for all plants. Here, we relax the restriction implicit in ref. 14 that $\rho$ is constant and allow it to differ among plant species and to vary with time. Equations (2) and (3) can be combined to give

$$\frac{dD}{dt} = \left(\frac{3C_B}{2\rho}\right) D^{1/3} \quad \frac{dM}{dt} = \left(\frac{C_B C_D}{C_D^2}\right) D^2$$

where $C = 1/4C_B C_D^{1/3}$. This can be integrated to give
Traits modulate the scaling of whole plant growth rate
See Enquist et al. 1999 and Enquist et al. 2007

Scaling stem diameter growth rate with stem diameter
\[
\frac{dM}{dt} = b_0 M^{3/4}
\]
Scaling of whole plant growth rate

Scaling stem diameter growth rate with stem diameter
\[
\frac{dD}{dt} = \left( \frac{3\left[1/4C_D^{2/3}b_0\right]}{2\rho} \right) D^{1/3}
\]
Note sensitive to wood density and \(b_0\) (other leaf traits)

Scaling biomass growth rate with stem diameter
\[
\frac{dM}{dt} = \left( \frac{b_0}{C_D^2} \right) D^2
\]
Independent of wood density but sensitive to these other traits too

Can predict growth rate from more fundamental traits and measures of plant size
Basis for understanding how species can differentiate from each other.
A handful of key traits appear to determine variation in plant growth rate and possibly ecosystem fluxes.

Let the concept of trait be functional!

Cyrille Vièlle, Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel and Eric Garnier

Cyrille Vièlle (cyrille.vieville@ecofev.cnrs.fr), Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel and Eric Garnier. CNRS, Centre d’Ecologie Fonctionnelle et Evolutive, UMR 5179, 1919, Route de Mende, FR-34293 Montpellier Cedex 5, France. MLN also at: Montpellier Supagro, 2 Place Viola, FR-34060 Montpellier Cedex 1, France. D.V. also at: Département de Biologie, Université de Sherbrooke, Sherbrooke (QC), Canada, J1K2R1.
Predicting Growth from Traits

Can derive the trait basis for scaling normalization

Production driven by key traits that govern scaling of metabolism
Builds on and is consistent with plant growth analyses (e.g. Poorter 1989)

\[
\frac{dM}{dt} \propto N_L = b_0 M^\theta
\]

\[
\frac{dM}{dt} \approx \frac{c}{\omega} \left[ \left( \frac{a_L}{m_L} \right) \left( \dot{A}_L \right) \right] \beta_L M^\theta
\]

Enquist, Kerkhoff, Stark et al. (2007) *Nature*
Predicting Growth from Traits

\[
\frac{dM}{dt} \approx \frac{c}{\omega} \left[ \left( \frac{a_L}{m_L} \right) \left( A_L \right) \right] \beta_L M^\theta
\]

Enquist, Kerkhoff, Stark et al. (2007) Nature
Traits underlie the scaling of plant growth

**Predicted Normalization Value**

Angiosperm $\beta_G = 2.43 \, g^{\frac{1}{4}} \, yr^{-1}$; 
95% CI = 0.44–11.92

Gymnosperm $\beta_G = 1.35 \, g^{\frac{1}{4}} \, yr^{-1}$; 
95% CI = 0.41–4.42

**Observed Normalization Value**

Angiosperm $\beta_G = 4.44 \, g^{\frac{1}{4}} \, yr^{-1}$; 
95% CI = 1.77–11.09

Gymnosperm $\beta_G = 1.36 \, g^{\frac{1}{4}} \, yr^{-1}$; 
95% CI = 0.80–2.40

\[
\frac{dM}{dt} = \frac{c}{\omega} \left( \frac{a_L}{m_L} \right) (\hat{A}_L) \beta_L M^\theta
\]

Enquist, Kerkhoff, Stark et al. (2007) *Nature*
Take an example of examining tree growth in different light environments. We know that some traits change in sun vs. shade leaves. How do these trait changes influence plant growth rates? We can use this trait based growth formulation to ask if the direction of trait shifts with light could in principle compensate for the observed light levels.

Tree growth could compensate for differences in light levels if traits shift directionally so that values of $b_0$ are similar in sun vs. shade trees.
Some literature cited

• [https://link.springer.com/content/pdf/10.1007/BF00650112.pdf](https://link.springer.com/content/pdf/10.1007/BF00650112.pdf)