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Power law relationships in the branches of loblolly pine, red maple and sugar maple trees

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Abstract: Power laws are interesting patterns that exist over wide ranges. Power laws may be used to determine the organization of countless networks in nature. The purpose of this study was to test whether the distribution patterns in shoot lengths of three popular tree species follow a power law. This study not only adds to the general knowledge base for these species but also may be used to make predictions about other species. Three common tree species were included in this study: loblolly pine (*Pinus taeda*), red maple (*Acer rubrum*), and the sugar maple (*Acer saccharum*). The height and all shoot lengths of five individuals of each tree species were measured, recorded and sorted. Loblolly pines and sugar maples followed the same power law at individual and species level. Most of the red maple individuals did not follow a power law although they followed a power law at the species level. One possible reason might be that the red maple trees measured were too young and were in strong competition for resources with other tree species.

Additional key words: Branch, Trees, Patterns, Species

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Introduction

Life on Earth is characterized by the diversity of organisms and their habitats. Due to the sheer number of species that exist, the amount of diversity is overwhelming. For example, trees have a wide range of taxonomic and structural diversity. However, vast diversity of tree forms may be reduced to a few architectural models and all trees may be composed of few basic, repeating structural elements (Hallé et al. 1978). Much of diversity follows particular patterns that can be described by a simple mathematical function, the power function. The patterns of organization described by this function are called power laws (Brown et al. 2002).

Patterns from power laws are visible in the organization of natural systems of organisms in many differ-

ent environments (Brown et al. 2002). For example, the relationship between the metabolism of an organism and the body mass of the organism (e.g., West et al. 1999, Muller-Landau et al. 2006) has been described by a power law. Power laws describe many other qualities of animals, such as their heart rate, life span, and population growth (e.g., Peters 1983). Power laws describe some characteristics of river systems (e.g., Hack 1957) and wildfires (Malamud et al. 2005). Power laws can characterize ecological patterns that repeat themselves over broad scales, so they are considered as "general features of complex systems" (Brown et al. 2002). The organizational limits caused by power laws possibly stem from natural laws and basic principles of mathematics. The basic characteristics of natural systems provide clues about the power laws that govern them. Power-law behavior is considered as

evidence that ecological systems are self-organized to ensure that energy is dissipated at the maximum rate across all scales (Malamud et al. 2005).

Power laws are also frequently used to investigate tree structure, such as diameter and tree height, branch radius and number of leaves, and branch radius and branch length (Kaitaniemi and Lintunen 2008). Tree branches are responsible for two primary functions. The first function is to dictate the organization of the leaves and the second main function is to provide supporting infrastructure to the tree (Watt et al. 2005). The branches of trees are organized in networks. Evolutionary pressures may have played a large role in the development of tree growth systems to maintain the maximum health of the tree as a whole (e.g., Watt et al. 2005; Suzuki and Suzuki 2009). These branching networks may also have developed due to the functional requirements of the branches, such as water and nutrient transport, leaf display, and support (Suzuki and Suzuki 2009). Because the branches of a tree are a self-organized network, all shoots may be predicted to follow a power law (Kaitaniemi and Lintunen 2008).

Among the patterns of branch growth that have been described by power laws is the shoot growth found in many pine species (Suzuki and Suzuki 2009). There are large differences in the annual growth of branches in different parts of trees; however, hierarchal shoot growth occurs when annual growth of branches is higher among lower-order branches. There is an obvious internal control that governs hierarchal shoot growth and maintains the consistency of the growth pattern (Suzuki and Suzuki 2009). This internal control that regulates tree and branch growth is likely related to a power law.

The objective of this study is to test whether or not the branching patterns (e.g., all shoot lengths) of each sampled tree of some common species follow a power law. Primarily, the results of this study will contribute to the general knowledge regarding the structural organization of trees. The findings of other studies on the power laws that describe the growth of trees have allowed for the development of several simple equations that are used to predict some of the most important economical functions of trees, such as cycling of nutrients and carbon in forests and inventories of greenhouse gases (Zianis et al. 2005). Understanding power laws on a small scale may enable the extension of power laws to larger scales (Kaitaniemi and Lintunen 2008) and thus allow for greater understanding of Earth's natural diversity. This will directly show the similarity and difference in architecture or geometry of different tree species. Results from this study may help to explain the complexity of many ecological systems and increase the understanding of the principles of mathematics and science that underlie biodiversity (Brown et al. 2002).

Methods

Study area and tree species

The data for this study was gathered at two different sites in Huntsville, Alabama. The measurements for loblolly pine (*Pinus taeda*) and red maple (*Acer rubrum*) were recorded from trees found at the Winfred Thomas Agricultural Research Station, a research farm owned by Alabama A & M University. Overstory was absent for both loblolly pine and red maple trees. The measurements for the sugar maples (*Acer saccharum*) were taken at Monte Sano State Park in Huntsville, Alabama. Sugar maple trees were at the understory of an oak-hickory forest with a canopy height of approximate 30 m and 60–90% overstory density.

The loblolly pine is widespread in the southeastern United States and ranges as far west as Texas and extends as far north as Delaware (Schultz 1997). Once a loblolly has reached maximum height around 30 m, vertical growth stops but growth in diameter continues. The loblolly pine is very important for economic and ecological reasons. Economically, because the wood of the loblolly is strong and easy to cut, the loblolly is most widely used timber species in the United States as far back as the seventeenth century (Schultz 1997). The loblolly pine is also very important to maintaining the balance of many ecosystems. Because the loblolly grows and reproduces quickly in a variety of environments, it is often used to help restore areas that were affected by fires or logging because these trees can rapidly produce a litter layer that helps increase soil fertility (Schultz 1997). Loblolly pines also provide habitats for a vast array of animal species (Schultz 1997).

Red maples are common in the eastern United States but can be found as far west as New Mexico and as far north as Canada. Red maples usually reach heights between thirty and forty meters tall (van Gelderen 1994). Red maples usually grow in acidic soil and can adapt to many other types of soil (Le Hardy de Beaulieu 2003). Red maples are an important economic species. Their soft wood is ideal for making wooden tools and utensils. Also, tourists often come to see the red leaves in the fall time (van Gelderen 1994).

Sugar maples are deciduous and widespread throughout North America. They are especially common in the Great Lakes region (Le Hardy de Beaulieu 2003). Sugar maples often reach forty meters in height but maximum height tends to vary among different subspecies (van Gelderen 1994). Sugar maples are not very adaptable and grow best in moist, fertile soil (Le Hardy de Beaulieu 2003). Sugar maples have very hard wood and are often used for construction and for hardwood floors in both homes and public

buildings. The sugar and the sap from sugar maples are also useful (van Gelderen 1994).

Measurements

Only healthy and accessible specimens were chosen to be measured for this study. If a tree was partially damaged or too small (still a seedling), it was not used for this study. Five healthy individuals with intact canopy were selected randomly. Loblolly pines and red maples were found and measured at the Wilfred Thomas Agricultural Research Station. Loblolly pines were located at a pine plantation and the heights were about 3-5 m. Red maples were in a restored plant community at an oldfield and their heights were about 1-1.5 m. Sugar maples were found and measured in a forest with an average height of 30 m at Monte Sano State Park and the heights of sugar maple were about 3-5 m. All measurements for this experiment were made with a metric tape with an accuracy of 1 cm. For every tree, the length of each shoot and stem height of the tree were measured and recorded. The shoot length is chosen here because this variable is related to both tree morphology (e.g., cone) and functions (e.g., biomass and water transportation).

Data sort and analysis

The lengths of all shoots for each tree were sorted based on the length increase of every 20 cm. For example, a tree with a height of 120 cm has the following length categories: [0, 20), [20, 40), [40, 60), [60, 80), [80, 100), and [100, 120). The number of shoots within each length category was counted. For each tree, a table was made showing the percentage for the number of branches within each length. Finally, a figure with the logarithm of each length (middle value)

and the logarithm of the frequency of each branch length was produced. A linear regression line was fitted for every tree based on the popular least-square method. The slope equality for fitting lines of all trees within and among species was tested using the method from Sokal and Rohlf (1981).

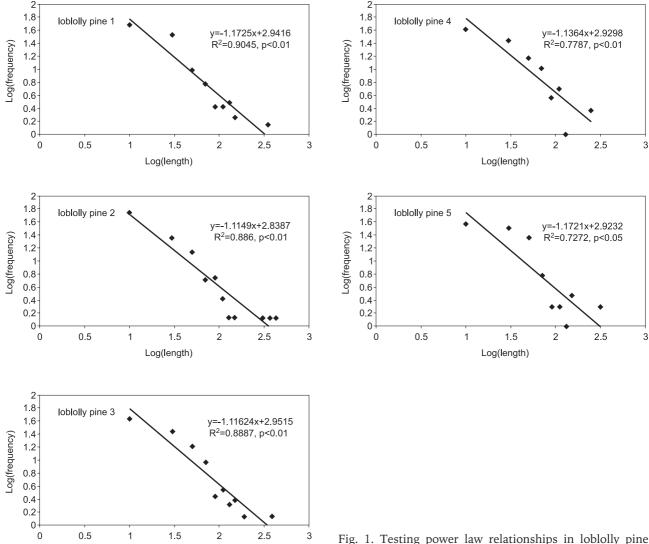
Results and discussion

The shoot quantity of measured trees varied from 8 to 313 and most shoots ranged between 0-50 cm (Table 1). The shoots of each loblolly pine follow a power law with an average exponent of $-1.1517 (\pm 0.0252)$ (Fig. 1) and the slopes of the fitting lines are statistically equal $(F_s < F_{0.01})$. The overall shoots of five loblolly pine trees also follow a power law with an exponent of -1.1725 ($R^2=0.9045$, p<0.01). For sugar maple individuals, shoots follow a power law with an average exponent of -1.1677 (± 0.0408) (Fig. 2) and slopes are also statistically equal $(F_s < F_{0.01})$. The overall shoots of five sugar maple trees follow a power law with an exponent of -1.0818 ($R^2=0.8558$, p<0.01), which is not statistically different with the overall shoots for loblolly pine. However, for the red maples, most individuals do not follow a power law and the slopes of fitting lines are not statistically equal (Fig. 3). The overall shoots of red maple trees follow a power law with an exponent of -1.0087 ($R^2=0.8425$, p<0.01), which is different from those of loblolly pine and sugar maple. The overall shoots of three species follow a power law with an exponent of -1.1725 $(R^2=0.9045, p<0.01).$

If the insignificant power law correlations are used to estimate the exponent of red maple species, the relationships of both tree heights vs exponents of power law and shoot quantity vs exponents of power

Table 1. The distribution of measured number of branches for each tree at each 50 cm shoot lengths (50 cm length is used here for saving space)

Length (cm)	0–50	50-100	100–150	150-200	200–250	250-300	300–350	350-400	400–450	Total
Pine #1	208	22	11	0	0	0	1	0	0	242
Pine #2	258	45	7	0	0	0	1	1	1	313
Pine #3	218	44	11	4	0	0	0	1	0	278
Pine #4	116	23	6	0	2	0	0	0	0	147
Pine #5	81	14	1	2	0	0	1	0	0	99
Red maple #1	24	5	1	0	0	0	0	0	0	30
Red maple #2	7	1	0	0	0	0	0	0	0	8
Red maple #3	6	1	0	0	0	0	0	0	0	7
Red maple #4	6	1	0	0	0	0	0	0	0	7
Red maple #5	10	1	1	0	0	0	0	0	0	12
Sugar maple #1	117	14	1	0	0	0	0	1	0	133
Sugar maple #2	38	3	0	1	0	0	0	0	0	42
Sugar maple #3	138	13	0	0	0	1	0	0	0	152
Sugar maple #4	105	10	2	0	0	0	1	0	0	118
Sugar maple #5	101	12	2	0	0	0	1	0	0	116



law are not obvious. There are large deviations (negative and positive) from the estimated average exponent (-1.1577) of all species when tree height is below 150 cm or when shoot quantity is less than 150 (Fig. 4).

Log(length)

Our results only partially confirm the existence of a power law in tree shoot lengths. The data collected from this experiment indicated that the shoot lengths of overall individuals of each species and overall individuals of all three species follow a power law, but at species level loblolly pine and sugar maple follow a power law different than that of red maple. At the individual level, only loblolly pines and sugar maples follow the same power law.

It was expected that each individual of three species would follow a power law because the tree shoots are a network and networks in nature are usually considered to follow power laws (Brown et al. 2002). Further, shoot growths of other pine species were also found to follow a power law (Suzuki and Suzuki 2009). Another case of pine branches that has already

2.5

2.5

3

been discovered to follow a power law is the relationship between the diameters of the branches and stem of Pinus radiata (Watt et al. 2005).

Power laws were also found in other patterns of pine trees, such as diameter of xylem conduits. Coomes et al. (2007) indicated that tree conduits grow narrower in a pattern which follows a power law. The environmental factor that caused the shoot growth to be governed by a power law was not discovered, but ecological interactions (e.g., competition) can cause variations in exponents of power law (Kaitaniemi and Lintunen 2008). It is likely that a hormone or other chemical growth regulator was responsible for the growth patterns in the four species (Suzuki and Suzuki 2009). In this study, both red maples and sugar maples are both under strong ecological interactions with surrounding other plants, but sugar maples still follow the same power law with that of loblolly pines.

It was expected that the shoots of the red maple trees would also follow a power law. However, this

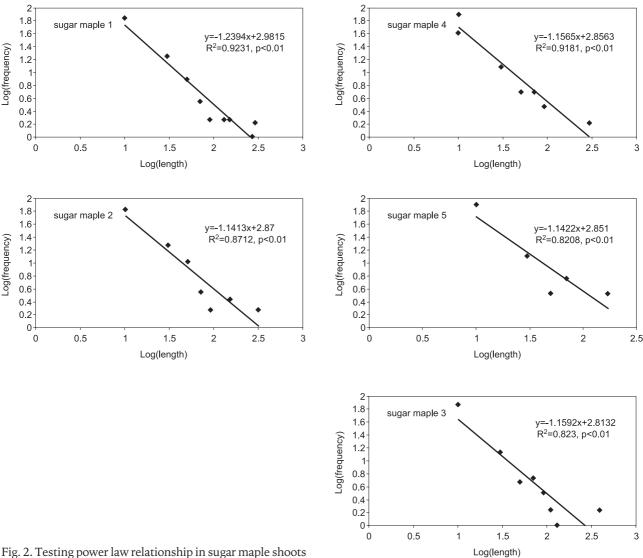


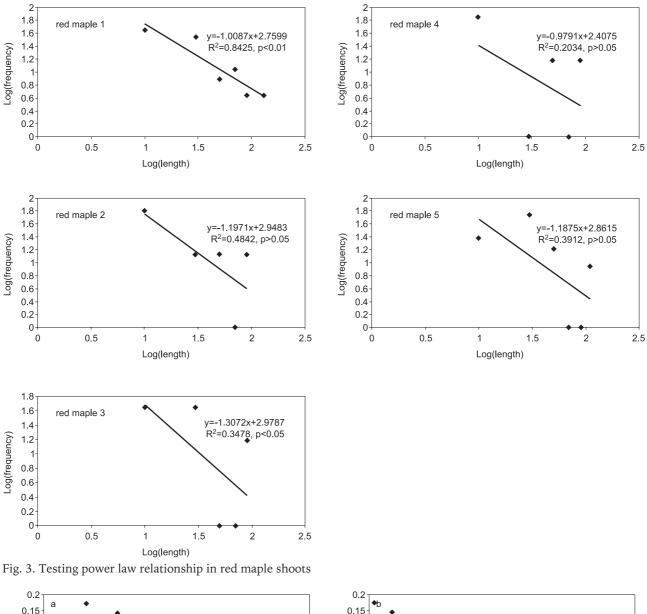
Fig. 2. Testing power law relationship in sugar maple shoots

was not the case. The shoot lengths of the most red maple individuals in this experiment do not follow a power law although shoots from all individuals still follow a power law. This likely occurred because the red maples were not fully mature. Specimens were approximately three to five years old and their canopy tops were similar in height to the surrounding plant community. Since tree height covaries with tree age, tree height may be one of the potential factors in this study. Also, the canopy of each red maple was not fully developed. It is possible that they were still competing strongly with surrounding species for resources. Based on this idea, the relationships between tree height vs exponent and shoot quantity vs exponent were investigated. It appeared that there was a bifurcation of deviations in average exponent when tree height is below 150 cm or when shoot number is below 150, although taller trees are needed for further study. This may support that power laws may not apply to immature trees or trees under environmental stress (Chen and Li 2003).

This study showed that two of the most common tree species in North America, loblolly pine and the sugar maple, have branch systems at the individual and species level that follow the same power law. However, immature trees of red maple do not follow the power law. A further study of power laws at different stages of tree growth is needed. The findings of this study contribute to what is already known about power laws and trees, especially for loblolly pines, red maples, and sugar maples. With power laws, research performed on a small scale can often be used to make predictions about patterns in larger scales. However, the predictive power of power laws and its limitations should be tested by more tree species and science will continue to grow closer to understanding the underlying factors of Earth's vast biodiversity.

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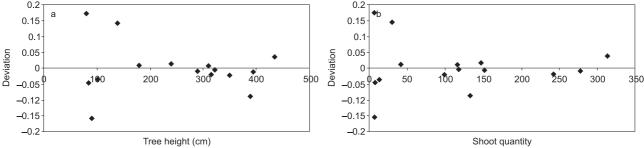


Fig. 4. Deviations (negative and positive) from the average exponent along tree height (a) and shoot quantity (b)

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References

Brown J.H., Gupta V.K., Li B.L., Milne B.T., Restrepo C., West G.B. 2002. The fractal nature of nature: power laws, ecological complexity and biodiver-

sity. The Philosophical Transactions of the Royal Society 357: 619–626.

Chen X.W., Li B.L. 2003. Testing the allometric scaling relationships with seedlings of two tree species. Acta Oecologica 24: 125–129.

Coomes D.A., Jenkins K.L., Cole L.E.S. 2007. Scaling of tree vascular transport systems along gradients of nutrient supply and altitude. Biology Letters 3: 86–89.

- Hack J.T. 1957. Studies of longitude stream profiles in Virginia and Maryland. USGS Professional Paper 294-B: 45–97.
- Hallé F., Oldeman R.A.A., Tomlinson P.B. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin.
- Kaitaniemi P., Lintunen A. 2008. Precision of allometric scaling equations for trees can be improved by including the effect of ecological interactions. Trees 22: 579–584.
- Le Hardy de Beaulieu A. 2003. An illustrated guide to maples. Timber Press, Portland, USA.
- Malamud B.D., Millington J.D.A., Perry G.L.W. 2005. Characterizing wildfire regimes in the United States. Proceedings of National Academy of Sciences USA 102: 4694–4699.
- Muller-Landau H.C., Condit R.S., Chave J., Thomas S.C., Bohlman S.A., Bunyavejchewin S., Davies S., Foster R., Gunatilleke S., Gunatilleke N., Harms K.E., Hart T., Hubbell S.P., Itoh A., Kassim A.R., LaFrankie J.V., Lee H.S., Losos E., Makana J.R., Ohkubo T., Sukumar R., Sun I.F., Supardi N.M.N., Tan S., Thompson J. Valencia R., Munoz G.V., Wills C., Yamakura T., Chuyong G., Dattaraja H.S., Esufali S., Hall P., Hernandez C., Kenfack D., Kiratiprayoon S., Suresh H.S., Thomas D., Vallejo M.I., Ashton P. 2006. Testing metabolic ecology theory for allometric scaling of

- tree size, growth and mortality in tropical forests. Ecology Letters 9: 575–588.
- Peters R.H. 1983. The Ecological Implications of Body Size. Cambridge University Press.
- Schultz R.P. 1997. Loblolly Pine: The Ecology and Culture of Loblolly Pine (*Pinus taeda L.*). U. S. Department of Agrciculture, Forest Service, Washington, DC.
- Sokal R.R., Rohlf F.J. 1981. Biometry: The Principle and Practices of Statistics in Biological Research. Second Edition. W.H. Freeman and Company, NY.
- Suzuki A.A., Suzuki M. 2009. Why do lower order branches show greater shoot growth than higher order branches? Considering space availability as a factor affecting shoot growth. Trees 23: 69–77.
- van Gelderen D.M. 1994. Maples of the world. Timber Press, Portland, USA.
- Watt M.S., Moore J.R., McKinlay B. 2005. The influence of wind on branch characteristics of *Pinus radiata*. Trees 19: 58–65.
- West G.B., Brown J.H., Enquist B.J. 1999. A general model for the structure and allometry of plant vascular systems. Nature 400: 664–667.
- Zianis D., Muukkonen P., Mäkipää R., Mencuccini M. 2005. Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs 4: 1–63.