

Research Paper

https://journals-crea.4science.it/index.php/asr



A narrow size diameter class model for tree growth and yield simulation in a mahoe (*Talipariti elatum* (SW.) Fryxell, *Malvaceae*) plantation in Puerto Rico

Jimena Forero Montaña^{1*}, Jess K. Zimmerman², Thrity Vakil³, Mark Nelson^{3,4}, Marìa Eglee Perez^{5,} Joaquin Medin⁶

Received 11/03/2019 - Accepted 18/06/2019 - Published online 30/11/2019

Abstract - Forest management planning requires forest growth models that provide a reliable way to forecast growth, calculate yield, and examine the effects of silviculture. Here we used a size stem frequency approach based on differential equations to developed a growth simulator system to guide the management of mahoe (*Talipariti elatum* (SW.) *Fryxell*) in a small plantation in Puerto Rico. We estimated the optimal harvest age using the Faustmann model, and evaluated alternative harvesting schemes using sensitivity analyses. The growth simulator system predicted that tree volume at first rises quickly, reaches a maximum value, and then decreases because of a lack of natural regeneration in the plantation. Thus, harvesting must be followed by replanting and large and healthy trees must be maintained as seed sources. The optimal harvest age was 43 years for a discount rate of 2.5% and 19 years for 5% interest. Analysis for alternative management schemes based on selective harvesting of the largest tress showed that 5%, 15%, or 30% of the trees ≥54.5 cm dbh could be harvested in cycles of 1, 5 or 10 years respectively, without drastically decreasing the basal area. The sustainability of these management schemes will depend on the costs of management, as well as the responses of mahoe to selective harvesting.

Keywords - forest management modelling; optimal harvest age; selective harvesting; system dynamics.

Introduction

Forest plantations help to meet the global demand for wood and have been increasingly established in the tropics to cope with the process of land degradation (Parrotta el al. 1997, Lamb et al. 2005, ITTO 2009,) and advance rural development (ITTO 2009). In the Caribbean island of Puerto Rico, for example, more than 38,200 hectares of degraded lands were reforested during the twentieth century prior to 1980 (Birdsey and Weaver 1982) and reforestation efforts have continued over the last four decades. Systematic trials included more than 100 exotic timber tree species, but only 19 produced satisfactory growth, and merely nine were later extensively planted (Francis 1995). Records of early growth and survival provided good information of the range of sites where these species can succeed (Francis 1995). However, the overall successes and the current area of forest plantations are not known. Moreover, few plantations are currently harvested or managed, and to our knowledge tree growth and yield models for planning management have been

not developed for these timber species. Developing methods to more thoroughly assess the sustainability of these forest plantations is therefore clearly needed.

Forest management planning requires growth models to forecast forest growth, examine the effects of management, and calculate yield of different management strategies (Vanclay 1994, Pretzsch 2009). Whole stand models have been traditionally used to model growth and yield in pure even-aged forest stands such as plantations when the main focus is the production of a single product in one rotation (Vanclay 1994, Pretzsch 2009). The stand level approach uses stand parameters such as tree density (No trees/ha), basal area, and volume to predict growth. Whole stand models require the lowest resolution and level of abstraction of forest models, but consequently provide rather general information of the future stand structure (Vanclay 1994, Pretzsch 2009). On the other hand, single tree models which use individual trees as the basic unit of modelling provide detailed information of stand structure (Vanclay 1994, Palahí et al. 2003, Pretzch 2009). Tree

- 4 Institute of Ecotechnics (US/UK), Santa Fe, New Mexico, United States
- 5 University of Puerto Rico Rio Piedras, Mathematics, San Juan, Puerto Rico

¹ University of Puerto Rico Rio Piedras, Faculty of Natural Sciences, Department of Biology , San Juan Puerto Rico

² University of Puerto Rico Rio Piedras, Environmental Sciences, San Juan Puerto Rico

³ Tropic Ventures Research and Education Foundation, Patillas, Puerto Rico

⁶ University of Puerto Rico in Bayamon, Physics, Bayamon, Puerto Rico

^{*}Corresponding author: forero.jimena@gmail.com

growth models with finer resolution, however, are susceptible to higher estimation errors, which may compromise the estimation accuracy desired for forest management decision making (Ferraco Scolforo et al. 2019). Stand oriented growth models can reveal some aspects of stand structure by considering steam number frequencies in diameter classes (Vanclay 1994, Pretzch 2009). These models predict not only stand mean values, but also changes in the diameter frequency distribution as result of growth, removal, and mortality (Pretzch 2009). The forest growth models described above represent different approaches in describing stand development. None of these models can be replaced entirely by one another, each modeling approach provides specific knowledge of forest growth, yield, and stand structure (Vanclay 1994, Pretzch 2009). Therefore, the aim and purpose of a model, as well as the stage of knowledge about the system considered determine the degree of complexity necessary or possible and its temporal and spatial resolution (Pretzsch 2009). In this study we used a size frequency approach based on differential equations to model tree growth and yield in mahoe (Talipariti elatum (SW.) Fryxell, Malvaceae), a valuable hardwood tree native to Cuba (Adams 1971) and Jamaica (Little et al. 1977), in a 25 year old enrichment plantation to guide its management in a subtropical wet secondary forest in Puerto Rico. The modeling approach was a compromise resolution between whole stand models and individual tree models. The system breaks down the stand into many narrow size classes of 1 cm and therefore permits simulations of growth with detailed information of stand structure (Muller-Landau et al. 2006), but keeping the model conceptually and operationally simple. Tree growth was modeled over a nine-year period using nonlinear equations and the optimal time for harvesting was calculated using the Faustmann (1849) formula to combine biological and economic risks (Chang 1998, Buongiomo 2001, Buongimo and Gilles 2003). Sensitivity of the optimal management schedule to changes in the discount rate, timber prices, and harvesting costs was analyzed. Finally, alternative management schemes based on selective harvesting of the largest trees were examined using sensitivity analysis.

Methods

Study area description

The study was conducted at Las Casas de la Selva (here after LCS), 376 ha of private land located on the south flank of the Cordillera de Cayey in the municipality of Patillas, Puerto Rico. The topography is mountainous and characterized by steep slopes that vary from 300 to 600 m in elevation. The forest is classified as subtropical wet forest in the Holdridge life zones system and is locally known as "tabonuco forest", with *Dacryodes excelsa* Vahl. being a dominant species. Annual rainfall averages 3,000 mm and annual temperature 22 °C (Nelson et al. 2010).

Las Casas de la Selva is owned and operated by Tropic Ventures, a joint venture between Global Ecotechnics Corporation and Decisions Team Inc. Before 1983, when Tropic Ventures acquired the land, it was mainly used for traditional cultivation of coffee, and a smaller part was cleared for grazing cattle. Between 1984 and 1989, valuable introduced hardwood species such as mahoe (T. elatum), and mahogany (Swietenia macrophylla x S. mahago*ni*), some native hardwood species, and Caribbean pine (Pinus caribaea Morelet) were planted on approximately 78 ha of the property (Nelson et al. 2011). The plantation of mahoe was mainly established on nine hectares of abandoned pastures. All mahoe trees were planted in a few months but the specific date of planting of each tree is not known. The initial stand density was 330 saplings ha⁻¹ with 10 m spacing from line to line and 3 m spacing within the lines. During planting, larger native hardwoods were left untouched when they were present in the tree lines (Nelson et al. 2011). The plantation currently has reached full canopy closure with 38 associated species and a total density of 571 trees ha-1 with a basal area of 37.43 m² ha-1 (Forero-Montaña 2015). Most of the associated trees are native species (95%) and comprise 61% of the stems > 10 cm dbh, but in general these trees are small and do not compete directly for light with mahoe. Indeed, mahoes had outgrown the other species and represent 49% of the trees and 72% of the total basal area (Forero-Montaña 2015).

Table 1 - Stand characteristics of the mahoe plantation at LCS in each inventory, showing mean values with standard errors when applicable.

Year	Number of stems ha ⁻¹	Mean dbh (cm)	Mean total height (m)	Basal area (m² ha⁻¹)	Volume (m ³ ha ⁻¹)
2003	285	22.09 (0.48)	16.04 (0.24)	11.82	112
2011	278	27.5 (0.62)	19.35 (0.29)	19.27	207

Annals of Silvicultural Research - 43 (2), 2019: 52-61

Forest inventories

In 2003, a 1.2 ha permanent plot was established to monitor tree growth and survival in 342 mahoes \geq 3.5 cm dbh. Diameter at breast height (1.3 m) (dbh), total height, and commercial height were measured on each mahoe using standardized methodology (Nelson et al. 2011). A second inventory was carried out between 2010 and 2011. Tab. 1 summarizes the characteristics of the stand in each inventory.

Data analyses

Tree growth simulator system

The growth simulator system was implemented in STELLA 9.0.9 (Richmond 2001). The basic structure of the model consisted of 66 one-cm diameter classes ranging from 9.5 to 54.5 cm that correspond to the stocks, which are connected by flows or processes that change the number of trees in each diameter class during a time step. The main processes of yield include ingrowth, outgrowth, mortality, and harvesting. The model was formulated as a set of differential equations that altogether change the number of trees in Diameter Class, with the form:

 $\frac{\Delta(DiameterClass_l)}{\Delta t} = \frac{\Delta(Ingrowth)}{\Delta t} - \frac{\Delta(Outgrowth)}{\Delta t} - \frac{\Delta(Mortality)}{\Delta t} - \frac{\Delta(Harvesting)}{\Delta t}$ (1)

The time step Δt was set as a discrete interval of one year. The differential equations of each process were mathematically disaggregated into sub-functions (control functions) to facilitate the model formulation. The distribution of tree numbers into the diameter classes at t_0 was taken from the first inventory. The tree numbers from t_0 to time t_n were obtained by stepwise integration of the differential equations in each time step. The new tree numbers in each size class were used as input variables for the control functions in the subsequent step. The major components of the model were implemented in STELLA using a design were ingrowth, outgrowth, mortality, and harvesting are the parameters to be set:

Ingrowth

Ingrowth or recruitment is the number of trees entering into the smallest stem diameter class in each year. Natural regeneration of mahoe has not occurred in the LCS plantation. Seedlings emerge in the forest but die apparently because they are not shade tolerant. Thus, recruitment into the first class was simulated assuming that harvesting must be followed by replanting. Stand density was reduced from 330 trees ha⁻¹ to 285 trees ha⁻¹ during the ~25 years since the plantation was established. Therefore, we considered it conservative to assume that 80% of the planted trees survive and enter into the smallest size class. In addition, because there is no information on growth of mahoe saplings, it was assumed that the planted trees that survive enter into the smallest diameter size class (3.5 cm) in a period of five years. For the other diameter classes outgrowth from the smaller size class represented ingrowth into the next larger diameter class.

Outgrowth

Outgrowth is the number of trees moving from each diameter class to the next higher diameter class in each year. The largest class serves as a container for very large trees and therefore its outgrowth is null. Outgrowth was defined as:

```
Outgrowth = Diameter Class_i \times Transition rate_i (2)
```

where the transition rate is the probability that a surviving tree moves from its Size $class_i$ to the next larger Diameter $class_{i+1}$ in one time step. The transition rate was calculated as:

Transition rate_i
$$= \frac{1}{\alpha} \times Id_i$$
 (3)

where *a* is the width of Diameter class_i, defined as 1 cm in this study, and Id_i is the estimated diameter increment for an average tree in the *Size clas* s_i . Diameter increment is a function dependent on tree size and stand density, and it was modeled using nonlinear equations by means of the methods explained below in the diameter increment model section.

Mortality

The number of dead trees in Diameter $class_{i}$ in each year was defined as:

 $Mortality = Diameter Class_i \times Mortality rate_i$ (4)

where mortality rate is the probability of a tree in Diameter class, dying in a year. It is usually a function of tree size and total basal area because higher probabilities of mortality typically occur at smaller sizes and in crowded stands. Mortality rate, however, was very low during the study period, only nine trees died, and mortality was independent of tree size. Therefore, annual probability of mortality was introduced in the growth simulator system as a constant value to randomly kill 0.003% (9/342 over nine years) of the trees in each time step.

Harvesting

Harvesting is defined as the number of live trees

in Diameter class. harvested per area in each cutting cycle. The system was first formulated to simulate growth in absence of harvesting with the aim of estimating the optimal harvest age or time for harvesting all mahoes followed by replanting applying the principles of the Faustmann formula for even-aged stands. Then, alternative management schemes were simulated to explore other possible scenarios for the management of the plantation that allow for periodic revenue without having to wait a long period to harvest all the trees (i.e., clear cutting). With this aim the model was constructed to simulate selective harvesting of the largest diameter size (i.e., $dbh \ge 54.5 cm$) trees to provide revenues, which also enables release of small trees and faster growth of a now less crowded stand. We explored numerous scenarios with different cycles and levels of harvesting to find a management scheme that produces the highest sustained yield without reducing the residual basal area to lower levels than the initial value in 2003 (i.e., $12 \text{ m}^2 \text{ ha}^{-1}$) with the aim of maintaining a reserve of trees that allow adequate growth. For all the scenarios we assumed that harvesting is followed by replanting to replace both the trees that are harvested and the trees that die by natural causes, thus maintaining the number of trees in equilibrium. To be as realistic as possible, harvesting started at the 16th year of the simulations corresponding to the state of the stand at the first inventory.

Fig. 1 shows the complete system dynamics diagram of the tree growth simulation system as it was implemented in STELLA. The diagram consists of an array that includes all diameter classes with the connected flows in one, the relationships shown in Fig. 1 are in effect for each diameter class. The complete set of model equations and variables as shown in Fig. 1 are listed in Anx. 1.



Figure 1 - Complete system dynamics diagram of the tree growth simulation model implemented in STELLA.

Diameter increment model

Growth calculations were performed for trees that were measured in both inventories without large or evident mistakes. Trees with negative dbh increment and extreme outliers were excluded from the analyses. Annual diameter increment was calculated as:

$$\frac{(dbht1-dbht2)}{(date\ 1-date2)} \times 365$$
(5)

where subscripts refer to successive forest inventories and time is measured in days. Traditional analyses of growth rates are based on linear models that assume constant absolute growth rate. However, the rate of biomass accumulation, almost universally slows as plants grow (Paine et al 2012). This decrease in growth results from a combination of factors that affect plants ontogeny such as accumulation of non-photosynthetic biomass in the form of stems and roots, self-shading of leaves, and decline in local concentrations of soil nutrients (South 1995). Nonlinear models provide the best method to account for slowing growth during plant ontogeny (Paine et al 2012). In this study, we used the nlsList function of the nlme package in the R statistical language to fit independent nonlinear functions to model tree growth of mahoe using the Gauss-Newton algorithm (Pinheiro and Bates 2000). Mean annual diameter growth rates within 1 cm dbh classes were calculated to facilitate the calibration of the growth simulator system. A power law function was used to model the relationship between diameter increment and initial size to allow for the assumption of slowing growth during tree ontogeny (Paine et al. 2012).

Height static equation for volume estimation

Analysis of the height data revealed obvious and large errors in the measurements of the first inventory that did not allow for the estimation of a height or volume increment model. Therefore, a static height model was constructed using the measurements of the second inventory. The relationship between total height and dbh was also modeled using a power law function to allow for the assumption of slowing height growth during tree ontogeny. This allometric equation served to calculate total height from dbh and was incorporated into the growth simulator system at the end of each time step to estimate mean volume of each diameter class using the relationship:

 $Tree \ volume = 0.5 \times basal \ area \times total \ heigh \ (6)$

Model validation and harvesting optimization

Once the growth simulator system was calibrated, its forecasting accuracy was assessed by comparing the observed size distribution in the second inventory with the distribution predicted by the model in the year ninth of the simulations using a Two-sampled Kolmogorov-Smirnov test (Crawley 2013). In addition, long-term steady states predicted by the model were also checked for quantitative plausibility of the model.

The specific age of harvesting that generates the maximum sustained yield depends on annual volume increment and socio-economic factors such as wood prices, costs of management, and discount rate, which account for the costs of waiting to realize profits. The problem of optimal harvest age for the management of even-aged stands such as plantations involves choosing the optimal time for clear-cutting followed by replanting and subsequent development of a new even-aged stand (Nautiyal 1988, Buongiomo 2001).

Using discounted cash flow techniques Faustmann (1849) provided a method to integrate biological and economic risks to the problem of land valuation to decide when to cut the forest (Chang 1998, Buongiomo 2001, Bungimo and Gilles 2003). The harvest age that maximizes the land value can be found using the following mathematical expression:

$$FEV = \frac{pV_t - C}{1 + r^t - 1} - C \quad (7)$$

where FEV is the forest expectation value that includes the value of the land plus trees, p is the net price of wood per unit of volume at age t, C is costs of replanting, and r is discount rate. For even-aged stands the net present value is basically formed by a continuous periodic series of harvesting revenues minus costs of harvesting at the end of every rotation of t years.

Given that the aim of this study was to use discounted cash flow techniques and sensitivity analysis to explore possible scenarios for management, rather than assess the absolute economic value of the LCS mahoe plantation, the capital value of the land was neglected and for simplicity it was assumed that future wood prices and costs remain constant or increase regularly in the future. The forest expectation value of different harvesting cycles was calculated for various combinations of costs, revenues and discount rates. In 2003, Tropic Ventures started selling mahoe in niche markets for expensive tropical hardwoods in the United States at a relatively stable price of US \$10 per board foot (0.002 m³). A previous evaluation at LCS determined a cost of production of US\$ 3 dollars per board foot (Vakil 2005 unpublished data). So, we included a net wood price of US \$7 per board foot and a base cost of US\$ 25.000 ha⁻¹ for replanting after clear cutting the whole stand. This corresponds to a full-time salary for a worker with minimum federal wage (US\$ 7.25) for less than two years in Puerto Rico. We explored the sensitivity of the optimal harvest age to a 1% annual increment in wood prices and a 20% increment in the costs of reforestation on the basis of the Puerto Rican Senate project Law 1195 of September 24 2014, which seeks to gradually increase the minimum wage from US\$ 7.25 to \$ 15 hr⁻¹ in 2025.

Results

Annual stem diameter increment model

Annual stem diameter increment and size (dbh) exhibited a positive relationship with clear deviations from linearity and high individual variability. The best model had the form:

$$F(x) = \alpha \times dbh^{\beta}$$
(8)

with $\alpha = 0.043 \pm 0.009$ (1 standard error) and $\beta = 0.77 \pm 0.06$ (1 standard error, n= 38) and explained 86% of the variation (residual standard error 0.082, df= 36). The exponent value indicated that diameter increment progressively decreases as stem diameter increases (Fig. 2).



Figure 2 - Data and fitted power law function for the relationship between mean annual dbh increment and 1-cm diameter size classes for mahoe.

Height static equation for volume estimation

Total height and dbh exhibited a positive relationship (Fig. 3). The power law function that best fitted the data had the form:

$$F(x) = \alpha \times dbh^{\beta}$$
(9)

with $\alpha = 5,61 \pm 0,69$ and $\beta = 0,37 \pm 0,03$ (n=41) (residual standard error 2.389, df=43) and explained 79% of the variation. The value of the exponent indicates that tree height slowly decreased as dbh increases (Fig. 3).



Figure 3 - Data and fitted power law function for the relationship between total height and stem diameter at breast height (dbh) for mahoe.

Model validation

The growth simulator system predicted a total volume of 173 m³ ha⁻¹ in the ninth year of the simulations, while the observed mahoe volume in 2011 was 207 m³ ha⁻¹. The growth simulator system likely underestimated tree volume increment because the simulations accumulated the largest trees in the 54.5 cm diameter class, while mahoe can grow to more than 70 cm. However, the predicted size and tree volume distributions in the ninth year of the simulations were not statistically different to the observed



Figure 4 - Comparison between observed and predicted distributions by the tree growth simulator system in the year ninth of the simulations. a) Tree size distribution, b) Tree volume distribution.

number of trees (D= 0.09, P> 0.05) and observed volume (D=0.15, P>0.05) in each size category in 2011 (Fig. 4). These results indicate that the growth simulator system provides accurate predictions for mahoe growth and yield at LCS.

Optimal harvest age

The model predicts that in absence of management tree volume will initially increase quickly, reach a maximum value of $714 \text{ m}^3 \text{ ha}^1$ at the age of ~80 years, stay relatively constant for few years, and then progressively decline because natural regeneration is absent in the plantation (Fig. 5).



Figure 5 - Predicted annual volume increment for 100 years (right) and forest expectation value (FEV) (left) showing optimal harvest age for 2.5% and 5% discount rates. Notice different scales in the y axis.

The harvest age that maximizes the land expectation value, when the net price of wood was \$7 per board foot, was 43 years with a discount rate of 2.5% and 19 years with a discount rate of 5%, and yielded a volume of 445 m³ ha⁻¹ and 134 m³ ha⁻¹, respectively (Fig. 5). In contrast, one-time changes in both wood prices and costs of reforestation modified the FEV, but did not change the optimal harvest age. A 1% annual increment in wood prices prolonged the optimal harvest age to 47 years with a 2.5% discount rate, but did not change the harvest age with a 5% discount rate. A 20% annual increment in the costs of reforestation decreased the optimal harvest to 19 years with a 2.5% discount rate, but it did not alter the optimal harvest age with a 5% discount rate (Tab. 2).

Selective harvesting schemes

The growth simulator system showed that 5%, 15%, or 30% of the trees \geq 54.5 cm dbh could be harvested in cycles of 1, 5 or 10 years, respectively, without severely decreasing the basal area (Fig. 6). The

J. FORERO-MONTAÑA¹, J. K. ZIMMERMAN², T. VAKIL³, M. NELSON^{3,4}, M. E. PEREZ⁵, J. MEDIN⁶ A narrow size diameter class model for tree growth and yield simulation in a mahoe (*Talipariti elatum* (SW.) Fryxell, *Malvaceae*) plantation in Puerto Rico

r	p (US\$ BF)	C (US\$ ha⁻¹)	FEV (US \$ ha⁻¹)	Optimal harvest age (yr)	Yield (m³ ha⁻¹)
	7	25'000	557'633	43	445
	10.5	25'000	817'926	43	445
2.5	7	50'000	494'679	43	445
	8.96	25'000	684'917	*47	509
	7	25'000	478'857	*19	134
	7	25'000	168'196	19	134
	10.5	25'000	751'345	19	134
5	7	50'000	127'430	19	134
	7	25'000	168'196	*19	134
	7	25'000	168'196	*19	134

Table 2 - Op	timal harvest age and	forest expectation value f	or different wood prices	, costs of reforestation	, and discount rates.
--------------	-----------------------	----------------------------	--------------------------	--------------------------	-----------------------

Net wood price (p), costs of reforestation (C), forest expectation value (FEV), board foot (BF). Asterisk correspond to the optimal harvest age for 1% annual increment in wood prices and 20% increment in costs of replanting starting with a US \$7 BF and a US \$ 25,000 ha⁻¹ respectively at 19 years of age.

dynamics of the residual basal area follows a similar trend to volume increment without harvesting. As result the harvested volume initially increases, reaches a maximum value, then progressively declines, but it recovers after some years because the model assumes that planting takes place regularly to replace the trees that die by both harvesting and natural causes (Fig. 6). The annual harvesting scheme involves harvesting between one to a maximum of four trees per year, the five year cycle scheme starts harvesting one tree and reaches a maximum of 15 trees at the age of 65 years, finally the ten year cycle scheme starts harvesting 2 trees and reaches a maximum of 31 trees at the age of 65 years. The sustainability of these management schemes will depend on mahoe responses to partial canopy opening, as well as on the costs of management, as we discuss below.



Figure 6 - a) Residual basal area and b) Number of trees harvested in each cycle for the alternative management schemes based on selective harvesting of trees ≥ 54.5 cm dbh.

Discussion

In this study we developed a narrow size diameter class model based on differential equations for tree growth and yield simulation in mahoe. Given the initial condition of the stand, the model predicted the state of the stand after given years with the alternative assumed prescriptions. Our approach has low complexity and is useful for users that have a small data set, thus it is easy to use for forest management planning. We examined two management possibilities: first, we allow the trees to grow and clear cut the whole stand when it reaches the optimal harvest age using the Faustmann formula. And second, we explored alternative harvesting schemes using sensitivity analysis based on selective harvesting of the largest mahoes, which would allow a steadier revenue stream, while small promised trees are released.

The optimal harvest age was 43 years for a discount rate of 2.5% and 19 years for a discount rate of 5%. Thus, given that the plantation is currently 25 years old under a high interest scenario the plantation must be harvested as soon as possible. The analysis of alternative scenarios for selective harvesting suggests that 5%, 15%, or 30% of the mahoes \geq 54.5 cm dbh could be harvested in cycles of 1, 5 or 10 years respectively, without severely decreasing the basal area. The sustainability and economic viability of these management schemes will depend on the costs of both harvesting and replanting, and ultimately on the responses of mahoe to selective harvesting.

Our data indicate that mahoe is shade intolerant and we do not know to what extent it could regenerate under partial canopy opening. Moreover, due to its rapid growth rate, mahoe is a high nutrient demanding tree (Kihlgren-Smith 2000). Therefore, it is vital to maintain soil productivity after harvesting. Cleaning, weeding, and soil fertilization are labor intensive operations that can be especially expensive in the tropics where soils are susceptible to erosion and nutrient loss, and where large canopy openings can trigger the growth of vines and grasses that obstruct regeneration (Wadsworth 1997). Thus, a management scheme should be selected to maintain the stand basal area low enough to maximize growth, but at the same time avoid severe canopy and soil disturbance to ensure adequate regeneration (Hutchinson 1993, Wadsworth 1997). It is important to avoid removing only the most valuable trees of the stand leaving behind mostly damaged diseased or genetically inferior trees with little potential for future growth. On the other hand, sick trees or tress with defects such as poor form, low forks, or too many large branches, which will never produce a high-quality saw log, should be eliminated (Hutchinson 1993). Trees of undesired species that are inhibiting growth of mahoes with high potential should be eliminated too. If two healthy vigorous mahoes are competing with one another, one should be harvested (Hutchinson and Wadsworth 2006, Wadsworth and Zweede 2006). Moreover, given that natural regeneration is currently absent at LCS any management scheme that is adopted must leave large and healthy trees as seed sources.

The modeling approach of this study can help to answer key questions of forest management planning. However, the deterministic nature of both the forest growth model and the classic Faustmann analysis , limits its accuracy to predict tree growth, estimate the optimal harvest age, and examine different silvicultural options. The classic Faustmann analysis considers that tree growth, wood prices, and costs remain constant over time or can be predicted with certainty. These assumptions, however, are not generally true. Variation in tree growth, wood prices, costs of reforestation, and discount rates, are the rule rather than the exception (Chang 1998, Buongiomo 2001).

Storms and hurricanes are important stochastic processes that shape tree growth in the secondary forests of Puerto Rico (Uriarte et al. 2004, 2009). Thus, consideration of natural risks is essential to improve our ability to model tree growth and guide management of mahoe in Puerto Rico. Montecarlo modelling techniques have been used to include natural risks such as storms and insect attacks in forest optimization models (Dieter 2001). This technique, however, requires the incorporation of empirical survival probabilities and specific information on the volume that can be harvested after a perturbation. This is information that we don't have for mahoe yet. Nonetheless, when risk is considered, the forest expectation value tends to decrease and the optimal harvest age becomes shorter (Dieter 2001). So, risks of storms would shorten the optimal harvest age of mahoe at LCS.

Our analysis showed that annual increments in wood prices tend to delay the optimal harvest age, while annual increments in the costs of reforestation and harvesting tend to shorten it. Prices respond to changing supply-demand balances that are not always predictable. Indeed, wood markets are continually undergoing dynamic changes (Bumgardner et al. 2014). Currently, there is a trend towards a reduction on the demand for tropical hardwoods in the international market because some species have been substituted by other woods or materials. Moreover, environmental concerns about tropical wood production represent a major challenge for exporters of tropical wood products. There is the expectation, however, that the implementation of the European Union Timber Regulation in 2013 would increase the demand for certified tropical woods (Bumgardner et al. 2014). The emergence of niche markets for fine tropical hardwoods in the USA represents a good commercial opportunity for mahoe, which is perhaps the only commercial hardwood in the world that has a blue heartwood color. Mahoe is now in low supply and it is only seen in small sizes and quantities in the market. Thus, prices of mahoe might likely increase in the near future.

Costs of management and production would likely change mainly in response to changes in labor expenses. For example, if the costs of replanting increase by 20% every year, in line with the Project Law 1195 of the Senate of Puerto Rico, the optimal harvest age of mahoe will decrease to 19 years with a discount rate of 2.5%, indicating that under this scenario the plantation would be not economically viable unless the prices of wood rise enough to cover the costs of management. Nevertheless, given the current fiscal deficit of the government of Puerto Rico salaries are likely to remain stable or even could decrease, which will prolong or not change the optimal harvest age of mahoe in the short term.

Conclusions

The model approach of this study made the best possible use of the existing data. The model is conceptually and operationally simple and can address strategic questions for the sustainable management of mahoe at our study area. The model approach was chosen on base of the existing data and the component functions were grounded on existing theories of forest growth. However, direct experimentation on selective harvesting is required to evaluate mahoe responses to partial canopy opening. Moreover, in order to reliably predict outcomes for different harvesting strategies for sustainable management, it is necessary to add to our database information on growth and survival of mahoe saplings, as well as estimate the real costs of selective harvesting and reforestation at LCS. Finally, risks of tropical storms and hurricanes is another aspect that must be considered to improve the prediction accuracy of the model. This will require evaluation of hurricane effects on vegetation structure and growth dynamics to determine survival probabilities and gather specific information on the volume that could be harvested after a perturbation.

Acknowledgements

This work was supported by the Center for Applied Tropical Ecology and Conservation (CREST-CATEC) under the Grant HRD 0734826, and the Luquillo LTER Program under the Grant DEB-1546686 to University of Puerto Rico. We thank support by The Earthwatch Institute and the work of Earthwatch volunteer groups from 2001-2012 in the collection of the data on tree growth at LCS. We also thank Dr. Fumero-Cabán and two anonymous reviewers for their valuable comments and criticism, which improved the manuscript.

References

- Adams C.D. 1971 The blue Mahoe and other bush: an introduction to the plant life in Jamaica. McGraw-Hill. Singapore. 159 p.
- Birdsey R.A, Weaver P.L. 1987 Forest area trends in Puerto Rico. New Orleans (LA): United States Department of Agriculture Forest Service Southern Forest Experiment Station. Research Note SO 331.
- Buongiomo J. 2001 Generalization of Faustmann's formula for stochastic forest growth and prices with markov decision process models. Forest Science 47(4): 466-471.
- Buongiomo J., Gilless J.K. 2003 Decision methods for forest resource management. Academic Press San Diego.439 p.
- Bumgardner M., Johnson S., Luppold W., Maplesden F., Pepke E. 2014 - Markets and market forces for lumber. In: "The global forest sector: changes, practices and prospects" Hansen E., Panwar R., Vlosky R., Ed. CRC Press: 41-76.

Crawley M.J. 2013 - *The R Book*. Second Edition. John Wiley and Sons, Ltd London. 975 p.

- Chang S.J. 1998 A generalized Faustmann model for the determination of optimal harvest age. Canadian Journal of Forest Research 28: 652-659.
- Dieter M. 2001 Land expectation values for spruce and beech calculated with Monte Carlo modelling techniques. Forest Policy and Economics 2: 157-166.
- Faustmann M. 1849 On the determination of the value which forest land and immature stands pose for forestry. In:

"Martin Faustmann and the evolution of discount cash flow" Gane M. Ed., Commonwealth Forestry Institute, Oxford Institute Paper 42, 1968.

- Ferraco Scolforo H., McTague J.P., Burkhart H. Campoe O., Stape J.L., Roise J. 2019 - Eucalyptus growth and yield system: Linking individual-tree and stand-level growth models in clonal Eucalypt plantations in Brazil. Forest Ecology and Management 432:1-16.
- Forero-Montaña J. 2015 Potential of subtropical secondary forests for sustainable forestry in Puerto Rico. Doctoral dissertation, University of Puerto Rico, Río Piedras, San Juan, PR.
- Francis J.K. 1995 *Forest plantations in Puerto Rico*. In: "Tropical Forest: Management and Ecology" Lugo A. E. and Lowe C. Ed., Springer-Verlag New York: 210-223.
- Hutchinson I.D. 1993 Puntos de partida y muestreo diagnóstico para la silvicultura de bosques naturales del trópico húmedo. Colección Silvicultura de Bosques Naturales 7. CATIE Turrialba. 32 p.
- Hutchinson I.D., Wadsworth F.H. 2006 *Efectos de la liberación en un bosque secundario de Costa Rica*. Recursos Naturales y Ambiente 46: 155-160.
- International Timber Organization (ITTO) 2009 Encouraging industrial forest plantations in the tropics: Report of a global study. Technical Series 33. 141 p.
- Kihlgren-Smith J. 2000 An Assessment of blue mahoe (Hibiscus elatus) growth using topographic, soil, and litter properties in St. Vincent, West Indies. Master Thesis, the University of Calgary. Calgary Alberta.
- Lamb D., Erskine P.D., Parrota J.A. 2005 Restoration of degraded tropical forests lands. Science 316: 1628-1632.
- Little E.L. Jr., Woodbury R.O., Wadsworth F.H. 1977 Trees of Puerto Rico and the Virgin Islands, second volume. Agricultural Handbook 449. Washington, DC; U.S. Department of Agriculture, Forest Service. 596 p.
- Muller-Landau H.C., Condit R., Chave J., Thomas S.C., Bohlman S.A., et al. 2006 - *Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests.* Ecology Letters 9: 575-588.
- Nautiyal J.C. 1988 Forest economics: Principles and applications. Canadian Scholar's Press Inc. Toronto. 569 p.
- Nelson M., Silverstone S., Reiss K.C., Burrows P., Joglar R., Robertson M., Vakil T. 2010 - The impact of hardwood line planting on tree and amphibian diversity in a secondary subtropical wet forest of southeast Puerto Rico. Journal of Sustainable Forestry 29: 503-516.
- Nelson M., Silverstone S., Reiss K.C., Vakil T., Robertson M. 2011 - Enriched secondary subtropical forest trough line-planting for sustainable timber production in Puerto Rico. Bois et forests des Tropiques 309 (3): 51-61.
- Palahí M., Pukkala T., Miina J., Montero G. 2003 Individual-tree growth and mortality models for Scots pine (*Pinus sylvestris* L.) in north-east Spain. Annals of Forest Science: 60: 1-10.
- Paine C.E.T., Marthews T.R, Vogt D.R., Purves D., Rees M., Hector A., Turnbull L.A. 2012 - How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods in Ecology and Evolution 3(2): 245-256.
- Parrotta J.A., Turnbull J.W., Jones N.1997 Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management 99: 17.
- Pinheiro J., Bates D. 2000 Mixed-effects models in S and S-PLUS. Springer Verlag New York. 528 p.
- Pretzsch H. 2009 Forest dynamics, growth and yield. Heidelberg Springer, Berlin, Germany. 664 p.
- Richmond B. 2001 An introduction to systems thinking. Stella Software. High Performance Systems Inc. Hannover. 165 p.

South D.B. 1995 - *Relative growth rates: a critique*. South African Forestry Journal 173: 43-48.

- Uriarte M., Canham C.D., Thompson J., Zimmerman J.K. 2004 - A maximum-likelihood, spatially-explicit analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs 71: 591-614.
- Uriarte M., Canham C.D, Thompson J., Zimmerman J. K. 2009 - Understanding natural disturbance and human land use as determinants of tree community dynamics in a subtropical wet forest: Results from a forest simulator. Ecological Monographs 79: 423-443.
- Vanclay J.K. 1994 Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, UK. 312 p.
- Wadsworth F.H 1997 Forest production for tropical America. U.S. Department of Agriculture, Forest Service Washington DC. 563 p.
- Wadsworth F.H., Zweede J.C. 2006 Liberation: Acceptable production of tropical forest timber. Forest Ecology and Management 233: 45–51.