

An Examination of Individual Tree Diameter Growth of Laurel  
(*Cordia alliodora*) in a Panamanian Lowland Moist Tropical Forest

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The assessment of tree growth is critical to our understanding of forest dynamics and for making economic decisions. Based on crossdated increment cores, yearly tree diameters were reconstructed for 21 laurel (*Cordia alliodora*) trees growing in a secondary natural forest on Gigante Peninsula (GP), Panama. Ages ranged from 14 to 35 years with an average of 25 years. Tree growth typically slowed at age seven indicating competition effects from the closure of gaps in the forest canopy. Tree diameter growth rate was modeled using the Bertalanffy-Richards growth function. Four different growth patterns were found, of which 52% were sigmoidal, 20% were inverse sigmoid, 14% were convex, and 14% were monomolecular. Environmental reasons for the growth patterns are discussed.

## 1. INTRODUCTION

Laurel (*Cordia alliodora* (Ruiz and Pav.) Oken) is a tropical hardwood with an extensive natural range extending from Mexico to Argentina, 25° N to 25° S. The other commonly used commercial name for *C. alliodora* is salmwood. It is an important timber species, and is frequently used in agroforestry as shade for cacao,

coffee, other agricultural crops and farm animals. Laurel grows to 25-45 m in height and 60-100 cm in diameter under optimum conditions. More commonly, it reaches 20 m in height and 46 cm in diameter (Somarriba and Beer 1987, Liegel and Whitmore 1991). In seasonally dry lowland tropical forests, most tree species lose their leaves during the dry season; but in Panama, laurel becomes deciduous for several months after the rains begin (Foster 1985). It is now understood that laurel is “evergreen as a seedling, semi-deciduous (in the dry season) as a sapling, and deciduous (in the wet season) as a mature tree” (Menalled et al. 1998).

To fully exploit the potential of this species, a better understanding of its growth dynamics is needed. A number of studies of laurel growth have been conducted. Some studies have concluded that there are several factors that contribute to the survival and growth of *C. alliodora*, including physical and chemical soil characteristics, site physiography, and the management of the trees with associated crops (Menalled et al. 1998, Hummel 2000a, Somarriba et al. 2001). Somarriba et al (2001) determined that the style of plantation management accounted for 56% of the variation in the site index values; while soil and mineral factors accounted for only 3 to 10% of the variation in the site index values. Site index is the average height of the dominant and co-dominant trees in an even-aged stand. The index age is normally chosen to be around the mid-point of the life of the tree species or harvest age. In this case, the index age was five years. The plantation types that offered the greatest amount of open space in well drained, fertile soils were most likely to have the largest amount of growth. Although my study involves diameter and not height, it is important to know the optimum growing conditions for laurel, whether it occurs in a plantation or in a natural stand.

Schlönvoigt and Beer (2001) also agree that laurel requires a great amount of space for initial growth. They used an altered Nelder-fan design to study the effects of tree-crop distance on the growth and development of this tree. The Nelder-fan is a circular design plot that allows the plants to be spaced at ever increasing distances in order to study density relationships. There was no significant difference between the growth of the seedling when it

was planted with corn versus in a monoculture, where all of the trees are of the same species. However, laurel was completely inhibited while it grew under the shade of the crop plant cassava. Cassava grows twice as high as corn. The tree seedling crowns never penetrated the crowns of cassava, but it is interesting to observe how the laurel seedlings reacted to the harvesting of the cassava plants in this study since it might mimic the conditions of a sudden clearing in a natural forest stand. Once the cassava plants were harvested, the seedlings were released from suppression and continued to grow with renewed vigor (Schlönvoight and Beer 2001).

It is not unlikely that a young suppressed laurel tree would suddenly begin growing rapidly in the event of a new gap in the forest near the tree. However, the present study will show that a few of the mature trees between ages 7.4 to 14.5 years also experienced renewed growth, thus following a non-typical growth pattern. The significance of these studies is that *C. alliodora* shows the greatest amount of growth when it has little or no competition for light. This tree is considered a pioneer species in that it tends to be one of the first to invade clearings such as pastures, burned sites, and new gaps in the forest. Laurel also has difficulty with weed competition in regards to nutrient absorption (Menalled et al. 1998). Some grasses, such as *Melinis minutiflora* P. Beauv., can even have an allelopathic effect on laurel. Laurel has a narrow, self-pruning tree crown so a fairly large diversity of plants can grow beneath it (Hummel 2000b). Although Laurel reacts poorly to being shaded out, it does have the advantage of “high initial productivity and rapid canopy and root-system closure” (Haggar and Ewel 1995); unlike another pioneer species, *Eucalyptus deglupta* Blume, which when slightly overtopped, can quickly become suppressed and die (Evans 1992).

According to Johnson and Morales (1972), who reviewed laurel range, biology, and growth habitats, the best stands are located on the Caribbean coast of Honduras, Nicaragua, and Costa Rica. Growth data collected in old natural laurel stands in the Atlantic lowlands of Costa Rica reveal diameters (outside bark) at breast height (1.3 m) (referred to as dbh) of 79, 89, and 91 cm for 40-, 50-, and 60-year-old trees, respectively. Rosero and Gewald (originally published in Liegal and Whitmore 1991) reported mean dbh of laurel

growing in pastures and agricultural fields in Costa Rica as shown in Table 1. Liegal and Stead (1990) reported mean diameters for laurel growing in six plantations across Puerto Rico as shown in Table 2. These data are mentioned for comparison with the present study. The objectives of this study are: 1) to discover the pattern(s) of growth displayed by the trees on Gigante Peninsula (GP) in Panama, 2) draw inferences about growth of laurel in this secondary natural forest, and 3) make comparisons with laurel growth at other sites.

Table 1. Mean diameters by age class for laurel growing in agroforestry sites in Costa Rica compared with Panama's Gigante (Liegal & Whitmore 1991).

Site	Mean dbh (cm)	Estimated age (years)	Associated crops
Costa Rica			
Siquirres	35.3	15-20	Cacao
Cahuita	37.5	27-32	Pasture
Bribri	41.1	22-27	Cacao
Bajo Chino	30.7	17	Coffee
La Suiza	16.9	3-7	Coffee/Erythrina
La Suiza	21.5	3-15	Bamboo
La Suiza	22.7	15	Grassland
Panama			
Gigante	26.0	25	None

Table 2. Mean diameters by age for laurel growing in plantations in Puerto Rico (Liegal and Stead 1990).

Site	Mean dbh (cm)	Estimated age (years)	Life zone
Catalina	11.9	10	Subtropical wet
Tract 105	7.1	6	Subtropical moist
Luquillo	8.9	8	Subtropical moist
Carite	12.7	9	Subtropical wet
Guilarte	2.4	6	Subtropical wet
Guánica	9.0	10	Subtropical dry

## 2. METHODS

### 2.1. *Study site*

The area from which the trees were selected is a secondary forest in GP, Panama (9° 10' North latitude, 79° 51' West longitude). The site is directly across Gatun Lake from well known Barro Colorado Island (BCI). Gigante Peninsula as well as BCI were formed between 1910 and 1914 when the Chagres River was dammed. Today, GP is part of the BCI Nature Monument, which was established in 1977, so the area is protected from disturbances such as shifting agriculture and selective cutting. The last major disturbance occurred in 1937 with the banana blight. Gatun Lake is part of the Panama Canal and the area is considered an intermediate moist climate zone, one of three possible climatic regions in Panama. The three forest type regions in Panama are dry, moist and wet (Foster 1985). The average annual temperature in a clearing at BCI is 27°C with a diurnal range of 9°C. The potential evapotranspiration in the area is approximately 12 cm/month (Dietrich et al. 1982).

The rainy season in Panama extends from part of April through November, which is the wettest month (Foster 1985). Ninety per cent of the 2600 mm of annual precipitation happens during the rainy season (Dietrich et al. 1982). Most of the rainfall occurs during short-term storms in the early afternoon. During the dry season, the rain is light and sporadic (Rand and Rand 1982) because convective storms are turned away by trade winds (Dietrich et al. 1982).

The terrain has many hills with sedimentary rock containing volcanic debris. The soil is rich in clay; so the permeability is poor, particularly below the fine root zone, which includes the top 10 to 20 cm of the generally 50 cm depth of soil (Dietrich et al. 1982). Laurel has a high rate of mortality at sites with poor drainage, soil compaction, and a common occurrence of flooding (Somarriba et al. 2001). Soils that are rich in clay are highly susceptible to soil compaction; thus in areas where cattle may also be grazing, there would be a negative effect on tree growth because of laurel's

“behavior of developing only a lateral, superficial root system within its first years” (Bergmann et al. 1994). The roots of a mature laurel tree are far reaching in depth and in lateral growth (Haggard and Ewel 1995) with a limited amount of branching, a structure that is typical for plants that require large amounts of nitrogen. In fact, concentrations of nitrogen as high as 4% have been found in the leaves of *C. alliodora* in Costa Rica (Bergmann et al. 1994, Menalled et al. 1998). It is suggested that in plantation settings, laurel should be mixed with nitrogen fixing species to improve afforestation practices (Bergmann et al. 1994); however, some studies show that additional fertilization with nitrogen has a negative effect on laurel growth (Johnson and Morales 1972), perhaps because of the reduced need to grow more to attain the needed nutrient.

## 2.2. *Measurements and data description*

With the use of an increment borer, 21 laurel trees growing on GP were sampled during August of 1991 and 2 cores per tree were collected by Bernard Parresol and Margaret Devall of the USDA Forest Service; I accompanied them in 1993 for the collection of tree cores from *C. alliodora* and two additional tree species located in Panama. The 1991 data were used instead of the 1993 data because that was the dataset made available to me by the Forest Service (B. Parresol, personal communication).

Tree cores in this study were collected approximately at breast height (1.3 m); and diameter (inside bark) at each year for each tree was determined by cumulatively summing the ring widths of the two cores per tree. If a core missed the pith, the number of years and distance to pith were estimated. This permits analysis of diameter growth rate and total diameter growth. There is no bark within a tree core; so diameters determined from tree cores are inside bark. In order to measure the diameter outside bark, one would have to measure the same individual every year or per week in the case of a seedling. For a description of how the cores were prepared and crossdated see Devall et al. (1996). There were 457 diameter by age data points available for fitting the Bertalanffy-Richards function. A

brief summary of the raw data follows. The final breast height ages for the trees ranged from 14 to 35 years with mean and standard deviation (SD) of 24.5 and 6.0, respectively. The final tree diameters (inside bark) ranged from 15.7 to 41.9 cm with mean and SD of 26.0 and 6.1. Diameter growth rates ranged from 0.16 to 4.23 cm/yr with an average of 1.0 and SD of 0.67.

### 2.3. Growth analysis

The Bertalanffy-Richards growth model is a mathematical expression of the essential causes of the growth phenomenon, with parameters that possess a gross physiological or biological interpretation. Pienaar and Turnbull (1973) pose this model and its corresponding principles as a general theory of growth of broad and general validity. While some researchers question the legitimacy of the theoretical foundations (e.g., Ricker 1979), this model has nonetheless enjoyed widespread use. This equation is valued for its accuracy and is used more than any other function in studies of tree and stand growth (Zeide 1993).

#### 2.3.1. The classic Bertalanffy-Richards growth model ( $0 < m < 1$ and $\eta, \gamma > 0$ )

The Bertalanffy-Richards model expresses rate of growth of an organism as the difference between anabolic rate (constructive metabolism) and catabolic rate (destructive metabolism). It is

$$\frac{dD}{dt} = \eta D^m - \gamma D \quad (1)$$

where  $D$  is the organism dimension of interest, typically volume, but in this case tree diameter, the derivative  $dD/dt$  is the dimension growth rate,  $\eta$  and  $\gamma$  are the parameters of the anabolic and catabolic terms, respectively and  $m$  is the allometric constant or shape parameter.

The physiological processes involved in catabolism remain fairly constant throughout an organism's life, so according to von Bertalanffy, the catabolic term can be expressed linearly. The

catabolic term is proportional to the volume of an organism. The anabolic processes or the growth physiology changes through time and is generally categorized as youth, maturity, and senescence. Von Bertalanffy used a power function on the anabolic term in order to allow the shape to form a non-linear curve that reflects the natural growth of an organism. This power function represents the allometric relationship between dimensional elements of an organism, such as tree diameter and height. The anabolic term is proportional to the surface area of an organism. Von Bertalanffy fixed the exponent on the anabolic term to the value  $2/3$  based on empirical studies of many aquatic and terrestrial organisms. In other words, his data revealed this value as a constant. However “Richards (1959), in studying plant growth, and Chapman (1961) the growth of fish, both argued that von Bertalanffy’s allometric constant of  $2/3$  was too restrictive to apply to many forms of life;” (Pienaar and Turnbull 1973) therefore the model was generalized by Richards and Chapman to include the allometric parameter  $m$  instead of the constant  $2/3$ . Equations (1)-(7) are given in Pienaar and Turnbull (1973).

Integration of Equation (1) yields

$$D_t = \left\{ \frac{\eta}{\gamma} - \frac{\eta}{\gamma} \times \exp[-\gamma(1-m)(t-t_0)] \right\}^{\frac{1}{1-m}} \quad (2)$$

where  $D_t$  is the dimension at time (or age)  $t$ , given the initial condition that at time  $t = t_0$ ,  $D_{t_0} = 0$ . For tree diameter,  $t_0$  is the age when diameter at breast height becomes measurable, that is, when tree height reaches breast height (1.3 m). As  $t \rightarrow \infty$  an upper asymptote denoted  $A$ , where  $A = (\eta/\gamma)^{1/(1-m)}$ , is reached. Therefore  $\eta/\gamma = A^{1-m}$ , and if  $\gamma(1-m) = k$ , then substituting these relationships into Equation (2) and simplifying the expression results in the classic Bertalanffy-Richards yield equation

$$D_t = A \left\{ 1 - \exp[-k(t-t_0)] \right\}^{\frac{1}{1-m}} \quad (3)$$



The function defined by Equation (3) is sigmoidal (S-shaped) when  $m > 0$  with a point of intersection with the time axis at  $t_0$ , an upper asymptote equal to  $A$ , and an inflection point (Figure 1). To summarize, parameter  $A$  is the equation asymptote or the largest size the organism is likely to reach, parameter  $k$  is related to the organism growth rate, parameter  $t_0$  is the location parameter, and  $m$  is the allometric constant or shape parameter.

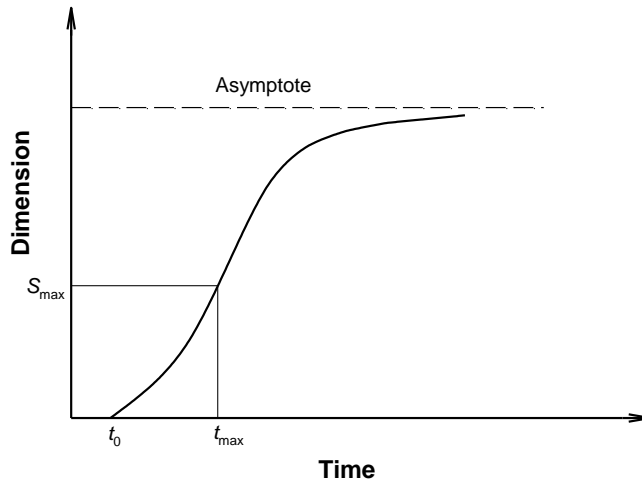


Figure 1. Sigmoidal form of Equation (3) with  $0 < m < 1$  and  $\eta, \gamma > 0$ .

### 2.3.2. Sigmoidal function characteristics

Three characteristics that can be determined from the sigmoidal form of Equation (3) are: (1) the size (organism dimension) at which the maximum growth rate occurs ( $S_{\max}$ ), (2) the maximum growth rate ( $R_{\max}$ ), and (3) the time when this occurs ( $t_{\max}$ ).

$$S_{\max} = Am^{1/(1-m)}, R_{\max} = Akm^{m/(1-m)}, t_{\max} = [kt_0 - \ln(1-m)]/k \quad (4)$$

In Figure 1, it is readily seen that the inflection point corresponds to  $(t_{\max}, S_{\max})$ .

The growth rate/age curve is obtained by differentiating Equation (3) with respect to  $t$ , and in the forestry literature it is known as the

periodic annual increment (PAI) curve. It is called this because tree growth occurs on an annual basis.

$$\frac{dD}{dt} = \left( \frac{1}{1-m} \right) A \left\{ 1 - \exp[-k(t-t_0)] \right\}^{\frac{m}{1-m}} k \exp[-k(t-t_0)] \quad (5)$$

The graph of Equation (5) is mound shaped and the peak of the curve occurs at  $(t_{\max}, R_{\max})$  (Figure 2a). Another revealing curve is the growth rate/size curve obtained from Equation (1). The function can be expressed in terms of the parameters  $A$ ,  $k$ , and  $m$  by substituting  $kA^{1-m}/(1-m)$  for  $\eta$  and  $k/(1-m)$  for  $\gamma$  to obtain

$$\frac{dD}{dt} = \frac{kA^{1-m}}{1-m} D^m - \frac{k}{1-m} D \quad (6)$$

Similar to the graph of Equation (5), the graph of Equation (6) is mound shaped and the peak of the curve occurs at  $(S_{\max}, R_{\max})$  (Figure 2b).

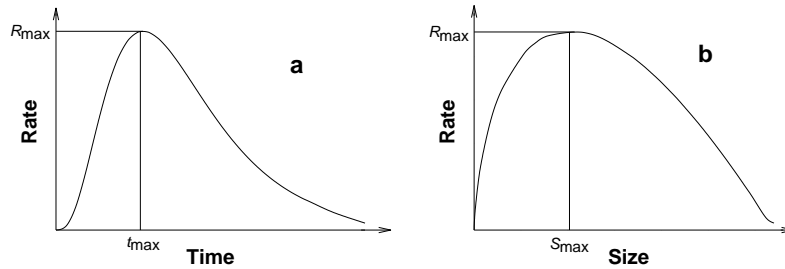


Figure 2. (a) Typical graph of rate over time from sigmoidal Bertalanffy-Richards function and (b) rate over size.

### 2.3.3. Bertalanffy-Richards for the case $m \leq 0$ and $\eta, \gamma > 0$

Many sources relate that tree growth is sigmoidal in form (Husch et al. 1972, Pienaar and Turnbull 1973, Clutter et al. 1983); however Lei et al. (1997) present practical situations where growth follows a non-sigmoidal form, such as fast-growing sub-tropical and tropical forests that appear to be in a sustainable growth. Lei et al. found that

the growth curves of such forests do not possess a point of inflection and have a convex shape as in Figure 3. They showed that the Bertalanffy-Richards curve as given in Equation (3) is convex in shape for the case  $m \leq 0$  and both  $\eta$  and  $\gamma > 0$ . The three characteristics  $S_{\max}$ ,  $R_{\max}$ , and  $t_{\max}$  are undefined in this case (the growth rate goes to infinity as  $t \rightarrow t_0$ ), except for  $m = 0$ , where

$$S_{\max} = 0, R_{\max} = Ak, t_{\max} = t_0 \quad (7)$$

In this instance the Bertalanffy-Richards function simplifies to the monomolecular growth function, a special case of the convex pattern. In the monomolecular growth function, the anabolic term is constant and the catabolic term is a linear function increasing with tree size; hence, the growth rate decreases in a linear fashion. For the convex case, the growth rate/age curve as given by Equation (5) and the growth rate/size curve as given by Equation (6) resemble a reversed J-shape when plotted (Figure 4a and 4b). However, for the case of monomolecular growth, the graph of growth rate over size is a descending straight line.

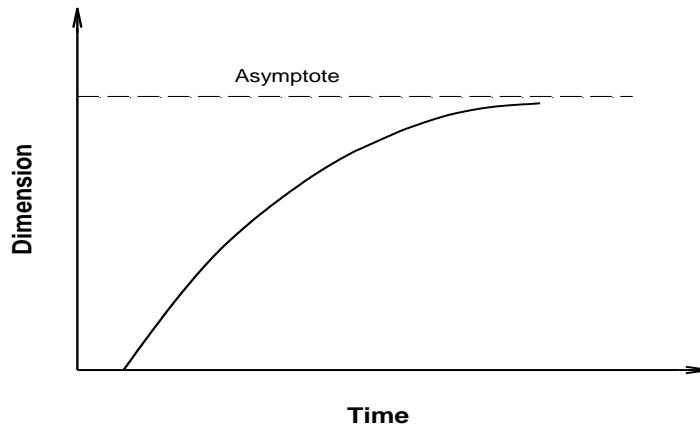


Figure 3. Convex form of Equation (3) with  $m \leq 0$  and  $\eta, \gamma > 0$ .

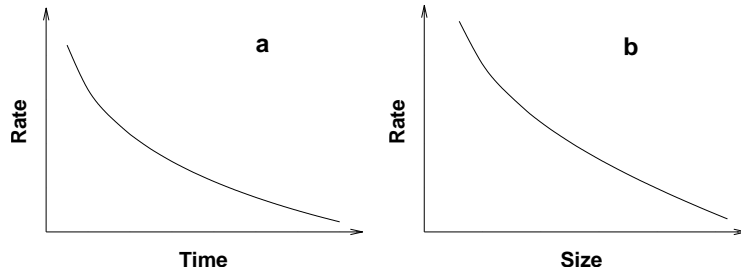


Figure 4. (a) Typical graph of rate over time from convex Bertalanffy-Richards function and (b) rate over size.

#### 2.3.4. Bertalanffy-Richards for the case $m < 0$ , $\eta > 0$ , $\gamma < 0$ .

Bredenkamp and Gregoire (1988) found, in studying stands of *Eucalyptus grandis* Hill ex Maiden, a non-asymptotic growth form in stands with heavy mortality, that is, there was an upturn in the data values indicating renewed diameter growth. Lei et al. (1997) showed that the Bertalanffy-Richards function can describe this growth pattern as well. Making  $\gamma' = -\gamma$ , Lei et al. (1997) showed that Equation (1) can be reformulated as

$$\frac{dD}{dt} = \eta D^m + \gamma' D \quad (8)$$

where parameter  $m$  takes on a negative value and parameters  $\eta$  and  $\gamma'$  are positive. In order to understand the changes made by Lei et al., compare Equation (8) with Equation (1), which is the equation developed by von Bertalanffy (1951), with the parameter  $m$  in place of the value  $2/3$ . The integral form of Equation (8) (Lei et al. 1997) is

$$D_t = A \{ \exp[k(t - t_0)] - 1 \}^{1/(1-m)} \quad (9)$$

Equation (9) should be compared with Equation (3). Notice that in Equation (3) the exponential term is subtracted from one; while in Equation (9), one is subtracted from the exponential term. Equation (9) lacks an upper asymptote. The shape of the curve can be

described as inverse sigmoidal (Figure 5). The graphs of growth rate/age and growth rate/size are valley shaped (Figure 6a and 6b), hence in the inverse sigmoid form of the Bertalanffy-Richards function [Equation (9)] the characteristics of interest are: (1) the size (organism dimension) at which the minimum growth rate occurs ( $S_{\min}$ ), (2) the minimum growth rate ( $R_{\min}$ ), and (3) the time when this occurs ( $t_{\min}$ ). The equations for these three characteristics, as derived by Dr. Bernard Parresol, are:

$$S_{\min} = A(-m)^{1/(1-m)}, R_{\min} = Ak(-m)^{m/(1-m)}, t_{\min} = [kt_0 + \ln(1-m)]/k \quad (10)$$

Figures (6a) and (6b) were plotted from the following two equations also derived by Dr. Bernard Parresol (personal communication). Equations (10)-(12) have not appeared previously in any literature:

$$\frac{dD}{dt} = \left( \frac{1}{1-m} \right) A \{ \exp[k(t-t_0)] - 1 \}^{\frac{m}{1-m}} k \exp[k(t-t_0)] \quad (11)$$

$$\frac{dD}{dt} = \frac{kA^{1-m}}{1-m} D^m + \frac{k}{1-m} D \quad (12)$$

In Figure 5 it is obvious that the inflection point corresponds to ( $t_{\min}$ ,  $S_{\min}$ ). In Figure 6a the minimum occurs at ( $t_{\min}$ ,  $R_{\min}$ ) and in 6b the minimum occurs at ( $S_{\min}$ ,  $R_{\min}$ ).

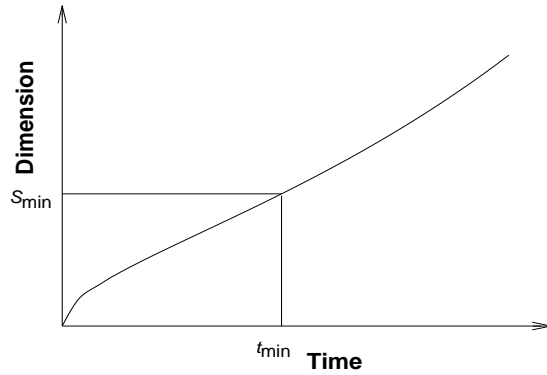


Figure 5. Inverse sigmoid form of Equation (9) with  $m < 0$ ,  $\eta > 0$ ,  $\gamma < 0$ .

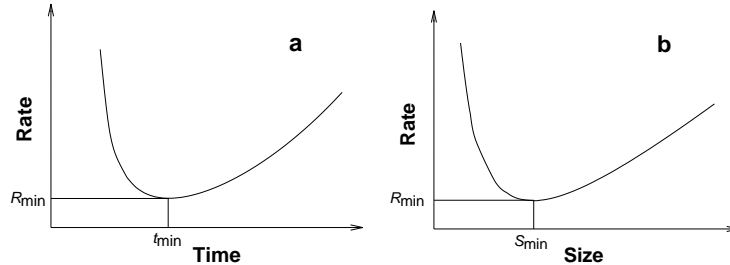


Figure 6. (a) Typical graph of rate over time from inverse sigmoid Bertalanffy-Richards function and (b) rate over size.

#### 2.4. The process of fitting the model and making the graphs

The Bertalanffy-Richards function was fitted to the data from each of the 21 trees using nonlinear least squares to determine values of  $A$ ,  $k$ , and  $m$ . Dr. Bernard Parresol wrote a program in the Statistical Analysis System (SAS) version 8 software (PROC NLIN, SAS Institute 2000) to estimate these parameters.

Normally, researchers know the actual age of a tree; but in this case, it is unknown. The location parameter,  $t_0$ , usually represents the age at which a tree reaches breast height. In most tree species, this is at about two to three years, so the coordinate of  $t_0$  would be (2,0) or (3,0), that is at age two or three, diameter at breast height is exactly zero, as demonstrated in Figure 1. However, the data from these tree cores begin at the age at breast height, so  $t_0$  has been set to zero in all equations. In other words, the coordinate of  $t_0$  in all of the graphs in this paper is (0,0).

For each tree, three graphs were created to show a plot of the fitted function, the growth rate over age, and the growth rate over size. Using Excel (Microsoft Corp. 2000), the author generated the graphs using Equations (3), (5), and (6) for the sigmoidal, monomolecular and convex patterns and Equations (9), (11), and (12) for the inverse sigmoid pattern. These graphs aid in interpreting results. Also in Excel, the author computed the values for  $S_{\max}$ ,  $R_{\max}$ , and  $t_{\max}$  listed in Equation (4) and  $S_{\min}$ ,  $R_{\min}$ , and  $t_{\min}$  listed in Equation (10).

### 3. RESULTS

Four of the trees could not adequately be fitted using Equation (3). For these trees Equation (9) was the appropriate model. The graphs of diameter over age, rate over age, and rate over size are given in Figure 7. Unexpectedly, not one or two, but four different growth patterns can be seen in the graphs of Figure 7: sigmoid, convex, monomolecular, and inverse sigmoid. Table 3 lists the fitted parameter values for each tree, identifies the growth pattern, and gives the Bertalanffy-Richards characteristics  $S_{\max}$ ,  $R_{\max}$ , and  $t_{\max}$  for the sigmoid and monomolecular patterns. These characteristics are undefined for the convex growth pattern. For the inverse sigmoid, the characteristics listed in Table 3 are  $S_{\min}$ ,  $R_{\min}$ , and  $t_{\min}$ . They are minimum values rather than maximum values because the inverse sigmoid starts out convex then shows a renewed surge in growth so the rate curve takes on a valley shape.

The asymptote values range from a low of 21.7 to 64 cm, well below the maximum size of 100 cm reported for this species by Liegel and Whitmore (1991). However, they report that 46 cm is more typical of maximum diameter size, which is only slightly above the 43 cm mid-range value for the laurel at GP. The interplay of all parameters determines the growth curve, but it is easy to see in Table 3 that the trees with the largest asymptote values generally have the smallest  $k$  values. It is possible that the growth rate computed from the Bertalanffy-Richards function is related to the product of  $A$  times  $k$ . Smaller values of  $k$  help offset large  $A$  values and regulate the functional growth rate in conjunction with the allometric constant.

As already stated, a sigmoid pattern corresponds to  $0 < m < 1$ . For these trees the mean of the three Bertalanffy-Richards function characteristics are:  $S_{\max} = 8.3$  cm,  $R_{\max} = 1.85$  cm/yr, and  $t_{\max} = 7.0$  years. The three monomolecular trees ( $m$  not significantly different from 0) have an average  $R_{\max}$  of 1.98 cm/yr. As given in Equation (7),  $S_{\max} = 0$  and  $t_{\max} = t_0$  (which is 0 in this study). Vega (1977) examined growth of laurel on different sites in Surinam and found that early growth on good sites varied from 2.1 to 3.5 cm/yr and at 7 years of age dbh frequently exceeded 22 cm. On poor sites the

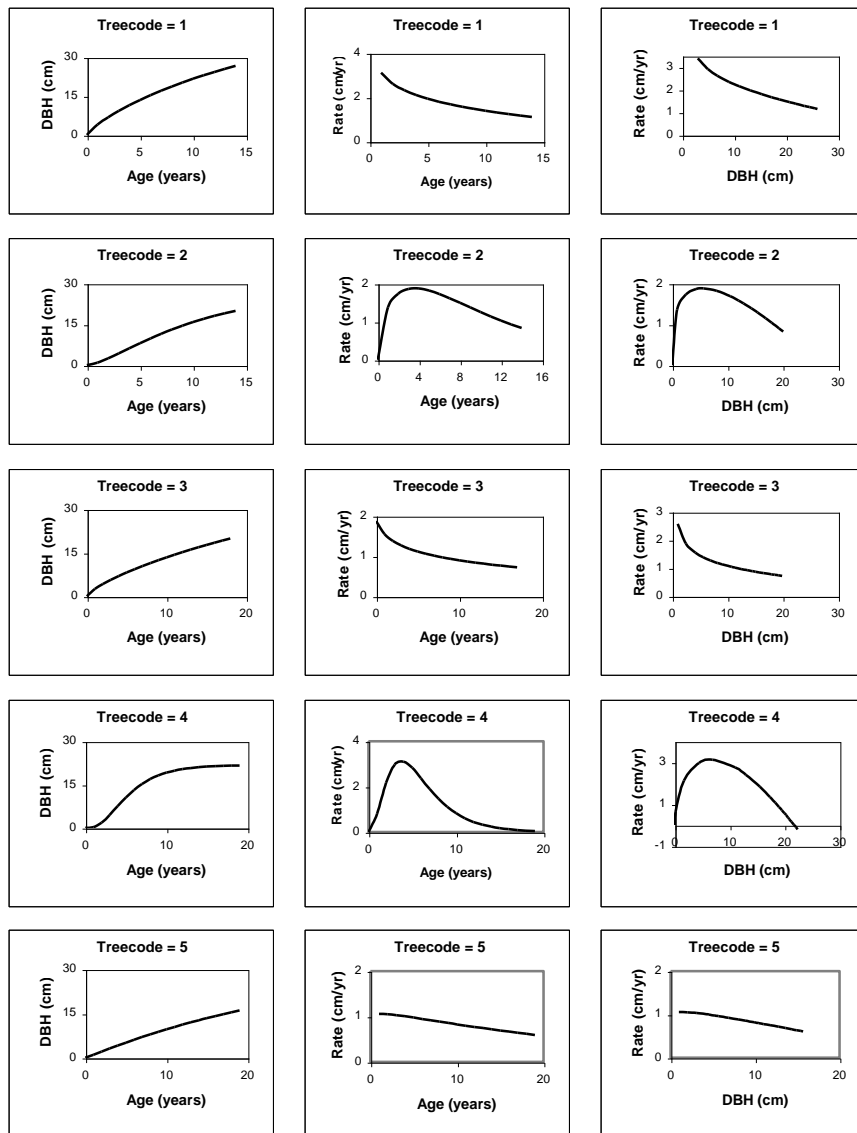


Figure 7. Results of fitting the Bertalanffy-Richards growth model to the 21 laurel trees from GP, Panama.



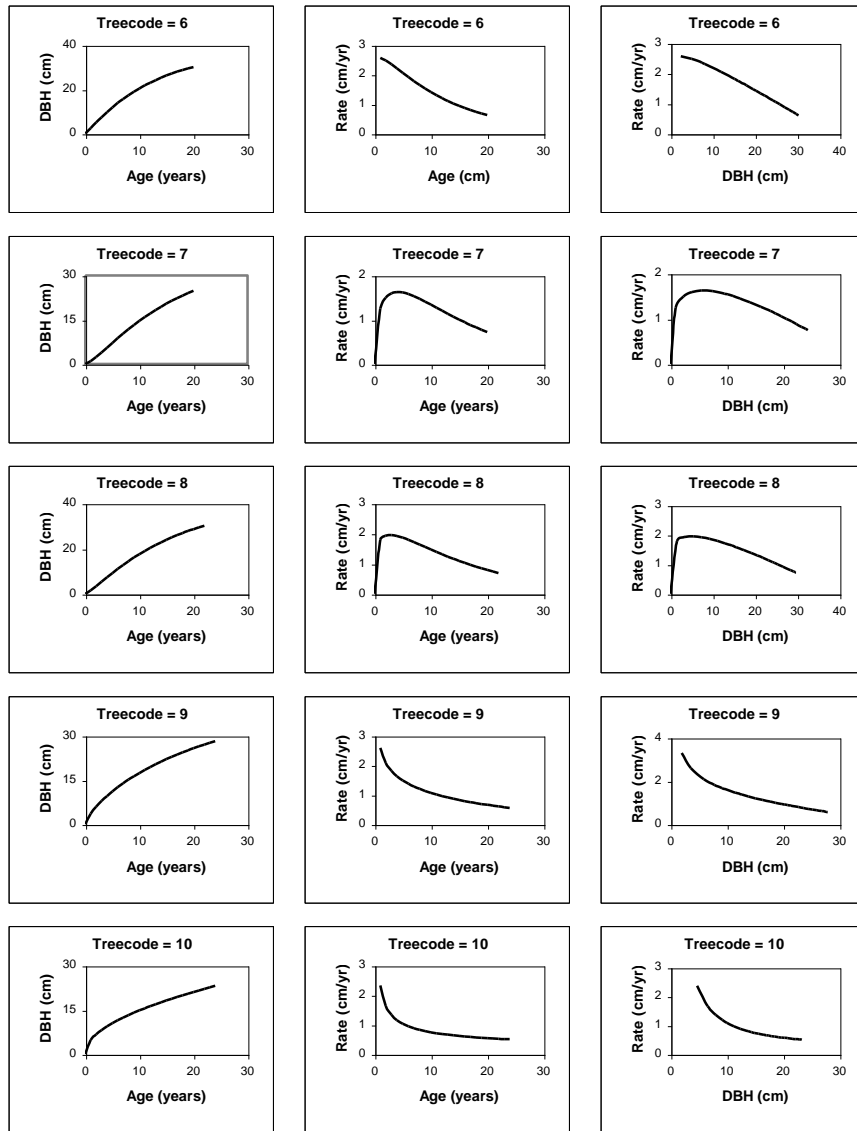


Figure 7. Continued.

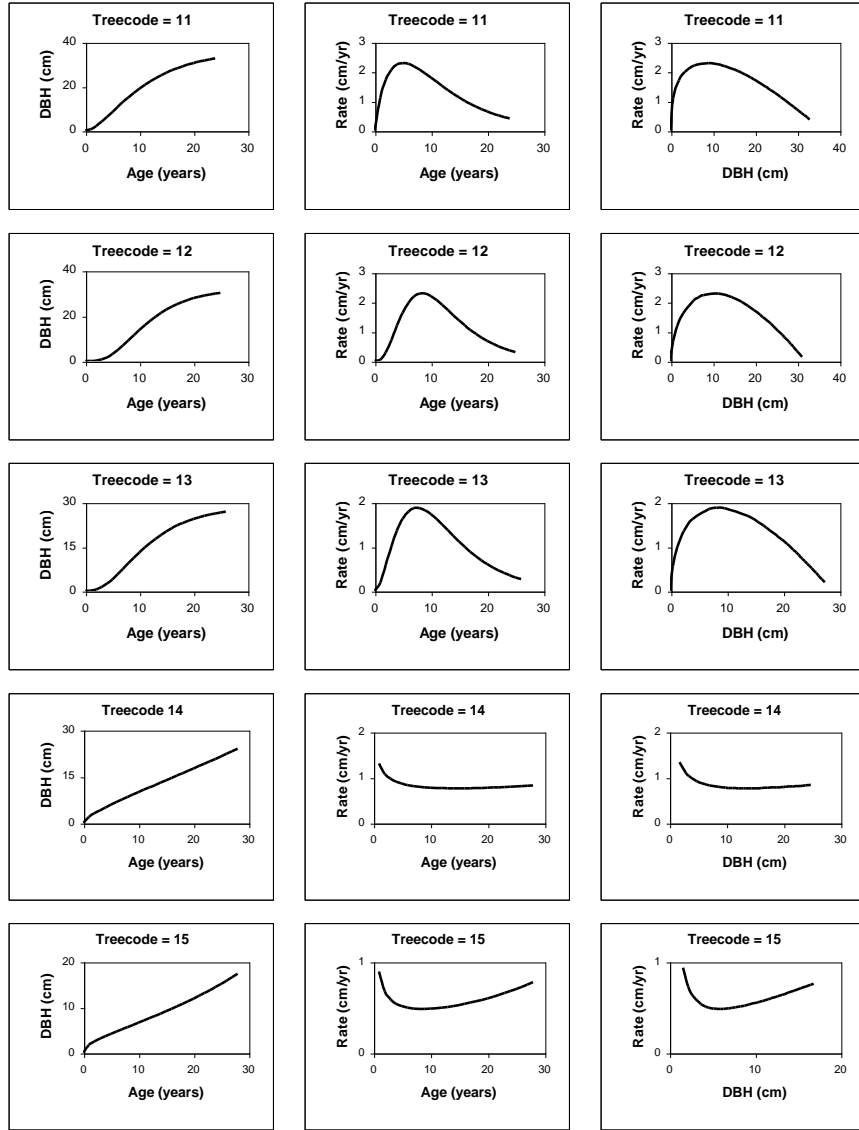


Figure 7. Continued.

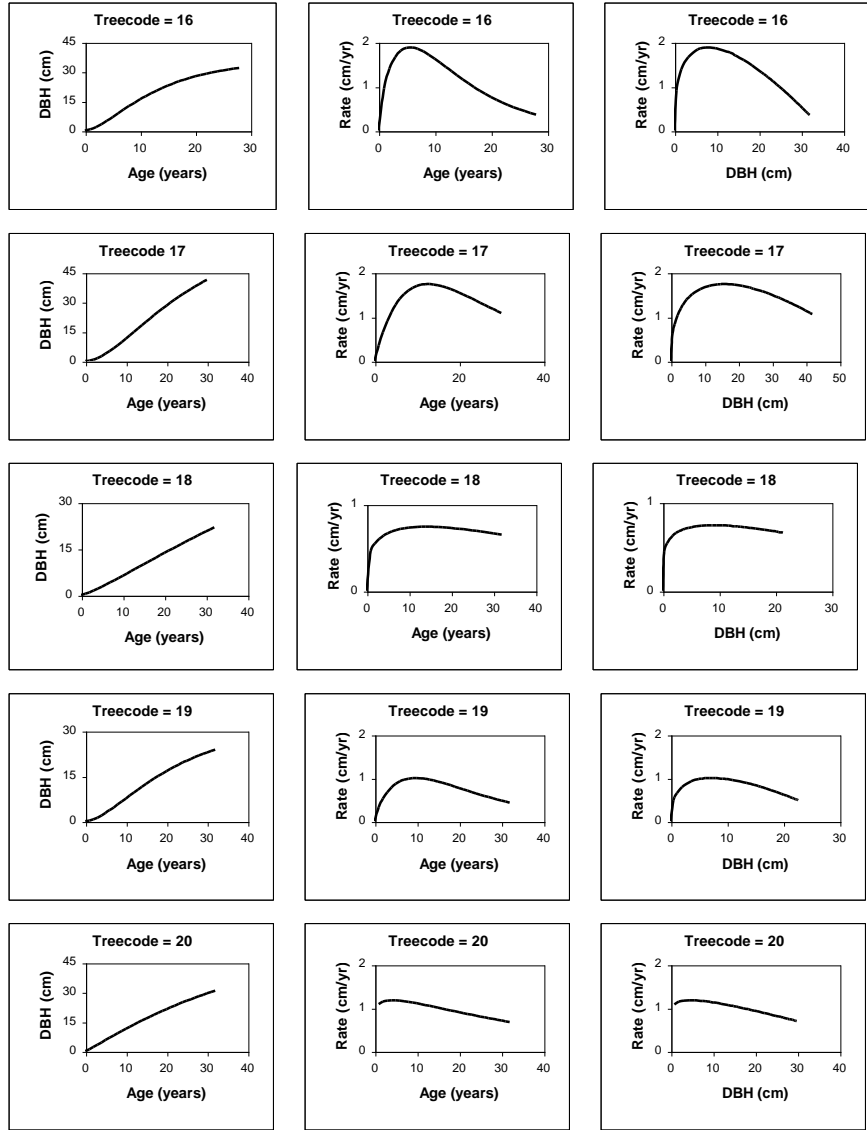


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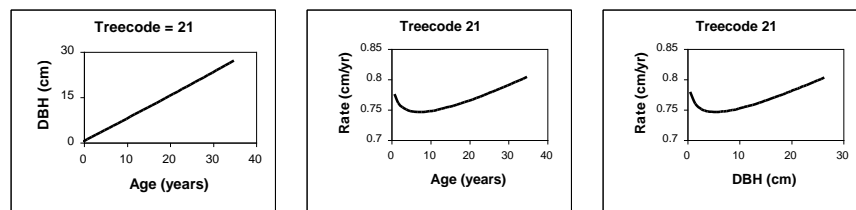


Figure 7. Continued.

Table 3. Parameter values, pattern, and characteristics from fitting the Bertalanffy-Richards function to the 21 trees from Gigante.

Tree	Final age	$A$	$k$	$m$	Pattern <sup>†</sup>	$S_{\max}$	$R_{\max}$	$t_{\max}$
1	14	50.5	0.0427	-0.2493	Convex	--	--	--
2	14	27.2	0.1225	0.3572	Sigmoid	5.48	1.88	3.6
3	18	58.8	0.0149	-0.3369	Convex	--	--	--
4	19	21.7	0.3319	0.7107	Sigmoid	6.67	3.12	3.7
5	19	31.4	0.0394	0.0497	Mono	0	1.24	0
6	20	37.5	0.0843	0.0753	Mono	0	3.16	0
7	20	34.7	0.0765	0.2756	Sigmoid	5.85	1.62	4.2
8	22	40.1	0.0708	0.1796	Sigmoid	4.95	1.95	2.8
9	24	43.1	0.0339	-0.3714	Convex	--	--	--
11	24	36.0	0.1241	0.4679	Sigmoid	8.63	2.29	5.1
12	25	32.0	0.1715	0.7652	Sigmoid	10.23	2.29	8.4
13	26	28.7	0.1477	0.6725	Sigmoid	8.54	1.87	7.6
16	28	35.6	0.0999	0.4312	Sigmoid	8.12	1.88	5.6
17	30	63.5	0.0546	0.498	Sigmoid	15.85	1.74	12.6
18	32	64.0	0.0177	0.2186	Sigmoid	9.15	0.74	13.9
19	32	31.2	0.0617	0.4518	Sigmoid	7.31	1.00	9.7
20	32	56.1	0.0275	0.1091	Mono	0	1.54	0
						$S_{\min}$	$R_{\min}$	$t_{\min}$
10	24	54.2	0.0066	-1.0672	Inverse	55.97	0.35	110.0
14	28	23.0	0.0258	-0.4554	Inverse	13.38	0.76	14.5
15	28	6.1	0.0779	-0.9646	Inverse	5.95	0.48	8.7
21	35	140.4	0.00473	-0.0356	Inverse	5.61	0.74	7.4

<sup>†</sup> Mono refers to monomolecular and inverse is short for inverse sigmoid.

the annual diameter increment was reduced to 0.6-1.1 cm/yr. Obviously the trees at GP fall between these cases. The  $R_{\max}$  range is from 0.74 to 3.16 cm/yr with a mean of 1.85 cm/yr at 7 years old. Piotto et al. (in press) report a mean annual increment (MAI) of 2.09 cm/yr for 5 to 10 year old pure laurel plantations in the Atlantic lowlands of Costa Rica. While the  $R_{\max}$  for the laurel at GP averages 1.85 cm/yr, the MAI (as reported in Section 2.2) is only 1.0 cm/yr for the 21 trees, whose average age is 25 years. So for 5-10 years of age the MAI for GP will lie between 1.0 and 1.85 cm/yr, well below the 2.09 reported by Piotto et al. Of course, the Atlantic Lowlands of Costa Rica are well known as an optimal site for laurel (Johnson and Morales 1972), and plantations usually outperform natural stands.

The four inverse sigmoid trees listed in Table 3 and graphed in Figure 7 as treecodes 10, 14, 15 and 21 are unusual cases. Something in the environment, perhaps a man-made or natural disturbance, caused these individuals to increase their growth rate (after age  $t_{\min}$ ) when the majority of trees are experiencing declining growth rates. Tree 10 in particular stands out because its inflection point occurs at  $t_{\min} = 110$  years, well beyond the life expectancy of this species. Tree 10 in essence looks like logarithmic growth, a non-asymptotic convex growth pattern. Excluding tree 10, the average characteristics for these inverse sigmoid trees are:  $S_{\min} = 8.31$  cm,  $R_{\min} = 0.66$  cm/yr, and  $t_{\min} = 10.2$  years.

#### 4. DISCUSSION

The trees from GP, quite unexpectedly, displayed an amazing degree of variation in form. Reports for most living organisms indicate that growth follows a sigmoidal pattern, with a small percentage differing from this classic form (Husch et al. 1972, p. 293; Pienaar and Turnbull 1973). Analysis of the laurel data showed that only 52% of the trees (11 of 21) followed this pattern. Three trees or 14% followed a convex pattern, which is regularly, though not commonly, reported for tree growth (Bredenkamp and Gregoire 1988, Lei et al. 1997). Surprisingly, for three trees the allometric constant,  $m$ , was not significantly different from zero, indicating monomolecular

growth. This is normally considered unrealistic for tree growth. Of the trees that were cored, none appeared suppressed but the site was suboptimal as confirmed by this analysis of the growth data.

It should be understood that the inverse sigmoid growth pattern applies to the range of the data only, because the data in this particular growth pattern do not reveal an asymptote. No living things grow to infinity, so an asymptote should eventually be reached. Extrapolation beyond the range of the data will result in unrealistic diameters. The point of the inverse sigmoid growth pattern is that the trees are experiencing renewed growth due to release from competition or other factors. The data do not indicate any potential asymptote, so future measurements would be needed to determine an upper limit.

In comparison to the Costa Rica agroforestry data of Rosero and Gewald (in Liegel and Whitmore 1991) listed in Table 1, the laurel at GP are about 15% smaller than the pasture trees at Cahuita and from 40 to 48% smaller than the coffee shade laurel of Bajo Chino and La Suiza. Niel and Jacovelli (1985) report that in agroforestry systems in Vanuatu, a small Pacific island nation, maturing laurel develops extensive shallow root systems that can compete strongly with adjacent agricultural crops. Laurel also develops a strong taproot in deep soils and this is the main factor in its ability to remain wind firm in the event of hurricane force winds; however, if the taproot cannot be established due to a thin soil layer such as on shallow coralline soils, the tree becomes more susceptible to blowing over under the stress of high winds (Grievess and McCarter 1990). Removed from forest competition and capable of developing vigorous root systems on agricultural soil, this analysis shows that agroforestry planted laurel grows better than in natural stands like at GP, where the soil is thin and rocky, and compare favorably with optimal natural sites like the Costa Rica Atlantic lowlands.

In comparison to the Puerto Rican plantation data of Liegal and Stead (1990) listed in Table 2, the laurel at GP are growing as well as the plantation trees at four of the sites (Catalina, Tract 105, Luquillo, Carite) and somewhat better at the remaining two sites (Guilarte and Guánica). Puerto Rico is at the northern boundary of the species' natural range, though this may or may not have any

bearing on the species' growth potential there. The site at the Guánica State Forest is listed as subtropical dry, which would explain its slower growth, as laurel does not do as well in drier areas (Johnson and Morales 1972, Liegel and Stead 1990, Liegel and Whitmore 1991).

Laurel is a gap pioneer species, characteristic of young forests. Pioneer species, including laurel, emerge in gaps of all sizes, but are usually restricted to gaps over 150 m<sup>2</sup>. Other tree species can exist as suppressed saplings in a closed forest until a gap forms, and then accelerate in growth (Brokaw 1982). Thus differing requirements of seedlings and saplings of various species lead to different growth patterns. Laurel that germinates in a gap typically has adequate resources at the time of germination and early growth. As the forest grows and the gap disappears, laurel typically occupies an intermediate to suppressed canopy position, and is then at a competitive disadvantage. The time when this occurs corresponds to  $t_{\max}$  for the sigmoidal pattern. According to Pienaar and Turnbull (1973), the inflection point, when the maximum growth rate is reached, is the point (i.e.,  $R_{\max}$ ,  $t_{\max}$ ) of measurable competition on the tree.

From Table 3 one can see that the range of  $t_{\max}$  is 2.8 to 13.9 years with a mean of 7 years. Gaps in the moist tropics tend to revegetate quickly, small gaps achieving canopy closure sooner than large gaps. One would expect natural stands to have variability in gap sizes and the  $t_{\max}$  values reflect this. Apparently on GP, gaps tend to close after about 7 years. For the trees displaying the inverse sigmoid pattern, the  $t_{\min}$  values ranged from 7.4 to 14.5 years, indicating an influence that caused renewed growth of the individuals. By age 7 *C. alliodora* trees have normally entered their maturity phase. Most species have lost their capacity to respond aggressively, that is, with a burst of growth, to a release event after becoming mature. Many species will respond positively to release from competition, but not to the extent of achieving sustained higher growth rates (Clutter et al. 1983). An extensive literature search found only one article that reported an inverse sigmoid pattern. Bredenkamp and Gregoire (1988), in studying *Eucalyptus grandis* in South Africa, found a resurgence of growth in stands that had

experienced heavy mortality. It would appear that *C. alliodora* has the same ability, an ability that few species seem to possess.

The Bertalanffy-Richards function is a useful tool for looking at tree growth because it is flexible enough, especially the alternate form, to reveal non-typical growth patterns like the convex, monomolecular, and inverse sigmoid, in addition to the standard sigmoidal growth pattern. It is significant that all four growth patterns were found in the natural stands at GP because it does not seem to have appeared in previous forestry literature. It may be that it does occur more frequently but has not been reported because the convex and inverse sigmoid growth patterns could not be revealed by the classic Bertalanffy-Richards function. It was Lei et al. (1997) who showed that by allowing the parameter  $m$  to go negative in the classic Bertalanffy-Richards function, that the convex growth pattern is revealed. They also derived an extension where  $m$  and  $\gamma$  are negative, which results in the inverse sigmoid growth pattern. The results in this study indicate that *Cordia alliodora* is amazingly resilient and has the capacity to assume different growth patterns under proper conditions. It would be interesting to see if further research in natural stands of laurel, especially with additional environmental data included, show similar results.

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