Patterns of Diametric Growth in Stem-Analyzed Laurel Trees (*Cordia alliodora*) in a Panamanian Forest

PATTERNS OF DIAMETRIC GROWTH IN STEM-ANALYZED LAUREL TREES (*CORDIA ALLIODORA*) IN A PANAMANIAN FOREST

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ABSTRACT—Based on cross-dated increment cores, yearly diameters of trees were reconstructed for 21 laurels (*Cordia alliodora*) growing in a natural secondary forest on Gigante Peninsula, Panama. From this sample of dominant-codominant trees, ages were 14–35 years with an average of 25 years. Growth typically slowed at 7 years old, indicating effects of competition from closure of gaps in the canopy. Rate of growth in diameter was modeled using the Bertalanffy-Richards growth function. Four patterns of growth were detected, of which 57% were sigmoidal, 19% were convex, 10% were monomolecular, and 14% were inverse sigmoid.

RESUMEN—Con base de testigos fechados de madera, diámetros anuales se reconstructaron para 21 árboles de laurel (*Cordia alliodora*) creciendo en un bosque natural secundario en la Peninsula Gigante, Panama. De esta muestra de arboles dominantes-codominantes, los edades varían de 14 a 35 años con un promedio de 25 años. Típicamente el crecimiento de los árboles disminuó a siete años de edad, señalando los efectos de competencia debido de la cierre de los claros en el dosel. La tasa de crecimiento diamétrico de los árboles se modeló usando la function de crecimiento Bertalanffy-Richards. Cuatro patrones de crecimiento se encontraron; 57 por ciento de los patrones eran sigmoideos, 19 por ciento eran convexos, 10 por ciento eran monomoleculares, y 14 por ciento eran sigmoideos inversos.

Growth of an individual tree is subject to complex interacting influences. In the early 20th century, there was a great deal of debate in ecology about aggregation versus nominalism (Mitman, 1992). Aggregation refers to grouping entities together on some basis and considering the assemblage as a whole. Nominalism rejects universals; it holds that the various objects labeled by the same term have nothing in common but their name. The aggregationists argued that nominalism is logically inconsistent: were there nothing in common among individuals, they could not be considered as members of the same species and combined under one name. Individuals share many common features and often exhibit aggregate behavior. It makes sense to use the average to characterize a population. Nominalists believe that models that deal with a population as a whole (aggregated large-scale models) are based on unrealistic assumptions, gloss-over ecological mechanisms and individual variability, and ignore reality. Aggregation violates the biological principle that each individual is different. Under the banner of nominalism, the future of ecology belongs to the individual-based modeling approach. Today, it is understood that the modeling paradigm depends on the objective for the model; both approaches are valid (Kaufmann and Ryan, 1986). In our study, we examined patterns of growth of individual laurels (*Cordia alliodora*),

an important tropical tree, to better understand dynamics of the population.

Laurels are tropical hardwoods with an extensive natural range extending from Mexico to Argentina, 25°N to 25°S. This tree is a pioneer species, invading clearings such as pastures, burned sites, and new gaps in forests. Laurels have a narrow, self-pruning crown allowing a diversity of plants to grow beneath it (Hummel, 2000b). As an important species for timber, the laurel frequently is used in agroforestry as shade for cacao, coffee, other agricultural crops, and farm animals. The commonly used commercial name for *C. alliodora* is salmwood. Laurels reach sexual maturity in 5–10 years (Liegel and Stead, 1990). Under optimum conditions, laurels can grow to 25–45 m in height and 60–100 cm in diameter. Typically, however, they grow to ca. 20 m in height and 46 cm in diameter (Somarriba and Beer, 1987; Liegel and Whitmore, 1991). In seasonally dry lowland tropical forests, most species of trees lose their leaves during the dry season, but in Panama, laurels become deciduous for several months after the rains begin (Foster, 1985). Laurels are 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 forestry and agroforestry potentials of this species, a better understanding of

dynamics of its growth is needed. Objectives of our analysis were to discover patterns of growth of laurels on Gigante Peninsula in Panama, draw inferences about growth of laurels in this secondary natural forest, and make comparisons with growth of laurels at other sites.

MATERIALS AND METHODS—We selected trees from a secondary natural forest on Gigante Peninsula, Panama (9°10′N, 79°51′W). The terrain had many hills with sedimentary rock containing volcanic debris. The soil was rich in clay, making permeability poor, particularly below the fine-root zone, which included the top 10–20 cm of the generally 50-cm depth of soil (Dietrich et al., 1996). The site was directly across Gatun Lake from Barro Colorado Island. Gigante Peninsula, as well as Barro Colorado Island, was formed during 1910–1914 when the Chagres River was dammed. Today, Gigante Peninsula is part of the Barro Colorado Island Nature Monument, which was established in 1977. The area is protected from disturbances such as shifting agriculture and selective cutting. The last major disturbance occurred in 1937 with 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 forested regions in Panama are dry, moist, and wet (Foster, 1985). Average annual temperature in a clearing at Barro Colorado Island was 27°C with a diurnal range of 9°C. Potential evapotranspiration was ca. 12 cm/month (Dietrich et al., 1996).

The rainy season was April–November, with November being the wettest month averaging 450 mm of rain (Foster, 1985). Of the 2,600 mm of annual precipitation, 90% was during the rainy season (Dietrich et al., 1996). Most rainfall occurred during short-term storms in early afternoon. During the dry season, rain is light and sporadic (Rand and Rand, 1996) because convective storms are turned away by trade winds (Dietrich et al., 1996).

During August 1991, we sampled 21 laurel trees growing on Gigante Peninsula. Using an increment borer, we collected 2 cores/tree. Only dominant or codominant trees were chosen. Cores were collected at about breast height (1.3 m). Diameter (inside bark) at each year for each tree was determined by cumulatively summing widths of rings of the 2 cores/tree. The current year was not measured because that growth was incomplete. If a core missed the pith, we estimated number of years and distance to pith. These data were collected originally for use in a dendroecological study. However, this type of stem-analyzed data permits analysis of rate of growth in diameter and total growth in diameter. For a description of how cores were prepared and cross-dated, see Devall et al. (1996). There were 457 diameter-by-age data points available for fitting the Bertalanffy-Richards function.

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) posed this model and its corresponding principles as a general theory of growth of broad and general validity. While some researchers question legitimacy of the theoretical foundations (e.g., Ricker, 1979), this model has enjoyed widespread use. This equation is valued for its accuracy and is used more than any other function in studies of growth of trees and stands (Zeide, 1993). Schnute (1981), working with populations of fish, has contributed greatly to our understanding of models of growth and Lei et al. (1997)

have shown equivalence between Bertalanffy-Richards and Schnute models.

The classic Bertalanffy-Richards model ($0 < m < 1$ and $\eta, \gamma > 0$) expresses rate of growth of an organism as the difference between anabolic rate (constructive metabolism) and catabolic rate (destructive metabolism). It is

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

where D is dimension of the organism of interest, the derivative dD/dt is the rate of growth in dimension, η and γ are parameters of the anabolic and catabolic terms, respectively, and m is the allometric constant or shape parameter (Pienaar and Turnbull, 1973).

Physiological processes involved in catabolism remain fairly constant throughout life of an organism, so the catabolic term can be expressed linearly (von Bertalanffy, 1951; Pienaar and Turnbull, 1973). Anabolic processes or the physiology of growth changes through time and generally is categorized as youth, maturity, and senescence. The Bertalanffy-Richards model (1) has an exponent on the anabolic term to allow the shape to form a non-linear curve that reflects natural growth of an organism (Richards, 1959; Chapman, 1961; Pienaar and Turnbull, 1973).

Integration of model (1) gives the classic Bertalanffy-Richards yield-equation:

$$D_t = A\{1 - \exp[-k(t - t_0)]\}^{\frac{1}{1-m}}, \qquad (2)$$

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 diameter of tree, t_0 is the age when diameter at breast height (dbh) becomes measurable; i.e., when height of tree reaches 1.3 m. In model (2), $k = \gamma(1 - m)$ and as $t \to \infty$ an upper asymptote denoted A, where $A = (\eta/\gamma)^{1/(1-m)}$ is reached. This function is sigmoidal (S-shaped) when $m > 0$ with a point of intersection with the axis of time at t_0 (Fig. 1a). Three characteristics that can be determined from the sigmoidal form of model (2) are: size (organism dimension) at which the maximum rate of growth occurs (S_{max}), maximum rate of growth (R_{max}), and time when this occurs (t_{max}). Formulas are

$$S_{max} = A m^{1/(1-m)}, \qquad R_{max} = A k m^{m/(1-m)},$$
$$t_{max} = [kt_0 - \ln(1 - m)]/k. \qquad (3)$$

In Fig. 1a, the inflection point corresponds to (t_{max}, S_{max}).

The curve for rate of growth/age is obtained by differentiating model (2) with respect to t and is the periodic-annual-increment curve:

$$\frac{dD}{dt} = \left(\frac{1}{1-m}\right) A\{1 - \exp[-k(t - t_0)]\}^{\frac{m}{1-m}} k \exp[-k(t - t_0)]. \quad (4)$$

The graph of model (4) is mound shaped and the peak of the curve occurs at (t_{max}, R_{max}; Fig. 2a). Another revealing curve is rate of growth/size obtained from model (1). The function can be expressed in terms of parameters A, k, and m by substituting $kA^{1-m}/(1 - m)$ for η and $k/(1 - m)$ for γ to obtain

$$\frac{dD}{dt} = \frac{kA^{1-m}}{1-m} D^m - \frac{k}{1-m} D. \qquad (5)$$

Similar to the graph of model (4), the graph of model (5) is
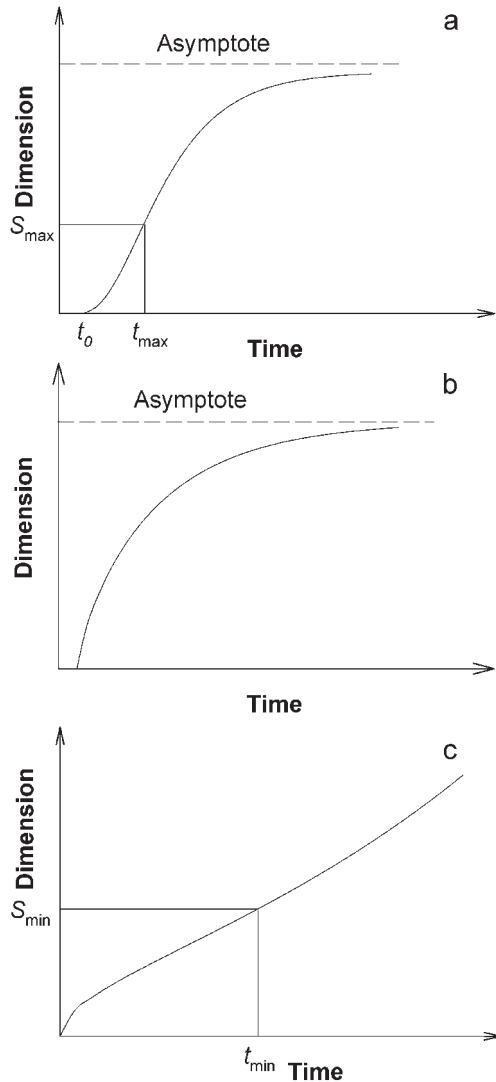
FIG. 1—(a) Sigmoidal form of model (2) with $0 < m < 1$ and η, $\gamma > 0$; (b) convex form of model (2) with $m \leq 0$ and η, $\gamma > 0$; and (c) inverse sigmoid form of model (8) with $m < 0$, $\eta > 0$, $\gamma < 0$.

mound shaped and the peak of the curve occurs at (S_{max}, R_{max}; Fig. 2b).

Many sources reported that growth of trees was sigmoidal in form (Husch et al., 1972; Pienaar and Turnbull, 1973; Clutter et al., 1983); however, Lei et al. (1997) presented practical situations where growth followed a nonsigmoidal form, such as fast-growing subtropical and tropical forests that appeared to be in sustainable growth. Lei et al. (1997) discovered that growth curves of such forests did not possess a point of inflection and had a convex shape as in Fig. 1b. They showed that the Bertalanffy-Richards curve, as given in model (2), is convex in shape for the case $m \leq 0$ and both η and $\gamma > 0$. The three characteristics S_{max}, R_{max}, and t_{max} are undefined in this case (the rate of growth goes to infinity as $t \to t_0$), except for $m = 0$, where

$$S_{max} = 0, \quad R_{max} = Ak, \quad t_{max} = t_0. \tag{6}$$

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 size of tree; hence, rate of growth decreases in a linear fashion. For the convex case, the curve for rate of growth/age as given by model (4) and the curve for rate of growth/size as given by model (5), resemble a reversed J-shape when plotted (Figs. 2c and 2d). However, for monomolecular growth, the graph of rate of growth plotted against size is a descending straight line.

Bredenkamp and Gregoire (1988) noted, in studying stands of the flooded gum *Eucalyptus grandis*, a non-asymptotic growth form in stands with heavy mortality; i.e., there was an up-turn in values indicating renewed growth in diameter. Lei et al. (1997) showed that the Bertalanffy-Richards function could describe this pattern of growth as well. Making $\gamma' = -\gamma$, Lei et al. (1997) showed that model (1) can be reformulated as

$$\frac{dD}{dt} = \eta D^m + \gamma'D, \tag{7}$$

where m takes on a negative value and η and γ' are positive. The integral form of equation (7) (Lei et al., 1997) is

$$D_t = A\{\exp[k(t - t_0)] - 1\}^{\frac{1}{1-m}}. \tag{8}$$

Model (8) lacks an upper asymptote. Shape of the curve can be described as inverse sigmoidal (Fig. 1c). Graphs of rate of growth/age and rate of growth/size are valley shaped (Figs. 2e and 2f). Hence, in the inverse sigmoid form of the Bertalanffy-Richards function, characteristics of interest are size (organism dimension) at which the minimum rate of growth occurs (S_{min}), minimum rate of growth (R_{min}), and time when this occurs (t_{min}). The equations for these three characteristics are:

$$S_{min} = A(-m)^{1/(1-m)}, \quad R_{min} = Ak(-m)^{m/(1-m)},$$
$$t_{min} = [kt_0 + \ln(1 - m)]/k. \tag{9}$$

Figures 2e and 2f were plotted from the following two models:

$$\frac{dD}{dt} = \left(\frac{1}{1-m}\right)A\{\exp[k(t - t_0)] - 1\}^{\frac{m}{1-m}}k\exp[k(t - t_0)], \tag{10}$$

$$\frac{dD}{dt} = \frac{kA^{1-m}}{1-m}D^m + \frac{k}{1-m}D. \tag{11}$$

Equations in (9) and models (10) and (11) have not appeared previously in the literature. In Fig. 1c, the inflection point corresponds to (t_{min}, S_{min}). In Fig. 2e, the minimum occurs at (t_{min}, R_{min}) and, in Fig. 2f, the minimum occurs at (S_{min}, R_{min}).

The Bertalanffy-Richards function was fitted to the data from each of the 21 trees and fitted to all data combined using the model procedure (PROC MODEL) in SAS (version 9.2; SAS Institute, Inc., Cary, North Carolina, USA) to determine values of A, k, and m. The location parameter, t_0, would be the age when a tree reaches breast height. However, data from these cores can give us only the age from when trees reached 1.3 m in height; actual ages of the trees are unknown. So, t_0 has been set to zero in all equations and it should be understood that age is from breast height. Because stem analysis is a form of repeated measures, serial correlation could exist. We used generalized Durbin-Watson statistics (version 9.2; SAS Institute, Inc., Cary, North Carolina, USA) and examined first through fourth order autocorrelation. Only first-order serial correlation existed in
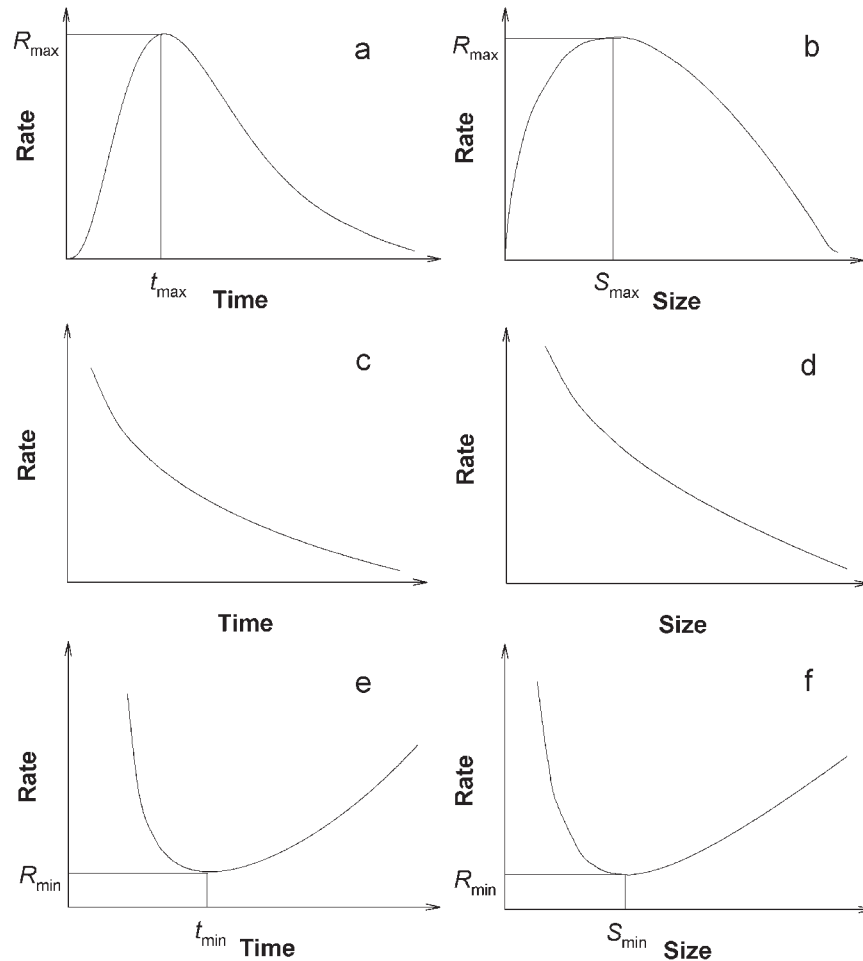
Fig. 2—Typical graphs of Bertalanffy-Richards function of (a) rate plotted against time and (b) rate plotted against size from the sigmoidal function; (c) rate plotted against time and (d) rate plotted against size from the convex function; (e) rate plotted against time and (f) rate plotted against size from the inverse sigmoid function.

residuals ($P < 0.05$); therefore, we refit regressions using a first-order autoregressive process.

We were able to statistically test the significance of patterns of growth depicted by the Bertalanffy-Richards model. The test of interest is on parameter m, which determines pattern of growth. In general, if k and A are positive, it can be shown that η, γ, and γ' have to be positive. Parameters k and A are positive in all regressions. Therefore, to test patterns of growth, one needs to examine the significance (at an appropriate alpha level) of the estimated parameter m against a null of 0, which is the monomolecular shape. If m is positive and significantly different from 0, then statistically, you accept the sigmoid shape. If m is negative and not 0, then you have the convex shape. If the data cannot be fitted to the standard Bertalanffy-Richards model, and they fit the alternate formulation, then this gives the inverse sigmoid pattern.

For each tree and the combined data, three graphs were created to show a plot of the fitted function; rate of growth plotted against age and rate of growth plotted against size. Values for graphs were computed using models (2), (4), and (5) for the sigmoidal, monomolecular, and convex patterns, and models (8), (10), and (11) for the inverse sigmoid pattern. These graphs aid in interpreting results. Also we computed S_{max},

$R_{max,}$ and t_{max} from the equations in (3) and S_{min}, R_{min}, and t_{min} from the equations in (9).

RESULTS—Final ages at breast height for trees were 14–35 years (mean $= 24.5 \pm 6.0$ years SD). Final diameters of trees (inside bark) were 15.7–41.9 cm (mean $= 26.0 \pm 6.1$ cm). Rates of growth in diameter were 0.16–4.23 cm/year (mean $= 1.0 \pm 0.67$ cm/year).

Three trees could not be fitted adequately using model (2). For these trees, model (8) was appropriate. Selected graphs of diameter plotted against age (which show pattern of growth), rate plotted against age (the periodic-annual-increment curve, whose shape reflects pattern of growth as illustrated in Figs. 2a, 2c, and 2e), and rate plotted against size (whose shape reflects pattern of growth as illustrated in Figs. 2b, 2d, and 2f) are given in Fig. 3. Four different patterns of growth can be seen in the graphs of Fig. 3; sigmoid, convex, monomolecular, and inverse sigmoid. Table 1 lists fitted parameters for each tree and the combined data, gives the probability value on estimates of m against a null of 0, identifies pattern of growth, and gives the Bertalanffy-Richards characteristics S_{max}, R_{max},

and t_{max} for sigmoid and monomolecular patterns. These characteristics are undefined for the convex pattern of growth. For inverse sigmoid, characteristics in Table 1 are S_{min}, R_{min}, and t_{min}. They are minimum values rather than maximum values because the inverse sigmoid begins convex, then shows a renewed surge in growth so the curves for rate become valley shaped.

Asymptote values were 21.7–68.9 cm, well below the maximum size of 100 cm reported for this species by Liegel and Whitmore (1991). However, they reported that 46 cm was more typical of maximum diameter, which is in line with the 45-cm mid-range for laurels at Gigante Peninsula. Significance for m was judged using $\alpha = 0.1$ to protect against Type II errors. As already stated, a sigmoid pattern corresponds to $0 < m < 1$. There were 12 trees significant for the sigmoid pattern (Table 1). For these trees, means of the three characteristics of the Bertalanffy-Richards function were $S_{max} = 8.03$ cm, $R_{max} = 1.92$ cm/year, and $t_{max} = 6.6$ years. The two monomolecular trees had an average R_{max} of 1.27 cm/year. As given in (6), $S_{max} = 0$ and $t_{max} = t_0$ (which was 0 in our study). There were four trees with the convex pattern, three significant for the pattern and one nonsignificant (Table 1). The three inverse sigmoid trees (two significant for the pattern, one nonsignificant) listed in Table 1 as trees 14, 15 (Fig. 3), and 21 were unusual cases. Something in the environment; perhaps, a human-made or natural disturbance, caused these individuals to increase their rate of growth (after age t_{min}) when the majority of trees were experiencing declining rates of growth. Average characteristics for these inverse sigmoid trees were $S_{min} = 9.38$ cm, $R_{min} = 0.67$ cm/year, and $t_{min} = 11.7$ years. For all trees combined, one would expect an overall pattern of sigmoid for the stand, which was significant (Table 1), with $S_{max} = 6.25$ cm, $R_{max} = 1.50$ cm/year, and $t_{max} = 5.1$ years.

DISCUSSION—While the overall pattern of growth of the stand was sigmoidal, trees from Gigante Peninsula displayed an amazing degree of variation in growth form (Fig. 3). 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; Pienaar and Turnbull, 1973). Analysis of data from laurels showed that 57% of trees (12 of 21) followed this pattern. Four trees (19%) followed a convex pattern, which occasionally is reported for growth of trees (Bredenkamp and Gregoire, 1988; Lei et al., 1997). For four trees, the allometric constant, m, was not significantly different from zero, indicating monomolecular growth. This usually is considered unrealistic for growth of trees. Of the trees that were cored, none appeared suppressed but the site was suboptimal as confirmed by our analysis of growth. Trees 5 and 20 in Table 1 (10% of trees) appear to be monomolecular in form, whereas tree 3 appears to be convex (although not significant for this pattern) and tree 21 appears to be inverse sigmoid (although not

significant for this pattern). Three trees (14%) followed the inverse sigmoid pattern of growth.

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

Several studies of growth of laurels have been conducted and some have concluded that there are several factors that contribute to survival and growth, including physical and chemical characteristics of soil, physiography, and management of trees with associated crops (Menalled et al., 1998; Hummel, 2000a; Somarriba et al., 2001). Somarriba et al. (2001) determined that the style of management of plantations accounted for 56% of variation in index values of sites; while soils and minerals accounted for only 3–10% of variation in index values of sites. Plantations that offered the greatest amount of open space in well-drained, fertile soils were most likely to have the largest amount of growth.

Schlönvoigt and Beer (2001) also reported that laurels require a great amount of space for initial growth. They used an altered Nelder-fan design to study effects of tree-crop distance on growth and development of laurels. The Nelder-fan is a circular plot that allows plants to be spaced at ever-increasing distances to study relationships of density. There was no significant difference between growth of seedlings when planted with corn versus in a monoculture, where all trees were the same species. However, laurels were inhibited completely where they grew under the shade of the agricultural crop cassava (*Manihot esculenta*). Cassava grows twice as high as corn. Crowns of seedling laurels never penetrated the crowns of cassava, but it is interesting to observe how seedlings reacted to harvesting of cassava plants in this study because it might mimic conditions of a sudden clearing in a natural forest. Once cassava plants were harvested, the seedlings were released from suppression and continued to grow with renewed vigor (Schlönvoigt and Beer, 2001). Although laurels react poorly to being shaded, they have the advantage of high initial productivity and rapid closure of canopy and root system (Haggar and Ewel, 1995); unlike another pioneer species, rainbow eucalyptus (*Eucalyptus deglupta*), which when slightly overtopped, quickly can become suppressed and die (Evans and Turnbull, 2004).

It is likely that a young suppressed laurel would suddenly begin growing rapidly in the event of a new gap in the forest near the tree. However, our study showed that a few of the mature trees (ages 7.4–14.5
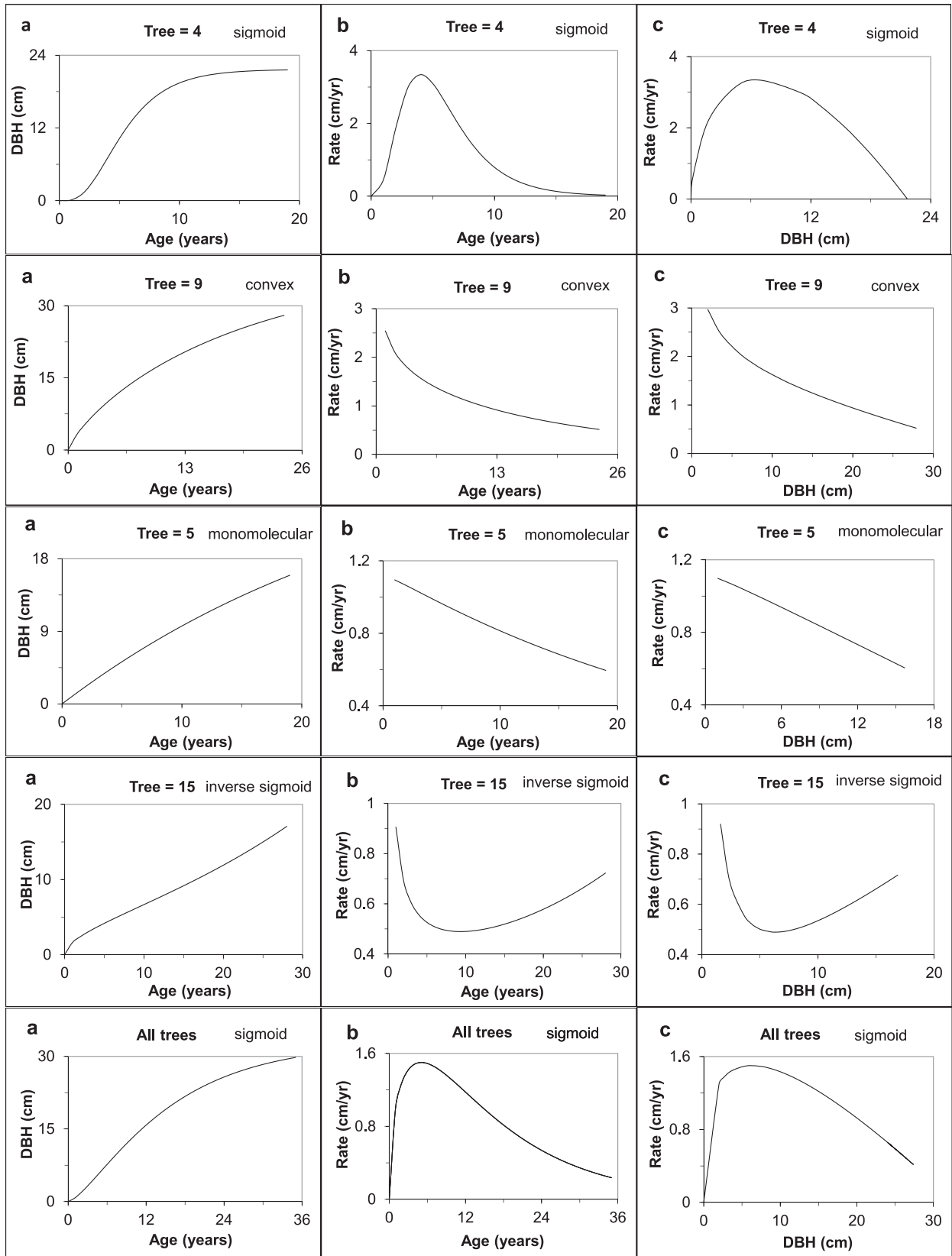
FIG. 3—Results of fitting the Bertalanffy-Richards growth model to laurel trees (*Cordia alliodora*) from Gigante Peninsula, Panama: (a) diameter plotted against age; (b) rate of growth plotted against age; and (c) rate of growth plotted against size. Trees 4, 5, 9, and 15 as identified in Table 1 are plotted as well as the fit to all 21 trees.

Table 1—Parameters, pattern, and characteristics from fitting the Bertalanffy-Richards function to the 21 laurel trees (*Cordia alliodora*) from Gigante Peninsula, Panama.

Tree	Final age	A	k	m	P[a]	Pattern	S_{max}	R_{max}	t_{max}	S_{min}	R_{min}	t_{min}
1	14	68.9	0.021	−0.411	0.038	Convex	—	—	—			
2	14	25.6	0.145	0.436	0.007	Sigmoid	5.88	1.95	4.0			
3	18	64.0	0.013	−0.355	0.111	Convex[b]	—	—	—			
4	19	21.7	0.370	0.771	<0.001	Sigmoid	6.96	3.34	4.0			
5	19	33.0	0.035	0.009	0.945	Monomolecular	0	1.16	0			
6	20	34.5	0.116	0.270	0.063	Sigmoid	5.73	2.46	2.7			
7	20	33.3	0.083	0.299	0.009	Sigmoid	5.96	1.64	4.3			
8	22	39.5	0.073	0.189	0.004	Sigmoid	5.06	1.96	2.9			
9	24	39.0	0.045	−0.268	0.015	Convex	—	—	—			
10	24	47.2	0.015	−0.719	0.005	Convex	—	—	—			
11	24	36.0	0.124	0.469	<0.001	Sigmoid	8.64	2.29	5.1			
12	25	32.5	0.163	0.747	<0.001	Sigmoid	10.26	2.24	8.4			
13	26	29.1	0.140	0.645	<0.001	Sigmoid	8.46	1.83	7.4			
16	28	36.1	0.095	0.400	<0.001	Sigmoid	7.85	1.86	5.4			
17	30	66.1	0.052	0.486	<0.001	Sigmoid	16.24	1.73	12.9			
18	32	61.7	0.018	0.203	0.015	Sigmoid	8.34	0.73	12.7			
19	32	29.4	0.066	0.457	0.002	Sigmoid	6.95	1.00	9.3			
20	32	57.7	0.024	0.019	0.896	Monomolecular	0	1.37	0			
14	28	27.4	0.022	−0.354	0.098	Inverse sigmoid				12.72	0.79	13.8
15	28	6.9	0.067	−0.864	0.002	Inverse sigmoid				6.34	0.49	9.3
21	35	133.4	0.005	−0.058	0.668	Inverse sigmoid[b]				9.08	0.74	11.9
All	35	32.8	0.079	0.328	0.001	Sigmoid	6.25	1.50	5.1			

[a] Probability for parameter m against a null hypothesis of 0.
[b] The pattern is not significant at $\alpha = 0.1$ based on the P value of m.

years) also experienced renewed growth; thus, following a nontypical pattern of growth. The significance of our studies is that laurels showed the greatest amount of growth when they had little or no competition for light. Laurels also had difficulty competing with weeds in regards to absorption of nutrients (Menalled et al., 1998). Some grasses, such as molasses grass (*Melinis minutiflora*), can have an allelopathic effect on laurels.

Laurels have a high rate of mortality at sites with poor drainage, compaction of soil, and frequent flooding (Somarriba et al., 2001). Soils that are rich in clay are highly susceptible to compaction and, with cattle grazing on such soils, there would be a negative effect on growth because laurels develop only a lateral, superficial root system within their first years (Bergmann et al., 1994). Roots of a mature laurel tree are far reaching in depth and in lateral growth (Haggar 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 detected in leaves of laurels in Costa Rica (Bergmann et al., 1994; Menalled et al., 1998). Bergmann et al. (1994) suggested that in plantation settings, laurels should be mixed with nitrogen-fixing species to improve afforestation practices. However, some studies have shown that additional fertilization with nitrogen has a negative effect on growth of laurels (Johnson and Morales, 1972); perhaps, because of the reduced need for expansion of roots to attain needed nutrients.

According to Johnson and Morales (1972), who reviewed geographic range, biology, and growth of laurels, the best stands are on the Caribbean coast of Honduras, Nicaragua, and Costa Rica. Data on growth from old natural stands of laurels in the Atlantic lowlands of Costa Rica revealed dbh-values of 79, 89, and 91 cm for 40-, 50-, and 60-year-old trees, respectively. Liegal and Whitmore (1991) reported mean dbh of laurels growing in pastures and agricultural fields in Costa Rica, and Liegal and Stead (1990) reported mean diameters for laurels growing in six plantations across Puerto Rico. In comparison to data on agroforestry from Costa Rica (Liegal and Whitmore, 1991), laurels at Gigante Peninsula were ca. 15% smaller than trees in their pastures at Cahuita and 40–48% smaller than their coffee-shaded laurels at Bajo Chino and La Suiza, Costa Rica. Neil and Jacovelli (1985) reported that in agroforestry systems in Vanuatu, a small Pacific-island nation, maturing laurels developed extensive, shallow root systems that could compete with adjacent agricultural crops. Laurels also developed a strong taproot in deep soils that allowed them to remain firm in hurricane-force winds. However, if the taproot cannot establish due to a thin layer of soil, such as on shallow coralline soils, the tree becomes more susceptible to blowing over (Greaves and McCarter, 1990). Removed from competition in forests and capable of developing vigorous root systems on agricultural soils, our analysis showed that agroforestry-planted laurels grew faster and larger than in natural stands such as at Gigante

Peninsula, where the soil was thin and rocky, and compare favorably with optimal natural sites like the Atlantic lowlands of Costa Rica.

In comparison to data from plantations in Puerto Rico reported by Liegal and Stead (1990), laurels at Gigante Peninsula were growing at a rate similar to four of their sites (Catalina, Tract 105, Luquillo, and Carite) and somewhat better compared to their other two sites (Guilarte and Guánica State Forest). Puerto Rico is at the northern boundary of the natural range of laurels, although this may not have any bearing on potential for growth there. The site at Guánica State Forest, Puerto Rico, was subtropical dry, which explains slower growth, because laurels do not thrive in drier areas (Johnson and Morales, 1972; Liegel and Stead, 1990; Liegel and Whitmore, 1991).

Vega (1977) examined growth of laurels on different sites in Surinam and noted that early growth on good sites was 2.1–3.5 cm/year, and at 7 years of age, dbh frequently was >22 cm. On poor sites, the annual increase in diameter was reduced to 0.6–1.1 cm/year. Trees at Gigante Peninsula were between these cases. The range in R_{max} was 0.73–3.34 cm/year with a mean of 1.92 cm/year at 6.6 years old. Piotto et al. (2003) reported a mean annual increment of 2.09 cm/year for 5–10-year-old laurels in pure plantations on the Atlantic lowlands of Costa Rica. While the R_{max} for laurels at Gigante Peninsula averaged 1.92 cm/year, mean annual increment was only 1.0 cm/year for the 21 trees whose average age was 25 years. For 5–10 years of age, mean annual increment for Gigante Peninsula was 1.00–1.92 cm/year, well below the 2.09 reported by Piotto et al. (2003). The Atlantic lowlands of Costa Rica are an optimal site for laurels (Johnson and Morales, 1972) and plantations in this region usually outperform natural stands.

The laurel is a pioneer species of gaps, characteristic of young forests. Pioneer species, including laurels, emerge in gaps of all sizes, but usually are restricted to gaps >150 m^2. Other species of trees can exist as suppressed saplings in a closed forest until a gap forms, and then accelerate in growth (Brokaw, 1996). Thus, differing requirements of seedlings and saplings of various species lead to different patterns of growth. Laurels that germinate in a gap typically have adequate resources at the time of germination and early growth. As the forest grows and the gap disappears, laurels typically occupy an intermediate to suppressed position in the canopy, and are 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 rate of growth is reached, is the point (i.e., R_{max}, t_{max}) of measurable competition on the tree.

The range of t_{max} was 2.7–12.9 years with a mean of 6.6 years (Table 1). Gaps in the moist tropics tend to revegetate quickly, small gaps achieving closure of canopy sooner than large gaps. One would expect natural stands to have variability in size of gaps and the t_{max}-values reflected this. Apparently, on Gigante Peninsula, gaps tended to close after ca. 7 years. For trees displaying the inverse sigmoid pattern, t_{min}-values were 9.3–13.8 years, indicating an influence that caused renewed growth. By age 7, laurel trees usually had entered their maturity phase. Most species had lost their capacity to respond aggressively; i.e., with a burst of growth to a release event after becoming mature. Many species respond positively to release from competition, but not to the extent of achieving sustained higher rates of growth (Clutter et al., 1983). An extensive search of the literature revealed only one article that reported an inverse sigmoid pattern. Bredenkamp and Gregoire (1988), in studying E. grandis in South Africa, documented a resurgence of growth in stands that had experienced substantial mortality. As demonstrated, laurels also are capable of resurgence of growth, a capability rarely reported.

The Bertalanffy-Richards function is a useful tool for assessing growth of trees because it is flexible enough, especially the alternate form, to reveal nontypical patterns of growth like the convex, monomolecular, and inverse sigmoid, in addition to the standard sigmoidal pattern of growth. It is significant that all four patterns of growth were in natural stands at Gigante Peninsula. All patterns simultaneously occurring in a stand have not been reported previously. It may be that all patterns of growth did occur but had not been reported because the convex and inverse sigmoid patterns of growth could not be revealed by the classic Bertalanffy-Richards function. It was Lei et al. (1997) who showed that by allowing m to become negative in the classic Bertalanffy-Richards function, that the convex pattern of growth is revealed. They also derived an extension where m and γ were negative, which resulted in the inverse sigmoid pattern of growth. Results of our study indicated that laurels are amazingly resilient and have the capacity to assume different patterns of growth under natural conditions. We anticipate that further research in natural stands of laurels; especially, with additional environmental data included, will show similar results.

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