

Article

## Variation in Fractal Symmetry of Annual Growth in Aspen as an Indicator of Developmental Stability in Trees

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**Abstract:** Fractal symmetry is symmetry across scale. If one looks at a branch of a tree its branching pattern is reminiscent of the tree as a whole. Plants exhibit a number of different symmetries, including bilateral, rotational, translational, and fractal; deviations from each of these types has been associated with organisms developing in stressful environments. Here, we explore the utilization and meaning of fractal analysis on annual growth ring production in woody plants. Early detection of stress in plants is difficult and the compounding effects of multiple or severe stressors can lead to irreversible damage or death. Annual wood production was used to produce a time series for individuals from stands classified as either high vigor or low vigor (a general measure of health). As a measure of symmetry over time, the fractal dimension of each time series was determined and compared among vigor classes. We found that individuals obtained from low vigor sites had a significantly lower fractal dimension than those from high vigor sites. These results agree with patterns found in a variety of other organisms, and we argue that the reduced fractal dimension is related to a loss in system complexity of stressed individuals.

**Keywords:** dendrochronology; fractal patterns; developmental instability; physiological response; plant stress; symmetry of scale

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## 1. Introduction

Evaluating plant health remains a challenge despite numerous studies and significant progress in the field (see below). There is currently no direct measure for plant health and in fact, there is not even a clear definition (reviewed in [1]). What can be agreed upon is that prolonged stress to an organism reduces vigor which in turn reduces that individual's general measure of health. Indicators of plant health are no different; typically defined on a comparative basis and measured indirectly through the description of observable traits (*i.e.*, crown loss [2], percent damage [3], photosynthetic rates [4], net photosynthesis [5], critical wilting [6], insect damage (but see [7]), and various imaging techniques [8]). The presence of measurable change, however, implies an advanced stage of health decline which may or may not be reversible [9]. One method to detect underlying stress in a population is through measurements of developmental stability [10,11]. Although fluctuating asymmetry (random deviations from bilateral symmetry) is the most commonly used measurement, others include phyllotaxy, equiangular spirals, and fractal dimension [12]. For this study we focus on the fractal dimension of annual growth rings in trees.

Fractals derive their name because in many, but not all, cases they have non-integer dimensions [13,14]. True fractals display symmetry of scale, and are infinitely complex. Although natural objects are only approximate fractals, fractal geometry and analysis serve an important role in the natural sciences. One example is the replacement of smooth, Euclidean shapes historically used in models by more accurate fractal shapes, representative of many natural objects such as coast lines, clouds, and tree crowns [15,16]. The fractal dimension of an object is often used to describe the roughness of its surface or edge [17,18]. This type of analysis describes the ability of the object to fill space, and is useful when considering things like photosynthetic surface area (canopy cover [19]), surface gas exchange (leaf or stem surface area [20]), and water or nutrient acquisition (root systems [21]). Fractals are also well known for their property of self-similarity or scale-independence. The concept of self-similarity is important for parsimony and design models (e.g., structure of a fern [22]), developmental stability [12], and the prevalence of self-similar systems present in the natural world gives rise to questions regarding order and fundamental rules of nature [23]. A third application of fractal analysis describes the roughness of a time series, displaying symmetry of scale over time [24,25]. This type of fractal application has been widely used in the medical field to monitor heart rate, brain wave, blood pressure, and other biological processes in humans ([26] and references therein); however, this technique has only rarely been used to evaluate developmental stability in plants [12,27].

Correlations between fractal dimension and stress have been observed in numerous animal species. The fractal dimension of behavior patterns have been measured and correlated to general health or stress in chimpanzees [28], fathead minnows [29], Iberian ibex [30], and domestic hens [31]. In plants, fractal analysis has been used to correlate the fractal dimension of physical measurements (self-similarity) to stress. Two examples are differential shoot branching patterns across grazing and water stresses in green pepper [32], and differential root branching across a nitrogen gradient in corn [33]. Finally, it is worth mentioning that fractal measurement and analysis of human system processes over time has been widely explored. For example, the fractal dimension of an individual's heart rate has been shown to be a reliable indicator of heart disease in humans [34,35], and the fractal dimension of electroencephalogram (EEG)

activity, which detects electrical activity in the brain, has been correlated to Alzheimer's [36]. In all of the cases described above, the fractal dimension of the measured trait decreased with increased stress.

Lipsitz [26] suggests that healthy organisms have complex systems. He argues that a complex system is better able to react to stress, and can do so quickly and on many levels. This idea is not a new one. Emlen *et al.* [37] outline what they refer to as the attractor hypothesis which is a theory that accounts for detailed adaptive responses of an organism to their continuously changing environments. In both accounts, disease or stress reduces the health of the organism, which can then impose a loss of complexity within the system and enhance susceptibility to additional diseases or stressors [26,37]. In the case of trees, growth depends on several variables, but, for example, is critically dependent on water availability. Precipitation is generally inconsistent with a high fractal dimension [38]. Individual trees respond to resource availability in a complex way. They grow more and store resources when resources available and less when they are limited. This is referred to as environmental buffering and the more successful an individual is in this buffering, the healthier it should be. In this study, we use fractal analysis to examine the time series produced from annual growth rings in low and high vigor trees. We then estimate and compare the fractal dimension of the time series between classifications to determine if the fractal dimension of annual growth can be used as an indicator of developmental stability in trees.

## 2. Methods

Eighteen trembling aspen (*Populus tremuloides* Michx.) increment cores were selected from a larger sample collected for a study on aspen decline in northern Minnesota. The subset of cores used in this study was selected based on age, with only the oldest trees being used due to the requirement of many annual rings needed to obtain an accurate estimate of fractal dimension. Tree age ranged from 62 to 118 years with an average age of 88.6 (Table 1). Samples were collected at breast height (1.4 m) in June and July 2009 (incomplete rings from 2009 were excluded from all analysis). All cores were prepared according to standard techniques [39], dated by hand, then read and cross-dated using COFECHA [40]. For this study, nine cores were selected from three stands classified as high vigor stands, and nine cores were selected from three stands classified as low vigor stands (for a total of 18 cores from six stands in two vigor classes). Vigor classification was based on visual assessment and verified with average annual stand growth over the last decade. High vigor stands were characterized by an average annual growth greater than  $816 \text{ mm}^2 \cdot \text{year}^{-1}$  and low vigor stands by an average annual growth less than  $452 \text{ mm}^2 \cdot \text{year}^{-1}$  [41]. Annual growth measurements are determined using basal area increment measurements. As the diameter of the tree increases, the same amount of wood production is represented by smaller and smaller rings. Therefore, ring width is a biased predictor of secondary growth so annual wood production, (*i.e.*, basal area increment), is used.

The set of basal area increment measurements for each tree was computed using ring widths and the dplr package for R [42] to produce a time series (Figure 1). The fractal dimension of each time series was calculated using a variation of the variogram estimator [25] which utilizes a lag ( $l$ ) of stationary increments. Specifically, if  $S(t, l)$  is the sample standard deviation of the time series from time  $t$  to time  $t + l - 1$  and  $R(t, l)$  is the range of the time series observations from time  $t$  to time  $t + l - 1$ , then  $\frac{R(t, l)}{S(t, l)}$  is known as the rescaled range. If we then let  $R(l)$  be the average of all the rescaled range values for a

given lag  $l$ , then the Hurst coefficient can be calculated by determining the slope of the line obtained from plotting  $\log(R(l))$  against  $\log(l)$  for multiple values of  $l$  (Figure 2 [43–45]). The Hurst coefficient ( $H$ ) is directly related to fractal dimension (FD) by the equation  $FD = 2 - H$  for a given time series. Below is a summary of the algorithm used to estimate the fractal dimension of a tree core:

- (1) Measure annual tree ring widths and determine corresponding tree diameters (DBH) by commutatively adding ring radii.

Calculate annual basal area (BA) and produce a time series.

$$BA = \pi \left( \frac{DBH}{2} \right)^2 \quad (1)$$

- (2) For each time lag (*i.e.*, scale)  $l = 3, 4, 5, \dots, 90$ .

Calculate the standard deviation,  $S(t, l)$ , and range,  $R(t, l)$ , of the time series observations from year  $t = 1$  to year  $t = l$ .

Repeat for all values of  $t$  applicable for the time series (*i.e.*,  $t + l - 1 =$  tree age).

Calculate the rescaled range,  $\frac{R(t, l)}{S(t, l)}$ , for each applicable  $t$  and the average rescaled range,  $R(l)$ , for each lag  $l$ .

$$R(l) = \frac{1}{t} \sum_t \frac{R(t, l)}{S(t, l)} \quad (2)$$

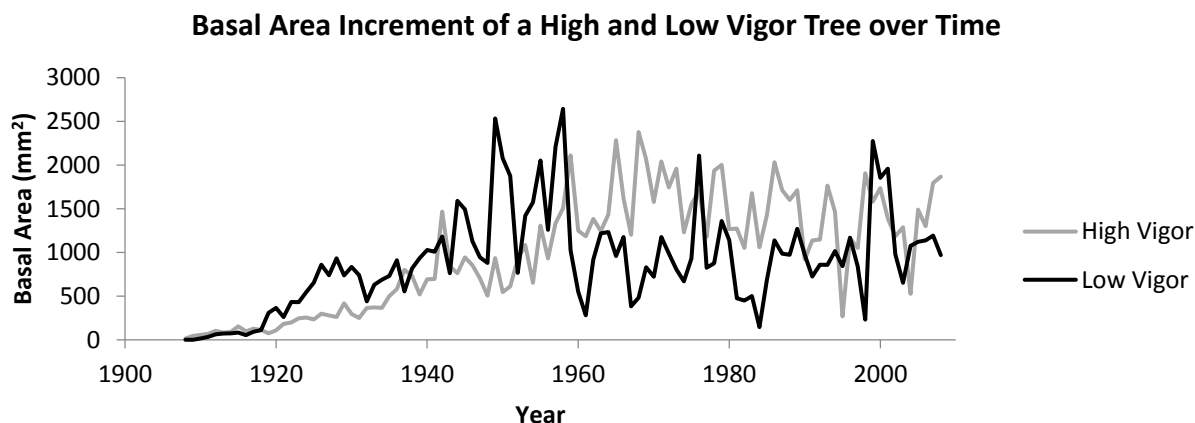
- (3) Plot  $\log(R(l))$  against  $\log(l)$  for all values of  $l$  and determine the slope of the line using least squares. The Hurst coefficient,  $H$ , is the slope of this line.

- (4) Calculate the fractal dimension, FD, using the equation:  $FD = 2 - H$ .

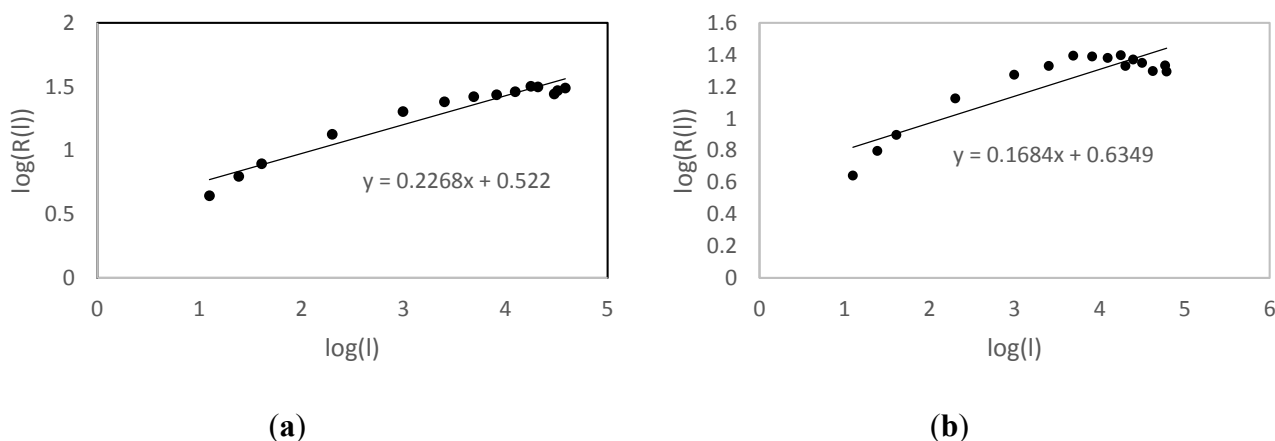
To determine if fractal dimension differed between vigor classes and if tree age had an effect on the results we used an ANCOVA with fractal dimension as the dependent variable, vigor classification as the independent variable, and age as the covariate (Table 1).

**Table 1.** Fractal dimensions (FD) and age of 18 aspen (*Populus tremuloides*) trees. Nine individuals came from stands of high vigor (High) and nine from stands of low vigor (Low).

Tree	FD		Age	
	High	Low	High	Low
1	1.802	1.728	79	96
2	1.736	1.741	100	100
3	1.818	1.779	72	91
4	1.805	1.773	116	86
5	1.829	1.729	118	89
6	1.814	1.779	118	90
7	1.819	1.728	71	73
8	1.756	1.744	79	87
9	1.766	1.824	68	62



**Figure 1.** Time series data for an aspen (*P. tremuloides*) individual from a low vigor stand (FD = 1.741) and an individual from a high vigor stand (FD = 1.818). The difference in roughness of the two time series can be seen. The high vigor tree has more peaks and troughs, but generally with smaller amplitude compared to the low vigor tree.



**Figure 2.** Log-log graph and corresponding slope ( $\alpha$  Hurst coefficient) and  $R^2$  values of the average stationary increment (or lag),  $l$  vs. the average rescaled range  $R(l)$  for all individuals in high and low vigor classes. (a) Low vigor,  $\alpha = 0.227$ ,  $R^2 = 0.938$ ; (b) High vigor,  $\alpha = 0.1687$ ,  $R^2 = 0.804$ .

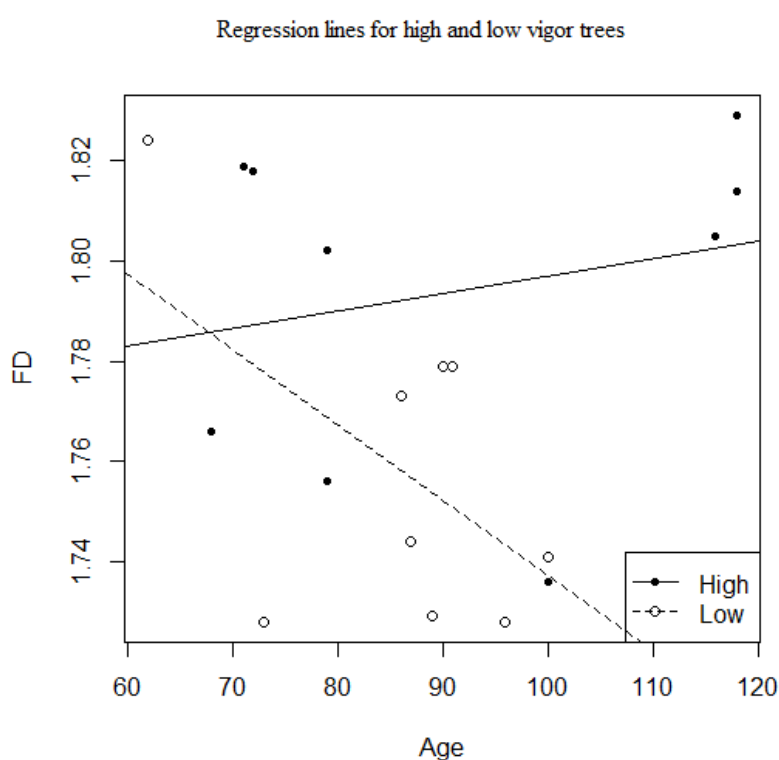
### 3. Results

Low and high vigor trees display significantly different fractal dimensions (Table 2). Low vigor trees have an average fractal dimension of  $1.758 \pm 0.033$  while high vigor trees have an average fractal dimension of  $1.794 \pm 0.033$ . The first ANCOVA model included age, vigor, and the interaction effect between age and vigor classification (Figure 2). Both age and the interaction between age and vigor classification were not significant ( $F = 0.045$ ,  $P = 0.835$  and  $F = 2.83$ ,  $P = 0.114$  respectively) while classification group was significant ( $F = 5.561$ ,  $P = 0.033$ ). The lack of a significant interaction effect indicates that the regression between age and fractal dimension is similar for both low and high vigor groups (Figure 3). A model without the interaction effect was then run. Again, age was not significant ( $F = 0.040$ ,  $P = 0.844$ ) while classification was ( $F = 4.95$ ,  $P = 0.042$ ). Finally, an ANOVA was used to

compare the two models ( $F = 2.835$ ,  $P = 0.1144$ ). Insignificant results indicate that the removal of the interaction effect does not significantly affect the fit of the model. The only significant effect on the fractal dimension of an individual was the vigor classification group it was assigned to.

**Table 2.** One-way analysis of covariance with fractal dimension as the dependent variable, vigor classification as the independent variable, and age as the covariate. \* indicates values significant at  $\alpha = 0.05$ .

Source of Variation	df	Sum of Squares	F	P
Age	1	$4.61 \times 10^{-5}$	0.040	0.844
Vigor Classification	1	$5.67 \times 10^{-3}$	4.954	0.042 *
Residuals	15	$1.72 \times 10^{-2}$	—	—



**Figure 3.** A scatter plot of tree age *versus* fractal dimension (FD) and corresponding regression lines for both high and low vigor trees. Despite appearances, there is no significant difference between the two slopes (High slope = 0.0003, low slope =  $-0.0015$ ,  $F = 2.83$ ,  $P = 0.1144$ ), indicating that the regression between age and FD is similar for both vigor classifications and there is no association between tree age and fractal dimension.

#### 4. Discussion

Our results indicate that stressed trees display a lower fractal dimension in their growth patterns compared to healthy trees and coincides with previous studies across a variety of organisms. One way to compare results among studies is to calculate the ratio between the Hurst coefficient (slope of the  $\log(l)$ - $\log(R(l))$  graph) of healthy and stressed groups. In this study the average Hurst coefficient of the high vigor group was 0.853 times that of the low vigor group ( $H_H/H_L$ ), a value comparable to values found in previous studies on animal behavior (0.803 [28]; 0.884 [29]; 0.74 and 0.798 [30]), plant growth

(0.854 [32]; 0.871 [33]), and time series analysis of heart rhythms (the difference between healthy and various diseases ranged from 0.79 to 0.941 [36]).

While average growth rates confirmed our vigor classifications at the stand level, a decline in growth within an individual tree does not necessarily translate to a decline in health. Growth of a complex organism like a tree requires a suite of interconnected physical (*i.e.*, apical and lateral growth, nutrient transportation, leaf and root production), chemical (*i.e.*, hormone production and regulation, photosynthesis, respiration), and biological (*i.e.*, dormancy, reproduction) processes. To help visualize how this complex system of processes may operate imagine a series of overlapping sine curves where the state space contains all vital life processes and the final output is growth. A system in its most basic state can be represented by a single curve (*i.e.*, carbon sequestration). Alone, however, this process cannot support the tree. As the system becomes more complex, the number of curves increases (representing processes such as water and nutrient uptake and transport, respiration, and hormone production), each with a different frequency or amplitude. This complexity allows the organism to function smoothly; curves compensate for each other as peaks and troughs overlap. Consider that each curve contributes in some way to our final output which is growth. When there is only one curve, growth occurs in fits and starts. When there are many curves, growth occurs at a fairly constant and close to ideal rate, although the curves vary continuously. (It is important to understand that the ideal growth rate will itself fluctuate based on the environment and available resources). When stress is introduced to the system, energy is required to alleviate that stress-energy that must come from somewhere within the system. As a result, the system experiences a loss in complexity, which in turn affects growth, until the stress is relieved and the system recalibrates [9,46]. Based on this idea, the theory proposed by Emlen *et al.* [37] and Lipsitz [26], and evidence provided by previous studies, our results suggest that the fractal dimension of the tree ring data reflects an individual measure of developmental instability. The lower fractal dimension seen in the low vigor trees could be indicative of a lower state of system complexity (as we observed) due to stress which has diminished those individuals' ability to respond dynamically to its environment. In another fundamental sense, the loss of dimension means literally a loss of the symmetry across time scales.

Growth and wood production (or biomass in general) is often used as a measure of health, and is thought to be a particularly sensitive indicator of stress [47]. Other energy and resource sinks including leaf, bud, and root production, maintenance, and storage tissue production all take precedence over secondary stem growth [48]. Reduced secondary growth is expected if there is a general lack of resources or if extra resources are required to fight disease, regenerate after defoliation, or otherwise respond to a disturbance. However, if there were little or no lasting effects of a stressful year on the individual, we expect that wood production would more or less reflect the environmental conditions of the year in which it was produced. In fact, this is often the case and a high correlation between annual precipitation and growth is a necessary assumption when tree ring chronologies are used to reconstruct historic climate data [49,50]. However, there are many studies that document the long term influence on growth by a single climatic [51] or herbivory [52] event (also see [1] and references therein).

The focus of this study was not to evaluate the mechanisms influencing stand vigor, only to examine the fractal dimensions within different vigor classes. However, the six stands represented in this study are similar with respect to soil, weather, and elevation; there is no natural gradient with which to further classify them, and all things being equal, we would expect the annual growth, vigor, and fractal

dimensions to be similar. Clearly, differences among local site conditions exist, some of which are responsible for the variation in stand vigor. Differential competition, insect damage, and local weather patterns are all possible factors affecting stand vigor. For this study, however, we did not identify which factor(s) affect stand vigor but instead focused on the correlation between fractal dimension and stand vigor class.

## 5. Conclusions

Our results support the idea that healthy individuals exhibit higher system complexity compared to stressed individuals which can be measured by fractal analysis. Higher system complexity in healthy individuals allows for more efficient reactions to a fluctuating environment, maintaining homeostasis. Individuals from stands that had low vigor were not producing consistently smaller basal area increments compared to individuals from high vigor stands, but the pattern with which wood was produced differed. A healthy individual from a high vigor stand produced wood dynamically resulting in a rough time series; differential production between years presumably correlates well with available resources. A stressed individual from a low vigor stand produced wood in a less dynamic pattern, resulting in a time series that was less rough. If our interpretation is correct, the fractal dimension of tree ring growth provides a measure of developmental stability over time in woody plants.

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## Author Contributions

JPS collected and processed tree cores, did the analysis and wrote the paper. DMK and JBB obtained funding for the collection of data and contributed knowledge of field site locations. DCF helped write the paper and made conceptual contributions.

## Conflicts of Interest

The authors declare no conflict of interest.

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