New Idea

Power scaling, vascular branching, and the Golden Ratio

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Abstract

The Golden Ratio (a ratio of ~1.618:1) appears repeatedly in nature including structural and functional traits of organisms (e.g. Fibonacci spirals of snail shells and certain seed heads), the spiraled shape of galaxies and hurricanes, and even in much cultural architecture and art. In the mid-19th century, branching structures in plant and animal vascular systems were found to follow the Golden Ratio; that is, successive branches in the vascular systems of plants and animals tend to follow a length ratio of about 1.618:1. Here we present a model that uses this empirical evidence as a branching ratio in theoretical vascular systems. We then use a defined mass of the model system as a predictor of log-log scaling of terminal units. In this model, log terminal units and log mass scale similarly with that of other models as well as empirical evidence, but with more parsimony and a perspective not yet offered among all available models of allometric scaling. This model invites novel and broad hypotheses on the influence of the Golden Ratio on power scaling in organisms.

Keywords: Golden Ratio; vascular branching; power scaling; allometry.

Introduction

Organismal power scaling is a well-established phenomenon in the field of biology (Rubner 1902, Kleiber 1932). Scientists have known for over a century that biological rates and processes scale at log-log slopes of less than one (Rubner 1902). We present a general model, which uses the golden ratio as the branching ratio (i.e. the ratio of the length of a single branch to the length of one of its successive branches) to describe power scaling in a defined vascular system predicted as the number of terminal units compared to the defined mass of the overall system.

In the mid-1800s, Adolf Zeising found that the arrangement of plant branches and leaf veins, as well as animal arteries, tended to follow the golden ratio. The golden ratio is a proportion of φ:1, where $\varphi \approx 1.61803399$. It is widely found in mathematical phenomena (e.g.. Fibonacci's sequence) as well as various natural and cultural phenomena such as human proportions, architecture, visual arts and music (Livio 2003, Putz 1995, Tool 2001).

Nearly two decades ago, West, Brown, and Enquist (West et al. 1997, hereafter referred to as WBE) published a model that mechanistically explained power scaling for all vascular organisms using first principles of physics. The WBE model uses branching ratios to predict the supply volume of vascular fluid to terminal units (e.g. capillaries or leaves).

WBE mathematically show that as organisms increase in size, and hence mass, the amount of tissue that each terminal unit must supply also increases. In essence, the logarithmic number of terminal units increases by about 3/4 for every logarithmic increase in the mass of organisms. In the WBE model it is assumed that terminal units are invariant in size and can supply
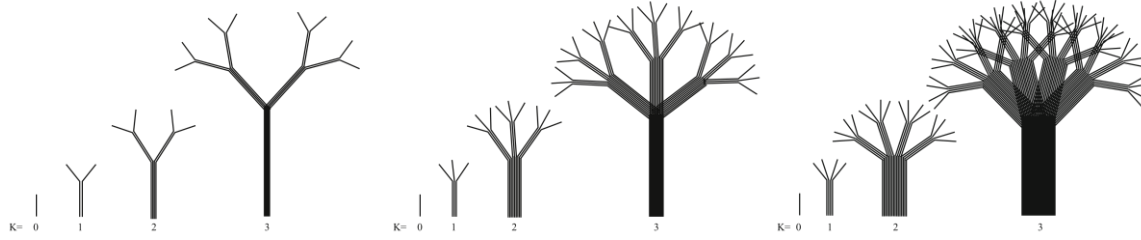
Figure 1. Model of Phi Branching Structure. Graphical depiction of the model of branching patterns where the base branch at each level $k+1$ increases by φ from the base branch at level k. The three graphs presented here represent the first three furcation levels that are discussed in the paper; bifurcation (n=2), trifurcation (n=3), and n=4.

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an invariant amount of fluid. Therefore, as mass increases, the amount of tissue that each terminal unit must supply also increases.

Zeising discovered that branches in the vascular systems of plants and animals were about φ times as long as a successive branch (Zeising 1854, 1856). Our model uses this ratio to determine length and mass of branches in a simulated vascular system. We show, using a simple model, the relationship between the defined mass of a model organism and the number of terminal units when the branching ratio follows the golden ratio.

Model

We define the model at the lowest branching level as a single vascular tube where the branching level (k) is 0 and the length and mass of the initial branch are each 1 (Figure 1). At successive levels of k, each branch diverges into n branching structures such that there are k branching points for each level of k. Therefore, each level of k could be thought of as representing an organism that has k-level branching points in its vascular system. For each level k this produces a number of terminal units such that

$$T_k = n^k$$

where T_k is the number of terminal units for an organism with k branching points and n is the number of branches that diverge at each branching point; n is a furcation constant that is defined *a priori* and represents the number of branches extending from the previous branch (Figure 1). In this model we simply count the number of terminal units; however, this could have a wide range of interpretation in biological reality ranging from capillaries in birds and mammals to leaves in plants. For sake of comparison we interpret terminal units the same as WBE (i.e. capillaries or leaves).

Additionally, we define length of the base vascular piece at each successive level as increasing at a ratio of φ : 1 such that,

$$l_{k+1} / l_k \equiv \varphi$$

where l_k is the length of the base branch at level k. We define mass of the initial branch as equal to 1; therefore, mass in the model is equivalent to the sum of lengths for all vascular tubes in the system. We assume that branches run continuously from source to terminal unit such that at level k there will be n^k vascular units of length φ^k. Therefore, the mass at each level of the model is as follows,

$$M_k = \varphi^k n^k + (M_{k-1} \cdot n)$$

where M_k is the mass of the model at branching level k and $\varphi \approx 1.61803399$.

Results and Discussion

The number of terminal units scales logarithmically with defined mass of the system at a slope near 2/3 when $n = 3$ and closer to 3/4 when $n = 4$. The relationship between $\ln(T_k)$ and $\ln(M_k)$ at $n = 4$ reveals a pattern that matches very closely with what WBE predict (Fig. 2). Note that this result holds true when the mass of a piece of the model vascular system is equal to its length. Changing this assumption would lead to a different result in the model output.

Interestingly, we can compare our model to the WBE equation for volume-preservation in the space-filling fractal (West et al. 1997), which is $\gamma_k^3 \equiv (l_{k+1} / l_k)^3 \approx n^{-1/3}$, where WBE derive as a scale factor for branch length between levels. Here n means the same as in our model, which is a furcation constant for each branching level. WBE essentially use γ and n along with β, a branch radii scaling factor, to derive the exponent that ultimately determines allometric scaling in organisms. We can compare the equation for γ to branching ratio in our model because we define mass of a vascular piece as being equal to its length. Therefore, if we take the last term in the WBE equation for γ and plug in different furcation levels we will see where γ for our model (which is φ) best fits. In order to do this, however, the last term in the WBE equation for γ must be inverted as M_k in our model builds on its previous branching level
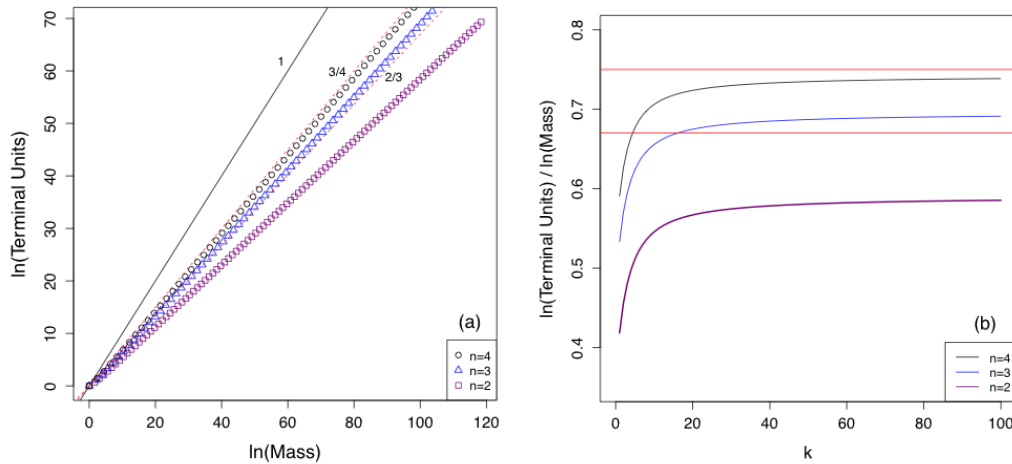
Figure 2. Results from the model. Subfigure (a) shows the correlation between ln(Terminal Units) and ln(Mass) for 100 branching levels. Slopes of 1 (black line), 3/4, and 2/3 (red dashed lines) are included for reference. Points for n=4 fall very closely in line with the 3/4 line predicted by WBE while points for n=3 are nearer to 2/3. However, the quadratic model described by Kolokotrones *et al.* (2010) fits points for $k = 100$ significantly better than the single-term linear model ($F_{1,97} = 6.58$, $p < 0.05$, ΔAIC=-4.6). Subfigure (b) shows the change in slope across levels of k. The y-axis represents the slope of the log-log relationship between terminal units and mass.

whereas the ratio for γ in WBE is compared to the subsequent k level. Inverting the last term in WBE reveals that when n=2 (which is basic bifurcation in branching) then $\gamma = 1.26$, when n=3 (trifucation), $\gamma = 1.44$, and when n=4, $\gamma = 1.59$, which is close to φ. Therefore, when we calculate the number of terminal units and mass using our model at $n = 4$ we see a pattern very close to what WBE predict (Figure 2a). WBE state that in their model the power scaling exponent is invariant of branching ratio, and the main reason for this is that the length ratio (γ) in branches changes with branch ratio (n) as seen above.

This observation invites novel and broad hypotheses about power scaling in organisms and its cause. Firstly, do all organisms follow the same power scaling patterns regardless of n? WBE state that allometric scaling does not depend on branching ratio (West et al. 1997); however, in our model the log number of terminal units corresponded to log mass at a ratio of 3/4 when $n = 4$, but as closer to 2/3 when $n = 3$. The mechanism behind the WBE model relates to how much body tissue can be supplied by terminal units, and that the number of terminal units does not scale as 1 with mass (but rather as 3/4). If terminal units actually scale differently between branching types, then according to our model exponents of power scaling will differ as well. Our simple model reveals a basic mathematical pattern between the number of terminal units of a vascular system and the system's branching ratio and furcation constant. This then brings up the question of what exactly did Adolf Zeissing measure? Did all of the organisms for which he measured branching ratio in animal vessels and plant stems have a furcation constant of 4? This seems unlikely (e.g. simply look at any tree and see how many branches stem at each node; rarely is it 4, although sometimes as in the case of pine and spruce trees it is greater than 4). It would be interesting to compare allometric scaling between organisms that are known to branch at $n = 3$ and those that are $n = 4$ to see how they differ. Additionally, it would also be interesting to measure the branch length ratios in these organisms to see if they all follow the golden ratio or if branch length ratios differ between them.

It is also interesting to note that there is a slight curvature in the trend presented in Figure 2a. This correlates nicely with the pattern found by Kolokotrones et al. (2010) which shows that basal metabolic rates in organisms follow a quadratic model quite well on a log-log scale. While this difference is difficult to discern a basic comparison of linear model fits between the linear vs. quadratic model shows a significant difference between the two models ($F_{1,198}= 19.448$, $p < 0.0001$), and the quadratic model exhibits a lower AIC value by about 16 (ΔAIC=16.3). This curvature in the output of the model can be readily seen in Figure 2b. Since Kolokotrones et al. (2010) measure basal metabolic rate

and our model relates to vascular scaling, this is only an interesting, notable correlation. However, WBE attempt to correlate metabolic rates with a vascular branching model that largely depends on the number of terminal units of a system. In essence, the number of terminal units among organisms that differ in mass determine metabolic rate in the WBE model.

Our model, just as every other model, is a simplification of nature in order to gain an understanding about certain components. Obviously we cannot take into account all biological realities such as known patterns in conduit packing and hydraulic architecture (Sperry et al. 2008) or differences in vessel structure between, say, furcating stems and reticulate leaves. Similarly, that mass equals the length of vascular units in this model is perhaps another overlooked reality as different structures on the same individuals perform different tasks and are likely to be composed of different materials consisting of different densities. While this would likely create problems in the model at higher levels of biomass (e.g. trees, where cellulose and lignin is used for structural support at the base of the vascular system), our goal was to get a broad overview of a very simple system across a wide range of branching levels to understand how fractal branching ratios near the golden ratio determine the physical structure of the system (in terms of terminal units, which provide the cells with the resources necessary for life). Although we have neglected some of these biological realities for the sake of parsimony we feel that this model reveals interesting correlations between a well-developed theory of allometric scaling and empirical measurements that follow patterns of a well-established mathematical relationship. The golden ratio is present in a wide variety of organismal traits (Mitchison 1977, Douady and Couder 1992) and represents a common thread among patterns in organismal structure. It is interesting that this ratio, which determines optimum form, could also lead to consistent patterns of scaling at constant branching ratios.

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