The Metabolic Scaling Relation for a Prostrate, Vascular Herb

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Abstract:

In this paper our group presents findings on the metabolic scaling law for *Chamaesyce setiloba.* We empirically determined that this herb constitutes a counter example to the conventional ¾ or 2/3 scaling law; adopting instead a near-linear relationship of mass to metabolism. We find that the most probable reason for this departure from theory is that the plant fails to be space-filling. In addition to these empirical results, we make several conjectures for more appropriate theories.

In the recent years much progress has been made in determining the origins of the ¾ scaling laws of biology. It has been convincingly shown that many of these relations can be determined by examining simple, biophysical constraints in fractal-like organisms. This method has been applied in botany with great success. In the case of vascular plants, the physical constraints that determine the scaling of metabolism are 1) the necessity to move water to great highs and 2) to use only use branches with sufficient length and girth to resist buckling under gravity[5]. Although these constraints can be applied to the many vascular plants, there are a significant number which derive their support from their environment. In this paper, we present the results of an experiment for the determination of the metabolic scaling relation in prostrate plants.

We expect that the plant should basically conform to the current theory. Specifically, we expect that the metabolism, B, of the plant should be approximated well by the relation:

$$B \approx M_0 M^a$$

(1)

Figure 1

where M_0 is a taxa-specific constant and a is a positive constant. There are three likely values for a: 2/3, 3/4, and 1. The first two options are direct results from the current theory of scaling. It has been show that in the case where 1) the leaves are of invariant size, 2) the vascular system can be approximated well by the pipe model, 3) and the plants attempt to maximize their use of the available volume, then a should be approxima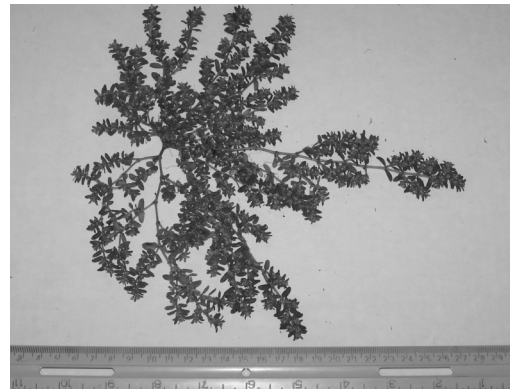tely d/(d+1). Here d is the number of Euclidian Dimensions occupied by the plant.[2] Because the plants we studied are prostrate, d should presumably be 2; from whence a=2/3. There is also an argument that a should be closer to ¾. All plants, obviously, are three-dimensional objects; thus even prostrate plants should scale according to the normal relation. It is entirely conceivable these plants would remain sufficiently three-dimensional in order to maintain the conventional scaling relation, rather than adopting the less efficient value of 2/3. The final possibility to be considered is that the metabolism of the plant will scale linearly with mass. The motivation for this prospect is that if the plant fails to conform to said assumptions, then the metabolism may be able to scale in an even more efficient manner than the aforementioned cases. In this case, linear scaling is a strong candidate as many other aspects of plant biology behave in this manner (e.g. reproductive biomass).[1,4]

Plant Materials)

There are two simple ways of gathering data from which one can glean the value of a. First, one can consider only individuals of a representative mass from a menagerie of different species and determine the metabolism for each. From this information, one can determine the metabolism of a species as a function of mass. The alternative is to consider only a single species. If this method is used, then one compares the metabolisms of many different individuals of varying mass. Both of these techniques typically

conform to equation (1). Due to a dearth of available species of prostrate plants, we chose the latter of these approaches. To this end we examined individuals of the species *Chamaesyce setiloba* (Figure 1). The goals of the data were to determine a and to test the assumptions that the plant is area-preserving and space filling. In order to find the metabolism of an individual, we used the number of leaves as a suitable proxy. Notice that the stem, though photosynthetic, is small compared to the total leaf area. In order to test the aforementioned assumptions we recorded data on the lengths and radii of the stem as a function of branching generation.

Our group used a total of 20 *C. setiloba* individuals as representative two-dimensional plants. Each plant was placed into one of 4 ranks according to its mass, M. The ranks were: small ($M<.5$ g, 8 individuals), medium ($.5$ g$< M <1$ g, 7 individuals), large (1 g$< M <5$ g, 4 individuals), and very large ($M > 5$ g, 1 individuals). The plants were collected from a sunny, well watered area.

Additional data were collected on the wet-weight of the aboveground biomass and total biomass of the plant. Due to the difficulty in removing the entire root, the total biomass of the plant was the largest source of error.

Number of Leaves and Dimensions)

The dimensions of each plant were determined from digital photographs. The NIH program ImageJ[6] was used to find the requisite lengths of the segments. We determined the radius, r, (as measured in the middle) and the length, l, of each inter-nodal segment. The plant only bifurcates at the end of a segment.

The number of leaves, n_L, refers to the total number of living leaves on a given plant. We determined n_L for each plant by hand. *C. setiloba* has simple leaves, thus there is no confusion in differentiating between leaves.

Results)

Our group was able to determine three interesting results from the data. First, the metabolism of the plant is a near-linear function of mass. This result runs counter to the current theory; in which the plant should scale with an exponent of 2/3 or 3/4. This outcome is elucidated by the second result: counter to previous theory, the branches tend toward an invariant length. Since the data counters the basic assumptions in the derivation of the d/(d+1) scaling exponent, then there is no reason to expect such a result. Finally, we found good evidence that this species might be area preserving.

The scaling of metabolism with mass)
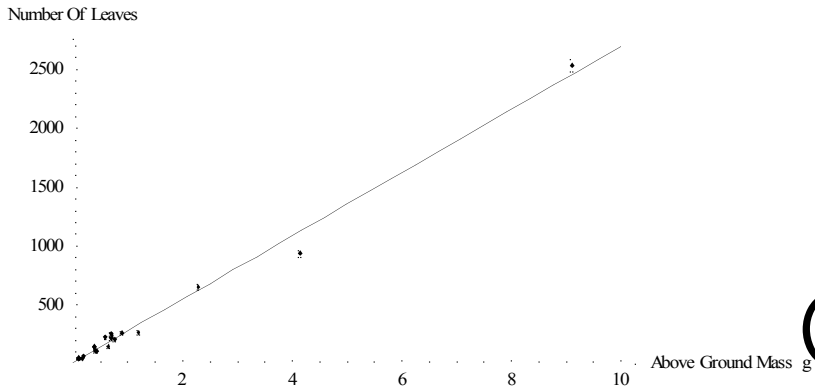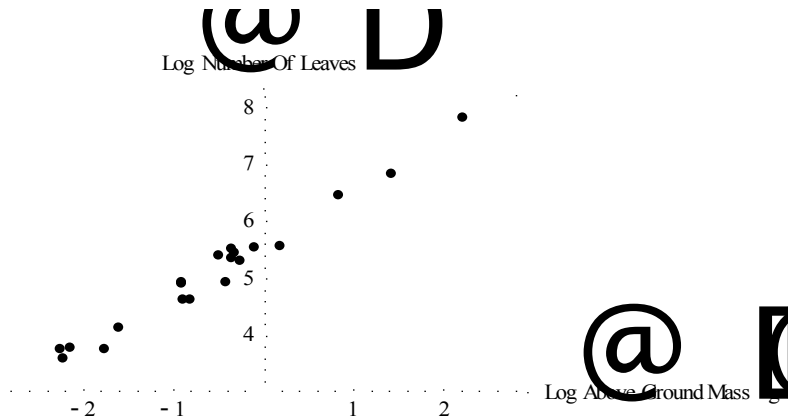

Figure 2

Our group found a roughly linear relationship between the mass of the plant in question and the number of leaves on the plant. This fit is consistent with data collected from plants with masses spanning two decades.

We assumed that the exact number of leaves, n_L, on a plant of known mass can vary according to a Poisson distribution. Therefore, we took the expected error in the number of leaves to be the square root of n_L. We then used the Method of Least Squares to find the line of best fit:

$$n_L=(268.62\pm6.27) \, M+(7.45\pm14.78) \tag{2}$$

where mass is given in grams. The data and line of best fit are shown in Figure 2.

Figure 3

We plotted our results on a Log-Log plot (Figure 3) in order to better discern the scaling exponent. To these ends we repeated the recent procedure, using the natural log of the data and mass. The result is that we found that the scaling exponent is actually slightly less than one. We found the line of best fit to be given by:

$$Ln[n_L]=(.91\pm.04) \, Ln[M]+(5.64\pm.04) \tag{3}$$

Thus, we find near-linear scaling.

Segment Length as a Function of Generation Number)

In the derivation of a=d/(d+1) it was assumed that the branches of the plant would conform to a space-filling constraint. This constraint manifested itself mathematically in the equation:

$$\gamma\equiv\ell_{k+1}/\ell_k=n^{-1/d} \tag{4}$$

where ℓ_k is the length of the kth segment from the center and n is the number of daughter branches from a given branch. We found this assumption does not hold for *C. setiloba*. Rather, γ is roughly one for the majority of branches.

Consider a branch with a total of N segments running from the center (k=0) to the edge (k=N). In order for the comparison of the length of a segment with its predecessor to be accurate, we needed to take into account two observations. First, at the time of collection the last segment is still growing; thus $\ell_N/\ell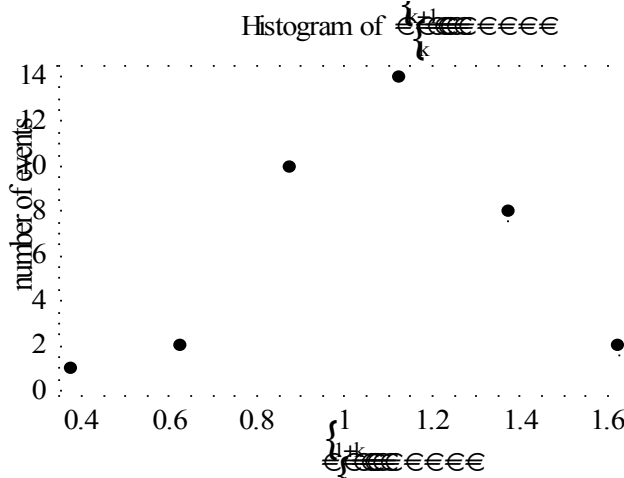_{N-1}$ is smaller than it would be at a later point. The second observation is that ℓ_0 and ℓ_1 are much smaller than any other branching segment. We conjecture that these branches tend to be shorter due to a limited number of leaves when these branches are grown.. Therefore, in the empirical determination of γ, we do not consider ℓ_0, ℓ_1, or ℓ_N.

Figure 4

Given the above considerations, we find that γ is normally distributed about $\mu=1.08$ with a standard deviation of $\sigma=.26$. This data is shown in Figure 4 as a histogram. This graph was made using 37 branches from six plants of varying mass. We compared the lengths of a total of 180 inter-nodal segments.

Evidence for Area-preserving Branching)

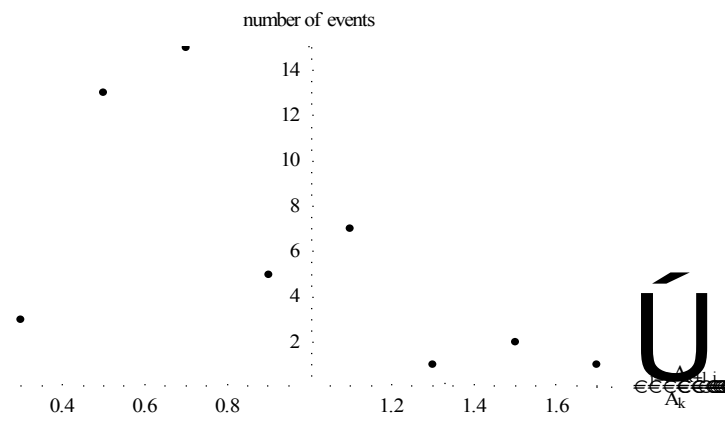*C. setiloba* has no heartwood, thus we expect that the pipe model of the vascular system should approximate well the actual xylem and phloem systems. Suppose that the cross-sectional area of a segment in the kth branching generation is A_k. Furthermore, let this segment split into n segments with areas denoted by: $A_{k+1,j}$ (j=1,2,3,…,n).According to the pipe model the transport tubes of the xylem and phloem have invariant radii. Therefore, as the number of pipes is nearly constant during a furcation,

Figure 5

er of the stem is large compared to the diameters of a xylem and phloem tubes. (Figure 5).

In order to test this assumption we created a histogram of the ratio $\sum A_{k+1,j}/A_k$. This ratio will be one in the case of area-preserving branches. We used 47 data points

from 6 plants to make this plot. The mean value was .78±.32. Therefore, the result neither confirms nor denies that the branches are area-preserving.

Discussion)

These results run counter to the current understanding of plant, metabolic scaling laws, and therefore warrant exploration. We present partial explanations for two aspects of these results.[2,3,5] First, we motivate the possible use of a hypothetical, allometric growth equation by showing that linear scaling can be deduced from standard assumptions in concert with an empirically derived equation for the placement of leaves. Furthermore, we motivate the observation that the segment lengths tend towards a constant by proposing a growth equation for this plant.

Motivation for linear scaling)

The result that this plant seems to have a linear relationship between mass and metabolism suggests that there is a theoretical departure from past formulations of scaling laws. We present a model that yields this linear relationship. It reviews the assumptions made in past derivations and corrects those postulates deemed empirically false. This model does not fully describe the very good relationship between the mass of a plant and the number of leaves.

Consider a fractal-like model of a prostrate plant with N branching generations and a branching ratio of n. Counter to past assumptions, suppose that the plant is both space filling and the branches are of invariant length. Furthermore, assume that at the end of each segment of the first N-1 there are m leaves. At the end of the Nth segment there are m_N leaves, which may be a function of N. These assumptions are consistent with observations of *C. setiloba*.

Clearly, the total volume of the non-leaf, above-ground biomass contained in the kth branching generation is:
$$V_k = A_k \, \ell_k \, n^k \tag{5}$$
By the aforementioned assumptions, this equation can be rewritten as:
$$V_k = A_N \, n^{(N-k)} \, \ell_N \, n^k \propto n^N \tag{6}$$
The total volume can be found by summing over k from 0 to N. Thus:
$$M_S \propto V \propto (N+1) \, n^N \tag{7}$$
Therefore, the mass of this aspect of the plant, M_S, is proportional to $(N+1) \, n^N$.

The total number of leaves can be calculated as above. The number of leaves in the kth generation is:
$$n_{L,k} = n^k \, m(k) \tag{8}$$
Where m(k) is given by:
$$\begin{cases} m & k \neq N \\ m_N(N) & k = N \end{cases} \tag{9}$$
Thus the total number of leaves on the plant is given by:
$$n_L = n^N \; \blacksquare_N \; \blacksquare \; \underline{} \; \frac{}{n-1} \; | \tag{10}$$

Our group has not formulated a closed form solution for the function dependence of m_N on N. However the data suggests that a linear function may be appropriate. We used nine branches from four plants to collect this data; from which we found:
$$m_N \approx (.73 \pm .13) \, N + (.44 \pm 1.16) \tag{11}$$
Thus, we determine that when n=2 equation (9) can be approximated by:
$$n_L \approx (.73 \pm .13) \, n^N \, (N + 3.21 \pm 2.50). \tag{12}$$
Thus, there is empirical data suggesting that $m_N(N)$ reduces equation (9) to a form where:
$$n_L \propto (N+1) \, n^N. \tag{13}$$
Equations (6) and (11) combine to show that the number of leaves is proportional to the mass of the non-leaf biomass. From this relation and the assumption that the leaves have mass per leaf, ρ, one can show that the total mass is given by:
$$M \approx (\zeta + \rho) \, n_L \tag{14}$$
where ζ is the constant of proportionality relating M_S to n_L. Therefore, the total number of leaves is proportional to the total aboveground mass of the plant.

Notice that this derivation did not explain the origin of the linear scaling law; rather it shifted one empirical result to another. The fact that the crux of the derivation relied on m_N behaving in a very special way suggests that this derivation is simply a demonstration of a much more general principal. The form of this derivation suggests that the evolution forced this plant to produce the exact number of leaves at the end of a branch as to maintain the linear scaling relation. The observation that the critical value is the number of leaves in the growing portion of the plant suggests that a growth equation may shed greater light on the situation. It may be possible to construct an allometric equation that determines the number of leaves that must be created in a growing region to add a segment with the restraints that the roots grow sufficiently to bring additional water and nutrients, and that the stem grows enough to minimize leaf overlap.

Motivation of Architecture)
C. setiloba has demonstrated a very peculiar architecture. As was discussed in Results, the segments begin stunted and then tend to an invariant length. This behavior is largely explainable using a growth equation.

The growth equation is the result of two simple assumptions stemming from two observations. Since the plant grows flat along the ground, there is no way to stack leaves in such a way as to profitably have leaves covering. This observation yields the assumption that the leaf area index should be close to one. Furthermore, if the segment lengths are small, then the amount of resources invested in stem is small, the water that needs to be gathered to maintain the transpiration-cohesion siphon is a minimum, and little time is needed for moving water from root to leaf. From these observations, we assume that the inter-nodal segments should be made as short as possible. Notice that the radii of the branches after the initial stem are fixed by assuming that the pipe-model holds.

These two assumptions can be implemented by considering the equation:
$$F_{a,b}(\ell) = A_{a,b}(\ell) - \beta \, \ell \tag{154}$$
where $A_{a,b}(\ell)$ is the amount of overlap between two leaves *a* and *b* at a distance ℓ, and β is a positive constant. Postulate that the ideal distance between a and b corresponds to a positive root of this equation. For each branching generation construct $F_{a,b}(\ell)$ for all possible a and b and find the appropriate values for each ℓ as so the magnitude of each

$F_{a,b}(\ell)$ is a minimum; after determination of the values of ℓ for a given generation, fix them for future reference. Notice that this method is distinct from the use of Lagrange Multipliers as neither overlap nor great distances are forbidden; rather these eventualities are simply punished.

A simple application of this concept proves an enlightening partial explanation for two aspects of the peculiar architecture. First, there is a propensity for the stem initially to split into four segments which then grow outward. Next, this model may produce the behavior that the first and second generations of segments are stunted relative to the others, which are roughly invariant.

When a seedling grows out of the ground it should eventually bifurcate (n is typically 2) twice into four segments. Consider the case where the first segments do not produce any leaves. Since the zeroth branching generation has no leaves, then:

$$A_{a,b}(\ell) \equiv 0 \qquad \forall a, b \qquad\qquad (16)$$

where a and b are potentially leaf producing areas in the zeroth generation. Thus, the only roots of equation (14) are when $\ell \equiv 0$. The result is that the next bifurcation seems to be produced directly from the roots. Thus this model is able to introduce a framework in which to consider the initial growth patterns of this plant.

Consider a special case, periodically seen in small plants, in which a branch grows additional segments without bifurcations and does so at a distance far enough from

Figure 6

the rest of the plant as to prohibit any inter-branch overlap. This is an interesting case as the growth of a segment can be considered in isolation. For an appropriate value of β, the roots of this equation are found when ℓ is such that the leaves just touch. This prediction is consistent with the plants (e.g. Figure 6).

If one can accurately model the branching pattern, then it would be possible find the appropriate lengths of every segment. As the branches become larger the self-interactions become progressively more important than other types. The result is that the lengths of each segment should depend critically on the branching pattern. Therefore, if the branching pattern is fractal-like, then the segment lengths should also become self similar. These conjectures could be tested rigorously by comparing actual plants to computer simulations grown in the aforementioned manner.

1) Niklas, K. J. (1994) *Plant Allometry: The Scaling of Form and Process* (Univ. of Chicago Press, Chicago)
2) West, G. B., Brown, J. H. &Enquist, B. J. (1997) *Science* **276**, 122-126
3) West, G. B., Brown, J. H. &Enquist, B. J. (1999) *Science* **284**, 1667-1679
4) Niklas, K. J., Enquist, B. J. (2003) *Evolutionary Ecology Research* **5**, 79-88
5) West, G. B., Brown, J. H. &Enquist, B. J. (1999) *Nature* **400**, 664-667

6) available online