

**AN INTEGRATIVE THEORY OF BIO-ENERGETIC
GROWTH, MORTALITY AND EVOLUTIONARY
OPTIMIZATION**

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ABSTRACT

AN INTEGRATIVE THEORY OF BIO-ENERGETIC GROWTH, MORTALITY AND EVOLUTIONARY OPTIMIZATION

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Growth is a universal energetic phenomenon for all living organisms, and is undertaken by meristematic and stem cells through energy metabolism. Most growth processes can be modeled with a sigmoidal function, meaning that early growth is near exponential and later growth declines with age or time until at a certain point (i.e., maturity), when evolutionary optimization is realized and a species should turn all or part of its growth energy into reproduction and then death occurs, consequently. This is usually called a life history process. Evolutionary optimization means that fitness should be supposedly maximized during this process for all species, but how it is realized for all species is still a challenge or gap in our knowledge. This dissertation is dedicated to fill this gap.

First, a general bio-energetic growth theory is presented here that assumes a dynamic universal energy pattern: a constant energy income rate deceleration with each cell reproduction, and a species- or clade-constant maintenance cost of cells. This pattern can produce the observed power relationships between energy metabolism and body size as described in Kleiber's law and the von Bertalanffy growth function. Secondly, the new growth theory and a related new bio-energetic definition of mortality are combined with a typical evolutionary optimization process to predict that maturity should begin when net energy income rate equals to the maintenance cost for all living activities and that

maintenance cost per mass integrated till maturity should be a defined constant. Two fish life history datasets were used to test the new theory, and the result supported the predicted relationships well. Thirdly, because leaves are the basic functional modules of plants, a comparable evolutionary life history theory for the leaf is developed. The theory predicted a similar energy equilibrium status between energy income (photosynthesis) and expenditure (maintenance) for mature leaves. A global leaf physiological trait dataset (GLOPNET) was used to test this prediction, and a large proportion of variation in photosynthesis of diverse mature leaves is explained ($R^2 = 87\%$ on mass-based metrics). Lastly, it is suggested that through an established relationship between leaf photosynthesis and seed energy income, there should also be an allometric relationship between leaf photosynthesis and seed mass. Using a large database of leaf traits and matched seed mass for the same species, it was shown that though a relatively small proportion (20%) of seed mass variation was explained by leaf photosynthesis, the predicted relationship is still generally supported.

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INTRODUCTION

1 Mass growth and energy metabolism are two complementary aspects of life in plants and animals

Growth is a fundamental activity of any living individual. Two types of growth have been recognized: determinate and indeterminate. Determinate growth is used to describe species that invest all growth energy into reproduction at maturity and are approaching their maximum body size at maturation, while indeterminate growth is for species that invest part of growth energy into reproduction and continue to grow after maturity with a smaller maturation size relative to maximum size (West et al. 2001; Kozłowski et al. 2004). Determinate growth is for all birds, some plants, insects and most mammals, and indeterminate growth are for fish, most plants and others (Karkach 2006). These two types may be mixed within one individual. For example, a plant's trunk and branches may grow indeterminately, while leaves, flowers and seeds grow determinately.

Changes in growth rate within the lifetime of an individual are called ontogenetic growth, and are essentially a result of cell level processes, because growth is fundamentally undertaken by only a few types of cells. Meristematic tissue in plants is responsible for the girth and height augmentation of stem, branch growth and the mostly planar expansion of leaves, while embryonic and adult stem cells in animals are responsible for all kinds of tissue differentiation and maturation. Meristematic and stem cell activity can be formulated not only as a mass growth process, but more importantly in terms of universal energy dynamics, such as energy production, metabolism and maintenance. The energy production units in plants are chloroplasts in leaves or stems, and photosynthesis is the universal metabolic process for capturing light energy and carbon in chloroplasts to produce all other types of structures and tissues in plants.

Animals depend on external resources to have energy production and metabolism. There is always a maintenance cost related to the above processes. For example, respiration of leaves is required to sustain a photosynthesis reaction, and other supporting costs are also inevitable for plants to achieve a structure and height to effectively capture light, while animals must spend certain amount of energy to maintain body temperature (i.e., endotherms) or to sustain basic functions of all tissues (measured by basal metabolic rate).

This bio-energetic perspective of growth has been noticed in some pioneering studies of ecology and a few more recent works. For example, growth in animals was often considered as a process of energy balance between build-up and break-down of tissues; von Bertalanffy (1938) specifically developed his well-known growth equation on this concept, and Kooijman (2010) had a dynamic energy budget theory on it. For plants, the energy budget of the whole plant or plant organs has been used to model plant or leaf growth (Kikuzawa 1991; Kikuzawa et al. 2006). However, better bio-energetic representations of growth are fundamental to advancing biological theory.

2 Growth or energy production is under evolutionary optimization

Since the discovery of Darwin's theory of evolution, the focus of ecology and evolutionary studies has been understanding how growth and reproductive processes are modulated by natural selection to define different life histories of various species. The central concept in evolutionary theory is fitness, which is defined as the lifetime number of offspring that can reproduce themselves as to maintain the continuity of life cycle, and it is generally assumed that this fitness has been maximized by evolutionary processes

during the long time of species formation and existence (Roff 1992; Stearns 1992; Kozłowski 1996).

The result of evolutionary optimization is optimized life history traits for separate species, i.e., life history traits should be closely coordinated with each other to achieve the overall goal of maximum fitness for the individual as a whole. In practice, it means that there should be general trade-off relations among traits of mass, energy and age for plants and animals as well.

The simplest trait relations in biology are bivariate correlations. Most bivariate relationships are defined by linear regressions on log transformed data. For example, traits of animals, such as basal metabolic rate (BMR), age of female at first reproduction, life expectancy at birth, instantaneous mortality rate, clutch size, reproduction output and individual lifespan are related to body mass raised to a power of α , and the values of α are usually around 2/3 to 3/4 or 1/3 to 1/4 (Sæther 1988; Harvey and Zammuto 1985; Ricklefs 2006; Charnov 1991 and 2005). Plant traits, such as growth rate, total pigment concentration, plant height and foliage/root/stem biomass are related to plant size in similar power relations (Niklas 2004; Niklas and Enquist 2001). Further, there are also allometric bivariate relations within and between plant organs, such as leaves and seeds. For example, leaf photosynthetic rate is related to respiration, leaf lifespan (LL), leaf mass per area (LMA), and leaf nitrogen (Reich et al. 1998a and 1998b; Poorter and Garnier 1999; Reich et al. 1997), and seed mass is associated with plant height, leaf photosynthetic rate, and relative growth rate (Moles et al. 2005). The many bivariate correlations within one species could be better understood when put together. For instance, because age at first reproduction scales as $m^{1/4}$, and instantaneous mortality rate

as $m^{-1/4}$, their product is a constant close to 2.1 (Beverton and Holt 1959; Charnov et al. 1991); and as lifespan scales as $m^{1/4}$, and reproductive output as $m^{3/4}$, life time reproductive energy per mass ≈ 1 to 2 for several animal species (Charnov 2005).

Another way of study trait relationships is to use a multivariate approach, typically reducing the dimensions of “multiple trait space” to facilitate biological interpretation. Such examples include a recent study that used principle component analysis to check the inter-correlations of up to six critical leaf traits, and it was found that there was a single major principle axis called “a leaf economics spectrum” that runs from slow carbon gain on investments of nutrients and dry mass to the fast opposite (Wright et al. 2004). Correspondingly, this latter work suggests a “fast-slow life history continuum” defined for animal species, where key life history traits of animals are distributed between two opposite trends: fast growth, early maturation, high fecundity and low adult survival as one extreme, and slow growth, late maturation, low fecundity and high adult survival as the other extreme (Bronikowski and Arnold 1999; Wiersma et al. 2007a; Wiersma et al. 2007b; Wright et al. 2004; Reznick et al. 1990; Roff 2007). Overall, given the seemingly great differences between plants and animals, it is striking to see how similar fundamental allometric scaling relationships actually are among them. This similarity leads the development of a recent theoretical framework called Metabolic Scaling Theory (MST) that refers to mainly biophysical reasons as the mechanism and resources of these universal patterns. However, the foundation and conclusions of this theory are vague, problematic and often rejected by reality (DeLong et al. 2010; Price et al. 2012; O’connor et al. 2007; Kozlowski et al. 2005).

3 Current growth and life history evolution theories and their limitations

Clearly, the universality of relations and life histories in plants and animals should be understood by similar bio-energetic optimization processes, because energy is the universal currency and metric for them especially plant leaves, and evolutionary optimization is a common constraining force for most if not all living organisms. Hence, modeling how the bio-energetic optimization process is undertaken to produce all kinds of trait associations or life histories for diverse species is a major challenge in ecology (Roff 1984; Stears and Koella 1986; Kozlowski 1996).

Currently, a typical optimization process in animals defines fitness as the product of two critical components: fecundity and survival rate. Fecundity is the lifetime offspring number, survival rate is the rate of the offspring surviving to its own reproduction stage. As fecundity is a function of body size, variation of body size with time, i.e., growth, is required to model fecundity. But the present growth functions are mainly empirical and focus on mass variation. Survival rate is mainly modeled from empirically fitted instantaneous mortality rate. As photosynthesis capacity in plants and the growth rate in animals usually decline with age (Kitajima et al. 2002), and the risk of mortality from mainly physiological and related factors increases with age, a growth process is thus optimized at certain age when reproduction should take over pure semantic growth to have the maximum number of offspring. This age is then determined by species-specific parameters from mass growth process and individual's independently estimated survival rate (Roff 1984). However, mass growth and survival rate are usually strongly correlated such that fast growth would correspond to low survival and vice versa (Charnov 1991), confounding possibly simpler but more fundamental constraint for

determining optimum maturity. Our present understanding to optimum age of reproduction therefore are mainly empirical, and life history constraint is also limited to various strong inter-correlations (Charnov 1993; Roff 2007).

Growth and life history theories for plants are especially rare and not well developed, because there are significant differences between plants and animals (Stearns 2000). The life history of whole individual of most tree species is difficult to quantify. Many plant species live many to hundreds of years, and contain large amount of living or dead mass that show great functional plasticity to outside conditions and thus are hard to precisely measure over a long period (He et al. 2009; Tjoelker et al. 2005; Wright et al. 2005). For example, most species traits tend to shift along climatic gradients (Wright et al. 2004; Mauseth 2009; Jin et al. 2008). More importantly, unlike unitary animals, plants are modular so that the concept of “individual” is often not strictly applicable. The above mentioned bivariate correlation and multivariate associations are usually also held within leaves and between leaves and seeds. There are models assuming that leaves are energy production unit and the net assimilation rate of a leaf should be optimized to have highest energy production rate (Kikuzawa 1991). However, such models are not compatible with the fact that leaves actually have largely varying net photosynthetic rates. For these reasons, plant ecologists are now suggesting that the functional trait variation of leaves and seed are themselves representing and defining whole plant life history strategies (Bonser et al. 2010; Poorter et al. 2006).

The specialty of plants compared to animals further necessitates a bio-energetic framework of growth and life history, because plant growth, especially that of leaves, is more related to energy budget that can be calculated from photosynthesis, respiration,

dead mass investment and related cost, and mortality may be more relevant to relative energy expenditure rate for functional maintenance. In other words, new insights in ecology can be raised if life history theory of animals and the energetic nature of plants are combined to provide a common mechanism for explaining their great similarity in growth-energy allometry and life histories.

Outline

In summary, there is a need for new theories to integrate three important aspects of plant and animal biology: (i) new bio-energetic growth process and survival rate with explicit relationship between them; (ii) simplified life history theory based on evolutionary optimization on them that can be applied to animals, plant or plant organs to provide explanations for their inter-specific life history variations; (iii) analyses of datasets that support the new framework. This dissertation research was conducted to fill the above-mentioned gaps. The following is an outline of the research:

In chapter 1, a bio-energetic growth model is developed. It is based on basic characteristics of energy dynamics, and is a universal bio-energetic form of various empirical von Bertalanffy growth functions (VBGFs). In chapter 2, the new growth model and a related energetic definition of mortality are integrated into a typical evolutionary optimization process. This produces a new life history theory in terms of energetic for animals. A large fish trait dataset was used to test it. Chapter 3 further extends the above study method by developing a similar growth and evolutionary optimization process for leaves. A global dataset (Wright et al. 2004) containing field measurements of critical mature leaf traits was used to test the leaf life history theory. Finally in chapter 4, seed mass is then linked to mature leaf photosynthesis because seeds

have a similar growth process from a general relationship between energy dynamics and mass growth. This prediction was tested by a large leaf trait and coupled seed mass dataset.

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CHAPTER 1. FROM CELLULAR BIOENERGETICS TO INDIVIDUAL GROWTH: A UNIFYING ENERGETIC GROWTH THEORY

Abstract

Inspired by an ontogenetic growth model (OGM) proposed in 2001 by West et al., a general bio-energetic growth theory was developed that assumes a universal energy dynamic pattern: a constant energy influx deceleration with each cell growth event in meristematic and stem tissues and a species or clade-constant maintenance cost of cells. This new growth theory links mass explicitly with energy, deduced a general form of the von Bertalanffy mass growth function and also explained the difficulty of determining a fixed power coefficient for the relationship between energy influx rate and body mass. This study helps improve understanding of power-scaling relations between metabolism and body mass.

Introduction

Growth is a fundamental biological process. Growth rates are rarely constant and changes in growth rate within an organism's lifetime are often referred as ontogenetic growth; one of the most fundamental processes in biology. This process has been studied mainly by modeling an individual's overall body size variation over its lifetime with empirical equations (Karkach, 2006). One such model that has been widely used is the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938):

$$\frac{dm}{dt} = a \cdot m^{\alpha} - b \cdot m^{\beta} \quad (1.1)$$

where m is body mass at time t , a and b are positive proportional coefficients, and α and β are two exponents relating energy influx (anabolism) and energy dissipation (catabolism) with body mass, respectively (Banavar et al. 2002).

While it has been generally accepted that energy dissipation, also referred to as ‘maintenance cost’, is proportional to body mass, i.e., $\beta=1$ (He and Stewart 2001; West et al. 2001), the selection of a specific value for α has been a subject of debate. For example, many empirical studies suggested from surface area versus volume scaling relationship that $\alpha = \frac{2}{3}$, while a new ontogenetic growth model (OGM) suggested that basal metabolic rate (*BMR*) is the source of anabolism and consequently suggested that $\alpha = \frac{3}{4}$, because there is a general 3/4-power relationship between *BMR* and body mass (known as “Kleiber’s law”) (McMahon 1973; Nunn and Barton 2000). However, this new OGM-based explanation of *BMR* to be energy influx rate is not strictly true (Makarieva et al. 2004), and the validity of Kleiber’s law itself is controversial because the power parameter of 3/4 is not supported in many cases (Dodds et al. 2001; O’Connor et al. 2007). It seems unlikely, based on these latter studies, that the value of α should be invariant. Thus, it is still unclear why there is a power relationship between energy influx and body mass and what specific value the power parameter α should assume under any given condition.

Here, we suggest that although VBGFs are useful models, new models should consider cell-level growth and energy dynamics, because all growth is undertaken principally by certain types of cells. Meristematic cells in plants are responsible for the girth and height augmentation of stems and branches, and stem cells in animals are the

ultimate sources of all types of tissues and organs. So we suppose a mechanistic link between energy influx and growth for these cell types. This link is scaled up to define a general VBGF form that itself represents a universal pattern of cell energy dynamics over an organism's lifespan and that its key coefficients are species-specific cell-level properties. This new theory also explains why it is difficult to distinguish a specific power parameter value of 2/3 from 3/4 in common VBGF models.

New Theory

1 Energy budget of cells

Living cells have two counterbalancing activities and functions: growth (including reproduction and other productive activities) and maintenance. Cell growth means reproducing a new differentiated or reproductive cell, and maintenance means using the cell's energy income to maintain its own viability and functionality. As a result, the energy budget of cells at certain time t can be generally separated into two parts (adapted from West et al. 2001):

$$\frac{B}{dt} = N_t \cdot B_c + E_c \cdot \frac{dN_t}{dt} \quad (1.2)$$

where $\frac{B}{dt}$ is the energy income rate of all cells, N_t is the number of cells, B_c is the maintenance cost or energy dissipation rate (for metabolic loss, mechanical support, and other energy costs dissipated irreversibly) of a cell, E_c is the energy required to reproduce a new cell, and dN_t is the number of newly produced cells.

Eq. (1.2) can be rearranged to make it more general as:

$$\frac{dN_t}{N_t} = \frac{\bar{B}}{E_c} - \frac{B_c}{E_c} \quad (1.3)$$

where $\bar{B}$ is the energy income rate of a cell, $\bar{B} \cdot N_t = B$.

Integrating eq. (1.3) over a certain time period 0 to t , the following function emerges:

$$N_t = N_0 \cdot e^{(\tau - \tau_{B_c})} \quad (1.4)$$

Where N_0 is the initial cell number at the beginning time 0, usually 1 if cell division

begins from one cell, $\tau = \int_0^t \frac{\bar{B}}{E_c}$ represents the total energy income over time t for a cell,

and $\tau_{B_c} = \int_0^t \frac{B_c}{E_c}$ represents the total maintenance cost over time t for a cell.

If the maintenance cost is zero, eq. (1.4) can be used to calculate cumulative energy income N_{tot} in terms of number of cells as:

$$N_{tot} = N_0 \cdot e^{\tau} \quad (1.5)$$

and cumulative growth efficiency can then be calculated as growth divided by the cumulative energy income:

$$\frac{N_t}{N_{tot}} = e^{-\tau_{B_c}} \quad (1.6)$$

Obviously, if there were no maintenance cost such that $\tau_{B_c} = 0$, the cumulative growth efficiency would be 1.

2 A pure energetic cell growth theory

As mentioned above, cell maintenance cost $\frac{B_c}{E_c}$ is usually viewed as constant for a species (West et al. 2001; Makarieva et al. 2008). The remaining critical relationship in

eq. (1.3) lies between $\frac{\bar{B}}{E_c}$ and $\frac{dN_t}{N_t}$, which is a proxy of relative growth rate (RGR).

One common observation for most if not all living organism is that RGR decreases with increasing body size (Falster et al.2008), suggesting that cell replication as the main part of body size growth has a negative feedback to cell energy influx rate. In the simplest case, this observation can be transformed into a linear relationship as this: energy income rate has a relative change of $(\alpha-1)$ each time a new cell is produced, and $\alpha < 1$. This assumption is similar to Newton's second law of motion regarding deceleration.

Mathematically, it can be expressed as:

$$\frac{d\bar{B}}{\bar{B}} = \frac{dN_t}{N_t} \cdot (\alpha - 1) \quad (1.7)$$

Eq. (1.7) indicates a simple, but critical, link between energy and mass.

Combining it with eq. (1.3) produces a new, purely energetic growth function, removing mass from the relationship:

$$\frac{d(1 - \frac{B_c}{\bar{B}})}{(1 - \frac{B_c}{\bar{B}})} = \frac{B_c}{E_c} \cdot (\alpha - 1) \quad (1.8)$$

This new bio-energetic growth eq. (1.8) describes the variation of instantaneous growth efficiency, defined as net growth energy $(\bar{B} - B_c)$ divided by gross energy income rate $\bar{B}$, i.e. $(1 - \frac{B_c}{\bar{B}})$, with time, or with each cell reproduction (in the latter case time is kept by tallying discrete events). It says that instantaneous growth efficiency has a relative declining rate of $\frac{B_c}{E_c} \cdot (\alpha - 1)$ with time or with each new cell reproductive event.

If we assume that the initial instantaneous growth efficiency is nearly identical to 1 at time zero, which is reasonable, then the integrative form of eq. (1.8) can be written as:

$$1 - \frac{B_c}{B} = e^{-\frac{B_c}{E_c} \cdot (1-\alpha) \cdot t} \quad (1.9)$$

Eq. (1.9) suggests a negative exponential curve in growth efficiency variation with time. As cumulative growth efficiency $\frac{N_t}{N_{tot}}$ is $e^{-\frac{B_c}{E_c} \cdot t}$ (see eq.(1.6)), eq.(1.9) can be transformed as:

$$1 - \frac{B_c}{B} = \left(\frac{N_t}{N_{tot}} \right)^{(1-\alpha)} \quad (1.10)$$

Eq. (1.10) means that an energetic growth process may also represent a power relationship between instantaneous and cumulative growth efficiency with the power parameter $(1-\alpha)$ being the only critical variable.

To test for the sensitivity of the relationship in eq. (1.10) to variation of $(1-\alpha)$, four commonly considered values of α : 1/2, 2/3, 3/4 and 4/5, and a common range of (0, 1) values for instantaneous and cumulative growth efficiency were used to produce four hypothetical growth relationships (Figure 1-1).

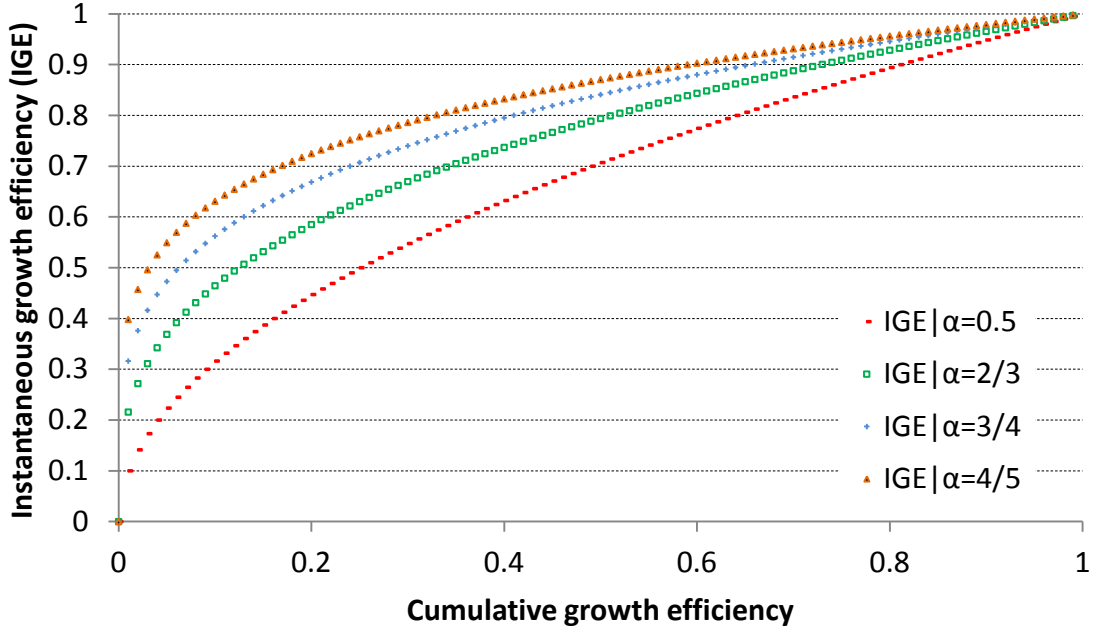


Figure 1-1. Instantaneous growth efficiency (IGE) vs cumulative growth efficiency for four different values of α . IGE| $\alpha=2/3$ represent instantaneous growth efficiency at $\alpha=2/3$, and the same for other legends. For interpretation of the reference to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

From Figure 1-1, it is clear that eq. (1.10) with different α values would produce quite different growth curves with similar forms. This is a mathematical property of the power relationship that has a power coefficient in the range of (0,1).

3 Linking the new energetic growth theory to traditional VBGF models

Because eq. (1.7) links energy with mass, the above pure energetic growth theory can be back-transformed into a traditional mass growth function. First, integration of eq. (1.7) gives:

$$\overline{B} = \overline{B}_0 \cdot N_t^{(\alpha-1)} \quad (1.11)$$

where $\overline{B}_0$ is the initial cell energy influx rate at time 0.

Eq. (1.11) has another form for an individual of N_t cells as:

$$B = \overline{B}_0 \cdot N_t^\alpha \quad (1.12)$$

Because maximum or asymptotic size N_T is reached when $1 - \frac{B_c}{B}$ is zero or $\overline{B} = B_c$, which means zero growth energy availability and thus a stabilized size, a new relation at maximum size from eq. (1.11) is:

$$B_c = \overline{B}_0 \cdot N_T^{(\alpha-1)} \quad (1.13)$$

Taking eqs. (1.11) and (1.13) together, we have:

$$\frac{B_c}{B} = \left(\frac{N_t}{N_T} \right)^{(1-\alpha)} \quad (1.14)$$

Substituting eq. (1.14) into eq. (1.9), a general mass growth function is deduced as:

$$1 - \left(\frac{N_t}{N_T} \right)^{(1-\alpha)} = e^{-\frac{B_c}{E_c} \cdot (1-\alpha) \cdot t} \quad (1.15)$$

Eq. (1.15) is a general form of VBGF, with the traditional VBGF growth coefficient K being replaced by $\frac{B_c}{E_c} \cdot (1-\alpha)$.

Discussion

The new growth theory presented here suggested that eqs. (1.9), (1.10), (1.12) and (1.15) are four inter-convertible ways for modeling the same growth process.

First, eq. (1.9) suggested a universal trend of exponential decreasing for instantaneous growth efficiency. This trend is observed in animals (West et al.2001; Banavar et al. 2002). Because this trend is also commonly observed in tree growth, dendrochronological studies have chosen it as the natural growth trend in trees to detrend

a ring-width growth pattern (Naurzbaev et al. 2004; Fritts 1963; Cook et al. 1990 p109), supporting the validity of eq. (1.9) in plants.

Second, it was deduced that this pure energetic trend can also be translated into a relationship between instantaneous and cumulative growth efficiency that was constrained only by a power parameter $(1-\alpha)$ (see eq. (1.10)). A higher α such as $3/4$ means that cumulative value would be $1/16$ for a specific instantaneous growth efficiency such as $1/2$, while a lower α such as $2/3$ would have a value of $1/8$ for the same $1/2$. Because instantaneous growth efficiency represents the relative proportion of total energy income available for growth, reproduction, and other related activities, the parameter α has a clear meaning: compared to species with lower α , species with higher α achieve higher excess energy for life history activities even at a later life stage with lower cumulative (overall) growth efficiency, or they achieve higher excess energy for life history activities at the same overall efficiency (Figure 1-1). A higher excess energy could then bring more flexibility, faster growth and more reproduction output to a species, which in the extreme case of $\alpha=1$ produces exponential growth (see eq. (1.1)). This is also obvious from eq. (1.7), as $\alpha \rightarrow 1$ the extent of negative feedback of growth on energy influx is lessened, and thus helps maintain a higher growth rate for a longer time. Conversely, lower α values such as $\alpha < \frac{2}{3}$ should be rare as they would significantly reduce growth efficiency. However, even if energy use efficiency relations systematically vary between taxa, eq. (1.10) and α values may need to be quite different to bring this variation to certain detectable difference level (Fig. 1.1), which is difficult when higher α values should be favored over lower ones in an evolutionary context.

Third, a general power relationship between energy influx rate and body mass was generated in eq. (1.12). When the power parameter $\alpha = \frac{3}{4}$, this relation is connected to Kleiber's law because energy influx rate and *BMR* are in fixed proportion in many cases (Rolfe and Brown 1997).

Fourth, it was shown in eq. (1.15) that the above pure energetic growth model about allometric relations between energy dynamics and mass is interchangeable with a general form of VBGF. Because VBGF is universally realized in various species, it is suggested that corresponding allometric rules about body mass and energy should also be quite universal, which has been shown by many studies (Hoppeler and Weibel 2005; Marquet et al. 2005; Agutter and Wheatley 2004). This new theory then provides a new universal basis for variability in allometric relationships between growth, mass, and energy scaling of biology.

This unification of several different mechanistic growth models helps to clarify apparent differences and universal energetic theme in general growth processes, such as various VBGFs in the form of eq. (1.1) that are widely accepted in biology (Chen et al. 1992). But since traditional FBGF coefficient K can be decomposed into two variables in the form of $\frac{B_c}{E_c} \cdot (1 - \alpha)$, it is inappropriate to validate a pre-determined α value by a statistical fitting of K like West et al. did (2001). It is then a challenge to determine which α is more appropriate for a specific species from growth data only.

Further, Figure 1-1 indicate that if the commonly argued values of 2/3 and 3/4 for α are considered, the $(1 - \frac{B_c}{B})$ values would have a difference of less than 11% across

the growth processes. And for possible cumulative growth efficiency of larger than 20% (Straile 1997; Reeve 1963), this difference would shrink to about 8%, which makes it difficult to be detected. For example, according to eq. (1.14), this variance between growth functions is the same as for the ratio between mass and maximum mass to have a variance of 25% if $\alpha = \frac{2}{3}$ to 35% if $\alpha = \frac{3}{4}$ within a growth function. In practice, that ratio could easily vary by 25-35%. For instance, Forsman (1991) found that maximum size is usually affected by prey body size and prey availability, and extrapolated maximum size is usually a function of growth curves which are affected by individual growth history, geographic location, disease, reproduction and other stresses. Therefore, it is really not easy to determine an exact α value from available growth or macro-level measurements on individuals.

As cumulative growth efficiency was quantified in equation (1.6), smaller cell maintenance cost $\frac{B_c}{E_c}$ would lead to higher cumulative growth efficiency over a certain period. Environmental factors such as cold temperature that may reduce maintenance cost should able animals to attain higher growth efficiency and larger body size under similar food resources. This conclusion might be underlying a phenomenon that most ectotherms grow slower but reach a larger maximum size when growing in colder temperature environments than in higher temperature ones (the “temperature-size rule”) (Kozłowski et al. 2004; Atkinson 1994)).

Finally, the new theory of growth could provide a more mechanistic understanding to other important aspects of biology that are related with growth, such as reproduction, mortality, life span and other important life history traits (Reich 2001;

Shmidt-Nielsen 1984; Peters 1986; Niklas and Enquist 2001; Qu et al., 2004). This will be shown in the next several chapters. Future studies also need to address an outstanding question: why should energy influx rate or growth efficiency decline a certain amount with each cell generation? Answers to this question may tap the more fundamental secrets about longevity and growth than are hidden within cells.

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CHAPTER 2. BIO-ENERGETIC EVOLUTION OF MATURITY: THEORY, ANALYSIS AND VALIDATION IN FISH

Abstract

Theories of life history evolution describe how physiological and demographic traits of an organism are optimized to produce the largest number of offspring that can reproduce themselves (maximizing fitness). One of the traits that is the focus of many optimization models is maturity in terms of age or size, because knowing how maturity is set by evolution may help determine most life history traits such as growth, lifespan, mortality rate and reproduction output (Charnov 1990; 1993; Wiersma et al. 2007; Roff 2007). However, present life history models on maturity are mainly empirical and fragmented (He et al. 2001; Charnov 2008), and a universal mechanism for detailing how maturity evolved is still lacking. Here, a new life history theory that integrates principles of bio-energetic growth and mortality processes with evolutionary optimization is advanced to provide a mechanism for determining maturity. This new theory proposes that maturity should occur when net growth energy and maintenance cost are at an equilibrium status, and thus the integrated maintenance cost per mass till this point should be a defined constant. One large growth and life history dataset for fish species provided support for the new theory. Finally, it is also discussed how this new understanding of maturity may help explain the variation of other life history traits such as lifespan, mortality, basal metabolic rate, reproductive effort and body size.

Introduction

Maturity is the time or size when reproduction begins. The time at maturity is measured as age, the size mass or length, and these two measurements are termed as age

and size at first reproduction, respectively. At maturity, the life history of an individual goes from immature growth into a reproduction-and-then-death stage, which makes maturity a critical turning point from an evolutionary perspective. Thus, understanding how this turning point is determined remains an important subject in life history and evolutionary studies (Charnov 1993; Kozłowski 1992).

Empirical studies indicate that maturity is closely related to other important life history traits such as growth, life-span, mortality and body size. For example, He et al. (2001) found that growth coefficients, such as the von Bertalanffy growth function (VBGF) coefficient K and asymptotic body length (L_{inf}) can empirically predict both age and size at first reproduction. Beverton and Holt (1959) supposed that length at first reproduction (L_r) is a fixed empirical ratio of L_{inf} for a group of fish species. The age of mammalian females at first reproduction (t_r) is strongly positively correlated ($R= 0.98$) with life expectancy at birth, a measure of mortality (Harvey and Zammuto 1985). Charnov (2005) and Calder (1984) both theorize that t_r and L_r are closely associated with adult life-span, basal metabolic rate (BMR , a measure of the pace of growth activities), and body size (M) in various forms. These empirical relationships have not been shown to be robust or universal, and not much theory was developed to explain the underlying mechanism that may help define and predict maturity in a mechanistic and robust way and explain its complex correlations with other life history traits. Ecological and evolutionary scientists then developed life history theory to fill these gaps gap (Stearns 1992; Roff 1992; Charnov 1993).

Life history theory deals with how evolutionary forces forged coordinated life history traits such as growth, maturity, mortality, life-span and size for a species to achieve maximum evolutionary success (Stearns 2000). This success is quantified by fitness. Traditional fitness definition is the overall lifetime mature offspring number. The maximization of this number is then defined as an optimization process that all living organisms should have fulfilled over their long evolutionary time. Hence, maturation puts a universal constraint on the variation and association of life history traits.

A typical optimization process in animals defines fitness as the product of fecundity and survival rate. Fecundity is the lifetime offspring number reproduced and is quantified as a function of body growth, survival rate is the rate of the offspring surviving to its own reproduction stage and is empirically estimated. As growth potential declines while mortality risk accumulates with age or size, maturity is a certain age when immature growth should be transformed into reproductive growth to have the maximum fitness. A resolution for maturity from such an evolutionary optimization process has been presented in Roff's classical life history theory framework as following (1992 and 2007):

$$t_r = \frac{1}{K} \cdot \ln\left(\frac{3K}{Z} + 1\right) \quad (2.1)$$

where t_r is maturity measured as age at first reproduction, Z is natural mortality (instant), and K is VBGF growth coefficient. Obviously, t_r is determined by growth and natural mortality together.

When both K and Z are estimated from empirical growth functions and field data, eq. (2.1) can provide quite a precise prediction about t_r (Roff 2007). But several questions

complicate use of eq. (2.1). First, K and Z are unstable and hard to get empirical parameters. In particular, though K has been thought as an empirical growth coefficient with no explicit biological meaning, it has the tendency to increase with all factors causing "stress" and an increase of oxygen consumption, such as increasing temperatures (Pauly 1980). Similarly, while Z is defined as all mortality from physiological/genetic reasons such as aging, disease, and the competition and predation without fishing, direct reports of Z are scarce and various convenient estimations are used instead (Pauly 1980; He et al. 2001). Second, there have been suggestions that K and Z should be biologically connected in some way (Charnov 1993; Jensen 1996). For example, both K and Z have the same unit of $1/t$ where t is time, both increase with stress and temperature, and empirical studies often found stable linear correlations between them (Jensen 1996; Charnov 1991). This induces a possibility of further simplifying eq. (2.1) to facilitate new understanding. But questions on how the simplification should be and what's the mechanism for doing that are still unanswered. Lastly, observed relations between maturity and many other life history traits as mentioned above have not been fully incorporated into and then explained by eq. (2.1).

So, here I ask several questions: (i) can we have a biological meaning for K and Z ? (ii) how should they then be connected by possible mechanism? (iii) what's the new simplified form of eq. (2.1) and its biological significance when K and Z are related? (iv) how would the new form provide a unified explanation to maturity and its multiple correlations with other traits?

In this chapter, a new life history theory is presented that begins with the concept and quantification of fitness, then develops general bio-energetic and mechanistic growth

and mortality models, next establishes their relationship, and finally applies the fitness optimization process to produce a unified bio-energetic function for determining maturity. This function and a deduced constraint are both tested using a large fish dataset. It lastly discusses possible mechanistic interpretations to many maturity-related correlations.

New Theory

Fitness concept and quantification

A common definition of fitness defines it as lifetime mature offspring number for a species at a demographically equilibrium or stable state (Kozłowski 1996; Lande 1982; Charnov 1990; Charnov and Skúladóttir 2000). From a bio-energetic perspective, it means that, over its life-span, an individual should transfer as much reproductive output (fecundity) to next mature generation as possible so that the energy flow within the species will be maximized. In general, fitness can be quantified as the product of fecundity and the survival to a mature state (Roff 1992 and 2007; Roff et al. 2006; Stearns 1992):

$$R_0(t) = f(t) \cdot l(t) \quad (2.2)$$

where $R_0(t)$ is fitness at time t , $f(t)$ is fecundity measured as reproductive output and $l(t)$ is the possibility of the output surviving to maturity. Note that these three terms in eq. (2.2) are all cumulative values because they are related with the fitness of an individual during its entire life-span.

Fecundity is usually proportional to body mass M as $c \cdot M$ (Sopow and Quiring 2004; Barnes and Hughes 1999), where c is a proportionality constant, so fecundity is a function of mass over time (i.e., growth).

Bio-energetic size/mass growth

Living organisms have two contrasting functions for consuming the energy acquired: growth (including reproduction) and maintenance. Growth is a process of using assimilated energy to produce new tissues, including the reproductive tissue. Maintenance is a process of maintaining the viability and effective functioning of whole body, and represents the share of acquired energy that is dissipated irreversibly. Thus, the energy budget of a living organism at time t can be generally quantified as (modified from West et al. 2001):

$$B = C + \frac{dM}{dt} \cdot E_m \quad (2.3)$$

where B is the energy income, M is body mass, C is the corresponding maintenance cost rate, $\frac{dM}{dt}$ is the new mass production rate, and E_m is the energy required to produce one unit mass and is usually constant for a species (West et al. 2001).

If B and C vary very little with time, eq. (2.3) becomes a traditional exponential growth equation, denoting that early growth follows an exponential trajectory (Karkach 2006). However, actual rates of these parameters can vary with time, making general sigmoidal curves more appropriate for describing growth. The VBGF is such a curve and has been widely used as one of the best in describing the whole body growth process (Chen et al. 1992). VBGF assumes that energy income rate (also “anabolism”) is proportional to mass raised to certain power and maintenance cost (also “catabolism”) is linearly proportional to mass (von Bertalanffy 1938; Banavar et al. 2002; also see Chapter 1), as follows:

$$\begin{cases} B = B_0 \cdot M^\alpha \\ C = C_m \cdot M \end{cases} \quad (2.4)$$

where B_0 is the initial energy income rate per mass^(1- α), α is a power parameter that is less than 1, meaning a declining energy income per mass, and C_m is a proportional constant that represents the maintenance cost per mass.

Taking eq. (2.4) into eq. (2.3), a general von Bertalanffy growth equation can be expressed as:

$$\frac{dM}{dt} = \frac{B_0}{E_m} \cdot M^\alpha - \frac{C_m}{E_m} \cdot M \quad (2.5)$$

where $\frac{C_m}{E_m}$ is the maintenance cost(energy dissipating rate) C_m per mass standardized by the energy contained within that mass, E_m .

The integrative form of eq. (2.5) is:

$$1 - \left(\frac{M}{M_{\max}}\right)^{(1-\alpha)} = e^{-\left(1-\alpha\right) \cdot \frac{C_m}{E_m} \cdot t} \quad (2.6)$$

where $M_{\max}$ represents the maximum body size when $\frac{dM}{dt} = 0$.

Eq. (2.6) is a typical VBGF, with the term $(1-\alpha) \cdot \frac{C_m}{E_m}$ being VBGF growth coefficient K .

It can be deduced from eqs. (2.4) and (2.5) that:

$$\left(\frac{M}{M_{\max}}\right)^{(1-\alpha)} = \frac{C}{B} \quad (2.7)$$

where $\frac{C}{B}$ represents the relative proportion of energy income that is used for maintenance.

Eq. (2.6) is used for fecundity quantification in eq. (2.2).

Bio-energetic survivorship

Because a standardized maintenance cost $\frac{C_m}{E_m}$ is an instantaneous rate equivalent to the relative energy dissipating rate for any bio-energetic process within living cells or tissues, it is assumed here that the standardized energy dissipation rate $\frac{C_m}{E_m}$ is also the bio-energetic instantaneous mortality rate for an individual. This pure energetic definition of survival is derived from the perspective of energy production and its sustainability, and can reflect the more general underlying origin of natural mortality Z .

So, similar to a method in population ecology for determining cumulative survival rate from instant mortality rate (Roff 2007), the cumulative survival rate of reproduction energy output can be quantified as following:

$$l(t) = e^{-\frac{C_m}{E_m} \cdot t} \quad (2.8)$$

This cumulative survival rate means that the reproductive output itself also has a maintenance cost or mortality rate until the next generation matures.

Fitness optimization

Substituting eqs. (2.6) and (2.8) into eq. (2.2), the optimization of equation (2.2) for fitness maximization is realized when:

$$B = 2C \quad (2.9)$$

The implication of eq. (2.9) is that when net energy income rate $\frac{dM}{dt} \cdot E_m$ ($= B - C$) equals to energy maintenance cost (or “mortality rate” in analog sense) C , the lifetime reproductive energy output to next generation of mature individuals should be maximized and reproduction should ensue at this time. Before this moment, growth is more energy-efficient because the net energy income per mass is larger than the possible maintenance cost of that mass; after this moment, reproduction, and then death, is more energy efficient because otherwise the possible maintenance cost would be larger than the net energy income itself. Therefore, a new physiologically-based bio-energetic definition of maturity is advanced here.

Also, a new rule is realized by substituting eqs. (2.9) and (2.7) into eq. (2.6):

$$(1 - \alpha) \cdot \frac{C_m}{E_m} \cdot t_r = \ln 2 \quad (2.10)$$

where t_r is the time point when maximum fitness is achieved, which also defines the optimal age at first reproduction.

Because $(1 - \alpha) \cdot \frac{C_m}{E_m}$ is the VBGF coefficient K , $t_r = \frac{1}{K} \cdot \ln 2$ occurs (from eq. (2.10)), which can be tested using real data if K and t_r are both available for the same species or population.

Table 2-1. Summary of parameters.

Parameters	Description	Units
L_{inf}	Asymptotic body length	m
L_r	Length at first reproduction	m
t_r	Age at first reproduction	year
K	VBGF growth coefficient	year ⁻¹
Z	Natural mortality (instant)	year ⁻¹
t	Age	year
$R_o(t)$	Fitness at age t	number
$f(t)$	Fecundity at age t	number
$l(t)$	Survival rate at age t	Unitless
M	Body mass or size at age t	kg
c	Proportional constant	$1 \cdot \text{kg}^{-1}$
B	Energy income rate	$\text{J} \cdot \text{s}^{-1}$
C	Maintenance cost	$\text{J} \cdot \text{s}^{-1}$
E_m	Energy for production of per new mass	$\text{J} \cdot \text{kg}^{-1}$
B_0	Energy income per mass at time zero	$\text{J} \cdot \text{kg}^{-(1-\alpha)} \cdot \text{s}^{-1}$
α	Power parameter	Unitless
C_m	Maintenance cost per mass	$\text{J} \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$
M_{max}	Maximum body size	kg

Methods

Application to fish

For fish, $L = b \cdot M^\beta$, where β is a power parameter, L is body length, and b is a proportional constant. At the time of maturity, since $\frac{C}{B} = 0.5$, eq. (2.7) can be written for fish as:

$$\frac{L_r}{L_{inf}} = 0.5^{\frac{\beta}{(1-\alpha)}} \quad (2.11)$$

Empirical studies showed that $(1 - \alpha)$ and β both vary within the similar narrow range of 1/3 to 1/4 (Enquist et al. 1999; Essington et al. 2001, Roff et al. 2006 and 2007; Lester et al. 2004). Assuming a value of 1/3 for all fish (He et al. 2008; Kalaycı et al. 2007):

$$\frac{L_r}{L_{\text{inf}}} = 0.5 \quad (2.12)$$

Fish dataset

Abundant life-history data are available for many fish species, especially for commercially important ones. Fish data are usually fitted with the VBGF, and the critical parameter-VBGF coefficient K is reported together with other life history data (Essington et al. 2001). He et al. (2001) collected such a comprehensive data set, including VBGF coefficient K , t_r , L_r , and L_{inf} , for 215 fish species from published studies; this data set was used to test the new theory.

Data analysis

The R package "smatr" for reduced major axis (RMA) was used for estimating the relationship between t_r and K , because it is appropriate when variance in dependent and independent variables are similar and the goal is the regression slope (Warne and Charnov 2008; O'Connor et al. 2007), as was the case here. Because maximum or asymptotic size is more precisely measured when compared to size at first reproduction, OLS was used for regression between length at first reproduction and maximum length.

Data points with $K > 1.0$ were not used (7 data points excluded in total) because the theory confines relative maintenance cost to be less than 1 and very high mortality rate as represented by K might not be due to physiological mortality defined above, and

only female data points were used as males and females are following different evolutionary routes (Roff 1992). After analyzing the available data with these constraints, it was determined that 78 points were available for testing the correlation between K and t_r , and 85 points were available for length correlation analysis.

Results

1 The relationship between L_r and L_{inf}

A statistically significant strong correlation between L_r and L_{inf} was found with a R^2 of 0.75 (Figure 2-1 and Table 2-2). The fitted slope of 0.49 was very close to the predicted one of 0.5, and its 95% confidence interval (CI) of 0.43 to 0.56 includes 0.5, indicating that eq. (2.12) can produce a good estimate of L_r if L_{inf} is reliably measured. However, the positive intercept for the fitted line is not zero, indicating a possible “nugget effect” that might cause the proposed model to underestimate actual L_r .

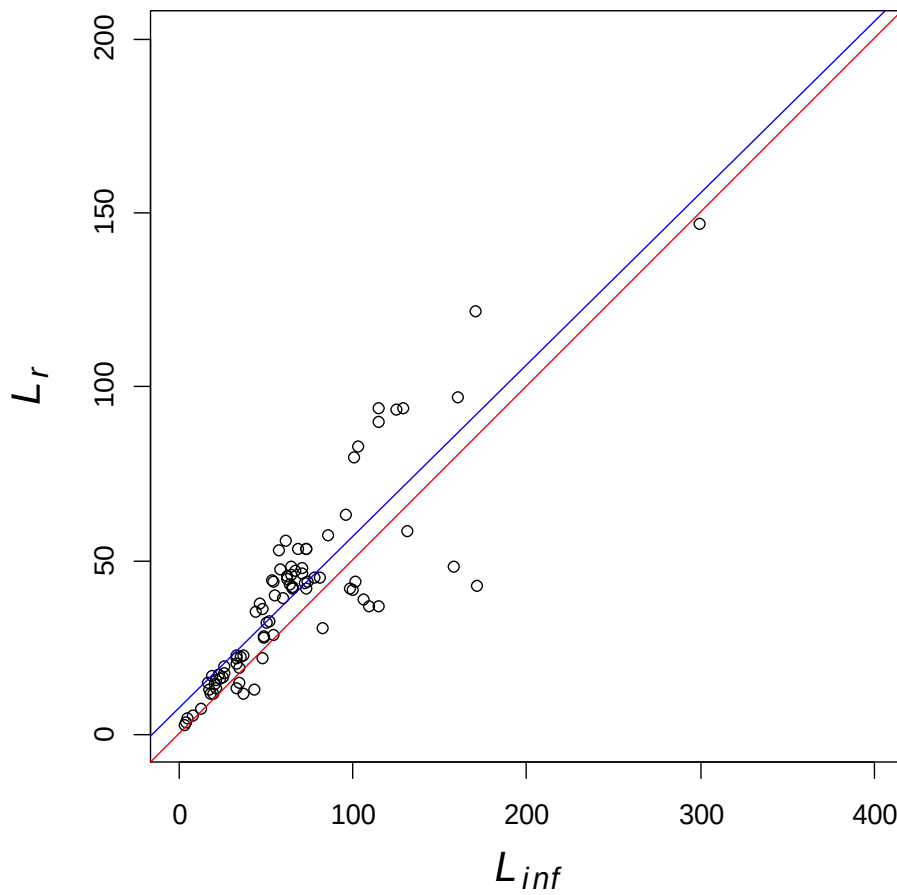


Figure 2-1. The relationship between L_r and L_{inf} . L_r : length at first reproduction, L_{inf} : maximum length. $n=85$, females only. Red line is the theoretical line with a slope of 0.5 and zero intercept, blue line is the fitted line with parameters in Table 2-2. Data is from He et al. (2001).

Table 2-2. Parameter values for Figure 2-1. R^2 is Pearson's correlation coefficient.

	Predicted coefficients	Fitted coefficients*	R^2
intercept	0	7.42 (2.45,12.38)	0.75
slope	0.50	0.49 (0.43,0.56)	

*number in parenthesis is the 95% lower and upper confidence limit, respectively.

2 The relationship between t_r and K

The regression between t_r and K showed support for eq. (2.10), with a R^2 of 0.70 (Figure 2-2 and Table 2-3). The actual fitted slope of -1.06 (95% CI is -0.93 to -1.20) was not different from the expected -1. More importantly, the predicted intercept of 0.69 ($= \ln 2$) was included in the back-transformed 95% CI ($0.66=10^{-0.18}$, $1.10=10^{0.04}$) of the fitted intercept. However, the most likely value for the intercept (the mean) was 0.85, which means that the theoretical value is at the lower bound of actual values (see discussion).

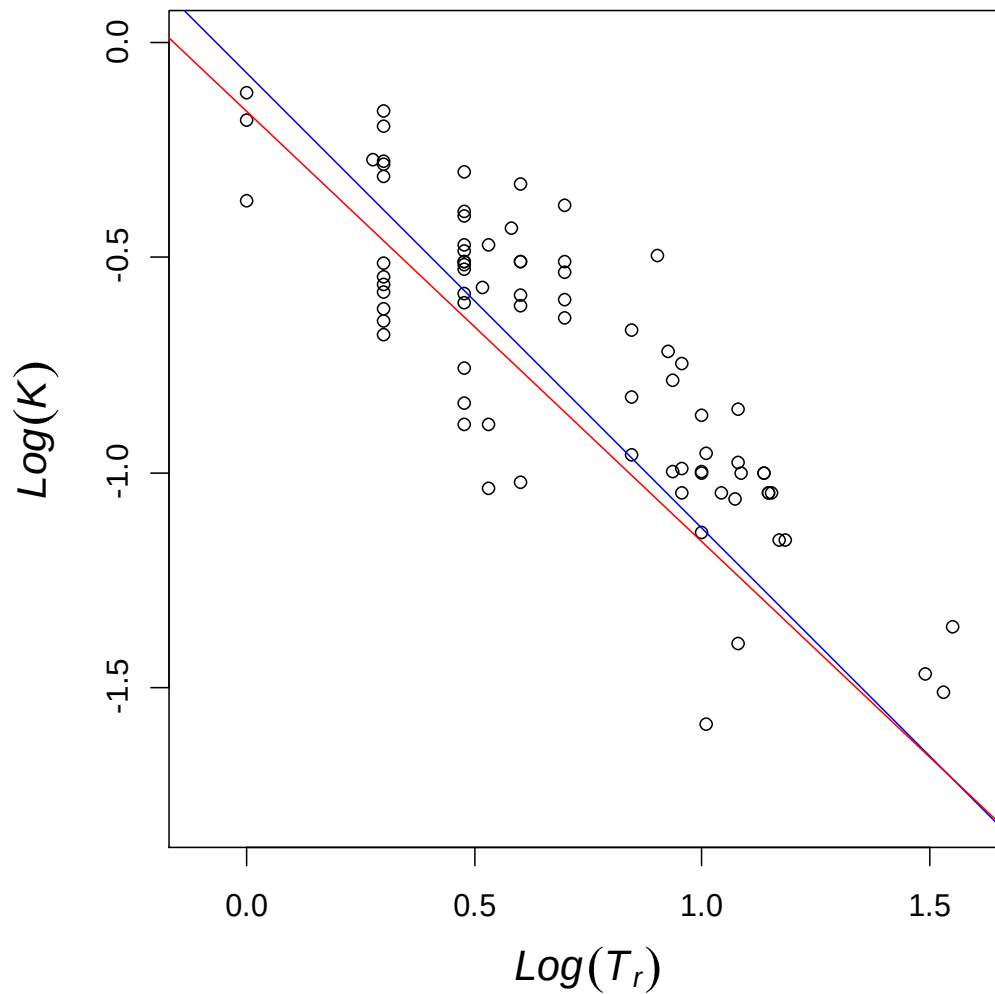


Figure 2-2. Relationship between $\log(K)$ and $\log(T_r)$. K is the von Bertalanffy growth coefficient. T_r (annotated as t_r in the text) is age at first reproduction, $n=78$ (sample size), females only. The red line is the predicted line with slope of -1 and intercept of -0.16(which equals to $\log(\ln 2)$), and the blue line is the fitted line with parameters in Table 2-3. Data from He et al. (2001).

Table 2-3. Parameter values for Figure 2-2. The parameters are from the RMA procedure.

	Predicted coefficients	Fitted coefficients*	R^2
Intercept	-0.16	-0.07 (-0.18, 0.04)	0.70
slope	-1	-1.06 (-0.93,-1.20)	

*number in parenthesis is the 95% lower and upper confidence limit, respectively.

Discussion

The theory described here provides a new framework that unifies previous empirical and theoretical understanding of maturity and the maturity-related life history rules. It thus may greatly advance our understanding of the evolution of maturity.

Table 2-4. Comparisons between the new theory and the existing rules*. Each is discussed, in turn, below.

names of new rules	new life history theory	current rules and the reference	
1 Natural mortality is standardized bio-energetic maintenance cost	$Z = \frac{C_m}{E_m}$	$Z / K = c_1$	second Beverton and Holt invariant (Beverton and Holt 1959).
2 Energy equilibrium at maturity	$B = 2C$ at maturity	None	
3 Length at maturity and asymptotic length	$L_r = \frac{1}{2} \cdot L_{\text{inf}}$	$L_r / L_{\text{inf}} = c_2$	third Beverton and Holt invariant (Beverton and Holt 1959).
4 Metabolic rate and body size	$BMR = \frac{1}{2} \cdot B_0 \cdot M^\alpha$, for mature individuals only.	$BMR \propto M^{\frac{3}{4}}$	Kleiber's law (West et al. 2001)
5 RE	$RE \propto BMR$	$RE \propto M^{\frac{3}{4}}$	Charnov et al. 2001b; Charnov 2001a
6 Life history invariant at maturity	$(1 - \alpha) \cdot \frac{C_m}{E_m} \cdot t_r = \ln 2$	$Z \cdot t_r = c_3$	first Beverton and Holt invariant (Beverton and Holt 1959; Charnov 1991b, 1993 and 2001b)).

* RE is reproductive effort, which is defined as the reproductive energy (or mass) devoted to reproduction, c_1 , c_2 and c_3 are undefined constants that are specific for certain populations, and other symbols and parameters are as mentioned in the text.

1 Natural mortality is standardized bio-energetic maintenance cost

Fecundity and natural mortality are two interconnected themes of living organisms, which are inextricably linked to fitness measures. Fecundity is usually proportional to mass which is easy to measure and describe (Roff 2007). As Einstein noted (Einstein 1935), mass and energy are essentially the same, so the VBGF, a widely used growth equation, can be easily combined with the first principle of energy conservation (eq. (2.3)) to have a bio-energetic mechanism for it, as presented here. Natural mortality, on the other hand, is previously viewed as an important empirical parameter, though it has some kind of intrinsic target range or value (Hewitt and Hoenig 2005). The present study provides a new definition for natural mortality: the standardized maintenance cost of energy. This new definition can be considered as an inherent energetic characteristic. This same energy depreciation rate is also explicitly present in the growth process, defining a factor limiting growth rate. It is then suggested that the finest level maintenance cost probably occurs intrinsically at cellular and tissue level, but it has an individual-level consequence: it may also determine an individual or population's natural mortality Z .

These new definitions simplify life history modeling and produced important life history constraints that can be validated by real data, as shown above. Therefore, $\frac{C_m}{E_m}$ might be a better proxy of Z than traditional population mortality rate. From $K = (1 - \alpha) \cdot \frac{C_m}{E_m}$ it is obvious that $K = (1 - \alpha) \cdot Z$. This may provide a mechanistic reason for the previously-viewed coincidence that Z has the same dimension of 1/time as

K and also for the “second Beverton and Holt invariant” which states a statistical relationship between Z and K (Beverton and Holt, 1959; Charnov, 2008).

2 Energy equilibrium at maturity and its significance

The new theory suggested that maturity means a special energetic relationship quantified by eq. (2.9), which leads to three important consequences:

2.1 maturity length is half of asymptotic body length

Measured maturity length is half of asymptotic body length just as predicted (Figure 2-1 and Table 2-2). However, there was a “nugget effect”, which represents a non-zero intercept value. This might be that one very large maximum length (L_{inf}) value of over 300 (cm) weighed too much. Excluding this value reduced the intercept to zero, and the slope was still close to 0.5 for fish.

Beverton and Holt (1959) proposed the concept of "third Beverton and Holt invariant" which states that L_r is certain fixed ratio of L_{inf} . This was accepted by Charnov (1993) as one of the life history invariants. Jensen (1996) further provided an explanation to it by assuming that reproduction should occur at the time of maximum mass production rate. However, his explanation is itself based on an assumption that was not validated. In contrast, the life history theory in this chapter deduced a definite evolutionary constraint for length at maturity, and the exact value for the ratio is established as 0.5.

2.2 BMR and M are related by life history evolution

The new relationship in eq. (2.9) means that there is a fixed energy relationship between maintenance cost (C) and energy income (B). Because B is empirically taken by

VBGF to be proportional to body size (M) raised to a power of α (see eq. (2.4)), and C is quantified mainly as BMR for animals, a parameter that measures the energy used to just maintain basic physiological activities (Rønning et al. 2007; Mckechnie and Wolf 2004), there should also be a relationship between BMR and M among species in the form of $BMR = \frac{1}{2} \cdot B_0 \cdot M^\alpha$.

The exact value of this power parameter α may vary, but two widely used VBGF has the following forms: $\frac{dm}{dt} = a_1 \cdot m^{\frac{2}{3}} - b_1 \cdot m$ and $\frac{dm}{dt} = a_2 \cdot m^{\frac{3}{4}} - b_2 \cdot m$, where a_1, b_1, a_2 and b_2 are proportional coefficients. Therefore, $2/3$ and $3/4$ are two possible values of α . Previous studies found that BMR and M really has a power relationship with power parameter ranging in $2/3$, $3/4$ or values between and around them (O'Connor et al. 2007; White et al. 2003).

Specifically, because $\alpha = \frac{3}{4}$ is a convenient average of possible values (Glazier 2005; Dodds et al. 2001), this special form of relation, $BMR \propto M^{\frac{3}{4}}$, is called Kleiber's law (West et al. 2001). This law is deemed by some scientists as universal and attracted many recent research interests (Kozłowski and Weiner 1997; West et al. 1997; Beuchat 1997; Enquist et al. 1999). The new relationship shown above suggests that Kleiber's law is only the average case for a diverse situation, and its validity lies in life history constraints that are reflected in the form and validity of VBGF. So these two quite general biological patterns are actually from the same origin (see Chapter 1 for further study).

2.3 Reproductive effort (*RE*) is proportional to *BMR*

If the net growth energy is to be distributed all (determinant growth) or proportionally (indeterminate growth) to reproduction at maturity, reproductive effort (*RE*) would be proportional to net growth energy that is equal to maintenance cost for mature individuals. As maintenance cost is *BMR* in animals, which itself proportional to *M* raised to certain powers such as 2/3 or 3/4, *RE* would also be connected with *M* raised to a power. The new theory hence defines mechanistic relationships among *RE* , *BMR*

and *M*. Charnov et al. found that *RE* is proportional to $M^{\frac{3}{4}}$ for mammals(Charnov et al. 2001; Charnov and Ernest 2006; Charnov 1993), which supports this new relation for *RE*.

3 Life history invariant at maturity rule may define a fast-slow life history spectrum

The energy equilibrium status at maturity combined with universal growth equation (2.6) further defines a new life history invariant rule, which is eq. (2.10). This expected relationship between t_r and *K* in eq. (2.10) was supported by fish data (Figure 2-2 and Table 2-3), supposing a universal constraint that relates maturation with the pace of life for animals.

Further, if $\alpha = 2/3$ in many cases (Glazier 2007), then $\frac{C_m}{E_m} \cdot t_r = 2.08$. Because

$\frac{C_m}{E_m}$ is also defined as mortality, there is a chance to experimentally test this relation.

Two studies showed the product of mortality and age at first production t_r to be 2.1 for parasitic nematodes and Pandalid shrimp (Charnov 2001) and 2.2 for some other groups (Charnov 1991). This relationship between mortality and age at first reproduction was also empirically recorded as “the first Beverton and Holt invariant” (Beverton and Holt

1959; Charnov 1991, 1993 and 2001). However, since they did not establish the value of the product and a mechanism as in eq. (2.10)., the “invariant”, up to this point, is only an empirical observation.

Eq. (2.10) also defines a possible "fast-slow life history continuum" through relationships between maturity and many other aspects of life. For example, larger t_r or smaller $\frac{C_m}{E_m}$ means later age at first reproduction and/or longer life-span, lower mortality rate, lower *BMR* (a slower life pace because any fast-pace physiological activity would require higher metabolic rate), and relatively lower *RE* per mass ($\propto M^{-(\alpha-1)}$), while smaller t_r or larger $\frac{C_m}{E_m}$ represents a faster life pace and other corresponding life history syndrome. This "fast-slow life history spectrum" was empirically observed (Bronikowski and Arnold 1999; Wiersma et al. 2007a). For example, it has been shown that tropical birds have later maturation, slower growth and metabolic rates, lower fecundity and higher adult survival rates than their temperate counterparts (Wiersma et al. 2007), while shorter / smaller species of fish have earlier maturation, faster growth and metabolism, higher fecundity and lower adult survival rate than longer ones (Roff 2007).

It is also worth discussing that the predicted value of 0.69 was not very close to the mean of 0.85 from real data (Figure 2-2 and Table 2-3). This means that the actual product of t_r and K is higher than predicted, and then either t_r or K or both tend to be measured higher. This is possible due to several reasons. First, the detection probability for capturing a first reproduction is pretty less than 1, and later detection is more likely to result in an increased age at first reproduction. Second, the estimation of K is negatively related with asymptotic size (Munro 1982), while asymptotic size is estimated by

maximum size when growth rate equals to zero under quite ideal natural conditions (Stamps et al. 1998; Hopkins 1992; Jennings et al. 1999). However, this maximum size when using observed maximum value will be a minimum possible asymptotic value due to detection problem and growth retardation from mostly inevitable environmental stresses and reproduction, leading to a underestimation of asymptotic size and overestimation of K . Therefore, the expected product value 0.69 of t_r and K should be a lower bound of the one in real world. This might explain the difference between 0.85 of real data and the expected 0.69.

Conclusion

In summary, the new theory suggests that a standardized bio-energetic maintenance cost is equivalent to the natural mortality rate Z , and the VBGF growth coefficient K equals to $(1-\alpha) \cdot Z$, where α is a power parameter connecting energy income rate with body mass. Therefore, eq. (2.1) can be simplified into interchangeable eqs. (2.9) or (2.10). These new equations are universal bio-energetic and evolutionary constraints. They contain a physiological and bio-energetic determination of maturity in eq. (2.9), and a eq. (2.10) that can further help explain most observed life history associations between maturity and other traits. In this way, previously empirical life history rules were explained with coherent and consistent mechanisms.

It is striking that Z is a key parameter identifying a species' characteristics and life history. This parameter encapsulates concepts from growth and energy metabolism to reproduction and evolution, and can be used to explain why growth, energy metabolism, reproduction and life history are all closely associated with each other to produce diverse life history syndromes or niches among a vast continuum of biological taxa. The work

presented here could be a demonstrated research approach that starts from macro-level phenomena, such as life history diversity, to arrive at micro level mechanisms, such as cell metabolism dynamics.

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CHAPTER 3. A NEW EVOLUTIONARY LIFE HISTORY THEORY FOR LEAVES CAN EXPLAIN THE VARIANCE OF LEAF PHOTOSYNTHETIC RATES AND CORRELATION WITH LEAF TRAITS

Abstract

The fundamental physiological processes in leaves involve two opposing functions: energy production by photosynthesis and energy dissipation from leaf maintenance costs such as dark respiration, mass investment, and protein turnover. Here, a mechanistic understanding of how these two functions of a leaf are optimized to have maximum energy output over its lifespan can advance our knowledge of plant ecology and evolution is provided. Specifically, the new theory predicts that the maximum energy output over a leaf's lifespan is achieved when there is an energetic equilibrium between net photosynthetic rate and leaf maintenance cost for mature leaves. Leaf trait data for C3 species from the Global Plant Trait Network (GLOPNET) are used to test this prediction. The result showed that 87% (mass-based) and 58% (area-based) of inter-specific variation in leaf photosynthetic rates can be explained by the predicted relationship. Further analyses on sub-groups of species suggest a leaf life history continuum that runs from “nitrogen-driven fast photosynthesis” type to “carbon-driven slow photosynthesis” type. The results also indicated that climate moderately affects the predicted relationships.

Introduction

Leaves are the most evolutionarily conserved functional units of life for diverse plant species that span eleven orders of magnitude in size (Niklas and Enquist 2001). In

particular, leaves undertake the fundamental processes of leaf energy metabolism (photosynthesis and respiration), gas and water vapor exchange between plants and environment, and material storage of nutrients, water and food for plants(though there are a few plants which have lost their capacity for photosynthesis and persist in mutualistic relationships with other plants, e.g., *Epifagus virginiana*). So, while plants are very different in appearance, their leaf is a proxy of the plant in many critical functional aspects, and there are theories that view the plant as tube or pipe bundles that begin from the root and end in the leaves where various energetic, hydraulic and nutritional processes are undertaken and/or modulated (the "pipe model"; see Shinozaki et al. 1964a and 1964b and Waring et al. 1982).

Leaves are also the basic compositional units of a plant species. For example, flowers and fruits are transformed leaves from a phylogenic perspective (Eames 1961), and other parts of plants such as stems, roots and branches are extended tissues of leaves for the function of mechanical support, water and nutrient exchange, and energy storage (Evert and Eichhorn 2004).

A leaf has its own life history that may be different than that of the whole plant: it grows as described by various sigmoidal growth equations, then reaches a stage where its size and form are stabilized and fixed (i.e., it exhibits determinate growth), and finally dies after a functioning period of photosynthesis (A), which captures light energy through carbon dioxide, oxygen and water vapor exchanges between cells and atmosphere, to finish what is called a leaf life-span (LL) (Groot and Meicenheimer 2000). The carbon energy a leaf harvested from photosynthesis has a maintenance cost that includes respiration (R), leaf structural mass investment per area (LMA), and leaf nitrogen (N)

related maintenance cost as N is critical to important photosynthetic proteins such as Rubiscos that are central in most metabolic processes within plant tissues (Wright et al. 2004; Atkin and Tjoelker 2003; Westoby et al. 2002). But these life history traits of leaves still represent important whole plant characteristics, indicating that the leaf is in certain extent a proxy of plants. For example, thin leaves with high photosynthetic rate are more easily decomposable, compared to thick leaves (Santiago 2007). Photosynthetic rate, LMA , R , and N were found to be positively correlated with RGR ($R = 0.90$), which is negatively correlated ($R = -0.9$) with LL (Reich et al. 1998a and 1998b; Poorter and Garnier 1999; Niinemets 2001; Poorter and Bongers 2006).

Life history traits of leaves are tightly correlated with each other. For example, R is critical to net assimilation rates of carbon dioxide (Hagihara and Hozumi 1991; Sprugel et al. 1995), a high LMA is usually related with longer LL , lower N and lower A (Wright et al. 2002), and A is strongly correlated with SLA , LL , and N (Reich et al. 1997; Shipley et al. 2006). When these leaf trait variation and associations are considered together across the whole plant biota, there is a universal leaf economics spectrum running from leaves with low A , long LL , high LMA , low N , and low R to leaves with opposite traits syndrome (Wright et al. 2004). Therefore, there seems to have universal constraints on bi- and multiple-leaf trait associations. But a mechanistic understanding to what the constraints are, why and how they are evolved for all plant leaves is still lacking (but see Shipley et al. 2006).

This challenge of understanding leaf-level trait variation and associations, as well as the functional and compositional importance of leaves as proxy of plants (Reich 2001), lead to the new idea here that as the plant is often clonal or modular with a population of

leaves with axillary bud and the attendant stem internode (Begon et al. 1996; Vallejo-Marín et al 2010; Herben 1994), selective evolutionary processes may have worked on leaves quite directly so that there should be a life history theory for leaves.

Life history theory is centered at the axiom that natural variation and patterns of traits, such as those related to development, growth, reproduction and mortality, are constrained by evolutionary optimization, which is the maximization of fitness measured as lifetime number of mature offspring. Though this theory has been successfully applied to the animal kingdom to provide a coherent and tractable mechanistic understanding of how individual trait variation and the tightly correlated trait syndrome among species are forged by evolution (Roff 1992; Stearns 1992; Chapter 2), it is suggested that the life history theory for unitary animals can't be directly applied to plants as they are modular (Vuorisalo and Mutikainen 1999; Stearns 1992). Thus, the above new idea also represents a new way for solving this difficulty. However, there has been very little research, to our knowledge, on how a life history theory for leaves should be developed. So the two specific questions are: (1) Can we have an evolutionary life history theory for leaves? (2) How would such a theory explain leaf life history, especially the variance of photosynthesis and correlation with other traits?

In this chapter, the above two questions are answered. First, a new and detailed life history theory for leaves is advanced. Second, this new theory is tested using the Global Plant Trait Network, or GLOPNET, database that contains field measurements of critical leaf traits and the associated climate factors for many species across the globe (Wright et al. 2004). The test results are analyzed and climate effects are also studied.

Finally, there is a discussion on the ecology and evolutionary significance of the new theory.

Theory

Fitness quantification

If a leaf is considered as an evolutionary selection unit like an individual organism, it must survive and reproduce and thus its evolutionary fitness can be described by the lifetime net output of assimilated energy standardized as the potential number of mature offspring (leaves/seeds) it produces. This definition is similar to the one for animals, where the fitness is quantified as the lifetime number of mature individuals (Roff 1992 and 2007; Stearns 1992). Under this definition, the fitness of a leaf can be quantified as the product of leaf fecundity and its survivorship to the leaf maturation stage, when the maximum fitness of a leaf is achieved and it's then optimal to transfer the net assimilated energy from its own growth to next generation in the form of assimilated energy:

$$R_0(t) = f(t) \cdot l(t) \quad (3.1)$$

where $R_0(t)$ is the leaf fitness, $f(t)$ is leaf fecundity measured as net output of assimilated energy and $l(t)$ is its possibility of surviving to maturity. Note that these three terms in eq. (3.1) are all cumulative values because they are related with the fitness of a leaf over its entire life-span (i.e., t is the time since the leaf bud breaks).

Net output of assimilated energy is proportional to leaf mass

Studies have demonstrated that $f(t)$ is usually proportional to mass (M) (Sopow and Quiring 1998; Barnes and Hughes 1999). Hence, there should be a descriptive function to model leaf mass variation with time, that is, a leaf growth function. Since leaf function is mainly quantified in energy terms, the leaf growth equation is to be modeled as a bio-energetic equation incorporating the dynamics of energetic traits such as photosynthesis, respiration, and other maintenance energy costs. Photosynthesis is the energy income-generating process of a leaf, and there are two contrasting channels for consuming this generated carbon energy: growth and maintenance. Growth uses energy and materials to produce new tissues and organs and maintenance maintains the viability and effective functioning of existing leaf tissues. In particular, the maintenance cost represents the assimilated energy that is dissipated irreversibly in the form of degradation or death of certain living cell parts or whole cells. Thus, the energy budget of a leaf at time t can be modeled as following (modified from West et al. 2001):

$$B = C + \frac{dM}{dt} \cdot E_m \quad (3.2)$$

where B is the assimilated energy income of a leaf from photosynthesis, C is the maintenance cost, E_m is the energy required to reproduce one unit leaf mass, and $\frac{dM}{dt}$ is the rate of new leaf mass production.

If B and C vary very little with time, we would have a traditional exponential growth equation. Studies have shown that early leaf growth usually follows an exponential trajectory (Groot and Meicenheimer 2000; Lamoreaux et al. 1978). However, overall leaf photosynthetic rate B shows a declination with time (Kitajima et al. 2002;

Kikuzawa and Ackerly 1999). Since leaves are determinate growers, general logistic functions, such as the von Bertalanffy growth function (VBGF), are appropriate in describing the mass growth process of leaves (Jackson 1984; Yin et al. 2003; Karadavut et al. 2010; Kirby 1988; Dennett et al. 1978).

The VBGF assumes that energy income rate (also “anabolism”) is proportional to mass raised to certain power, and maintenance cost (also “catabolism”) is linearly proportional to mass (von Bertalanffy 1938; also see Chapter 1). In terms of a leaf, these assumptions can be written as:

$$\begin{cases} B = B_0 \cdot M^\alpha \\ C = C_m \cdot M \end{cases} \quad (3.3)$$

where B_0 is the initial photosynthetic rate at time 0, M is leaf mass, α is a power parameter that typically varies between 2/3 and 3/4 (Banavar 2002; Dodds et al. 2001; O'Connor et al. 2007), and C_m is the maintenance cost per leaf mass, usually a constant for a specific-taxa (West et al. 2001).

Taking eq. (3.3) into eq. (3.2), a general VBGF is:

$$\frac{dM}{dt} = \frac{B_0}{E_m} \cdot M^\alpha - \frac{C_m}{E_m} \cdot M \quad (3.4)$$

where $\frac{C_m}{E_m}$ is the maintenance cost (energy dissipating rate) per mass standardized by the produced energy per mass.

The integrated form of eq. (3.4) is:

$$1 - \left(\frac{M}{M_{\max}} \right)^{(1-\alpha)} = e^{-\frac{C_m}{E_m} \cdot t} \quad (3.5)$$

where $M_{\max}$ represents the maximum leaf size when $\frac{dM}{dt} = 0$, and it can be deduced

that $(\frac{M}{M_{\max}})^{(1-\alpha)} = \frac{C}{B}$, where $\frac{C}{B}$ represents the relative proportion of leaf

photosynthesis that is used for maintenance.

Eq. (3.5) is a general bio-energetic mass growth equation (but still a VBGF) for leaves, and is used for fecundity quantification.

Survivorship of net energy output to maturity

The survivorship of the net output of assimilated energy to next mature generation can also be defined in energetic terms just as $(f(t))$ was (eq. (3.5), above). From eq. (3.4),

any mass production process should have a standardized maintenance cost $\frac{C_m}{E_m}$, which is

the instantaneous energy dissipating rate relative to the produced energy, just like mortality rate for individuals. So the cumulative survival rate of net output can be quantified analogous to a method in population ecology for determining cumulative survival rate from instantaneous mortality rate:

$$l(t) = e^{-\frac{C_m}{E_m} \cdot t} \quad (3.6)$$

where $l(t)$ is the cumulative survival rate of net output of assimilated energy to a certain time t in a leaf's life-span.

Fitness optimization for leaves

Taking eqs. (3.5) and (3.6) into eq. (3.1), the optimization of equation (3.1), which means the maximization of leaf fitness, is achieved when:

$$B = 2C \quad (3.7)$$

The implication of eq. (3.7) is that when net energy income rate $(B-C) = \frac{dM}{dt} \cdot E_m$ (i.e. the growth rate of mass) equals to the energy dissipating rate, (i.e., the maintenance cost rate of mass), the lifetime net leaf energy output to next mature generation should be maximized, and a leaf should at this time stop its own growth (thus determinant growth) and transport all available energy to produce new leaves or flowers and seeds. Thus, an evolutionary definition of leaf maturity in terms of bio-energetics is clearly specified by eq. (3.7). This equation can be tested with life history trait data from mature leaves.

Data and methods

GLOPNET dataset

Measurements of five critical leaf traits- LMA , LL , A_{mass} or A_{area} , and R_{dmass} or R_{darea} , N_{mass} or N_{area} were reported in the Global Plant Trait Network (GLOPNET) dataset, which includes 2,548 species from 219 families, representing 175 sites distributed from the arctic to the tropics (Wright et al. 2004). 196 species had all five traits measured, but 10 of them were C4 plants, i.e., do not use C3 carbon fixation as their metabolic pathway for carbon fixation in photosynthesis. Given the small sample size available for C4 plants and their very different photosynthetic physiology, only 186 species of C3 plants were used as the total sample frame for this study. Information on growth form, habitat type and climate for each species was given in GLOPNET as well. Three sets of sub-grouping were used to examine the predicted relationship of eq. (3.7) in them: (1): grass/herbs vs shrub/trees, (2): evergreens vs non-evergreens, and (3):

temperate forest vs woodland species. Only seven species from the tropical rain forest ecosystems were available, so data from this category were not analyzed as a sub-group separately.

Analytical Methods

A mechanistic model was developed to analyze the data in terms of the presented theory (Figure 3-1). Leaf energy influx was partitioned into two parts: the “working” part B for growth and the “lost” part C for maintenance. While B can be well quantified by photosynthetic rate (red arrow, Figure 3-1), the maintenance energy C was not available for direct measurement, so it had to be represented using a conceptual model (blue arrows, Figure 3-1): C is composed of a respiration cost for mobile tissue content (represented by leaf dark respiration rate) and a structural maintenance cost for mobile and immobile tissues. The latter is further decomposed into a lifetime mass investment cost for immobile cell parts (structural carbohydrates) and a replacement cost that compensates for the decay of mobile cell parts or critical live macromolecules, such as DNAs, RNAs and proteins. The lifetime mass investment can be represented by leaf dry mass since the mobile components of a leaf should be either eliminated or negligible in dry status, and this investment should be divided by leaf life-span to become a cost of rate because the immobile leaf dry mass functions over the whole life-span of a leaf. The replacement cost for the decay or turn-over of mobile cell parts was assumed to be proportional to nitrogen content, because nitrogen is the most important element in many mobile cell proteins and other structures (Wright et al. 2004; Loomis 1997).

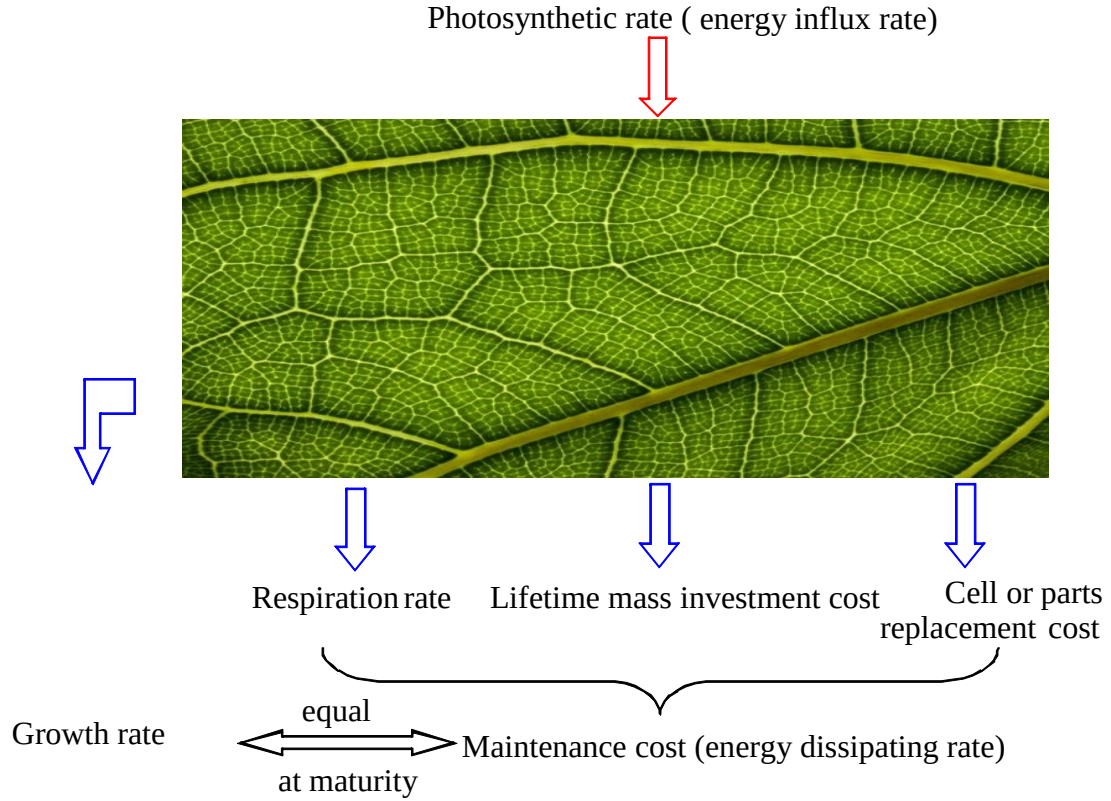


Figure 3-1. An illustrative figure showing how eq. (3.7) is formulated in plant leaves as shown in the text according to energy decomposition principles.

The GLOPNET variables were related to the conceptualization of eq. (3.7) in Figure 3-1, so that the data could be fit to the new model. An area-based bio-energetic relationship from eq. (3.7) is first derived according to Figure 3-1:

$$A_{area} = 2 \cdot R_{darea} + K_a \cdot LMA/LL + b_a \cdot N_{area} \quad (3.8a)$$

where A_{area} is photosynthetic rate per area of leaf, R_{darea} is dark respiration rate per area, LMA/LL represents the lifetime structural mass investment per area (LMA) distributed over entire leaf life-span (LL), N_{area} represents leaf nitrogen content per area, K_a is a parameter for the conversion of each unit structural mass investment into energy

cost, and b_a is a proportional constant representing the replacement cost related to per unit nitrogen content.

By dividing both sides of eq. (3.8a) with LMA , a mass-based equation is:

$$A_{mass} = 2 \cdot R_{dmass} + K_m / LL + b_m \cdot N_{mass} \quad (3.8b)$$

where A_{mass} is the photosynthetic rate per unit leaf mass, R_{dmass} is the dark respiration per unit leaf mass, K_m converts one unit mass of structural mass investment into energy units, N_{mass} represents leaf nitrogen content per mass, and b_m is a proportional constant relating replacement cost with per unit nitrogen content of leaves.

Because leaf nitrogen content is usually correlated with leaf lifespan (Wright et al. 2004; Reich et al. 1998a), two more models that did not include nitrogen content were added to compare with eqs. (3.8a) and (3.8b) to see if simpler models were sufficient:

$$A_{area} = 2 \cdot R_{darea} + K_a \cdot LMA / LL \quad (3.8a-1)$$

$$A_{mass} = 2 \cdot R_{dmass} + K_m / LL \quad (3.8b-1)$$

Model combination with climate factors

Leaf physiology is known to vary with climate as well as from intrinsic differences between species. Therefore, the models needed to account for possible effects from climate. Five key climate factors were available from the GLOPNET data: solar radiance (RAD), potential evapo-transpiration (PET), mean annual temperature (MAT), vapor pressure deficit (VPD), and mean annual precipitation (MAP). To determine which climate variables should be included in the model, generalized linear regression analysis was conducted relating each of the five climate factors to photosynthetic rate (Table 3-1).

Table 3-1. Summary of regression analyses of photosynthetic rate in relation to 5 climate factors.

	R^2	Intercept	<i>RAD</i>	<i>PET</i>	<i>VPD</i>	<i>MAT</i>	<i>MAP</i>
A_{mass}	0.26	489.0 ***	-2.87 ***	-0.002	18.48	4.51*	0.004

Notes: *** $P < 0.00$, ** $P < 0.001$, * $P < 0.01$.

The result suggested that *RAD* and *MAT* were significantly correlated with A_{mass} , so these two climatic variables were added as linear terms to produce new equations (3.8a-2) and (3.8b-2), assuming that climate effects are linear and additive effects and that the distributions of these two climate factors across sites are approximately normal (Wright et al. 2007). Notice that simpler eqs. (3.8a-1) and (3.8b-1) are not used in combination with climate factors, the reasons are presented in the result section.

$$A_{area} = 2 * R_{darea} + K_a \cdot LMA / LL + b_a \cdot N_{area} + K1 * MAT + K2 * RAD \quad (3.8a-2)$$

$$A_{mass} = 2 * R_{dmass} + K_m / LL + b_m \cdot N_{mass} + K3 * MAT + K4 * RAD \quad (3.8b-2)$$

where *K1*, *K2*, *K3* and *K4* are four new proportional constants.

In order to determine if only one of these two climate factors should be incorporated as they are often inter-correlated, two new equations were developed: *MAT* only and *RAD* only, for both area- and mass-based metrics:

$$A_{area} = 2 * R_{darea} + K_a \cdot LMA / LL + b_a \cdot N_{area} + K5 * MAT \quad (3.8a-3)$$

$$A_{mass} = 2 * R_{dmass} + K_m / LL + b_m \cdot N_{mass} + K6 * MAT \quad (3.8b-3)$$

$$A_{area} = 2 * R_{darea} + K_a \cdot LMA / LL + b_a \cdot N_{area} + K7 * RAD \quad (3.8a-4)$$

$$A_{mass} = 2 * R_{dmass} + K_m / LL + b_m \cdot N_{mass} + K8 * RAD \quad (3.8b-4)$$

where *K5*, *K6*, *K7*, and *K8* are four proportional constants.

Statistical analyses

The nls2 package in R (version 2.12.0) was used to estimate the coefficients in the above equations using non-linear, least-squares regression. To further analyze possible patterns of different sub-groups in driving photosynthesis (according to eq. (3.7)), three additional parameters were calculated as ratios relative to photosynthetic rate: (1) $2 \cdot R_{dmass} / A_{mass}$ (dark respiration rate/photosynthetic rate), representing relative respiration cost, (2) $b_m \cdot N_{mass} / A_{mass}$, representing relative replacement cost, and (3) $K_m / (A_{mass} \cdot LL)$, representing relative lifetime structural mass cost (all expressed on mass-base for simplicity). T-tests were used to test for significant differences in these three ratios between the paired plant sub-groups.

Reduced major axis (RMA) regression is used to test the relationship between the predicted and measured values, because variance in dependent and independent variables are similar and the goal is the regression slope (Warne and Charnov 2008; Swenson and Enquist 2008; Wright et al. 2005).

An AIC difference of 4-7 units can indicate distinguishable models, and differences of 10 units or more are considered to indicate a substantial difference (Burnham and Anderson 2002; Rose et al. 2009). So, two models were considered different when their AIC values differed by more than 10. For similar models, the ones with higher R^2 or fewer parameters were selected to observe the principle of parsimony.

Results

1 Best models with and without climate factors and their performance

For models without climate variables (the left side of Table 3-2), eqs. (3.8a) and (3.8b) were better than eqs. (3.8a-1) and (3.8b-1) in terms of lower AIC value and higher R^2 . For models with climate factors incorporated (Table 3-2, right side), eqs. (3.8a-2) and (3.8b-2) had the same R^2 and slightly lower but not significantly different AIC values than eqs. (3.8a-3) and (3.8b-3) respectively, so the latter two were considered better because they have only one climate variable included. Because eq. (3.8b-4) had lower R^2 and significant higher AIC value than eq. (3.8b-3), and eq. (3.8a-4) had lower R^2 and similar AIC values than eq. (3.8a-3), they were viewed as generally worse than eqs. (3.8a-3) and (3.8b-3) in performance and were both excluded from further analysis to keep consistency between area- and mass-based metrics. The four best models (in bold, Table 3-2) were further analyzed (Figure 3-2 and Table 3-3).

Table 3-2. Comparison of models

	3.8a	3.8b	3.8a-1	3.8b-1	3.8a-2	3.8b-2	3.8a-3	3.8b-3	3.8a-4	3.8b-4
R^2	0.58	0.87	0.57	0.84	0.63	0.88	0.63	0.88	0.61	0.87
AIC	1092	1883	1172	1966	1024	1864	1031	1872	1029	1883

For all plant species pooled together, eqs. (3.8a) and (3.8b) both fit the data well, but the area-based eq. (3.8a) with a R^2 value of 0.58 explained 29% less variation than the mass-based eq. (3.8b) with a R^2 value of 0.87 (Figure 3-2 (a) and (c)). The RMA

regression slope from eq. (3.8a) is the predicted 1.00, and the intercept of -0.95 is close to 0 with confidence intervals (CI) of (-2.42, 0.51) including 0. The RMA regression slope of 0.89 from eq. (3.8b) is close but slightly different from 1.00 (CI is from 0.83 to 0.96), and the intercept is close but different from zero (CI is from 0.44 to 16.1), indicating a possible "nugget effect" from the model. The discrepancy of slope from model prediction would be removed if the intercept is set to zero, meaning the slight bias is from non-zero intercept. This was further explored in the study of sub-groups that follows.

The addition of two climate variables in eqs. (3.8a-3) and (3.8b-3) had a small effect on the R^2 values, improving the fit of the models from a R^2 of 0.58 to 0.63 for area-based metrics and 0.87 to 0.88 for mass-based metrics, but it also produced a bias. This bias is reflected in both the higher than zero intercept values of 2.27 and 17.5 and the lower than 1.00 slopes of 0.78 and 0.83, respectively (Table 3-3). Specifically, the predicted photosynthetic rates were overestimated for leaves with smaller photosynthetic rates (less than 100 (mass-based) or 10 (area-based)), indicating a possible overestimation trend at this range. Similarly, area-based eq. (3.8a-3) had a 0.25 less R^2 than mass-based eq. (3.8b-3) (also see Figure 3-2 (b) and (d)). This suggests that though area- and mass-based equations were derived from the same mechanism, area-based metrics seem to be less closely related with leaf energetics and ecology than mass-based ones, which has also been supposed by other studies (Wright et al. 2004; Atkinson et al. 2010). Hence, only mass-based eqs (3.8b) and (3.8b-3) (in bold in Table 3-3) were selected to be applied to sub-groups to further explore their performance.

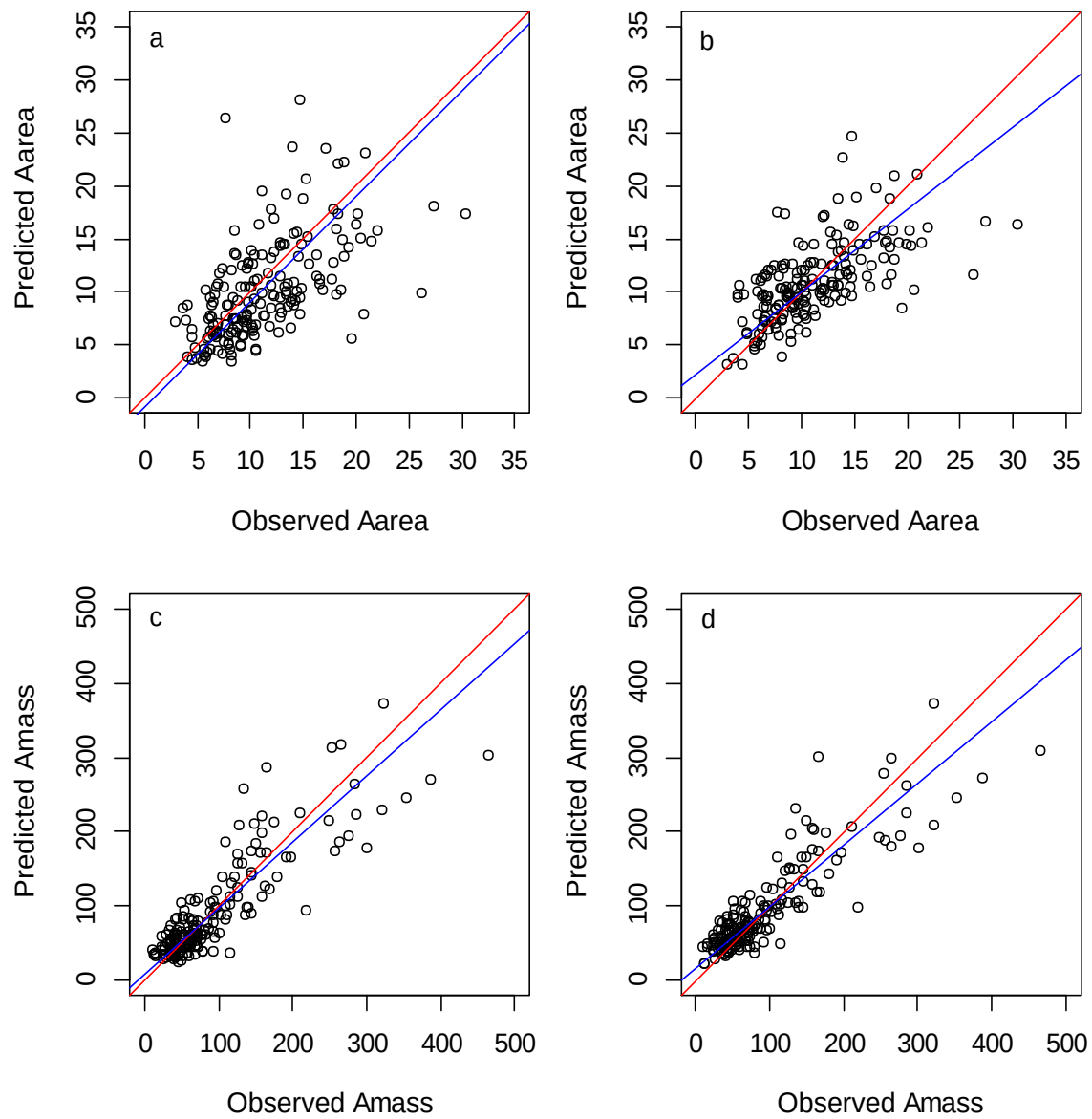


Figure 3-2. Predicted vs. measured A_{mass} for all species pooled together. (a) by eq. (3.8a) . (b) by eq. (3.8a-3). (c) by eq. (3.8b). (d) by eq. (3.8b-3). The red line is the 1:1 line through the origin, the blue line is the RMA regression line between measured and predicted values. All related parameter values are in Table 3-3.

Table 3-3. Parameter values for Figure 3-2.

	K_m	b_m	K5 for b and K6 for d	RMA Intercept	RMA Slope	R^2
a	0.22(0.02) ***	1.83(0.18) ***		-0.95(-2.42,0.51)	1.00 (0.89,1.12)	0.58/0.3 3
b	0.21(0.02) ***	0.47(0.22) *	0.28(0.03)* **	2.27(1.18,3.35))	0.78 (0.69,0.87)	0.63/0.3 9
c	212(19)** *	24.4(2.4)* **		8.26(0.44,16.1))	0.89(0.83,0.96) 6)	0.87/0.7 6
d	238(20)** *	14.8(3.5)* **	1.07(0.29)* **	17.5(10.5,24.5))	0.83(0.78,0.89) 9)	0.88/0.7 7

Notes: $n=186$, R^2 is the correlation coefficient of the regression model / the RMA regression, number in parenthesis is standard error or the 95% lower and upper confidence limit. ***: <0.000 , **: <0.001 , *: <0.05 .

2 Performance of mass-based models in three sub-groups

The comparison of model performance of eq. (3.8b) and (3.8b-3) in three sets of sub-groups is analyzed. For grass/herbs, the slope and intercept from eq. (3.8b) was not different from 1 and 0, respectively, with a R^2 of 0.73, and those from eq. (3.8b-3) had a slope significantly smaller than 1 and an intercept larger than 0 with slightly higher R^2 of 0.75, similarly indicating a biased result from including climate in the model for species with slower photosynthetic rates. For shrub/trees, there are higher R^2 values of 0.88 and 0.89 for eqs. (3.8b) and (3.8b-3), respectively, but the slopes of 0.92 and 0.87 are slightly or significantly different from 1 (CIs is from 0.85 to 0.99 and 0.81 to 0.93, respectively).

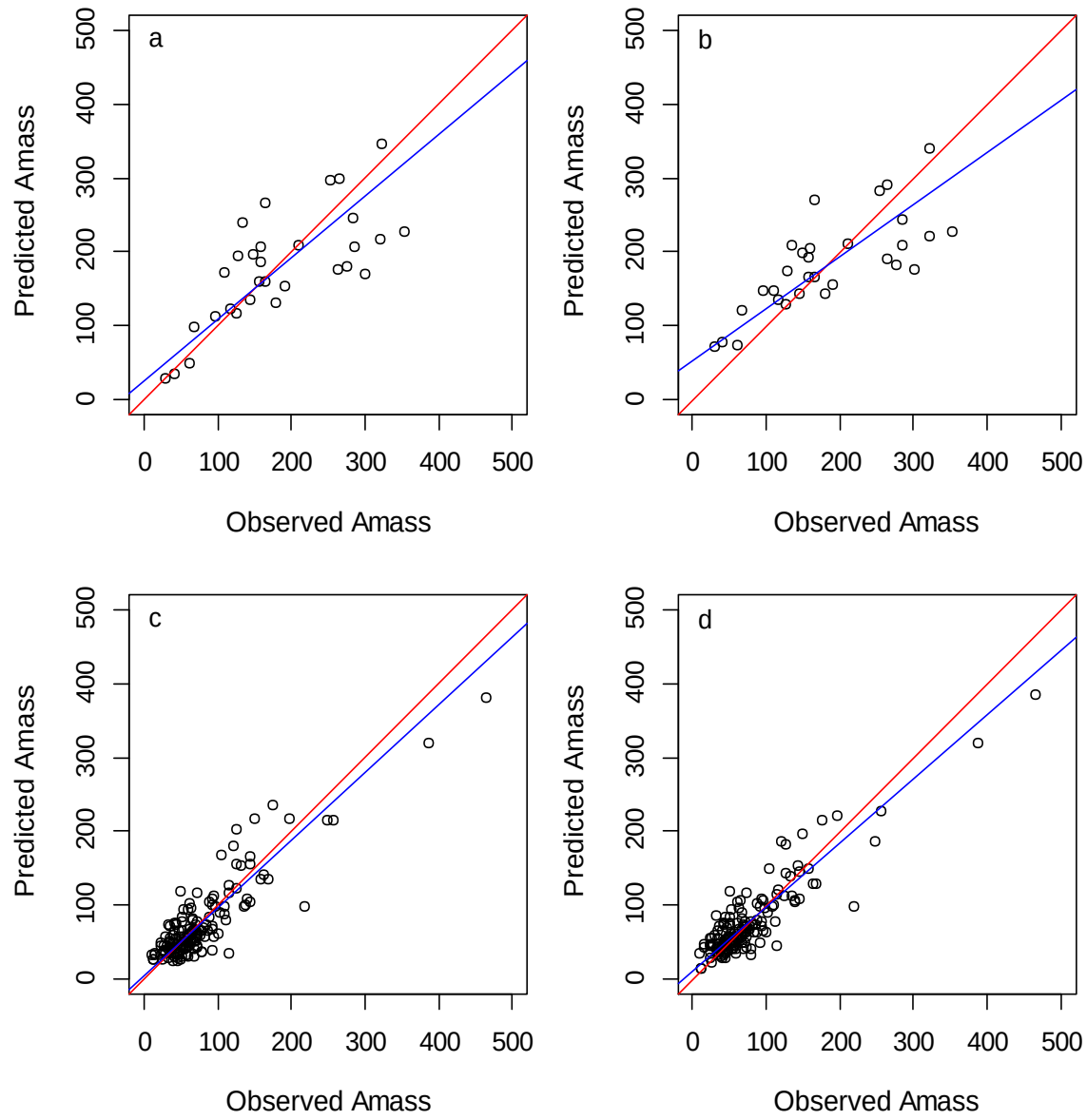


Figure 3-3. Predicted vs. measured A_{mass} for grass/herbs by (a) eq. (3.8b) and (b) eq.(3.8b-3), and shrub/trees by (c) eq. (3.8b) and (d) eq.(3.8b-3). The red line is the 1:1 line through origin, the blue line is the RMA regression line. All related parameter values are in Table 3-4.

Table 3-4. Parameter values for Figure 3-3.

	n	K_m	b_m	K_6	RMA intercept	RMA slope	R^2
a	30	195*** ^a (42)	22.1** ^a (7.8)		24.5 (-21.3,70.2)	0.84 (0.64,1.09)	0.73/0.53
b		196*** (41.0)	15.1* (8.8)	2.68 (1.72)	50.0 (16.6,91.4)	0.71 (0.55,0.91)	
c	156	379*** ^b (33)	15.9*** ^a (2.6)		4.62 (-2.07,11.3)	0.92 (0.85,0.99)	0.88/0.78
d		413*** (32)	4.54 (3.74)	1.04*** (0.26)	10.9 (4.86,16.9)	0.87 (0.81,0.93)	

Notes: n is sample size, R^2 is the correlation coefficient of the regression model / the RMA regression, the same letter indicates no statistical difference between sub-groups ($\alpha = 0.05$) for eq. (3.8b), while different letters indicate significant difference, number in parenthesis is standard error or the 95% lower and upper confidence limit. ***: <0.001 , ** <0.01 , * <0.05

The pattern from Figure 3-3 and Table 3-4 are largely seen in the next two sets of sub-groups (Figure 3-4 and Table 3-5; Figure 3-5 and Table 3-6). Specifically, the RMA regression slopes and intercepts from eq. (3.8b) were 1 and 0 except for non-evergreens, which had a slope of 0.80 (CI is 0.68 to 0.95) and an intercept of 32.1 (CI is 5.05 to 59.2). Those from eq. (3.8b-3) were biased for small photosynthetic rates with a slope lower than 1 and an intercept larger than zero. The R^2 ranged from 0.69 to 0.88, depending on sub-groups, but 6 out of 8 cases had a R^2 value ranging from 0.77 to 0.88, suggesting good fit of both equations to the data.

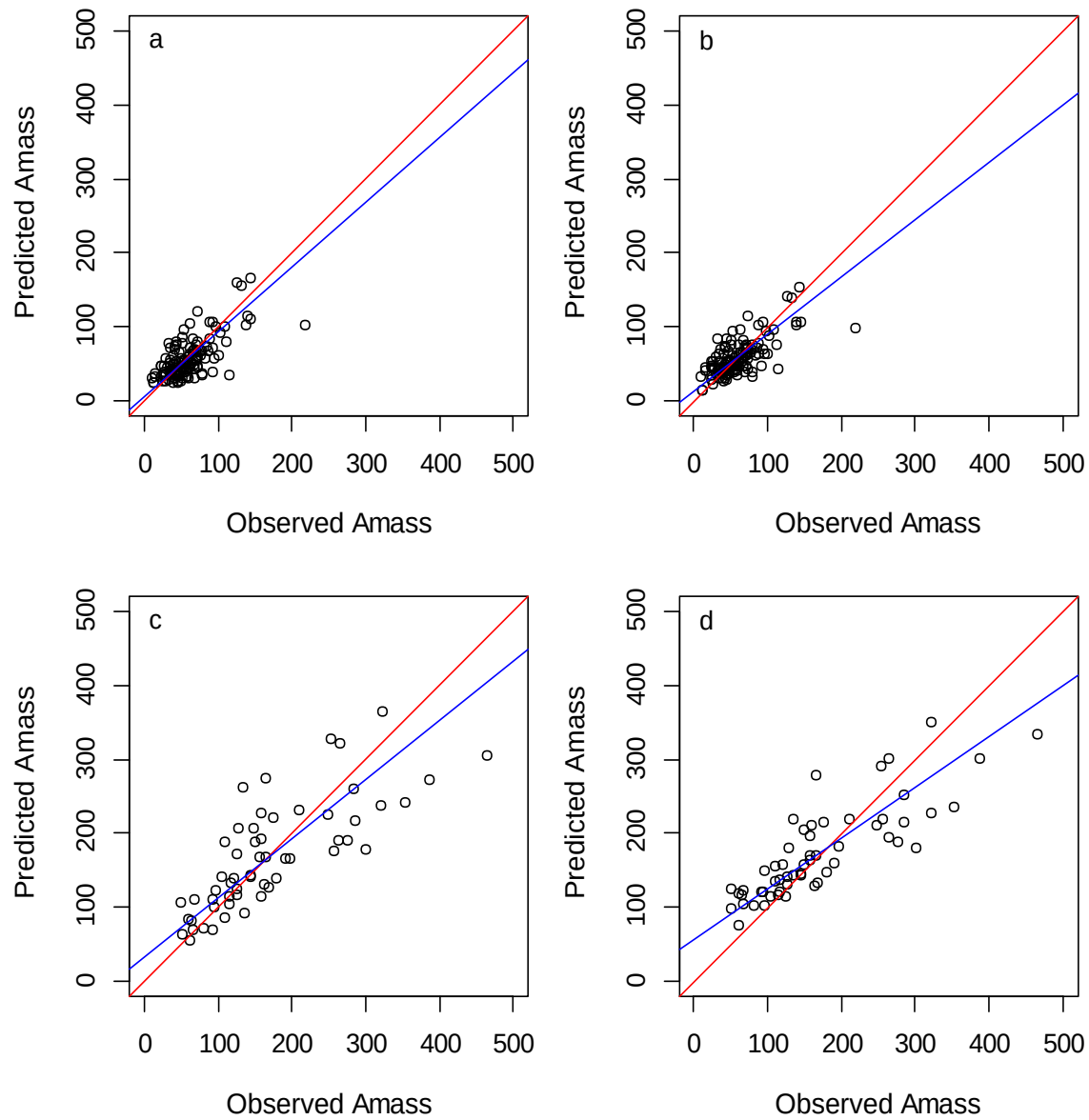


Figure 3-4. Predicted vs. measured A_{mass} for evergreens by (a) eq. (3.8b) and (b) eq.(3.8b-3), and non-evergreens by (c) eq. (3.8b) and (d) eq.(3.8b-3). The red line is the 1:1 line through origin, the blue line is the RMA regression line. All related parameter values are in Table 3-5.

Table 3-5. Parameter values for Figure 3-4.

	n	K_m	b_m	K6	RMA intercept	RMA slope	R^2
a		452*** ^b (82)	13.4*** ^a (3.6)		4.66 (-3.00,12.3)	0.88 (0.77,1.00)	0.69/0.47
b	132	408*** (80)	5.01 (4.36)	0.94** (0.29)	12.6 (5.92,19.3)	0.77 (0.68,0.88)	0.69/0.48
c		193*** ^a (36)	27.7*** ^a (5.6)		32.1 (5.05,59.2)	0.80 (0.68,0.95)	0.78/0.60
d	54	201*** (33)	16.6** (6.16)	2.60** (0.79)	57.8 (37.6,78.0)	0.68 (0.59,0.80)	0.83/0.69

Notes: n is sample size, R^2 is the correlation coefficient of the regression model / the RMA regression, the same letter indicates no statistical difference between sub-groups for eq.(3.8b) ($\alpha = 0.05$), while different letters indicate significant difference, number in parenthesis is standard error or the 95% lower and upper confidence limit. ***: <0.001 , **: <0.01 , *: <0.05 .

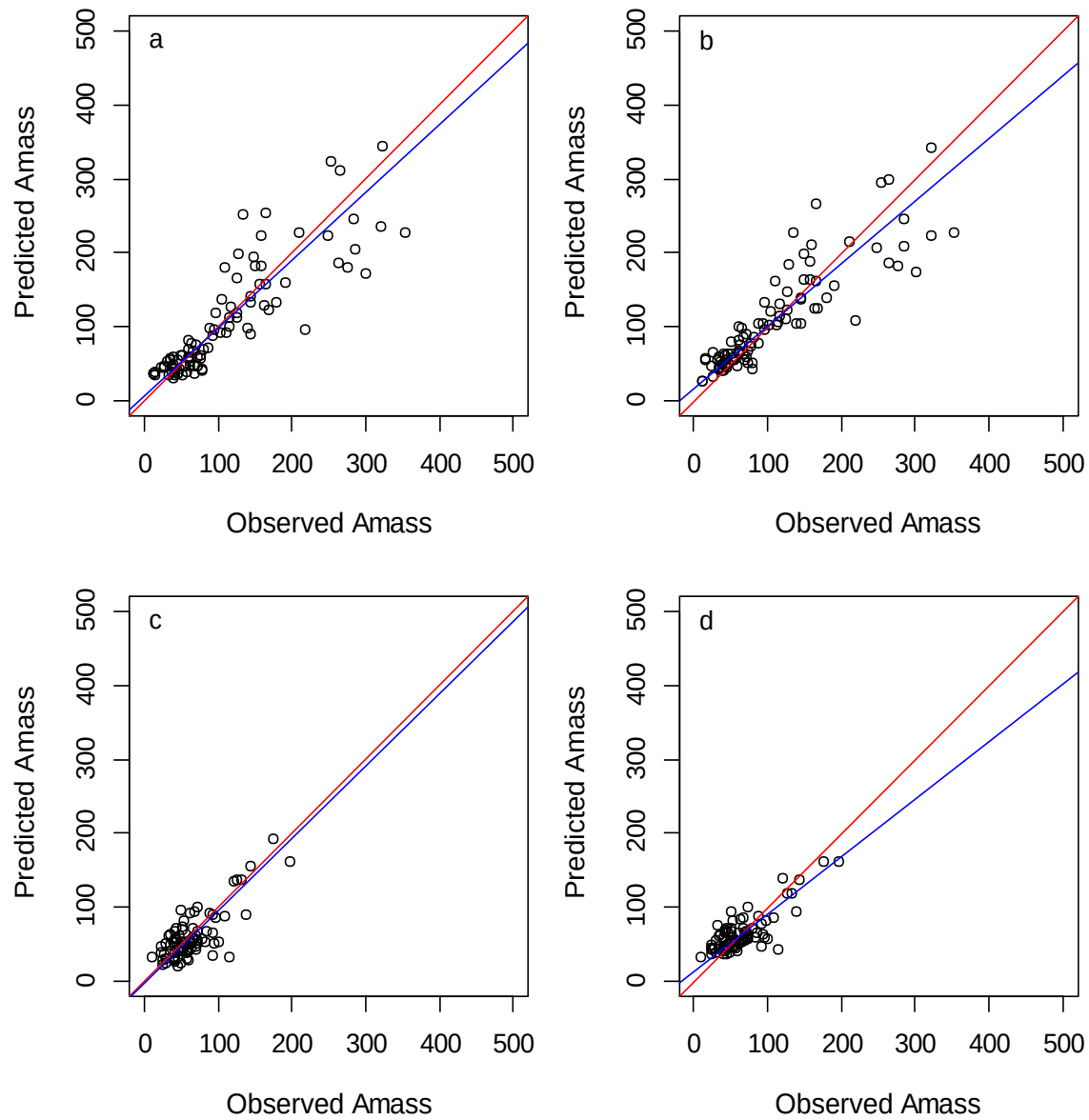


Figure 3-5. Predicted vs. measured A_{mass} for temperate forest species by (a) eq. (3.8b) and (b) eq.(3.8b-3),and woodland species by (c) eq. (3.8b) and (d) eq.(3.8b-3). The red line is the 1:1 line through origin, the blue line is the RMA regression line. All related parameter values are in Table 3-6.

Table 3-6. Parameter values for Figure 3-5.

n	K_m	b_m	$K6$	RMA intercept	RMA slope	R^2
a	172*** ^a (24)	28.1*** ^a (3.5)		5.22 (-8.00,18.4)	0.92 (0.83,1.02)	0.87/0. 75
b	191*** (24)	19.7*** (4.44)	1.46** (0.50)	18.0 (6.34,29.7)	0.84 (0.76,0.93)	0.88/0. 77
c	236*** ^b (48)	17.0*** ^a (2.9)		-2.49 (-12.6,7.67)	0.98 (0.85,1.12)	0.77/0. 60
d	264*** (44)	2.67 (4.22)	1.31*** (0.30)	14.5 (6.79,22.2)	0.78 (0.68,0.89)	0.79/0. 63

Notes: n is sample size, R^2 is the correlation coefficient of the regression model / the RMA regression, the same letter indicates no statistical difference between sub-groups for eq.(3.8b)($\alpha = 0.05$), while different letters indicate significant difference, number in parenthesis is standard error or the 95% lower and upper confidence limit. ***: <0.001 , ** <0.01 , * <0.05

It was shown here that although eq. (3.8b), which included N_{mass} is significantly better than eq. (3.8b-1), without it, there was a possible correlation between MAT and N_{mass} in some cases, because MAT caused the effect of N_{mass} to be insignificant in 3 out of 6 cases (Table 3-4 (d), -5 (b) and -6 (d)). This might contribute to the bias in eq. (3.8b-3)(see discussion).

For eq. (3.8b), K_m values were significantly different between contrasting sub-groups while b_m values were not. Further, K_m was negatively correlated with b_m across sub-groups (see Table 3-4,5 and 6 and Figure 3-6), i.e., a higher or lower K_m corresponded to lower or higher b_m , respectively, indicating that they are complementary (Figure 3-6). Therefore, plants can evolve to have either a lower-cost (lower K_m) or

"cheap" lifetime structure investment with higher-cost (higher b_m) or "expensive" replacement cost, or the reverse. High-photosynthesis sub-groups such as grass/herbs, non-evergreens, and temperate forest plants had "cheap" lifetime leaf structure and "expensive" maintenance replacement cost, while the contrasting low-photosynthesis ones had the opposite strategy. Analyses for eq. (3.8b-3) had similar results and are not shown here.

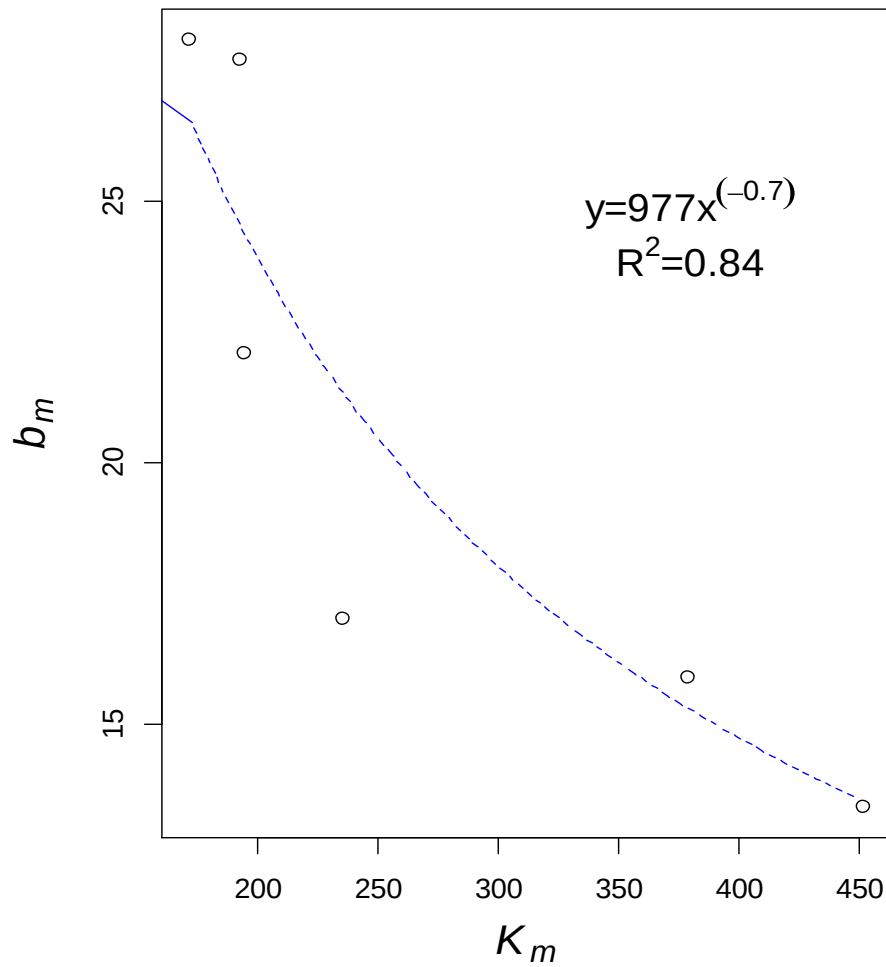


Figure 3-6. The relationship between K_m and b_m . Data points are for eq. (3.8b). The blue dashed line is the fitted curve with the equation and R^2 shown in the graph.

3 A pattern in the relative ratios of composite maintenance costs to photosynthesis

The $b_m * N_{mass}$, K_m / LL and dark respiration rate are three composites of leaf maintenance cost that indirectly drive photosynthetic rates for mature leaves through the energy balance requirement for leaf maturation (eq. 3.7). Their relative contribution to the photosynthetic rate (Figure 3-7) demonstrated that high-photosynthesis leaves had lower respiration/photosynthesis ratio ($2 * R_{dmass} / A_{mass}$), and a higher structural maintenance /photosynthesis ratio (the sum of these two ratios is 1), although this pattern was not significant for the grass/herb and shrub/tree sub-groups. The higher structural investment is mainly due to higher cell or parts replacement cost (higher $b_m * N_{mass} / A_{mass}$) but similar lifetime structural mass investment ($K_m / (A_{mass} * LL)$). The low photosynthesis leaves had the opposite characteristics. Therefore, the high and low-photosynthesis leaves represented two contrasting photosynthesis models.

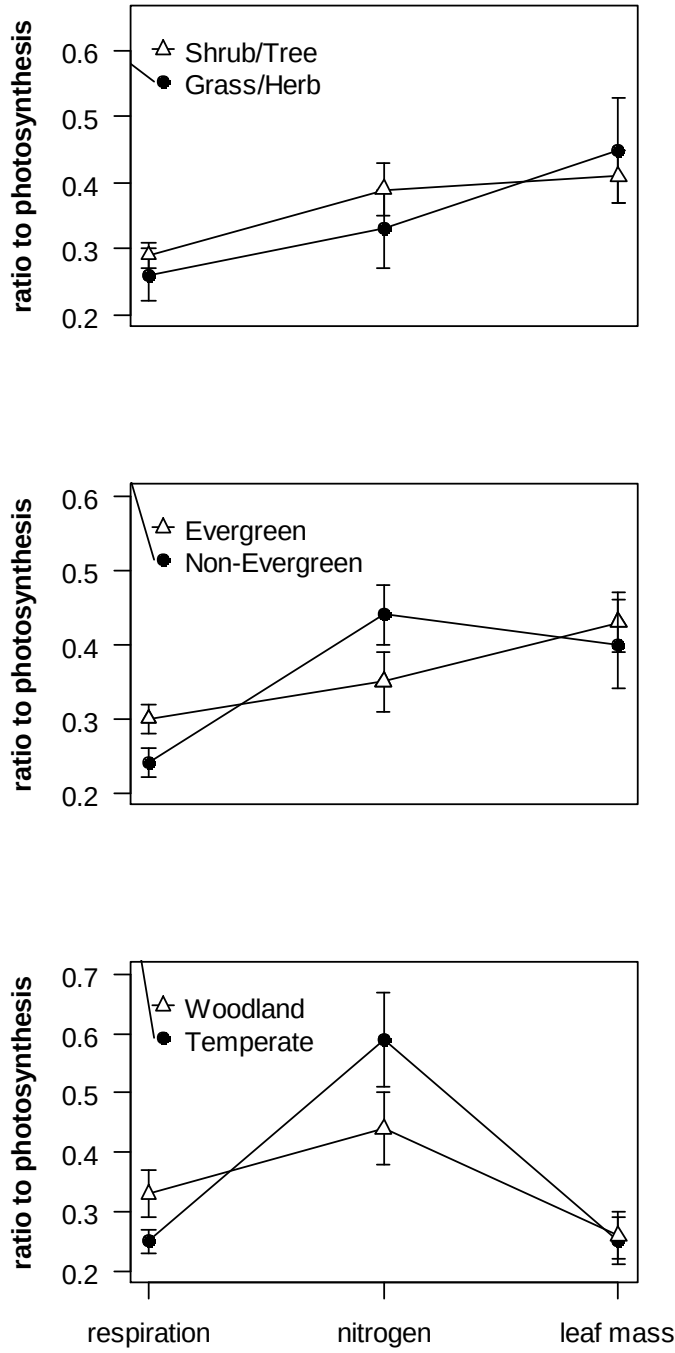


Figure 3-7. The relative ratios with 95% confidence intervals of respiration, nitrogen-related and leaf structural mass maintenance costs to photosynthesis, corresponding to $2 \cdot R_{dmass} / A_{mass}$, $b_m \cdot N_{mass} / A_{mass}$, and $K_m / (A_{mass} \cdot LL)$, respectively,

Figure 3-7 (cont'd). for three sets of sub-groups: shrub/trees vs grass/herbs, evergreen vs non-evergreens, woodland vs. temperate forest species.

Discussion

Here, an evolutionary life history theory for leaves was developed. It was based on bio-energetic leaf growth and maintenance/mortality processes, with a focus on how evolution has modulated leaf life history traits to maximize the lifetime net energy/carbon output to the next generation of leaves. The predictions of this theory were supported by a global leaf trait database and the theory can be discussed in terms of four major insights described below.

1 An evolutionary life history theory for leaves has significant meaning for plant functional traits studies

A major thread of studies in plant functional ecology is about evolution and the resulted trade-offs (Kikuzawa 1991; Reich et al. 2003; Donovan et al. 2011). For example, Reich et al. (2003) stated that it is necessary to analyze the adaptive significance of plant functional traits by modeling possible evolutionary constraints on them. However, not much has been done besides assumptive suggestions until this research. Kikuzawa (1991) and Kikuzawa et al. (1999) put forward a theory assuming that the net carbon assimilation rate of a leaf should be maximized by evolution. However, Kikuzawa's theory cannot explain why leaves obviously have so many different net assimilation rates, instead of just one optimized type with the highest net production rate for all plant species (Westoby et al. 2002). Clearly, individuals can be successful with higher survival rates as opposed to faster growth rates (Reich 2001), as evolution is generally more about lifetime fitness than speed or rate (Shipley et al. 2005). Besides, leaves are not purely

dependant functional organs, rather they should be reviewed from a holistic perspective of plant life history evolution (Reich et al. 2003).

The new theory presented here is based on a theory about leaf life history evolution that is similar to the theory for individual life history (Roff 2007): net energy output to the next mature generation of leaves (and by extension, flowers or seeds) over a leaf's lifetime should be optimized. This optimization theory was tested by the GLOPNET data, and its mechanism for each critical component is detailed: fecundity is in growth eq. (3.5), and survival in eq. (3.6). For all species pooled, the new theory without including climate effects provided a good fit to the GLOPNET data ($R^2=0.58$ and 0.87 on area- and mass-basis, respectively; see Figure 3-2). The predicted slope of 1.00 was realized on an area-basis but not on mass-basis although the latter has a slope of 0.89 with its upper 95% CI limit (0.96) close to 1.00 (Figure 3-2 (c)). Next, it was shown that this deviation can be removed when the new theory was fitted separately for four out of six sub-groups, and even for the two exceptions (shrub/trees and non-evergreens), the upper limits of (0.99 and 0.95, respectively) of 95% CIs of slopes are quite close to 1.

Reasons for possible small deviations in two sub-groups could be from three sources. First, there is a non-zero intercept value for deviated regression lines. If that value is set to zero, this deviation from predicted slope of 1 would disappear. Secondly, the A_{mass} used here is the photosynthetic potential of mature leaves, which may not be the same as the photosynthetic rate when leaves just mature because the concept of leaf maturity is not well studied and quantified previously and photosynthetic potential declines after the time of maturity (Kikuzawa and Ackerly 1999). Last, the coarse sub-grouping and sometimes small sample sizes for some sub-groups may hide

underlying patterns. For example, some pioneering evergreen pine species have been found to actually have high photosynthesis leaves (Reich et al. 2007), though evergreens on average have leaves with lower photosynthesis rates. And the sub-group of shrub/trees includes some fast-growing shrubs such as *Manihot esculenta* and *Atriplex stipitata* and trees such as *Solanum straminifolia*, and *Cecropia ficifolia* that are not different in functioning with grass/herbs. We hope that future studies that have more precisely measurements of A , R , SLA and N for more species, and not just for mature leaves, could allow for improved exploration of the new theory.

2 A photosynthesis variation continuum across species with two contrasting driving patterns

Recognizing that photosynthetic rates vary along a continuum from slow to fast with corresponding relationships to other leaf traits, the new life history theory for leaves provide a framework for exploring leaf trait variation. When paired sub-groups that have relatively contrasting leaf / plant life history characteristics (e.g., evergreens vs. non-evergreens) were examined (Figure 3-6 and 3-7), two contrasting photosynthesis types are obvious: the “nitrogen-limited, slow photosynthesis” type and the “carbon-limited, fast photosynthesis” type.

Although there is obvious variability within the coarse sub-groups, the slow-photosynthesis sub-groups: shrubs/trees, evergreens and woodland species, represented a trend toward the nitrogen-limited slow photosynthesis type, where mature leaves has a smaller nutrient-related maintenance cost relative to photosynthetic rates (lower $b_m * N_{mass} / A_{mass}$), but higher respiration costs (mainly in the form of carbon) driving photosynthetic rates (reflected in higher respiration/photosynthesis ratio), and leaf

structures made of more "expensive" materials (higher K_m) (see Figure 3-7). This photosynthesis pattern should be adaptive in areas with low nutrient concentration and other adverse conditions, because high rates of photosynthesis may be nutritionally unaffordable and energetically inefficient.

The other three sub-groups: grass/herbs, non-evergreens and temperate forest plants, generally demonstrated the characteristics of the opposite carbon-limited fast photosynthesis type, which occurs when, e.g., resource conditions are good and higher photosynthetic activities are possible. In this case, a species should perform optimally when sufficient nutrients, especially nitrogen, can facilitate fast photosynthesis, but when dark respiration of leaves is more limited. For these three groups, the ratio of nitrogen-related replacement maintenance cost to photosynthetic rate was higher, the respiration/photosynthesis ratio was correspondingly lower, respiration appeared more efficient (Figure 3-7), and leaf structures were made of "cheaper" material (lower K_m) (see Figure 3-6). A study by Reich et al. (1998b) compared evergreen tree taxa with relatively lower photosynthetic rates, such as *Pinus*, *Picea* and *Thuja*, to deciduous tree taxa with relatively higher photosynthetic rates, such as *Populus* and *Betula*, and showed that the former are usually distributed at sites with a low potential rate of resource capture, and the latter are usually colonizing high light early successional sites with high nitrogen uptake availability. Low-photosynthesis taxa such as *Pinus* contain relatively more cell wall materials such as lignin and cellulose and higher carbon level (more energetically expensive), while high photosynthesis taxa such as *Populus* have relatively more cytoplasmic elements such as proteins and sterols and a higher nitrogen:carbon ratio (Niemann et al. 1992). These studies above also suggest that the slower growers are

functioning as nitrogen-limited slow photosynthesis types, while the fast ones are operating under more of a carbon-limited fast photosynthesis type. Other studies have also suggested that the advantages of evergreen leaves are both energetic and nutrient-economic (Moore 1984; Moore 1980), and that slow-growing plant species are characteristic of higher respiration to photosynthesis ratio (Loveys et al. 2002; Way and Sage 2007).

Though the average trait values of the three paired sub-groups might be different, the overlap of data range is obvious (Fig. 3, 4 and 5). This is not only consistent with other empirical studies (Wright et al. 2004), but further supports that eq. (3.7) from the evolutionary perspective quantified here should be universally observed both within and among species groups. Thus, it represents a general constraint, meaning that an individual leaf may adopt a same or quite different photosynthetic rate according to its extant environments, as long as the leaf traits are associated in a way that satisfies the constraint. This can explain why different leaf types usually coexist in many different ecosystems. It also indicates that the widely used functional type classifications, which assume distinctly separated life history traits among groups (Bonan et al. 2003; White et al. 2000), might not be appropriate. However, the challenge is to determine the maintenance cost, which should be a fundamental characteristic of a leaf. The conceptual model in Figure 3-1 did not include possible costs such as internode, stem and roots, though there were evidence that these costs may affect leaf energy budget as well (Kikuzawa et al.1999)

3 Lifetime structural mass cost varies little between different leaves

A striking finding is that the lifetime mass investment cost relative to photosynthesis is actually similar or constant across all sub-groups, as indicated by

indifferent $K_m/(A_{mass}*LL)$ values (Figure 3-7). Given a constant K_m value within a species group, there should be a significant trade-off relationship between A_{mass} and LL . In fact, the correlation between A_{mass} and LL across all species is strong ($R^2=-0.83$), which has also been shown by more general correlation analyses to this trait-pair (Wright et al. 2004 and 2005), but the slope is not -1, though close to it (result now shown). This might be that the value of K_m , which is the energy cost per leaf mass, are different between groups (Table 3-2 and -3), and hence the negative correlation can't be appropriately fitted with one equation for all. Nevertheless, this trade-off suggests that the continuum of photosynthesis should be accompanied by a similar continuum running from short (at high A_{mass}) to long (at low A_{mass}) leaf life-span.

Also because this structural mass cost is relatively similar among sub-groups, relative carbon cost (mainly for respiration) and nitrogen cost (for maintenance replacement) are complementary so that the above "carbon-limited slow photosynthesis" is nitrogen-driven and vice versa. This trade-off theme between nitrogen and carbon is common in plant biology, but the theory presented here shows its possible evolutionary reason.

4 Temperature moderately influences photosynthesis and its association with other traits

MAT is selected in the model as an independent climate variable for explaining the variance of A_{mass} . It has been known that photosynthesis changes with temperature in a characteristic bell-shaped curve (Ehleringer and Sandquist 2010), and A_{mass} was

positively related to *MAT* (Reich et al. 2007). Adding temperature in eq.(3.8b-3) improved the explained variation in photosynthesis by 1% for all species pooled, and by 1-2% in five sub-groups and 5% in one sub-group, indicating very little temperature effects, as supposed by other studies (Wright et al. 2004). This could be that as long as a species adapts certain position in the photosynthesis continuum, it is set to be equally competitive to others in terms of fitness and largely independent of environmental conditions, which makes it hard to directly relate macro-climate with individual performance. However, including temperature in the model produced a overestimation bias for smaller photosynthetic rates and also caused N_{mass} effect to be negligible in several cases (Table 3-4 (d), -5 (b) and -6 (d)). The bias means a change of slope or intercept or both for the regression between A_{mass} and leaf trait association, which is in agreement with a finding that changes in growth temperature altered the scaling relationship between photosynthesis and leaf traits in certain leaves (Atkinson et al. 2010). As *MAT* overwhelmed N_{mass} in determining A_{mass} , its effect on non-linearly influencing different A_{mass} is possible. Specifically, species with higher photosynthetic rates may respond less to temperature, i.e., correlations between higher photosynthesis species and *MAT* should have lower slope than the ones between lower photosynthesis species and *MAT*. This was supported by data because climate-included eq. (3.8b-3) produced shallower slopes for high-photosynthesis sub-groups such as grass/herbs and non-evergreens than low-photosynthesis subgroups such as shrub/trees and evergreens (slopes were 0.71 and 0.68 vs. 0.87 and 0.77, respectively; see Table 3-4 and 3-5). Atkin et al. (2006a and 2006b) supposed that fast-growing species may have a greater ability to

acclimate than slow-growing species, meaning that high photosynthesis leaves are more likely to be less affected by temperature and have a higher degree of metabolic homeostasis than low photosynthesis leaves. Under different global change scenarios, it may further indicate that high-photosynthesis plant species should be able to cope with possible temperature increase better than the low-photosynthesis ones.

Conclusion

Leaves are basic structural, functional and physiological modules of plants. Though leaf characteristics, particularly functional and life history traits, are diverse, there are strong universal association patterns among them. Explaining why and how these patterns are formed remained an enduring challenge. Plant modularity studies have suggested looking for evolutionary constraints on leaves for possible answers, but not many testable theories have been advanced prior to this research. This paper confirmed that evolutionary constraint can explain the variation of photosynthesis and its association with other leaf traits across species. Analyses of the driving pattern for photosynthesis indicated that nitrogen content and carbon respiration are the two key driving components of photosynthesis that trades off with each other. Overall, this study could advance our understanding of plant evolution and ecology further from plant to leaf scale.

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CHAPTER 4. A LIFE HISTORY PERSPECTIVE ON THE LINKAGE BETWEEN SEED MASS AND LEAF PHOTOSYNTHESIS

Abstract

Seed mass is an important functional trait that defines the life history strategy of a plant. Variation in seed mass and leaf traits, especially photosynthetic rate, have been shown to be correlated, but of the mechanisms that underlie this empirical correlation are not well understood. To fill this gap, a new theory of seed growth based on a widely-used sigmoidal growth function and an energetic relationship between photosynthesis of mature leaves and seed energy income is proposed here. A mechanistic relationship between seed mass and leaf photosynthesis is produced by the new theory. A dataset including leaf trait and seed mass measurements of 102 species collected globally is used to test this relationship. The results indicate that, as predicted, there was a negative correlation between seed mass and leaf photosynthetic rate with a slope of -0.37, but only 20% of seed mass variation was explained. Additional proportions of variation in seed mass were explained by other leaf traits.

Introduction

Seeds represent a critical life stage of most plant species. The majority of plant types begin from, and reproduces by, seeds, including conifers, cycads, gnetophytes, and angiosperms. Some notable exceptions are seedless vascular plants, including bryophytes (mosses), pterophytes (ferns) and minor groups such as lycophytes (club mosses), but these also have a seed-like (spore) stage that begins and ends their life-cycles. A critical functional trait of seeds is their mass, because seed mass is directly connected with the reproduction strategy of a species, i.e., a plant may evolve to have many smaller seeds or

few larger ones. Seed mass varies over a range of over 11 orders of magnitude among species and 5-6 orders of magnitude within a given community (Moles et al. 2005b; Westoby et al. 2002). This variation is connected with different plant regeneration types that help define species niche (Perez-Ramos et al. 2010). In particular, large seeds have more energy reserve for greater initial seedling mass that can help plants to endure many different hazards, such as dryness, shade, poor soil nutrients and shallow soil, and thus to dominate closed or shaded environments (Grubb and Metcalfe 1996; Hewitt 1998; Paz and Martínez-Ramos 2003; Poorter and Rose 2005). On the other hand, small seeds are lighter, often wind-dispersible for large distances, and more abundant per area than larger ones, which may help plants to colonize new sites with abundant seedlings and confer them a direct fitness advantage under certain conditions (Muller-Landau 2010; Moles and Westoby 2006). Small seeds also tend to experience lower predation risks than the large ones whose survival is often depressed by predation pressure from animals such as rodents (Hulme 1998).

Leaf photosynthesis is another critical plant functional trait that helps define plant niche and life histories (Chapter 3). Especially, higher photosynthetic rate is related to a higher RGR and less shade-tolerance (Reich et al. 1998a). Photosynthesis is also related to other important leaf traits such as leaf dark respiration (R_{dmass}), leaf nitrogen content (N_{mass}) and lifespan (LL) (Chapter 3; Wright et al. 2004).

Because seed mass and leaf photosynthesis are two functional traits of the same species, it is hence reasonable to expect a relationship between them. This idea is supported by emerging evidence that variation in seed mass is indeed linked to leaf photosynthesis for some species (Reich et al. 2003). For example, seed mass is negatively

correlated with photosynthetic rate in the same individuals of several temperate plant species (R^2 up to 81%) (Reich et al. 1998a and 1998b), and also with RGR and diameter growth rates of adult trees as photosynthesis is in some taxa and habitats (Shipley and Peters 1990; Castro et al. 2008). But how general and in what form this negative relationship between seed mass and photosynthesis is across many species still remains a largely unknown question.

Further, correlation and causality are not the same thing, so it is important to seek a mechanistic explanation for the linkage between seed mass and leaf photosynthesis. Currently, such explanations are still rare, although phylogenetic and comparative perspectives are often supposed (Moles 2006; Moles and Westoby 2004b; Ackerly and Donoghue 1995; Reich et al. 2003; Reich et al. 1998a).

Here, new research was conducted to shed new light on seed mass-photosynthesis relationships. First, a sigmoidal growth process for seeds is proposed. Second, the energy metabolism of seed mass growth is linked to leaf photosynthesis. Finally, a large global dataset containing measurements on seed mass, photosynthesis and leaf physiological traits of diverse plant species was analyzed to test the theory.

Theory

General logistic functions, such as the von Bertalanffy growth function (VBGF), are appropriate in describing most growth processes. The VBGF assumes that energy income rate (“anabolism”) is proportional to mass raised to certain power as the following (von Bertalanffy 1938; Banavar et al. 2002; also see Chapter 1):

$$B = B_0 \cdot M^{\alpha} \quad (4.1)$$

where B is the energy income rate of a seed, M is seed mass, B_0 is constant for a given species, α is a power parameter that may vary between 2/3 and 3/4 (Dodds et al. 2001; O'Connor et al. 2007a and 2007b).

At maturity, leaves should stop growing and export available net assimilated energy to seed growth. This net assimilated energy can be calculated from the following relationship (see Chapter 3):

$$B_l = 2C \quad (4.2)$$

where B_l is gross photosynthetic rate or assimilated energy income, C is the leaf maintenance cost. The net assimilated energy output $(B_l - C)$ therefore is $\frac{1}{2}B_l$, and is used as the energy income rate, B , of a seed.

Next, seed mass should be related to leaf photosynthesis as the following in a mass-basis:

$$\overline{B_l} = k \cdot 2 \cdot B_0 \cdot M^{\alpha-1} \quad (4.3)$$

where $\overline{B_l}$ is mass-based photosynthetic rate, if seed mass is proportional to foliage mass as reflected in a parameter k (Niklas and Enquist 2001). This relationship can be tested with measurements of leaf photosynthesis and matched seed mass.

Methods

Analysis of seed mass and leaf traits

A global effort on collecting plant traits, namely Global Plant Trait Network (GLOPNET), has records of leaf trait measurements for many plant species distributed across the globe (Wright et al. 2004; see Chapter 3 for more details). These were matched

to a seed mass dataset provided by Moles et al. (2005b); 102 records of species were identified from both databases with both leaf trait and seed mass information and these data were used to test eq. (4.3). Because photosynthesis also correlates with R_{dmass} , LL and N_{mass} (Wright et al. 2004), possible correlations between seed mass and these indirectly linked variables were also tested.

All correlation analysis was conducted using reduced major axis regression (RMA). A dedicated software package, *smatr*, in R statistical software (ver. 2.15.0) was used to get slopes, intercepts and R^2 values.

Results

In general, photosynthetic rate explained 20% of variance in seed mass and the slope parameter was -0.35 (Figure 4-1), indicating the hypothesized negative correlation between them.

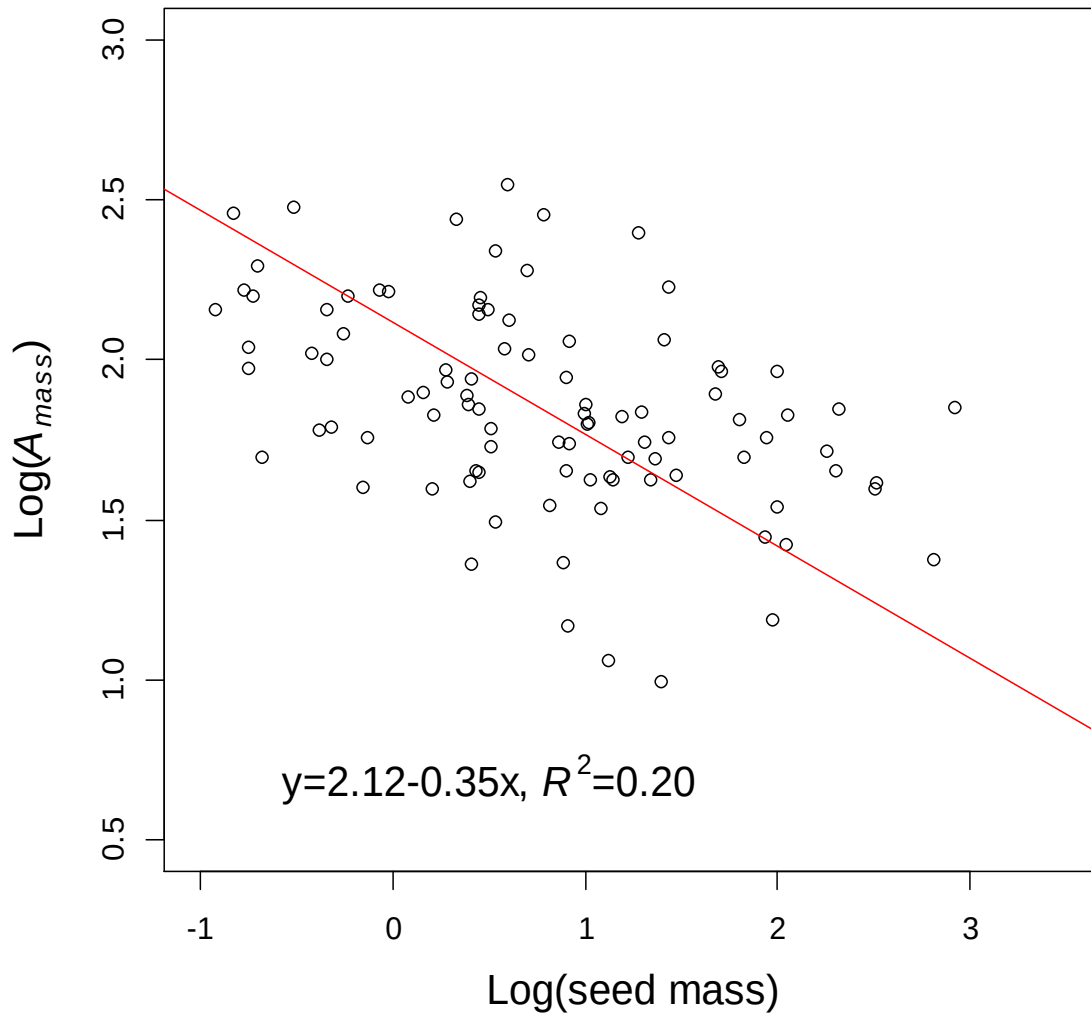


Figure 4-1. Correlation between photosynthetic rate and seed mass. $n=102$. The 95% confidence intervals (CIs) of the intercept and slope are (2.04, 2.20) and (-0.29, -0.41), respectively. The red line is the regression line from the regression equation displayed in the figure.

R_{dmass} , LL and N_{mass} each had certain predicting power for seed mass (Figure 4-2). N_{mass} was a relatively weaker predictor of seed mass ($R^2=0.13$), R_{dmass} and LL explained higher amounts of variance in seed mass ($R^2=0.22$ and 0.25 , respectively). Also consistent with established inter-relationships between these three leaf traits and

photosynthesis (Wright et al. 2004), R_{dmass} , and N_{mass} were negatively related to seed mass with slopes of -0.27 and -0.20, and LL was positively related to seed mass with a slope of 0.51.

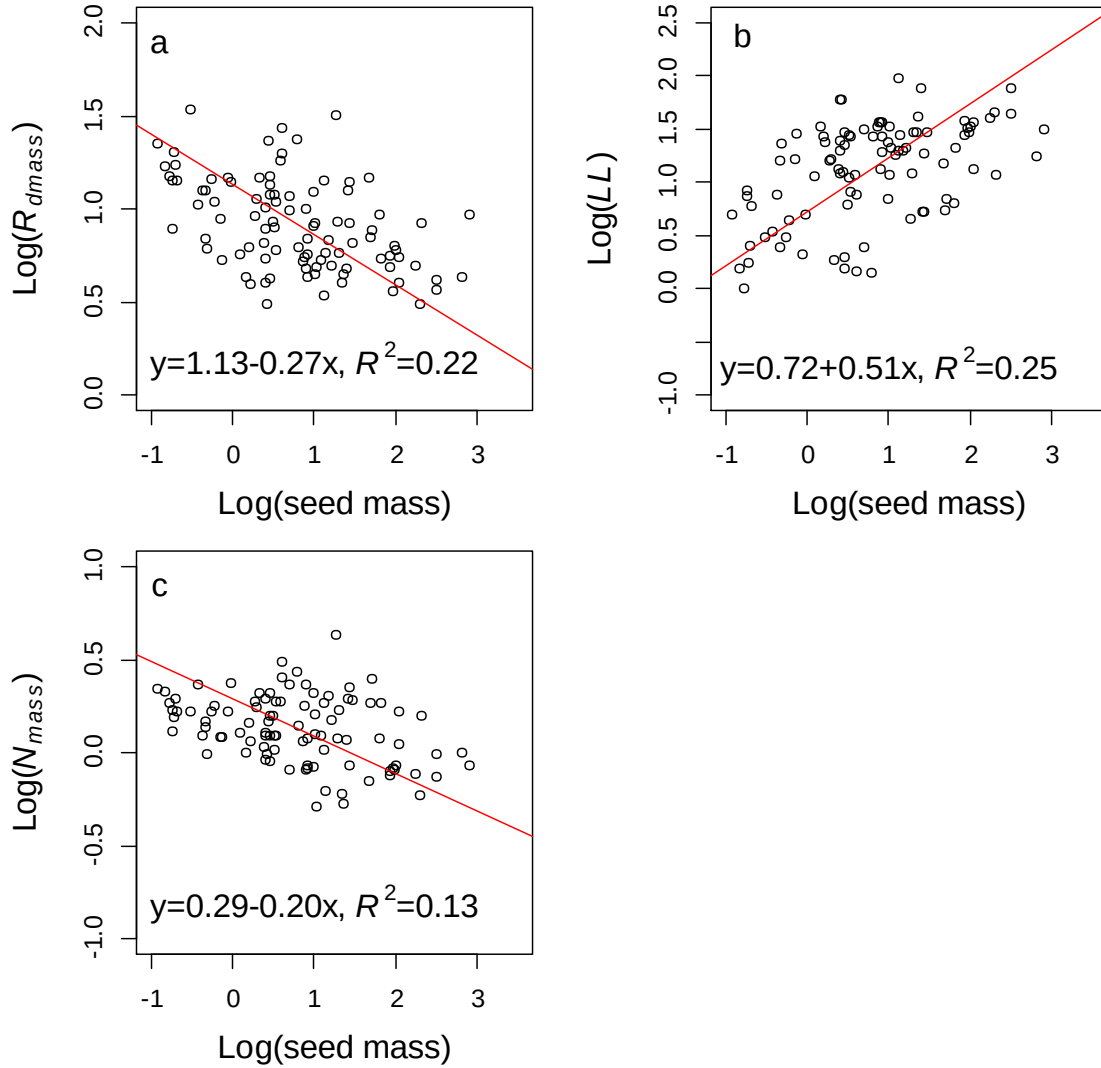


Figure 4-2. Correlations between seed mass and three leaf traits with 95% CIs of the intercept and slope: (a) respiration (R_{dmass}), (1.07, 1.20) and (-0.23, -0.33), (b) LL , (0.60, 0.83) and (0.43, 0.61), (c) nitrogen content (N_{mass}), (0.24, 0.34) and (-0.17, -0.24),

respectively. $n=102$. The red line is the regression line from the regression equation displayed in the figure.

Discussion

Seed mass varies locally or globally across species. Here, an allometric growth model linking leaf photosynthesis with seed mass was presented. This model suggests an explanation for the correlation between seed mass variation and leaf physiological traits across a wide variety of plant species occurring globally.

Growth is a universal phenomenon for living organisms including seeds. A typical growth process with time usually appears as a sigmoidal function. VBGF is such a well-know growth function widely used in many growth studies (Burd et al. 2006; Karkach 2006). The assumption of VBGF that energy income rate is related to mass raised to a power has been supposed to be underlying observed allometric scaling relations (Chapter 1 and 2), and are largely supported by real data from both animals and plants (Niklas and Enquist 2001; Enquist et al. 1999). Like leaves (in Chapter 3), seeds also have their own growth trajectories that can be described by sigmoidal growth curves such as VBGF. Therefore, there should be a power relationship between the energy income rate of a seed and it's mass. The energy income rate for seed growth is from leaves, and is especially tightly related to the mature leaf photosynthesis (eq.(4.2)). It was then predicted that seed mass should be allometrically related to mature leaf photosynthesis (eq.(4.3)). Data from 102 species collected throughout the globe supported the relationship (Figure 4-1). The indirect correlation between seed mass and other leaf traits were also supported (Figure 4-2). Though seed mass variation has been explored from various aspects, the new insight presented in this paper is to our

knowledge its first kind to directly relate leaf traits with seed mass in a quantitative and mechanistic model and to verify the generality of the relations in a large number of plant species.

Studies on allometric scaling between mass and metabolism supposed various values for the scaling parameter α that usually ranges around a span of 2/3 to 3/4 (DeLong et al. 2010; Sears et al. 2012), though recent arguments that 3/4 is a better value are highlighted (Enquist et al. 1998). The present study has the $(\alpha-1)$ value of -0.35, which seems to be close to -1/3 from a possible $\alpha = \frac{2}{3}$ case, and its 95% confidence interval of -0.41 to -0.29 did not include the value of -0.25 if $\alpha = \frac{3}{4}$. This is consistent with a near 2/3 relationship between energy income rate and mass for plant species that is derived from photosynthesis having a near 2/3 relationship with respiration which scales isometrically with mass (Reich et al. 2006). However, this 2/3 might be more of a convenient average of many possible values, and the actual α value should vary from species to species, as VBGF can use from 2/3 to 3/4 scaling depending on different cases (Banavar et al. 2002; Chapter 1).

The relatively low explained variance of 20% may be due to the fact that the seed mass data were compiled from literature and averaged for a species. It has been demonstrated that the correlation between seed mass and photosynthesis can be as high as 81% in more precise individual studies for the same plants of several species (Reich et al. 1998a and 1998b).

Photosynthetic rate in leaves has been used to define a possible "fast-slow photosynthesis continuum" of leaf life history (Chapter 3). As seed mass is linked to

photosynthesis in a mechanistic way here, it may help further extend that continuum to include seed mass. For example, higher-photosynthesis species should have smaller seeds, higher RGR and maintenance cost or mortality rate, and short leaf lifespan, while lower-photosynthesis species have the opposite trait syndrome. Through its link with photosynthesis, linkages between seed mass and other plant traits, such as plant height, stem diameter, time to first reproduction, plant mass, potential RGR, canopy area, and canopy volume (Moles et al. 2005b; Leishman et al. 2000; Castro et al. 2008; Moles and Westoby 2004b; Silvertown 1981) may also be explained. Together, they reflect the concept that seed mass is really an important plant functional trait representing certain ecologically important life history dimensions of plants (Westoby et al. 2002; Reich et al. 1998a, 1998b). But future studies are needed to test the suggested relationship here using larger datasets of precise measurements from the same individuals. Local environmental factors that might contribute to seed mass variation, such as climate and geographic effects, should also be taken into consideration (Moles et al. 2005b; Leishman et al. 1995). So far, these kinds of studies are still rare, and much is still needed to further our understanding of seed mass variation.

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SUMMARY AND FUTURE DIRECTIONS

In this thesis, a systematic bio-energetic theory for growth and life history of plants and animals was developed. It started with a new understanding to growth and mortality in terms of energy metabolism dynamics, and finished with a new evolutionary life history theory. From fishes to plant leaves and seeds, it has been shown that the new theoretical framework was generally well supported. In particular, this framework is centered on energy instead of mass, though both are tightly correlated. This idea of energy as both building blocks and regulators of development and life history has important biological significance. Meristem cells, for example, are supposed to be activated by plant energy supply and correlated hormones (Uggla et al. 2001; Borisjuk et al. 1998; Oribe et al. 2003; Druart et al. 2007), as well as prevailing physical conditions such as temperature, light and water availability. Studies have also shown that biological energy, in forms of glucose, ATP, protein or sugars, are critical developmental signals (Begum et al. 2007). The stress of the weight generated by a plant's own growth, as well as environmental stressors, can serve as developmental signals (Ko et al. 2004; Telewski 2006; Chehab et al. 2009). These all then point to the possibility of further testing the framework presented here at cellular level. Especially, is there a molecular mechanism within cells for the growth efficiency declination with age or each cell production (in Chapter 1)? How is the most important life history trait, i.e., relative maintenance cost or energetic mortality rate $\frac{C_m}{E_m}$, for a species (in Chapter 2) defined genetically or physiologically on cell level and affected by environmental factors?

Answers to them might reveal even more fundamental rules and biological mechanisms and pave the road for a grand unifying theory of ecology.

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