



# Growth equations and rotation ages of ten native tree species in mixed and pure plantations in the humid neotropics

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## Abstract

Ten percent of the world's forest consists of plantations, yet these plantations supply 37% of the world's timber. While plantations proliferate, local communities are looking for suitable native species to cultivate in plantations. This paper is a component of a larger project—trying to restore degraded areas with native plantations in ways that would financially benefit the surrounding communities. Growth equations have been constructed for ten native tree species, using 12 years of growth data from research plots in La Selva Biological Station, Costa Rica. Interpolative growth equations for *Terminalia amazonia* (J. Gmel) Exell., *Virola koschnyi* Warb., *Dipteryx panamensis* (Pittier) Record & Mell, and *Hieronyma alchorneoides* Allemao were constructed. A maximum sustained yield approach was used to determine the other six species' rotation age and the merchantable volume produced per hectare at time of harvest. In single-species plantations, *Jacaranda copaia* (Aubl.) D. Don., *Vochysia guatemalensis* Donn. Sm., and *Vochysia ferruginea* Mart. were the most productive species and, thus, are the recommended plantation species for the humid lowlands of Costa Rica. The data for this experiment suggest *J. copaia* has an ideal rotation age of 6.5 years, at which time the yield will be 255 m<sup>3</sup>/ha. *V. guatemalensis* has a rotation age of 13.5 years producing 417 m<sup>3</sup>/ha, and *V. ferruginea* has a rotation age of 13.3 years producing 363 m<sup>3</sup>/ha.

*J. copaia* and *V. guatemalensis* grew significantly faster in mixed plantations than in pure plantations. A mixed-species plantation comprised of *J. copaia*, *V. guatemalensis*, and *Calophyllum brasiliense* Cambess produces 21% more total volume of merchantable timber than a pure plantation of *J. copaia*, which grows the fastest of the three species. Restoring abandoned agricultural sites with *V. guatemalensis* will yield the most timber to landowners after one rotation.

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## 1. Introduction

As of 2000, 3.9 billion hectares of forest existed around the world. Forty-seven percent of these forests

are located in the tropics. Moreover, plantations compose 5% of forests around the world (FAO, 2001). What's more remarkable is that this 5% contributes over 20% of the world timber supply (Matthews, 2001). More importantly, the representation of plantations on the forested landscape is increasing. The tropics specifically have seen a 2% increase in plantations (by area) since 1990. This rise equates to the creation of over 4.5 million hectares of plantations annually (FAO, 2001).

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In Central America, many of these plantations are being established on abandoned agricultural land. Farmers are recognizing the potential for financial returns from plantations (Rheingans, 1996; Shelhas et al., 1997). Many of these farmers prefer to use native species, for which relatively little is known (ACEN, 1994; Butterfield and Fisher, 1994; Wightman et al., 2001; Piotto et al., 2003b). While establishment considerations and thinning effects are known for some native species, productivity levels of native species in plantations are by and large unknown (Montagnini et al., 1995; Piotto et al., 2003a). The next logical step in finding a species to endorse for reforestation efforts is determining each species' rotation age and how much timber it is capable of producing (Rheingans, 1996; Wright and Alder, 2000; Wightman et al., 2001). Many plantations comprised of these species have already been established, so this study is targeted at determining the productivities of the ten most commonly utilized, native, timber species for the Atlantic lowlands of Costa Rica.

Moreover, the diversity of species in plantations has been increasing (FAO, 2001). Many local farmers seek to use mixed-species plantations (Piotto et al., 2003b). Mixed-species plantations are often useful tools in restoration as they can ameliorate microsites to be more conducive to native tree seedling recruitment (Guariguata et al., 1995).

However, because most of the already established plantations with native species have yet to reach their rotation ages, questions about their productivity can be addressed through modeling. The growth data from the annual measurements of our experimental plantations at La Selva, Costa Rica has been stored in MIRA<sup>®</sup> (Ugalde, 2000), a continuous forest inventory database maintained by Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) based in Turrialba, Costa Rica. Data from the past 11 to 12 years for each of the plantations were used to construct growth models for ten species of trees indigenous to the humid lowlands of Central America. This study addressed four main research objectives. The main objective of this study was to construct growth equations for each of ten species growing in the plantations. Secondly, employing these equations, the rotation age and the merchantable volume produced at this age were extrapolated for each of the species. Then the productivity of these species was compared in order to

make recommendations to landowners. Finally, the productivities of pure and mixed-species plantations were compared. This study has implications for species selection and rotation lengths in plantations throughout Central America and even into parts of South America.

## 2. Materials and methods

### 2.1. Study site description

Experiments were established on abandoned pasture at La Selva Biological Station, Costa Rica—humid tropical lowlands (10°26'N, 86°59'W, 50 m mean altitude, 24 °C mean annual temperature, 4000 mm mean annual rainfall) (Fig. 1). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well-drained, stone-free, acidic (pH in water <5.0), with low or medium amounts of organic matter (2.5–4.5%), cation exchange capacity 10–14 cmol kg<sup>-1</sup>, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt, and 25–45% clay) (Sancho and Mata, 1987).

The area was cleared in the mid-1950's and grazed until 1981, a land-use pattern common in the region. The area is on flat, uniform terrain (<1 m average difference between lowest and highest points). At the time of clearing for the plantations, the area was covered with shrubs and early successional trees interspersed with patches of grass and ferns. In comparing soil chemical characteristics before planting, results showed that there were no significant differences among blocks within each plantation (Montagnini et al., 1993). According to standards set by the Costa Rican Ministry of Agriculture, fertility levels of the site were too low for conventional agriculture (Montagnini and Porras, 1998).

The plantations used in this research were established in 1991–1992. There are three plantations that originally contained four species each; two species have died, thus, leaving ten species for consideration. The ten species were as follows: Plantation 1—*Calophyllum brasiliense* Cambess, *Vochysia guatemalensis* Donn. Sm., and *Jacaranda copaia* (Aubl.) D. Don.; Plantation 2—*Dipteryx panamensis* (Pittier) Record & Mell, *Virola koschnyi* Warb., and *Terminalia amazonia* (J. Gmel.) Exell.; and Plantation 3—*Vochysia*



Table 1

Native timber species in mixed and pure plantations at La Selva Biological Station, Costa Rica involved in this study

Species	Common name	Family	Natural distribution
Plantation 1			
<i>C. brasiliense</i> Cambess	Cedro Maria	Clusiaceae	Mexico to N. South America
<i>V. guatemalensis</i> Donn. Sm.	Mayo, chanco	Vochysiaceae	Mexico to Peru
<i>J. copaia</i> (Aubl.) D. Don.	Jacaranda	Bignoniaceae	Guatemala to Brazil
Plantation 2			
<i>D. panamensis</i> (Pittier) Record & Mell	Almendro	Fabaceae-Pap.	Nicaragua to Colombia
<i>V. koschnyi</i> Warb.	Fruta dorada	Myristicaceae	Central America
<i>T. amazonia</i> (J. Gmel) Exell.	Roble coral	Combretaceae	S. Mexico to N. South America
Plantation 3			
<i>V. ferruginea</i> Mart.	Botarrama	Vochysiaceae	Nicaragua to Brazil
<i>H. alchorneoides</i> Allemao	Pilon	Euphorbiaceae	Mexico to Brazil
<i>G. americana</i> L.	Genipa	Rubiaceae	Tropical America
<i>B. elegans</i> (Ducke) Barneby & Grimes	Ajillo, guaitil	Fabaceae-Mim.	Tropical America

Source: Piotto et al. (2003a), Jiménez and Poveda (1997), González et al. (1990), Holdridge and Poveda (1975).

present in the three plantations. All of the thinnings done to the plantations were crown thinnings aimed at releasing the residual trees to maximize growth in the plot. While they aimed for maintaining a consistent spacing of a tree every 4 m (length and width), the actual spacing varied. When establishing subplots for measurement, the first inside 8 m on every side of the plot were discarded as having potential border effects. Instead, all of the trees inside a fourteen by 16 m subplot (eight rows of trees 16 m long) were measured and tallied (Rustagi, 1993). The corners of these plots were randomly chosen using a random number generator. A two-digit random number was produced and divided by four. Then its remainder (0, 1, 2, or 3) determined the corner of the plot at which the corner of the subplot was established.

All of the trees present in the subplot were measured. Each tree's diameter at breast height (cm) and total height (m) were measured (Hairiah et al., 2001). Both the area of each subplot and the volume of merchantable wood standing in the subplot were calculated. As trees were planted in rows on the border of the subplot, the length and width of the area-defining rectangle were found by extending the subplot 2 m on each side (to compensate for the crown width of the border trees). This measure allows the volume/ha statistic to be applicable when extrapolating to larger size plantations (Hairiah et al., 2001). When the plots were younger and comprised of trees with smaller crowns, the sides of the rectangle were

increased only by 1 m. All of the tree data from the 50 plots was then entered into 'Manejo de Información sobre Recursos Arbóreos, or Information Management for Tree Resources' (MIRA<sup>®</sup>) (Ugalde, 2000) to augment the previous 11-year database of growth measurements for these species and to perform calculations of tree productivity parameters (Piotto et al., 2003a). MIRA is an information management system that warehoused the past stocking levels of these stands. MIRA employs an allometric model for estimating stockings in stands.

### 2.2.2. Modeling

The total standing volume of wood (m<sup>3</sup>) in each plot was calculated using MIRA for each time it was measured through the plot's history. These volume/ha statistics along with the corresponding age of the plantation at the time of measurement were exported into an Excel<sup>®</sup> workbook. Growth equations were then calculated for each species via regression analysis, and these took the form of a third-degree polynomial (Singh et al., 1998; Borders and Bailey, 1986; Haggard and Ewel, 1997). Second-degree polynomials (interpolative equations) were assigned to the species whose growth was too premature for extrapolative modeling (indicated by the tertiary terms in the third-degree polynomials being positive).

The effects of thinning in the plots distorted the model predictions for two of the species. For *V. guatemalensis* and *V. ferruginea*, two separate growth

equations had to be constructed: one describing growth before thinning and one describing the growth of these species after thinning (Bailey and Ware, 1983; Farrar, 1985; Knoebel et al., 1986; Baldwin et al., 1988). The first equation is useful for interpolating growth estimates, and the second was used for extrapolating volume predictions (Smith and Hafley, 1986). The first equation was generated by a third-degree polynomial regression analysis (using the same procedure described above). The second was constructed using a weighted polynomial regression analysis in SPSS<sup>®</sup>. Because of the paucity of data points, future estimations of growth one year out were used to help true the equations (Wright and Alder, 2000; Johnson, 2003). These estimations were calculated using a time series analysis (fed from data previously recorded in the plots), which modeled proportional effects of reductions in growth rates with canopy closure after thinnings (Wright and Alder, 2000; Kennedy, 2001). For each discrete plot, the estimated future yield and the first year's response growth to the thinning were assigned half the power of the measured data in the regression analysis.

The mean annual increments (MAI) for each species were then computed from their respective growth equations. The age, at which MAI was maximized, was identified to the month. This age was deemed to be the optimal rotation age for the species under these conditions (Newman, 1988; Smith et al., 1996). The rotation age of *J. copaia* had to be determined by a visual approximation of its growth curve, which will be further discussed in Section 3. In addition, the volume of wood produced at this age was computed for each species by entering this age into the extrapolative growth equations produced earlier (Knoebel et al., 1986). This total volume was converted to merchantable volume (amount of timber in logs to be removed from the stand) by subtracting 15% from the total wood volume (Vanclay, 1996; Wright and Alder, 2000).

The calculated rotation ages and merchantable volumes yielded after a rotation were then used to compare the productivities of the species. Mean annual yields were computed for each species using each species' respective rotation age and predicted yield: mean annual yield = (merchantable yield after one rotation/rotation age). The mean annual yields for each species were then compared by ranking each

species in terms of productivity. Note that this comparison only included the species for which a rotation age could be determined.

### 2.2.3. Comparisons of pure and mixed-species plantations

The growth of trees in mixed plantations was compared to the growth of the trees of the same species in the pure plots in Plantation 1. The volumes of the individual, sampled trees present in both the pure and mixed plots were calculated using the formula  $V = \alpha B_{\text{dbh}} H$  (Montero, in press). The value of  $\alpha$  was set to 0.5 (Ugalde, 2000). An unpaired *t*-test was performed for Plantation 1 to test for significant differences between the average volumes of wood present in trees of the same species under the two growing regimes (Whyte and Woollons, 1990). The level of significance for this test was set at 0.05. Inconsistent sampling of the mixed plots in Plantations 2 and 3 precluded any analysis of the other species.

The productivity of the pure plots in Plantation 1 was then compared with the productivity of the mixed plots. A rotation age (assuming each plot is clearcut, or all species are harvested at the same time) and expected yield for this mixture of species was first determined by the methods described in Section 2.2.2. Then the rotation age and merchantable volume to be produced were used to computing respective mean annual yields. As these annual yields represent productivity, the productivities of the mixtures were compared with the productivities of the single-species plots to see which yielded more merchantable wood (Burkhardt and Tham, 1992; Kelty, 1992). In the mixtures, no differentiation amongst the types of wood was considered in the comparisons.

### 2.2.4. Sensitivity analysis

Lastly, a series of four sensitivity analyses was conducted to determine the solidity of our findings. The first sensitivity analysis (SA) involved manipulating time near each species' rotation age to see its effect on the merchantable volume produced. The rotation age for each species was increased and decreased by 10% (Chan et al., 1998) and then entered into the growth equations to compute new yielded volumes. The effects of manipulating the independent variable (time) on the dependent variable (merchantable volume produced) were expressed as a percentage

of the expected volume to be yielded at the actual rotation age. Comparing these percentages to the percent adjustment of time elucidated how the mechanics of the model processed the variables near the rotation age.

The second sensitivity analysis addressed how a change in rotation length would affect the productivity of a species. First, the rotation length for each species was increased by 0.5 years. Next, the new amount of merchantable volume to be produced at the end of a rotation was calculated from entering the new rotation age into the existing growth equation for the species. This new combination of rotation age and yield was used to determine the adjusted productivity for each species over a 100-year period. This process was repeated with a 0.5-year decrease in the rotation period. The effects of manipulating the rotation period on productivity were then judged. Finally, the actual productivity and adjusted productivities for each species were graphed and compared to the other species. Overlap in the breadths of productivity values for each species were noted to determine if timing in the harvest year would affect the productivity rankings of the species.

The third sensitivity analysis addressed the relative scatter of the data points used to generate the growth equations for each species. The most influential data point affecting the  $R^2$ -value of each growth was adjusted by increasing and decreasing its dependent

variable measures by 10%. This analysis aided in establishing the precision of the data used to construct the growth equations (Davis and West, 1981). The final SA, similar to the last, sought to observe the effects of adjusting a data point on the productivity of a species. First, the data point, whose adjustment would affect productivity the most, was increased and decreased by 10%. Regression analyses were conducted utilizing the new points to form two new growth equations for each species. From these equations, new rotation ages and harvesting volumes were computed for each species, and these, in turn, were used to establish new productivities for each species. Each species' range of productivities was again compared to determine if the initial ranking of species still holds (if no overlap exists amongst the ranges) (Davis and West, 1981).

### 3. Results

#### 3.1. Modeling predictions

The growth equations of six of the species were third-degree equations and, thus, they could be used for volume extrapolations (Table 2). The six species were *C. brasiliense*, *V. guatemalensis*, *J. copaia*, *V. ferruginea*, *G. americana*, and *B. elegans*. The growth equations for the other four species were

Table 2  
Growth equations for ten native species in plantations in the Atlantic lowlands of Costa Rica

Species	Growth equation <sup>a</sup>	$R^2$ -value
<i>C. brasiliense</i>	$V = -0.0711 t^3 + 2.6340 t^2 - 5.5421 t$	0.950
<i>V. guatemalensis</i>	$V = -1.2983 t^3 + 16.562 t^2 - 11.441 t, \forall t t < 8.3$ $V = -0.4939 t^3 + 13.437 t^2 - 55.039 t, \forall t t > 8.3$	0.967 0.738
<i>J. copaia</i>	$V = -0.1462 t^3 - 0.0343 t^2 + 52.615 t$	0.940
<i>D. panamensis</i>	$V = 0.9562 t^2 + 1.3287 t^b$	0.909
<i>V. koschnyi</i>	$V = 3.3494 t^2 + 1.0236 t^b$	0.937
<i>T. amazonia</i>	$V = 2.6515 t^2 + 0.7005 t^b$	0.958
<i>V. ferruginea</i>	$V = -0.5576 t^3 + 9.8208 t^2 - 15.719 t, \forall t t < 7.0$ $V = -0.5908 t^3 + 15.772 t^2 - 73.248 t, \forall t t > 7.0$	0.985 0.828
<i>H. alchorneoides</i>	$V = 0.3897 t^2 + 14.689 t^b$	0.897
<i>G. americana</i>	$V = -0.0184 t^3 + 0.4856 t^2 + 3.5484 t$	0.815
<i>B. elegans</i>	$V = -0.1351 t^3 + 2.4023 t^2 + 7.8420 t$	0.952

<sup>a</sup> As seen as variables in the above equations,  $V$  is volume of timber produced in  $m^3/ha$ , and  $t$  is time in years.

<sup>b</sup> These equations are valid for interpolative predictions only; limiting the modeling projections for plantations of these species to 12 years of age (11 years for *H. alchorneoides*).

second-degree polynomial equations. These four species were *D. panamensis*, *V. koschnyi*, *T. amazonia*, and *H. alchorneoides*. Rotation ages for these species could not be computed with these equations, for these equations are limited to interpolative uses. Two equations (one interpolative and one extrapolative) were generated for *V. guatemalensis* and *V. ferruginea*. All of the equations have high  $R^2$ -values. The  $R^2$ -value for the *G. americana* equation is the lowest, yet still high at 0.815. The extrapolative growth curves noticeably level off with age, and the interpolative growth curves seem to continue to exponentially increase without limit (Fig. 2).

Rotation ages and expected merchantable volumes to be yielded were calculated from the growth equations (Table 3). *J. copaia* and *B. elegans* had relatively short rotation ages—6.5 and 8.8 years, respectively. Their short calculated rotation age means that trees of these species slow down their growth early, which usually occurs in fast-growing species (Fry and Poole, 1980; Lamprecht, 1986; McDade et al., 1994). At this age, trees of these species are of merchantable size so they can be harvested (Butterfield, 1993). The calculated rotation ages for the other four species ranged from 13.2 to 18.5 years.

The rotation age of *J. copaia* had to be estimated visually from its growth curve (Fig. 2). Because of the nature of its growth equation, the MAI of *J. copaia* increases indefinitely as the rotation age approaches zero. Thus, its rotation age was approximated to be 6.5 years, for it has a noticeable decrease in growth at this age. The *J. copaia* growth curve still has use in interpolative applications. This species was not clumped with the other four undetermined species because its rotation age was not capable of being determined for a different reason. For this species,

the data yielded were not conducive to a MAI analysis because it appears to continually reduce its growth rate after its first year.

However, the short length of some of the rotations calculated here can be misleading, exemplified by *V. guatemalensis* and *V. ferruginea*. While these species have longer rotations, they produce much greater volumes of wood at the time of harvest than other species. The most productive species must strike a balance between short rotations and high volume yields. The productivity of these species is illustrated by determining the mean annual yields of merchantable timber they would produce in pure plantations over one rotation (Table 3). This analysis shows that the most productive species are *J. copaia*, *V. guatemalensis*, and *V. ferruginea*, whereas *C. brasiliense*, *B. elegans*, and *G. americana* are the least productive species, in order of decreasing productivity. *J. copaia*, *V. guatemalensis*, and *V. ferruginea* are more than twice as productive as *C. brasiliense*, *B. elegans*, and *G. americana* (Table 3).

### 3.2. Comparing mixed and pure plantations

When comparing individual tree growth in pure and mixed-species plots, all of the species in Plantation 1 had significantly different growth rates in the pure plots compared to the mixtures, when employing a 0.05 level of significance (Table 4). *J. copaia* and *V. guatemalensis* grew significantly larger in mixed plots of *C. brasiliense*, *J. copaia*, and *V. guatemalensis* than in pure plots of *J. copaia* or *V. guatemalensis*. *C. brasiliense* trees grew significantly larger in pure plots than *C. brasiliense* trees in mixtures containing *C. brasiliense*, *J. copaia*, and *V. guatemalensis*.

Table 3  
Rotation age, yield, and relative growth rates for six native species in plantations, determined through maximum sustained yield

Species	Rot. age (years)	M. vol. at harvest (m <sup>3</sup> /ha)	Mean annual yield (m <sup>3</sup> /ha/year)	Rel. growth (ranking)
<i>C. brasiliense</i>	18.5	296	16.0	4
<i>V. guatemalensis</i>	13.5	417	30.9	2
<i>J. copaia</i>	6.5	255	39.2	1
<i>V. ferruginea</i>	13.3	363	27.3	3
<i>G. americana</i>	13.2	76	5.8	6
<i>B. elegans</i>	8.8	139	15.8	5

Rot. age: rotation age; M. vol. at harvest: merchantable volume yielded after one rotation; Rel. growth: relative growth.

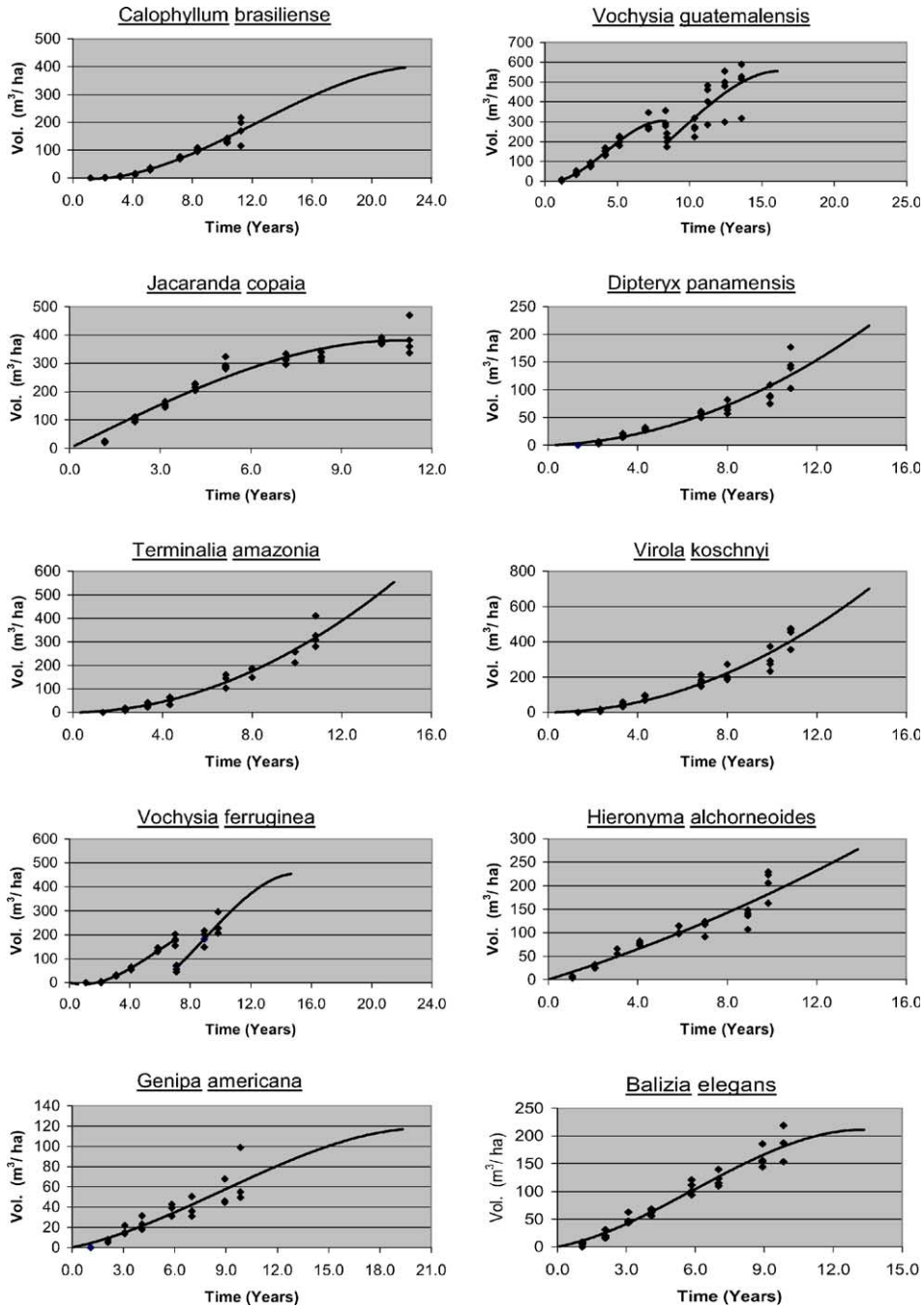


Fig. 2. Growth curves for ten native species in the Atlantic lowlands of Costa Rica.

Two of the three species comprising the Plantation 1 mixtures grew faster in mixtures than pure plots. However, not only did the third species *C. brasiliense*

grow significantly slower in the mixed-species plots, but also the relative abundance of this slow-growing species was decreased. By determining the ideal

Table 4

Differences in growth amongst pure and mixed plantations of plantation 1 determined by way of an unpaired two-tailed *t*-test

Species	$\bar{x}_{\text{Pure}}$ (m <sup>3</sup> )	$\bar{x}_{\text{Mixed}}$ (m <sup>3</sup> )	<i>P</i> -value	Conclusion
<i>C. brasiliense</i>	0.22	0.05	1.86E–09	Pure > mixed
<i>J. copaia</i>	0.47	0.82	1.83E–09	Pure < mixed
<i>V. guatemalensis</i>	0.63	0.94	3.4E–04	Pure < mixed

Level of significance,  $\alpha = 0.05$ .

rotation age of the mixtures to be 8.5 years and calculating its corresponding yield to be 403 m<sup>3</sup>/ha, the productivity of the mixed-species plots was compared to the productivities of each of the single-species plots in Plantation 1 (Table 5). The mixed-species plots produced more merchantable wood over time than any of the other pure plots from this plantation. The mixture was about 21% more productive than the most productive of the single-species plots.

### 3.3. Sensitivity analyses

Time has a linear effect on volume production near each species rotation age (Table 6). When the length of the rotation was increased or decreased by 10%, the merchantable volume predicted to be produced after

one rotation was increased or decreased by about 10%, i.e. if the trees were left to grow 10% longer, the plot would yield 10% more merchantable volume. A slightly larger alteration in merchantable volume always resulted from shortening the rotation period than from lengthening the rotation period, which is to be expected of trees that slow their growth with age. *J. copaia* was least affected by manipulations in rotation age, due in part to its much shorter rotation length.

The third sensitivity analysis involved moving each of the data points to note the precision of the data from which each of the ten growth equations were constructed. Adjusting the average plot-volume by 10% is gratuitous. In a plot of *B. elegans* having an average diameter at breast height of 27 cm, this would mean every tree would have to be either under-measured or

Table 5

Comparing single-species plantations with mixed-species plantations: yield produced at their rotation age and mean annual yield in plantation 1

Species	Rot. age (years)	M. vol. at harvest (m <sup>3</sup> /ha)	Mean annual yield (m <sup>3</sup> /ha/year)
<i>C. brasiliense</i>	18.5	296	16.0
<i>V. guatemalensis</i>	13.5	417	30.9
<i>J. copaia</i>	6.5	255	39.2
Mixed species	8.5	403	47.4

Rot. age: rotation age; M. vol. at harvest: merchantable volume yielded after one rotation.

Table 6

Sensitivity analysis of time near the predicted rotation ages in the extrapolative growth equations

Species	Act. rot. age (years)	Mer. volume gained (w/10% increase in age) (%)	Mer. volume loss (w/10% decrease in age) (%)
<i>C. brasiliense</i>	18.5	9	11
<i>V. guatemalensis</i>	13.5	10	10
<i>J. copaia</i>	6.5	7	8
<i>V. ferruginea</i>	13.3	9	11
<i>G. americana</i>	13.2	9	11
<i>B. elegans</i>	8.8	9	11

Act. rot. age: actual rotation age; Mer. volume gained: merchantable volume gained; Mer. volume loss: merchantable volume loss.

over-measured by nearly 3 cm; or all of the trees would have to be under-assessed or over-assessed consistently by more than 2 m.

This manipulation had little effect. The lack of influence on the  $R^2$ -values was due to the large number of sample points used in the construction of each growth equation (Campolongo and Braddock, 1999). This analysis also suggests that all of the data closely fit the regression line, indicating a high degree of precision. *G. americana* was the most affected species in this SA, for many of this species' experimental plots were adversely affected by hot and dry weather conditions immediately following this plantation's establishment (Montagnini et al., 1995). After one of the *G. americana* sample plots was spayed by disease in 1997, the data of remaining years for this plot were not used in the construction of the growth equation for this species, and were not considered in the analysis.

The last SA illustrated the effects of data manipulation and potential experimental bias on productivity. Whether the equations were increased or decreased to cause the greatest possible effect on productivity, the relative productivity rankings of the top three species still hold. The range of productivities for each of these species does not overlap. The ranges of productivities for *C. brasiliense* and *B. elegans* do, however, overlap. This indicates that in extreme scenarios it is possible that *B. elegans* would produce more wood than *C. brasiliense*. More pragmatically, this occurrence suggests that their growth rates should not be considered significantly different. Perhaps, valuations of the timber produced from each species will be required to set the rotation times of these two species (ACEN, 1994).

## 4. Discussion

### 4.1. Productivities

The most productive of the six native species, for which growth equations could be constructed, were *J. copaia*, *V. guatemalensis*, and *V. ferruginea*, respectively. These findings are in accordance with what is presently known about the growth of these species in plantations in the same region (Holdridge and Poveda, 1975; Montagnini et al., 1995; Montagnini and Porras, 1998; Piotto et al., 2003a,b).

However, in addition to high productivity, uses and market values of the species are important factors determining their preferences by farmers. For example, *V. guatemalensis* is one of the most preferred species in the region for reforestation of degraded pastures while *J. copaia* is not preferred because it has low local economic value (Montagnini et al., 2003). *V. guatemalensis* is probably the most frequently planted species in the Caribbean lowlands of Costa Rica, and knowledge exists regarding several aspects of this species' domestication, including seed collection and germination, vegetative propagation, and preliminary stages of tree genetic improvement (Montagnini et al., 2002). In contrast, despite of its good growth, farmers are not planting *J. copaia* due to its poor timber quality. *V. ferruginea* is also preferred by farmers due to its good timber quality. Under plantation conditions in the experimental site, *V. ferruginea* had abundant leaf litter production that covered the ground and protected against soil erosion, an additional advantage in the use of this species when grown on degraded sites (Horn and Montagnini, 1999; Stanley and Montagnini, 1999).

The least productive of the six species was by far *G. americana*. This species is not well adapted to the environmental conditions of the region since it grows naturally in drier regions (Montagnini et al., 2003), and thus presented high mortality (sometimes 80%) and poor growth.

*C. brasiliense* and *B. elegans* exhibited similar productivities although their productivities were less than half the productivities of *V. ferruginea*, *J. copaia*, and *V. guatemalensis*, which is in line with findings from Little and Wadsworth (1964), Jordan and Farnworth (1982), Butterfield and Espinoza (1995), Wightman et al. (2001), Montagnini et al. (2003) and Piotto et al. (2003a,b). The sensitivity analyses conducted show that these productivity rankings are relatively firm. Because *C. brasiliense* yields very high-quality timber though grows slowly, combining it with other species in silvopastoral systems is a good alternative. Earlier earnings from the cattle products could help offset the relatively high maintenance costs and longer rotation times (Montagnini et al., 2003). Pruning practices are needed for this species to maintain good tree form. Moreover, pruning is needed to allow the light that is needed for pastures to grow to reach the understory. In contrast, *B. elegans* is not being planted in the

region due to its lower timber quality and poor tree form. At La Selva, tree form in *B. elegans* plots was variable: some trees had several twisted stems, but many trees had acceptable form (Montagnini et al., 2003).

*V. koschnyi* at the time of the measurements had a little over 420 m<sup>3</sup>/ha of merchantable timber standing in its twelve-year old plots. Even if it was harvested at that time, the amount of volume obtained from a premature harvesting cycle would rank *V. koschnyi* second amongst the species for which predictions were made. This species' ability to rank just below *J. copaia* with an imperfect rotation age suggests it has potential to be one of the most productive species (Holdridge and Poveda, 1975; Butterfield and Espinoza, 1995; Montagnini et al., 1995; Piotto et al., 2003b). Though this cannot yet be quantified until its true rotation age and yield is determined, this trend is worth noting. In addition, *V. koschnyi* has a dense canopy and, thus, does not need to be pruned. Farmers prefer it, and it is suitable for planting in low density in silvopastoral systems (Montagnini et al., 2003). Moreover, the other three species, for which rotation ages could not be determined, exhibited moderate growth. This was also seen in studies conducted by Clark and Clark (1992) and Wightman et al. (2001).

At La Selva Biological Station, trees do most of their growing during the six-month rainy season (McDade et al., 1994; Brunner, 2003). Consequently, a series of step-wise growth equations may depict the growth of these species more accurately (Borders and Bailey, 1986). However, one would usually seek to harvest a plantation at the end of the current year's

growing season (Lamprecht, 1986). This decision should be regardless of the specific nature of the rotation ages given in Table 3 because the original establishment of each plantation can vary over the year, making this level of specificity futile. Consequently, the volumes projected for each species' rotation should vary with the rotation age, varying no more than 0.5 years in either direction. The varied rotation ages and their corresponding yields are shown to differ little from the yields projected from the ideal rotation ages (Table 7). While the  $\pm 0.5$  years is useful in mimicking step-wise growth, landowners should round the rotation ages presented in Table 3 to the end of the growing season.

Also, this did not cause a significant difference in the productivities of the species, for the species still held their rankings. This small degree of change was expected. Because this last year of growth before being harvested is not one of the years exhibiting the highest levels of growth, manipulating it should not have major impacts on yield. Although the *J. copaia* simulations do not conform to the trends in simulations of other species, for reasons previously discussed, this species still holds its first-place ranking in productivity when its rotation age is varied over a year. Also noteworthy, *C. brasiliense* is only very slightly impacted by rotation length changes. In fact, the differences in production it exhibits over 100 years result in less than 1 m<sup>3</sup>/ha of merchantable wood.

The year after this research was completed, the plantations were measured again. The volumes calculated from the field measurements were compared with the estimations obtained by using the growth

Table 7  
Sensitivity analysis on volume produced after one rotation, manipulating rotation length

Species	Rot. age (years)	M. vol. (m <sup>3</sup> /ha)	Tot. vol. (m <sup>3</sup> /ha)	Lengthened 6 months			Shortened 6 months		
				Rot. age (years)	M. vol. (m <sup>3</sup> /ha)	Tot. vol. (m <sup>3</sup> /ha)	Rot. age (years)	M. vol. (m <sup>3</sup> /ha)	Tot. vol. (m <sup>3</sup> /ha)
<i>C. brasiliense</i>	18.5	296.0	1601	19.0	304.2	1600	18.0	288.2	1600
<i>V. guatemalensis</i>	13.5	417.1	3090	14.0	431.6	3083	13.0	399.7	3075
<i>J. copaia</i>	6.5	255.0	3923	7.0	269.0	3843	6.0	240.4	4007
<i>V. ferruginea</i>	13.3	362.8	2728	13.8	374.8	2716	12.8	347.5	2715
<i>G. americana</i>	13.2	76.0	577	13.7	78.4	574	12.7	72.7	574
<i>B. elegans</i>	8.8	139.0	1574	9.3	146.7	1572	8.3	130.8	1571

Rot. age: rotation age; M. vol.: merchantable volume yielded after one rotation; Tot. vol.: total merchantable volume produced over a 100-year period.

equations for the six species of the present research (Alice et al., in press). For *V. guatemalensis* and *V. ferruginea* the volume estimated from the growth equations was very close to the volume estimated from the field measurements: the growth equations gave a figure only 3 and 6.9% larger than the field measurements, respectively. For *B. elegans* the growth equations underestimated the volume measured in the field by 9%. For *J. copaia*, *C. brasiliense*, and *G. americana*, the use of the growth equations resulted in substantially larger volumes than those measured in the field (over 10% discrepancies).

Because *J. copaia* (grown for 12 years) had almost doubled its estimated rotation length, a considerable decrease in its growth by 2003 is expected. In the case of *G. americana*, its lack of adaptability to the site has resulted in significant decreases in growth and even higher mortality than in previous years. Therefore, to find lower volumes in the field than those expected from the equations is not surprising. One of the four plots of *C. brasiliense* also had high mortality, resulting lower field volumes than expected (Alice et al., in press).

#### 4.2. Productivities in pure plantations versus mixtures

The arrangement of *J. copaia* and *V. guatemalensis* in mixed-species plantations mimics stands with well-spaced crowns. When a 27 m tall *J. copaia* tree is adjacent to a 17 m tall tree, its crown is effectively released on that side. By having shorter *C. brasiliense* trees interspersed amongst *J. copaia* or *V. guatemalensis* trees, essentially these larger trees are closed on fewer sides and, thus, they will be able to have larger crowns (due to a reduction in crown shyness), receive more radiation, be able to fix more carbon, and exhibit faster rates of growth than trees in pure plantations (Fry and Poole, 1980; Reukema and Bruce, 1977; Lamprecht, 1986). The opposite is true for the shorter tree species *C. brasiliense*, which is overtopped by *J. copaia* and *V. guatemalensis* in mixtures. Because other *C. brasiliense* trees will not overtop each other in pure plantations, they will exhibit greater reduced growth in the mixtures than in pure plantations (even if their crowns are closed on all sides). This coincides with earlier findings in these plantations (Montagnini et al., 1995).

The mixed-species plots in Plantation 1 are more productive than the pure plots because they are able to

usurp more of the available growing space, by growing in strata (Lamprecht, 1986; Whyte and Woollons, 1990). Also, the relatively large increase in volume productions in *J. copaia* and *V. guatemalensis* offset the relatively small reduction in volume seen in the *C. brasiliense* trees, which are disproportionately under-represented in the plots anyway.

#### 4.3. Future perspectives

This study has provided a solid foundation upon which to expand research to continue to provide important, relevant information to plantation owners and local farmers considering establishing plantations. This experiment can be followed up with a few well-fitted, ensuing studies. The obvious recommendation would be to continue to measure *D. panamensis*, *V. koschnyi*, *T. amazonia*, and *H. alchorneoides* until decreases in their growth rates are detected. Then rotation ages and yields can be successfully extrapolated and used to compare these species' productivities to the productivities of the original six species. In addition, continuing to measure *C. brasiliense*, *V. guatemalensis*, *J. copaia*, *V. ferruginea*, and *B. elegans* will provide an opportunity to validate the established equations, by comparing actual volumes with predicted volumes.

Also, current information is needed on uses and market prices of the species of this research. Stumpage prices for each species should try to be matched to predicted yields and factored into the analysis. The rotation ages should then be redefined using a Faustmann approach instead of maximum sustained yield. The Faustmann Approach entails using a net present value analysis to determine the financial rotation ages for the species (Newman, 1988; Smith et al., 1996). Then, the species that will bring the most revenue to the landowner will be predicted. Information relating to the management objectives of the plantation (production, restoration, or a combination of both) can be more important than productivity alone.

## 5. Conclusions

Although accessing the growth potential of some of the slower growing species is premature, the relative productivities of many of the species are evident.

Of the six species analyzed, *J. copaia*, *V. guatemalensis*, *V. ferruginea*, and *V. koschnyi* were (in terms of merchantable volume per hectare) the most productive timber species on abandoned agricultural land. Sensitivity analyses have confirmed that this finding and the predicted yields for these species are precise.

*V. guatemalensis* is one of the most preferred species in the region for reforestation of degraded pastures, while *J. copaia* is not preferred because it has low local economic value. *V. ferruginea* and *V. koschnyi* are also planted by farmers in the region. Thus, *V. guatemalensis*, *V. ferruginea*, and *V. koschnyi* are the most recommended species with which abandoned agricultural land in the humid lowlands of Costa Rica should be restored if using single-species plantations and the landowner is seeking to maximize the productivity of an area. Of the three species, *V. guatemalensis* will provide landowners with the most merchantable timber after a single rotation. Lastly, the single-species plots analyzed in this Plantation were shown to be less productive than mixed-species plots composed of the same selection of species. Establishing productive mixed-species plantations is also advantageous in that more flexibility is provided by having a variety of products to supply to an uncertain market.

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