Enriched secondary subtropical forest through line-planting for sustainable timber production in Puerto Rico

Article in Bois et Forets des Tropiques - January 2011

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Entre 1984 y 1990, se establecieron plantaciones lineales de diferentes especies nobles, autóctonas o introducidas, como la caoba, *Swietenia macrophylla*, o majagua, *Talipariti elatum*, en un centenar de hectáreas de una zona de bosque tropical húmedo al sudeste de Puerto Rico. Habida cuenta del incremento anual del área basal (BA) de los mejores tallos de caoba (25%), serían necesarios 176 años después de la siembra para lograr un área basal promedio por árbol de 0,20 m², correspondiente a un diámetro a la altura del pecho (DBH) de 50 cm de promedio. En cuanto a majagua, el incremento del área basal es tres veces más rápido que en la caoba, lo que proporcionaría un área basal promedio de 0,20 m² en 57 años. Actualmente, en el cuarto superior de majagua, ésta supera 0,10 m² por unidad, haciendo ya posible una cosecha selectiva. Los ensayos en especies autóctonas (*Coccoloba pubescens*, *Calophyllum brasiliense* y *Cedrela odorata*) arrojaron los mejores resultados en términos de porcentaje de incremento en altura con una buena tasa de sobrevivencia, pero es necesario realizar estudios a más largo plazo para confirmarlo. Las plantaciones lineales en zonas forestales secundarias como las de Las Casas pueden incrementar el valor de los bosques secundarios garantizando, al mismo tiempo, una producción sostenible de madera y la preservación de la biodiversidad, así como las demás ventajas ambientales derivadas de la protección de la cubierta forestal. El enriquecimiento y el manejo de bosques secundarios merecen un mejor enfoque, prometedor para una silvicultura sostenible.

**Palabras clave:** caoba, majó o majagua, plantación lineal, enriquecimiento de bosque secundario, manejo sostenible, bosque húmedo subtropical.
Introduction

Most of the original forests of Puerto Rico were logged then converted for agricultural uses over the last several hundred years. A decline in agricultural land use and social and economic changes have permitted these lands to revert to secondary forests. Puerto Rico is one of the few countries in the world reporting large amounts of forest gain, an increase of 211,650 ha from 1980 to 2003. Currently, forests cover 57% of the land surface of Puerto Rico, a sharp increase from a low of around 17% forest cover in the 1930s (BRANDEIS et al., 2007). Secondary forests can be broadly defined as poorer successional forests which result after logging or conversion of primary forest. As CHOKKALINGAM, DE JONG (2001) note secondary forest can result from natural or man-made disturbance, over short or longer time frames, and with significant differences in the naturally regenerating forest from the original forest in forest structure, canopy and/or species diversity. Secondary forests are increasing in extent worldwide, especially in tropical forest regions where replanting, managing of naturally regenerating forests and sustainable use of timber trees is still only practiced on a small percentage of forest (LAMB et al., 2005).

Research into the ecological management of tropical secondary rainforest and wet tropical forests for sustainable timber production for profit could contribute to preservation of biodiversity by offering alternatives to forest clear-cutting or conversion to agriculture (MONTAGNINI et al., 1997). One reason secondary tropical forests are little utilized is that they are seen as uneconomic since regenerating timber species typically take a very long time to be harvestable (WADSWORTH, ZWEDE, 2006). But with restricted access to primary forest, secondary forests may become more valuable a resource in the future. Studies have shown that in cut-over forest, remaining trees benefit from lack of competitors and access to crown exposure, significantly lowering time to maturation of some of the remaining trees (WADSWORTH et al., 2010). Another option for forest regeneration and economic enhancement of secondary forests is enrichment planting, where valuable tree species are planted in cleared lines or blocks, simulating forest openings when tall trees fall, within current forest vegetation, offering soil erosion protection and facilitating forest development (SHONO et al., 2007). MONTAGNINI et al. (1997) make the case that including species with shorter times to harvest may improve economic viability of forest enrichment.

In Puerto Rico enrichment planting could also make a considerable contribution to the local island economy by replacing some imported wood with local production, providing income to landowners and employment in timber industries. Puerto Rico currently imports nearly all of its timber from the United States. WADSWORTH et al. (2010) pointed out that secondary forest deserves more attention and at least 48% of the timber could be produced in Puerto Rico’s secondary forests without conflicting with agricultural land use, reducing the island’s net imports and providing large increases in local employment. This would be particularly significant in rural undeveloped areas such as Patillas (the Puerto Rican Municipality in which the project we report

Study area

Las Casas de la Selva (LCS) is an experimental sustainable forestry and rainforest enrichment project in southeastern Puerto Rico in the Cordillera mountains, a part of the island’s Upland province (MONROE, 1980). The 409 hectares (ha) forest is located on steep slopes at an average elevation of 600 m and receiving an average annual rainfall of over 3,000 mm. Because of heavy rainfall, high relief and generally steep slopes, most of the Upland province is highly subject to severe erosion and landslides, even when well covered with forest. Most of the land was logged and then converted to coffee plantation. Some of its acreage was cleared for grazing land, with serious erosion ensuing. It is characterized as subtropical wet in the Holdridge life zone system (EWEL, WHITMORE, 1973), and known locally as “tabonuco forest”, with candletree (Dacryodes excelsa) being a dominant tree. NELSON et al. (2010) provide more detail on the study site and forest enrichment strategy. This experimental project, LCS, lies within the Central Volcanic-Plutonic Sub-province.

LCS occupies a valuable land area adjoining the Carite State Forest and thus expanding the continuity of forest habitat. The LCS property includes a number of ridgetops and streams which feed Lake Patillas. This reservoir is the main supply of water for irrigation, other industries, and potable water for approximately forty thousand people in the region.
Review of prior work with mahogany, *Swietenia* sp. pl., and mahoe, *Taliparti elatum*, in forest enrichment

Among the species first utilized for forest enrichment at Las Casas de la Selva was mahogany, *Swietenia* sp. pl., one of the most valuable timber species of the Neotropics. Mahogany is difficult to regenerate in logged over natural forests, which has led to it being listed in CITES Appendix 2 which requires producing countries to develop sustainable management methods (Snook, 2005). Introduced to Puerto Rico in 1906, mahogany has become naturalized on the island and line planted mahogany was extensively tested in secondary forest in the Luquillo Mountains (Weaver, Bauer, 1983). Line plantings were established in 1963 using 3 x 3 meters (m) spacing within the lines with subsequent control of competition. In 1975 a thinning removed about 30% of the trees. An 18-year re-measurement in 1981 showed a mean annual increment of 1.4 cm/yr in trunk diameter at breast height (DBH) and 1.0 m/yr in height. Weaver, Bauer (1983) concluded that line planted mahogany could be used to enrich subtropical secondary forest.

Mahogany enrichment plantings have also been established outside of Puerto Rico. Mahogany trees in Uxpana, Mexico, grew most rapidly in height in completely open areas. The highest survival rate was in areas where all vegetation with a DBH greater than 12 centimeters (cm) was removed during the first year (Ramos, Del Amo, 1992). In southern Para, Brazil, logging companies tested line planting in 2-3 m wide bands at 10 m intervals. Growth was very slow, attributed to lianas being allowed to compete and the fact that they did not remove enough of the natural forest canopy (Verissimo et al., 1995). In the Yucatan Peninsula of Mexico, Snook (2005) reviewed forest enrichment and management by community foresters who reported optimal mahogany establishment in cleared areas of 5000 m² and virtually no mahogany survival when line-planted under forest cover. Mayhew, Newton (1998) recommended that keeping undisturbed forest vegetation between the lines provides lateral shade, which is desirable since it encourages straight growth of the planted trees.

Mahoe, *Taliparti elatum* (formerly *Hibiscus elatus* Sw.), also known as “Blue Mahoe” for the characteristic coloration of its wood after milling, is a native to Jamaica and Cuba (Francis, 1989). A volunteer species, characteristic of open disturbed habitats and also found, due to its shade tolerance, as an understory tree in secondary forests, mahoe grows to 25 m tall and upwards of 100 cm DBH (Kimber, 1970). It was recognized as a potentially important timber species for plantation and forest enrichment after a survey by Jamaican foresters (Long, 1963 cited in Kimber, 1970). An excellent wood with rich variety of colors and attractive grain (photograph 1), it has been likened to teak, *Tectona grandis*, (Ashton et al., 1989) although very little mahoe is currently produced. The fast-growing tree tolerates a range of day length conditions and thrives at sites with rainfall exceeding 1,500 mm (though in lowland areas it can survive with rainfall down to 1,150 mm/yr). The first plantings in Puerto Rico were in the 1940s. Mahoe has become naturalized in Mexico, Peru, Brazil, southern Florida and the West Indies (Chudnov, 1982).

In Puerto Rico, mahoe was planted between 1960 and 1980 in 34 areas of subtropical moist, tropical wet and lower montane wet forests, with rainfall from 1,500-3,000 mm/yr and with varying soil types and pH. The stands were relatively dense, ranging from 300-2,100 stems/ha and thirty-one of the stands having more than 800 stems/ha. Growth and development was assessed for stands at differing ages. Early success with mahoe in Puerto Rico led to a 22 ha mahoe plantation project between the northern limestone hills of the Rio Abajo Forest where sawmill timber volume was reported to be 128 m³/ha (Francis, Weaver, 1988).

In other Caribbean locations, where it was becoming favored as a plantation tree, mean annual DBH increment (MADI) was 0.9-3.0 cm/yr and mean annual height increment (MAHI) 0.9-2.1 m/yr. Early work in Hawaii showed mahoe to be promising in most of the sites chosen (Weaver, Francis, n.d.). In Jamaica, earlier work showed 15-16 yr old mahoe stands with basal areas of 16-20 m²/ha and DBH and height for dominant mahoes (not the mean) of 21-30 cm and 18-31 m height (Little, Wadsworth, 1964). There are widely differing relationships between individual mahoe DBH and total height, depending on spacing and growth conditions. Since the tree has a relatively short history of use for plantation, spacing and thinning guidelines are poorly developed (Ashton et al., 1989).

Photograph 3.
Mahoe trees after 20 years of growth in secondary tropical forest, Las Casas de la Selva, Patillas, Puerto Rico. Photograph T. Vakil.

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<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Family</th>
<th>Common Names</th>
<th>Uses</th>
<th>Successional Status</th>
<th>Light Preferences</th>
<th>Rates of Growth</th>
<th>Environmental Conditions</th>
<th>Literature Cited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calophyllum brasiliense Britton (Calophyllum calaba L.)</td>
<td>Clausiaceae</td>
<td>Antilles calophyllum; Santa María</td>
<td>Planted as ornaments, shade and timber; construction uses include posts, flooring, shingles, furniture, cabinets, and framing; commonly used in reforestation and rehabilitation of degraded sites.</td>
<td>Established during secondary succession; do not typically serve as pioneer species due to susceptibility to desiccation in full sun; once mature they are classified as canopy trees.</td>
<td>Young seedlings prefer light shade; susceptible to desiccation in full sun; exhibit poor growth rates in full shade; once established, trees require full sunlight.</td>
<td>Growth rates typically slow; increases in height range from 0.6-1.4 m/yr; diameter increases range from 5.6-13.8 mm/yr; mature trees can reach heights up to 45 m however in Puerto Rico they typically range from 12-20 m tall and 45 cm in diameter.</td>
<td>Grows well in degraded soils; tolerant of a variety of growing conditions.</td>
<td>BURNS, HONKALA, 1990</td>
</tr>
<tr>
<td>Cedrela odorata L.</td>
<td>Meliaceae</td>
<td>Spanish cedar; Cedro Hembra</td>
<td>Used for shade in residential areas and in coffee and cacao plantations; high levels of insect repelling resins, especially useful for exterior construction; exhibits high resistance to attack by both termites and fungus; used to build storage boxes for clothing.</td>
<td>Classified as a late successional species.</td>
<td>Prefer high light environments at all stages of development; seedlings can tolerate shade however will suffer damage if then exposed to sun leaving them susceptible to insect attack.</td>
<td>Once established, exhibits rapid growth rates of 2 m/yr in height and 2.5 cm/yr in diameter. Mature trees can be 20-40 m tall and 50 cm in diameter.</td>
<td>Rates of growth are dependent on environmental conditions, in particular rainfall; does best in seasonally dry climates; does not tolerate soils with poor drainage.</td>
<td>BURNS, HONKALA, 1990</td>
</tr>
<tr>
<td>Cocoloba pubescens L.</td>
<td>Polygonaceae</td>
<td>Grandleaf seagrape; Moralón</td>
<td>Planted as ornaments; wood is hard and heavy and resists termite attack; used to make furniture and in general construction.</td>
<td>Late successional species.</td>
<td>Seedlings prefer light shade.</td>
<td>Exact rates of growth for Moralón were not cited however they are known to be slow growing trees; mature trees can be 20 m tall and 60 cm in diameter.</td>
<td>Commonly found growing in humid mountainous limestone regions; can be successfully grown in other soil types.</td>
<td>LITTLE, WADSWORTH, 1964</td>
</tr>
<tr>
<td>Cordia alliodora (Ruiz &amp; Pav.) Oken</td>
<td>Boraginaceae</td>
<td>Spanish elm; Capa Prieto</td>
<td>Planted to provide shade in coffee and cacao plantations; leaves and seeds have been used medicinally; fruits can be eaten though consumption is not widely noted; wood used in fine carpentry and general construction.</td>
<td>Considered a pioneer species commonly found in disturbed areas, along roadsides, and where gaps have occurred in mature forest; part of the dominant canopy.</td>
<td>Prefer full sunlight at all stages of development.</td>
<td>Reproductive maturity reached in 5-10 years; growth rates are rapid, with height increasing ranging from 2-3 m/yr; mature trees up to 30 m tall and 100 cm in diameter under ideal conditions; in Puerto Rico typically reach 20 m in height and 45 cm in diameter.</td>
<td>Growth rates depend largely on age of trees, water availability, soil quality, and region; poor drainage can damage trees, however soil degradation does not appear to limit growth.</td>
<td>BURNS, HONKALA, 1990</td>
</tr>
<tr>
<td>Swietenia macrophylla King</td>
<td>Meliaceae</td>
<td>Honduras mahogany; Caoba</td>
<td>Prized wood used for furniture and other fine crafts; can be used in construction however given its beauty it is more popular for fine carpentry.</td>
<td>Late successional species.</td>
<td>Seedlings need light shade when young however extreme shade can sometimes stunt growth; once established, trees will flourish with ample sunlight.</td>
<td>Growth rate of approximately 1 cm/yr in diameter; mature trees have been documented at over 45 m tall however they typically grow to 20 m tall and 60 cm in diameter.</td>
<td>Growth rates highly variable and depend largely on environmental conditions and age of trees; rainfall, soil, drainage, slope aspect, and crown position can all impact growth rates.</td>
<td>SNOOK, 2006</td>
</tr>
<tr>
<td>Taliparti elatum (formerly Hibiscus elatus Sw.)</td>
<td>Malvaceae</td>
<td>Mahoe</td>
<td>When used in construction, wood is highly resistant to attack by decay fungi; fine wood for artisan uses from musical instruments, fine cabinetry to construction.</td>
<td>Early successional species.</td>
<td>Tolerant of understory shade and direct sunlight.</td>
<td>Grows to 25 m in height with a straight trunk 50 cm or larger in diameter.</td>
<td>Generally thrives at rainfall &gt; 1,500 mm/year but can grow in lowland conditions at 1,150 mm/yr. Can tolerate tight spacing when young. Elevation from coastal to 1,000 m.</td>
<td>FRANCIS, WEAVER, 1988; WEAVER et al., n.d.</td>
</tr>
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</table>
Table II.
Growth measurements for mahogany and mahoe.

<table>
<thead>
<tr>
<th></th>
<th>Mahogany</th>
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<th>Mahoe</th>
<th></th>
<th>T-Value</th>
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<tr>
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<td>Unit</td>
<td>Value</td>
<td>Standard Error</td>
<td>Value</td>
<td>Standard Error</td>
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<td>Number of Trees</td>
<td>trees</td>
<td>543</td>
<td>292</td>
<td>292</td>
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<tr>
<td>Total Plot Area</td>
<td>hectares</td>
<td>7.6</td>
<td>1.2</td>
<td>1.2</td>
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<tr>
<td>Tree Density</td>
<td>trees/ha</td>
<td>71.4</td>
<td>243.3</td>
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<tr>
<td>Mean Time Since Planting</td>
<td>year</td>
<td>17.7</td>
<td>22.7</td>
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<tr>
<td>Mean DBH</td>
<td>cm</td>
<td>12.45</td>
<td>0.24</td>
<td>27.2</td>
<td>0.61</td>
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<tr>
<td>Mean Commercial Height (H_c)</td>
<td>m</td>
<td>9.76</td>
<td>0.13</td>
<td>19.73</td>
<td>0.31</td>
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<tr>
<td>Mean Canopy Width^</td>
<td>m</td>
<td>3.10</td>
<td>0.06</td>
<td>5.89</td>
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<td>Mean Basal Crowding^</td>
<td>stems</td>
<td>7.18</td>
<td>0.11</td>
<td>7.49</td>
<td>0.14</td>
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<tr>
<td>Mean Basal Area (BA)</td>
<td>m²/tree</td>
<td>0.0146</td>
<td>0.0005</td>
<td>0.0674</td>
<td>0.0029</td>
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<tr>
<td>BA Increment</td>
<td>m²/tree/yr</td>
<td>0.0008</td>
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<td>0.0030</td>
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<tr>
<td>Stand BA</td>
<td>m²/ha</td>
<td>1.04</td>
<td>18.15</td>
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<tr>
<td>Mean Tree Volume</td>
<td>m³/tree</td>
<td>0.0704</td>
<td>0.0030</td>
<td>0.4360</td>
<td>0.0270</td>
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<tr>
<td>Volume Increment</td>
<td>m³/tree/yr</td>
<td>0.0040</td>
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<td>0.0192</td>
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<tr>
<td>Stand Volume</td>
<td>m³/ha</td>
<td>5.03</td>
<td>105.73</td>
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</tr>
</tbody>
</table>

* Signifies significant difference (p < 0.01).
\^ Comparison at 19 years for mahoe; no measures for latest sampling event.

Table III.
Growth measurements for upper quartile of mahogany and mahoe.

<table>
<thead>
<tr>
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<th>T-Value</th>
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<td>Standard Error</td>
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<td>Number of Trees</td>
<td>trees</td>
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<td>Total Plot Area</td>
<td>hectares</td>
<td>7.6</td>
<td>1.2</td>
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<tr>
<td>Tree Density</td>
<td>trees/ha</td>
<td>18</td>
<td>68</td>
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<tr>
<td>Mean Time Since Planting</td>
<td>year</td>
<td>17.7</td>
<td>22.7</td>
<td></td>
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</tr>
<tr>
<td>Mean DBH</td>
<td>cm</td>
<td>19.91</td>
<td>0.22</td>
<td>41.02</td>
<td>0.58</td>
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<tr>
<td>Mean Commercial Height (H_c)</td>
<td>m</td>
<td>12.52</td>
<td>0.19</td>
<td>23.30</td>
<td>0.68</td>
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<tr>
<td>Mean Canopy Width^</td>
<td>m</td>
<td>7.43</td>
<td>0.18</td>
<td>8.75</td>
<td>0.54</td>
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<tr>
<td>Mean Basal Crowding^</td>
<td>stems</td>
<td>4.35</td>
<td>0.10</td>
<td>7.16</td>
<td>0.24</td>
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<tr>
<td>Mean Basal Area (BA)</td>
<td>m²/tree</td>
<td>7.09</td>
<td>0.21</td>
<td>7.63</td>
<td>0.32</td>
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<tr>
<td>BA Increment</td>
<td>m²/tree/yr</td>
<td>0.0317</td>
<td>0.0007</td>
<td>0.1382</td>
<td>0.0056</td>
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<tr>
<td>Stand BA</td>
<td>m²/ha</td>
<td>0.57</td>
<td>9.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Volume</td>
<td>m³/tree</td>
<td>0.1644</td>
<td>0.0055</td>
<td>0.8550</td>
<td>0.0750</td>
</tr>
<tr>
<td>Volume Increment</td>
<td>m³/tree/yr</td>
<td>0.0093</td>
<td></td>
<td>0.0377</td>
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</tr>
<tr>
<td>Stand Volume</td>
<td>m³/ha</td>
<td>2.96</td>
<td>56.98</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Signifies significant difference (p < 0.01).
\^ Comparison at 19 years for mahoe; no measures for latest sampling event.
**METHODS**

**Line planting**

Between 1984 and 1990 some forty thousand tree seedlings were planted in lines in about 25% of the secondary forest (87 ha) at Las Casas de la Selva (LCS) (photograph 2, photograph 3). Ninety percent of the seedlings were mahogany; the other 10% was primarily mahoe. The steeper slopes of the forest were left untouched for fear of erosion and to provide areas to study natural succession of the forest. On the areas previously converted to grazing, Caribbean pine, *Pinus caribaea*, was planted to hold the soil and mahogany and mahoe interplanted once the pines had established. In 2000, 22 randomly selected 0.4-ha plots were established including 19 plots of mahogany and three plots of mahoe, reflecting the greater use of mahogany in the line-planting.

In 2003, five 0.4-ha plots of mixed broadleaf tree species were planted to evaluate the potential timber production using a wider range of species. The species included were capa prieto or Spanish elm, *Cordia alliodora*, moralon or grandleaf seagrape, *Coccoloba pubescens*, santamaria or Antilles calophyllum, *Calophyllum brasiliense*, Honduras mahogany, *Swietenia macrophylla*, and cedro español or Spanish cedar, *Cedrela odorata*. Table I summarizes the trees being trialed at LCS with some of their ecological and silvicultural characteristics.

Throughout LCS, line planting was at approximately 3 m spacing within the lines and 10 m spacing from line to line under a canopy of secondary forest. The initial planting density for mahogany was approximately 370 trees/ha and for mahoe 415 trees/ha. It was anticipated that hurricanes, vine-overgrowth, natural die-off and landslides would significantly reduce the density of planting, perhaps reducing the density to one-third that of planting even before thinning might be needed. During planting, large native trees of valuable timber species were left untouched with gaps in planting lines around them.

**Field measurement**

Diameter at breast height (DBH) and total height for mahogany plots were measured in 2001-2002 and again in 2004-2005 (at a mean of 17.7 years since planting). DBH and total height for mahoe plots were measured in 2002-2003 and again in 2010 (at a mean of 22.7 years since planting). Height was measured in mixed hardwood plots at planting in 2003-2004 and annually through 2007.

DBH was measured for each species using a standard tape measure. Total height was measured using a Brunton Clinomaster Clinometer to identify angle to tree top and angle to tree base and a tape measure to record distance from the observer to the tree. Commercial height was estimated from the lowest major fork or branch. Canopy crown width was calculated as the mean extent of the canopy along and perpendicular to the planted line. A measure of forest crowding around each tree was taken using a 2.5 factor basal area prism. This measure should not be confused as a measure of stand basal area, as the observer did not pivot around a central point but rather pivoted around the entire base of each line planted tree.

**Data Evaluation**

Only trees with a complete data record were included in the analysis, and data greater than two standard deviations of mean species DBH and/or total height were excluded. From field measurements of DBH, total height, and commercial height, standard measures of forest productivity were calculated, including tree basal area (BA):

\[
\text{Tree BA} = \pi \times \text{DBH}^2/4 \quad \text{(equation 1)}
\]

where tree BA (basal area) was in m²/tree and DBH was in meters. Tree volume was calculated as:

\[
\text{Tree Volume} = \pi \times \text{DBH}^2/4 \times H_c \times 0.7 \quad \text{(equation 2)}
\]

Where tree volume was in m³/tree, DBH was in meters, and \(H_c\) (commercial height) were in meters. Commercial height (\(H_c\)) was used so that tree volume reflected merchantable tree volume, and a 0.7 factor was used to estimate tree taper. These measures of forest productivity were compared between all mahogany and mahoe trees and for trees in the upper quartile DBH. Differences in forest growth variables were compared using a 2-sample t-test with unequal variance in Minitab version 15.1.30.0.

Based on calculated annual increment for tree BA, estimates were calculated for the length of time for mahogany and mahoe to reach various mean basal area tree. Incremental measures of BA are preferred as a measure of timber increase over DBH, as BA correlates linearly with volume and provides a more easily interpreted stand parameter.

### Figure 1.

DBH size class distribution for mahogany (17.7 years; blue) and mahoe (22.7 years; green).
Results

There was a larger number of mahogany trees in this study (total number of measured trees \( n = 543 \)) compared to mahoe trees (total number of measured trees \( n = 292 \)), since there were 19 plots of mahogany and three plots of mahoe. The average stocking density was 71.5 trees/ha for mahogany and 243.3 trees/ha for mahoe due to higher mahogany mortality and higher initial planting density for mahoe.

Mahoe had significantly greater growth than mahogany for all variables (table II). Basal crowding was not significantly different between mahogany and mahoe. Mahoe had significantly greater tree volume than mahogany. Annual BA increment for mahogany was significantly less than for mahoe; likewise, annual volume increment was significantly different between mahogany and mahoe. Analysis of the upper quartile of mahogany and mahoe trees showed significantly greater growth measurements for mahoe in all categories except commercial height (table III).

Mean annual BA and volume increments were used to project the length of time from planting that mahogany and mahoe seedlings would need to reach seven specific BA classes from 0.03-0.20 m²/tree (table IV). For the upper quartile of mahogany trees, an estimated 32 years from planting is required to reach the marketable 0.07 m²/tree BA class. The upper quartile of mahoe already exceeds the first five BA classes (figure 1).

Survival rates for mahogany were estimated at 38% for mahogany at Las Casas. The site elevation at Las Casas de la Selva of 600 m means the slopes are severely affected by the prevailing easterly winds, and since line planting occurred, Hurricanes Hugo (1989), Hortense (1996), Georges (1998) and tropical storm Jean (2004) did considerable damage within the forest. The higher survival rate for mahoe, estimated at 66% of plantings, is probably due to its resilience to hurricane damage.

Survival rates were high for the younger hardwood plantings, ranging from 69-100% (table V). Growth rates were expressed as the mean annual growth rate expressed as a percentage of the original height at planting (% change/yr). Coccoloba pubescens, Calophyllum brasiliense, and Cedrela odorata had the greatest change in height in the semi-shaded plots. These three species were all more successful in the semi-shaded plots than in full sun based on seedling survival. In full sun plots, Calophyllum brasiliense had the greatest change in height over the four years of measurement. Results from the mixed hardwood plantings are too premature to judge which of the additional species will perform well at LCS, and analysis of longer-term survival and growth dynamics should be monitored.
Discussion

The Las Casas de la Selva (LCS) enrichment planting was designed to test the efficacy of line-planting enrichment in the wet forest life zone as a means of achieving both economic return and protection of natural biological resources. If valuable economic returns are achieved from line planting efforts, LCS could provide a model for future sustainable forestry initiatives in secondary forest management.

At LCS mahoe has been far more successful than mahogany in terms of wood production with mahoe tree volume more than three times greater than mahogany. This may be because conditions at LCS are similar to the humid cool mountains of mahoe’s native range in the Caribbean (Wadsworth, 1999). In contrast, mahogany is a low-elevation species common on relatively dry sites like the Yucatan (Mayhew, Newton, 1998). Other factors that may have led to mahogany being less productive than mahoe include inherently slower annual growth rates, early competition from other trees and from vine overtopping, and stand damage from three hurricanes and one tropical storm that have impacted Las Casas in the last two decades.

Given the relatively young age of the trees and a sigmoid shaped model growth curve, we predicted that the trees were still experiencing near linear incremental growth rates. At the upper end of these estimates, this assumption may fail; however, to date there are no long-term estimates of terminal tree age or size for either species in Puerto Rico (Francis, Weaver 1988). In the short term, linear estimates of annual incremental diameter and height growth as used in this study may mimic actual stand growth. At current annual rates of increase it would take the mahogany at LCS another 48 years to reach a mean tree BA class of 0.07 m²/tr, which is the minimum BA considered suitable for harvest, giving a total time from planting to harvest of 66 yrs. Even the upper quartile mahogany trees have not yet reached a mean BA class of 0.07 m²/tree.

For comparison, in the Yucatan peninsula of Mexico, where mahogany is native, a study of regeneration and growth following disturbance such as hurricane, fire or other episodes, which open up the forest for enough light to permit mahogany recruitment and growth, mahogany was reported to have a mean 3.1 ± 0.2 cm DBH after 15 years, with an annual increase of 0.20 cm; an average DBH of 19.4 ± 2.8 cm and an increase of 1.09 cm/yr at 30 years; at 45 years an average of 25.0 ± 2.3 cm DBH with an annual increase of 0.44 cm/yr; and at 75 years an average DBH of 37.2 ± 1.2 cm with an annual increase of 0.38 cm/yr (Snook, 2003). These results were for mahogany planted in relatively large cleared areas of 5000 m², as opposed to the line-planting at LCS where the secondary forest was far less disturbed. The mahogany trees at LCS have a DBH of 12.45 (0.24 cm standard error, SE) (table II), and average DBH is projected to reach 20 cm after 32 years, 25 cm after 48 years and 30 cm after 66 years (table IV).

But the situation with mahoe is very different: it is currently possible to selectively harvest marketable wood from the mahoe stand at LCS (photographs 4 and 5). The relative superiority in growth for mahoe compared to mahogany was unanticipated and if known, would have led to mahoe being planted in larger numbers. Having harvestable wood some twenty years after planting makes mahoe a good candidate for sustainable timber production in subtropical secondary forests where both ecological and economic interests compete. The findings are supported by earlier work by Kimber (1970) who suggested in its native range mahoe may reach merchantable size in 7-10 yrs and lumber size in 20-30 yrs. Marketing and selling of this quite rare but very attractive hardwood mahoe tree has already proved it to be well accepted by artisans and fine woodworkers.
Future challenges with the mahogany and mahoe plantations will involve working out the best thinning and replanting strategies. Other methods, such as liberation thinning, which can accelerate maturation of both the line-planted and valuable naturally growing native timber trees by removal of competitor trees and lessening of forestry density (Wadsworth, Zweede, 2006), are also being researched in trial and control plots in the forest.

There are numerous ancillary benefits to forest enrichment and the maintenance of forest versus alternatives of conversion to pasture land or other agricultural uses. Since enrichment planting combines planting, or agroforestry, with maintenance of natural regenerating forest, which provides protection and shelter wood, it retains forest characteristics with their greater biodiversity and ecological functions (Michon et al., 2007 cited in Paquette et al., 2009). A number of studies have pointed out that secondary forests grow rapidly, accumulating and maintaining large amounts of aboveground biomass and increasing soil organic matter. Utilization of forests through management of natural regeneration or through forest enrichment prevents the release of carbon, which ensues from loss of forest cover (e.g. Paquette et al., 2009; Montagnini, Nair, 2004; Stanley, Montagnini, 1999). Biodiversity in forest regions are greater than in forests converted to agricultural uses. Forest cover also prevents soil erosion and downstream/downslope deterioration of water resources. It is estimated that some 300 million people worldwide depend on the products and services of secondary forests and providing livelihood and economic returns is crucial in improving their lives and giving incentive to the maintenance and improvement of the world’s forests (Lamb et al., 2005).

**To draw an inference from this study**

Mahogany and mahoe productivity to date suggest that line planting within secondary forests such as those at Las Casas de la Selva (LCS) can provide both sustainable timber production for profit and preservation of biodiversity. Studies have found that tree diversity and amphibian diversity and abundance have not been negatively impacted by line-planting (Nelson et al., 2010). Observations indicate that mahoe seedlings are establishing near the line-planted trees (but not yet mahogany as the trees for the most part have not begun flowering and seeding), and there appears to be increased recruitment of valuable native hardwoods. Seedlings of ausubo, Manilkara bidentata, caimitillo, Micropholis chryso-phylloides, camasey, Miconia prasina, granadillo, Buchenavia capitata, and tabonuco, Dacyroydes excelsa are increasingly apparent. The shade of the mahogany and mahoe has probably helped with regeneration, as most native Puerto Rican hardwood seedlings are sun-intolerant (Burns, Honkala, 1990). These results indicate forest enrichment should be further tested and applied as a promising approach to maintaining secondary forest, increasing economic value from the forests and in developing locally appropriate forms of sustainable tropical forestry.

**Acknowledgements**

The authors gratefully acknowledge the continuing support by The Earthwatch Institute and the work of Earthwatch volunteer groups from 2000-2010 in the collection of the data on tree growth at Las Casa de la Selva. They are indebted for the invaluable advice and methodological help given by Frank H. Wadsworth and Peter L. Weaver of the International Institute of Tropical Forestry, Jess K. Zimmerman, of the Luquillo Long-Term Ecological Research Program (Luquillo LTER), University of Puerto Rico, and Jill Thompson from the Big Grid species study and the El Verde Field Station at El Yunque. The Puerto Rican Department of Natural Resources (DNR) helped with species selection, tree seedlings and provided support for planting costs. Special thanks and appreciation are given to Global Ecotechnics Corporation (www.globalecotechnics.com) for project support for over two decades, and to the staff at Las Casas de la Selva, Andrés Rúa and Joseph Sanquilla, for help in field expeditions, computer mapping and data management.

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