

# A SIMILARITY CRITERION FOR FOREST GROWTH CURVES

Georgii A. Alexandrov<sup>1</sup> and Georgy S. Golitsyn<sup>1</sup>

<sup>1</sup>A.M. Oboukhov Institute of Atmospheric Physics, Russian Academy of Sciences, Pyzhevsky 3, Moscow, Russia  
Correspondence and requests for materials should be addressed to G.A.A. (g.alexandrov@ifaran.ru)

Comparison of forest growth curves has led many to the conclusion that there is a similarity between forest stands growing in different conditions. Thus, in the beginning of the past century Alexander Turin, a well-known forest scientist, made an important empirical generalization: "The normal pine stands with equal heights at a certain age had the same growth in the past and will have the same growth in the future regardless of where they grow."<sup>1,2</sup> This empirical generalization (like other generalizations of this sort) defines similarities between growth curves in a quantitative way.

Here we treat the same subject from the viewpoint of similarity theory. Since the concept of biological similarity is extensively reviewed in the seminal work of Stahl<sup>3</sup>, we omit a detailed explanation of the general methodology that underlies our research and proceed to its goal.

Our goal is to form a dimensionless ratio of biophysical entities that could parameterize the diversity of forest growth curves. Such ratios are called *similarity criteria*. Similarity criteria for growth are often formulated in the form  $(1/B)(dB/dt)\tau$ , where B stands for biomass, for example, and  $\tau$  is a time constant, such as generation time. A criterion of this kind parameterizes the family of exponential curves. However, an exponential curve can approximate only a short part of a growth curve, because growth slows down with age.

Jorgensen and Svirezhev<sup>4</sup> explain the slowdown in growth as follows. The input of energy is proportional to the surface area of an organism, whereas its metabolism is proportional to its volume (or biomass). The surface area generally grows slower than volume. Therefore, the rate of energy supply comes in balance with the rate of energy dissipation. The generation time – that is, the period of more or less significant growth – is proportional to two-thirds power of the maximum size of the organism (so-called, Bonner's relation). The Boner's relation holds if the shape of the organism is relatively simple (e.g. spherical). However, if the surface of an organism is a fractal with dimension greater than 2 (but less than 3), then the exponent in the Bonner's relation should be higher than 2/3. That is why Bonner's relation works well in the case of mammals, and does not work well in the case of trees.

Application of the Jorgensen-Svirezhev theory in the study of forest growth led to conclusion that the biomass of a stand should be proportional to the four-fifths power of its biological age<sup>5</sup>. This recalls the well-known application of similarity theory that allowed Sir Geoffrey Taylor to evaluate the yield of an atomic explosion using only its photographs published in newspapers<sup>6</sup>. Therefore, we suppose that it might be a meaningful analogy between tree crown growth and atomic explosion. If so, we get a fresh insight to the physical nature of tree crown growth, which is essential for choosing the right biophysical entities for our similarity criterion.

The application of similarity theory to the atomic explosion is justified by the fact that the shape of the blast wave remains constant within certain time interval. Due to this reason one may apply the method which is known as the *dimensional analysis*<sup>7,8</sup>. The radius (R) of the blast wave is determined by the energy (E) released by the explosion, air density ( $\rho$ ), and time (t). Thus,  $R=F(E,t,\rho)$ , where F is an unknown function. On a certain time interval, F could be approximated by the monomial  $E^a \rho^b t^c$ , where a, b, c are unknown numbers. Let us find a, b, c at which the dimension  $[E^a \rho^b t^c]$  of the monomial  $E^a \rho^b t^c$  coincides with the dimension [R] of R.

Taking into account that

$$[E]=ML^2T^{-2}, [\rho]=ML^{-3}, [t]=T, [R]=L \text{ (where } M, T, \text{ and } L \text{ are dimensions of mass, time, and length, respectively)}$$

we get

$$[E^a \rho^b t^c]=M^{a+b}L^{2a-3b}T^{-2a+c}$$

and then

$$a+b=0; 2a-3b=1; -2a+c=0.$$

Thus

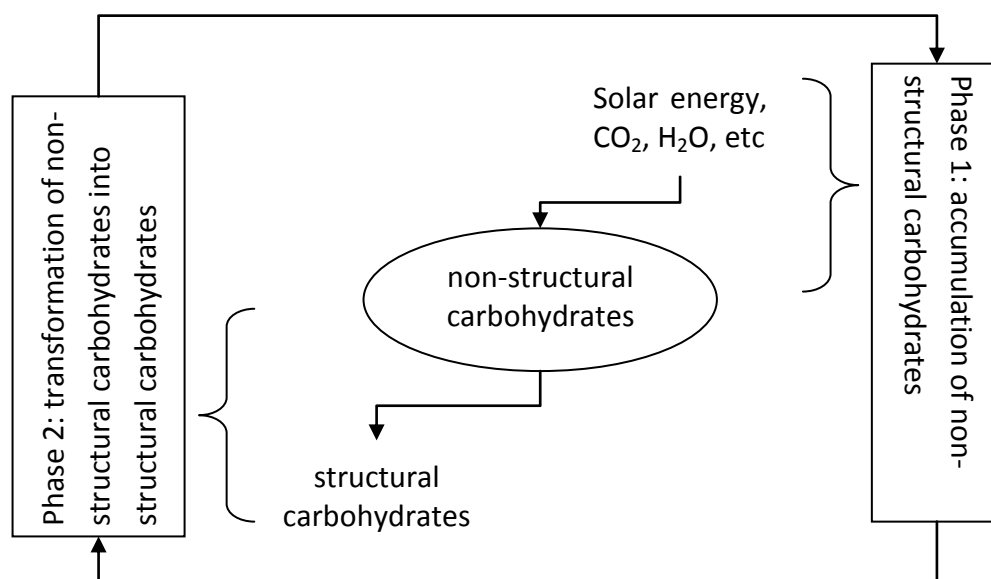
$$a=1/5, b=-1/5, c=2/5,$$

and

$$R=c_0(E/\rho)^{1/5}t^{2/5},$$

where  $c_0$  is a dimensionless constant.

The analogy between tree crown growth and blast wave propagation is easier to see in the case of deciduous species with spherical crowns. A typical deciduous tree accumulates non-structural carbohydrates during the growing season, keeps them over the dormant period, and then, in spring, translocates them to the buds, where they are transformed into structural carbohydrates of growing shoots and leaves (Figure 1)<sup>9,10,11</sup>. Since the rate of translocation is higher than the rate of transformation, the flow of non-structural carbohydrates achieves the tips of branches and enables the radial growth of crown. If the rate of translocation would be lower than the rate of transformation, all non-structural carbohydrates will be consumed inside the crown and nothing remains for its expansion.



**Figure 1. Conceptual scheme of tree crown growth.** (NB: one may distinguish two phases in the annual cycle of growth: accumulation of non-structural carbohydrates and their transformation to structural carbohydrates.)

The rate of radial growth ( $dR/dA$ ) thus depends on tree age ( $A$ ), the energy ( $E$ ) embedded in translocated non-structural carbohydrates, and crown density ( $\rho$ ) – that is,  $dR/dA = F(E, \rho, A)$ . (The crown density,  $\rho$ , is defined as the ratio of crown biomass to crown volume,  $V = (4/3)\pi R^3$ .) Let us assume that  $F$  could be approximated by the monomial  $E^a \rho^b A^c$  within each 1-year interval of tree growth (that is, when  $A_i \leq A < A_i + 1$ , where  $A_i$  stands for the tree age at the beginning of the  $i$ -th 1-year interval). Then we can find  $a, b, c$ , at which the dimension  $M^{a+b} L^{2a-3b} T^{-2a+c}$  of the monomial  $E^a \rho^b A^c$  coincides with the dimension  $L T^{-1}$  of  $dR/dA$ :

$$dR/dA = c_{0i} (E/\rho)^{1/5} A^{-3/5} \quad (A_i \leq A < A_i + 1)$$

If  $c_{0i} = c_0$  for each interval of tree growth, and  $E/\rho = \text{const}$ , then integration of the above equation results in

$$R = (5/2) c_0 (E/\rho)^{1/5} A^{2/5}.$$

Tree crowns cannot grow freely in a forest stand: space is limited there. If there would be no competition for space, the projective area of each crown ( $S_k$ ) would grow proportionally to the radius squared, and hence  $S_k$  would be proportion to the stand age ( $A$ ) raised to the 4/5-th power:

$$S_k = c_{1k} (E_k/\rho_k)^{2/5} A^{4/5}$$

The total projective area of crowns ( $S$ ) would grow in similar way:

$$S = \sum S_k = (\sum c_{1k} (E_k/\rho_k)^{2/5}) A^{4/5}$$

where  $\sum c_{1k} (E_k/\rho_k)^{2/5}$  can now indicate the class of growth (stand productivity) and can be identified by the  $S/A^{4/5}$  ratio.

Since competition for space changes the growth of an individual tree, we cannot expect that coefficients  $c_{1k}$  remains constant. We may only hope in this case that the sum  $\sum c_{1k} (E_k/\rho_k)^{2/5}$  remains constant. This may really happen in the *normal* forest stands. Normal stands are the stands where the density of forest cover is the highest among the stands of the same age and the same class of growth either due to optimal forest management or due to natural conditions. The negative effects of competition are minor there because the number of trees decreases in an optimal way. Hence  $S$  should be proportional to  $A^{4/5}$  in normal forest stands, and the curves displaying  $S$  growth in different normal stands should form an anamorphic spectrum, where each curve is identified by a single number which is equal to  $S/A^{4/5}$ .

The density of forest cover is characterized in practice by the stand basal area  $S_b$ . (The basal area is easier to measure than the total projective area of crowns.) Let us assume that  $S_b$  provides an indirect measure of  $S$ . Then we can suppose that  $S_b$  grows proportionally to  $A^{4/5}$  (like the projective area of crowns), and propose the following similarity criterion for normal stands:

$$\Pi_n = \frac{S_b/A^{4/5}}{\max_{A_l} [S_{b,l}/A_l^{4/5}]}$$

where  $S_l$  and  $A_l$  refer to the case of the  $l$  class growth.

The result of our study provides some theoretical ground for the empirical generalization made by Turin. We could explain now why the normal stands with equal heights at a certain age should have the same growth in the past and in the future. Our theory is as follows.

Every normal stand goes through the phase at which tree crowns are changing in scale, not in shape. During this phase (e.g. from age  $A_1$  till age  $A_2$ ) the basal area grows proportionally to the stand age raised to the 4/5 power. The coefficient of proportionality is completely determined by the basal area at a given age  $A^*$  that can

be taken arbitrarily from the interval from  $A_1$  to  $A_2$  ( $A_1 < A^* < A_2$ ). Due to this reason the curves displaying the growth of basal area cannot have common points within this interval: if two curves have a common point, they coincide. The same can be said about the height growth curves, because the average height of a normal stand and its basal area are linked by some allometric relationship.

It must be emphasized here that  $S$  grows proportionally to  $A^{4/5}$  only within a certain age interval. Our theory is based on the assumptions which are valid for a certain phase of stand growth. During this phase of growth  $\Pi_n$  remains relatively constant. However, one may distinguish three phases of stand growth: juvenile, mature, and senescent.  $\Pi_n$  increases during the juvenile phase, remains relatively constant during the mature phase, and decreases during the senescent phase. Hence, the similarity criterion for growth curves should be formulated as follows: *the growth curve of a normal stand can be identified by the maximum value that  $\Pi_n$  achieves over the whole period of growth.*

Figure 2 is to show how the similarity criterion could be applied to classification of growth curves. The upper left panel displays the growth of basal area in the normal stands of Siberian pine<sup>12</sup>. The changes in  $\Pi_n$  are displayed at the lower left panel. One may notice that  $\Pi_n$  remains relatively constant,  $0.8 \pm 0.025$ , over a span of 50 years (from 50 to 100 years of age). If a forest stand belongs to the I or III class of growth,  $\Pi_n$  varies in a wider range within the same age span (from 0.9 to 1.0 in the case of I class growth, and from 0.55 to 0.65 in the case of III class growth). Therefore, we can identify the class of growth based on  $\Pi_n$  calculated for a stand of any age that falls within this age span. If  $\Pi_n$  is above 8.5, the stand belongs to the I class of growth; and if it is below 7.5 (but above 0.5), the stand belongs to the III class of growth.

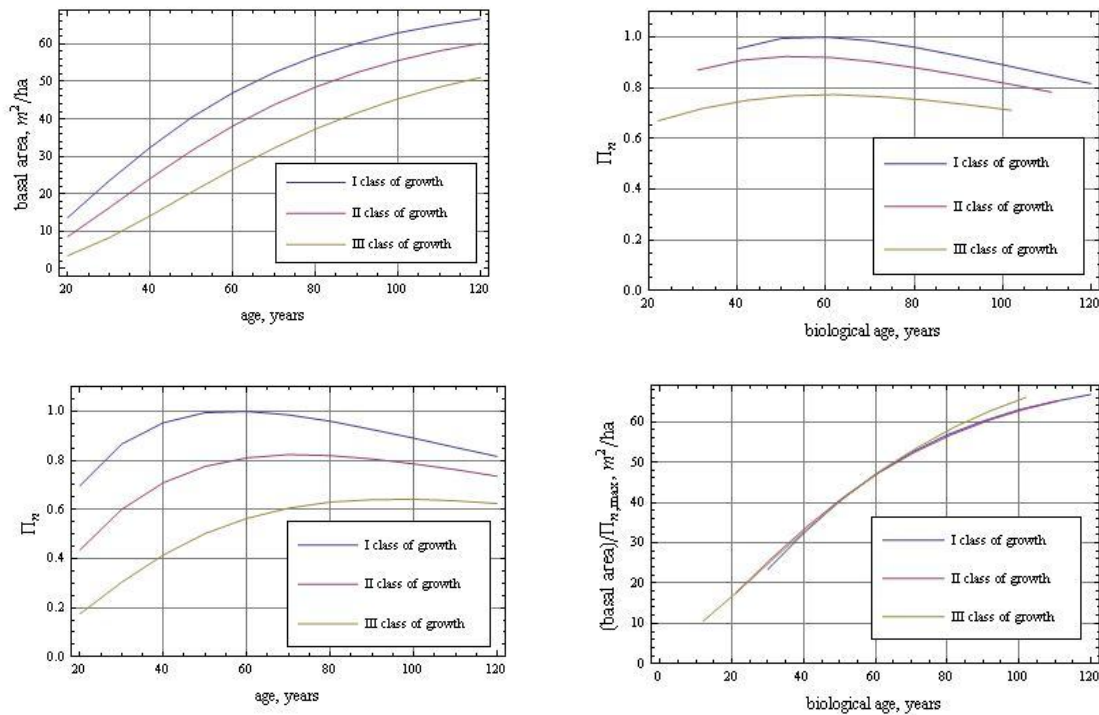
This case study suggests (in line with the empirical generalization made by Turin) that the variety of growth patterns can be represented by an one-parameter family of curves. However, it is almost impossible to prove the general validity of such a postulate on an empirical basis. Moreover, the Chapman–Richards model, which is often used in the studies of forest growth, generates a 4-parameter family of curves. Can we identify all the curves from the 4-parameter family by means of only one parameter?

As we can see in Figure 2, the highest value of  $\Pi_n$  ( $\Pi_{n,max}$ ) is achieved earlier in the more productive stand as compared to the less productive stands: at the age of 50 in the case of the I class of growth, at 70 in the case of the II class of growth, and at 90 in the case of the III class of growth. The delay in transition to the mature phase of growth can be conceptualized through the notion of biological age<sup>13,14,15</sup> and “rejuvenation bias”<sup>5</sup> (the difference between the calendar and biological age of the stand). The model  $S = (\sum c_{1k} (E_k / \rho_k)^{2/5}) (A - u)^{4/5}$ , where  $u$  is the rejuvenation bias, approximates well the Chapman–Richards model within the age interval corresponding to the mature phase of growth<sup>16</sup>. In other words, the middle part of a curve generated by the Chapman–Richards model for a set of 4 model parameters is determined by two parameters:  $\sum c_{1k} (E_k / \rho_k)^{2/5}$ , which characterizes stand productivity, and  $u$ . These two parameters are not independent: the higher is the first, the lower is the second. Hence, the middle parts of growth curves can be represented by an one-parameter family of curves.

In conclusion we would like to cite Zeide, who clearly depict the long-standing problem that we attack in our research: “Shortcomings of the presentation of growth by formulas are rarely discussed. Unlike equations for physical laws, functions used to describe tree or stand growth do not reflect the essence of growth.”<sup>1</sup>

We employed here the method which is commonly used to derive physical laws<sup>7,17,18</sup>. In contrast to the previous work<sup>5</sup> on the similar subject, we focus on the analogy to atomic explosion. A blast wave is formed when the rate of energy release is much higher than the rate of energy dissipation. The difference between the rates of energy release and dissipation is the essence of this phenomenon. The essential feature of crown growth is the difference between the rates of non-structural carbohydrate supply and demand. Since the rate of supply is much higher than the rate of demand, the flow of non-structural carbohydrates achieves the tips of branches and enables the radial growth of crown. (Otherwise, crowns would grow in weight, not in size.)

Proceeding from these ideas, we derived the similarity criterion which supposedly captures the “essence of growth” that emerges from the geometric similarity of tree crowns.



**Figure 2. Similarity criterion for the curves displaying the growth of basal area in the normal stands: the case study of Siberian pine.** The upper left panel shows the standard curves reported by Semechkin et al.<sup>12</sup> The lower left panel shows how the normalized similarity criterion ( $\Pi_n$ ) is changing along these curves. The upper right panel shows the changes in  $\Pi_n$  calculated proceeding from the biological age of the stands (rejuvenation bias is set at 9 and 18 years for the stands of II and III class of growth, respectively). The maximum values of  $\Pi_n$  ( $\Pi_{n,\max}$ ) are equal to 0.92 and 0.77 in the stands of II and III class of growth, respectively. At the lower right panel we plot the values of basal area divided by  $\Pi_{n,\max}$  against the biological age of the stands to show that the middle parts of the curves shown on the upper left panel can be approximated by an one-parameter family of curves.

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**NB.** This is a pre-publication release of research results that will be submitted for publication to a peer-reviewed journal.

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