Growth and development of loblolly pine in a spacing trial planted in Hawaii

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Growth and development of loblolly pine in a spacing trial planted in Hawaii

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Abstract

Loblolly pine (Pinus taeda L.) was planted at four square spacings (1.8, 2.4, 3.0, and 3.7 m) on the Island of Maui in 1961, and measured periodically for 34 years. Patterns of stand growth and development were examined and compared with yield model estimates of stand characteristics of plantations of the same initial spacings, ages, and site index in the southeastern United States. The Hawaiian plantings had much higher survival at all spacings and sustained high diameter growth in the face of intense competition. At Age 34, the 1.8 m spacing had 1585 stems/ha averaging 24.1 m tall and 28.8 cm DBH; the widest spacing (3.7 m) had 723 stems/ha, 26.1 m tall and 38.2 cm DBH. The highest basal areas (~100 m²/ha) were double maxima attained in the southeastern United States and were reflected in similar differences in volume yields. The Hawaiian plantings demonstrate that growth potential of loblolly pine is far greater than is apparent from observations on plantations in its native habitat. To capture this potential in other situations, research must identify the tree, stand, and environmental characteristics associated with low mortality rates and high diameter growth in Hawaii, and, conversely, the factors that limit loblolly’s potential in the southeastern United States. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pinus taeda; Stand dynamics; Stockability; Self-thinning; Growth and yield

1. Introduction

Loblolly pine (Pinus taeda) is the most common and commercially important pine species in the south-

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Retired.

eastern United States. It is well adapted to the wide range of soils, sites, and environments that occur over its natural range, which extends from southern New Jersey south to central Florida and west to eastern Texas (Baker and Langdon, 1990). Because of its rapid growth and adaptability it has been planted in a number of other countries, including Argentina, Australia, Brazil, China, New Zealand, South Africa, and also in the state of Hawaii, and found to perform
exceptionally well so that it is now grown commercially in many of these countries (Burns and Hu, 1983; Schultz, 1997). China and Brazil have the largest loblolly pine management programs. Annually they produce and plant more than 320 million seedlings (Schultz, 1997). The most successful plantings are usually between latitudes of 24° and 30° N or S, and at elevations of 500–900 m. In Brazil loblolly pine is grown on 15–25-year rotations for both fiber and solid wood products. Stand yields of 15–25 m³/ha/year are common and yields up to 35 m³/ha/year have been reported. Height growth curves indicate heights of 27–32 m by Age 20 on the best sites and 19–23 m on average sites (Machado, 1980). In South Africa loblolly pine is grown at rotational lengths of 18–35 years. Mean annual increment is ca. 18 m³/ha/year but can exceed 28 m³/ha/year on the best sites. Trees can reach a height of 30 m and a DBH of 45 cm at 35 years (Schultz, 1997). There are numerous published reports on individual aspects of the growth of loblolly pine planted in the subtropics, e.g., seed source (Baldanzo, 1978; Falkenhagen, 1978), environment (Burns and Hu, 1983; Harms et al., 1994; Schultz, 1997), site index (Machado, 1980), thinning (Machado et al., 1990), and carrying capacity and thinning (Strub and Bredenkamp, 1985), but few data or analyses of the quantitative aspects of stand dynamics and growth, especially as compared to growth of native plantations, have been published. One exception is a series of reports that examine the growth of a spacing trial planted in Hawaii to evaluate the potential for loblolly pine to augment the state’s softwood timber requirements. This spacing trial has been measured periodically for 34 years, and has provided a rich record of stand growth and development of an exceptionally fast-growing plantation. Two of the reports evaluate early survival, height, and diameter growth in relation to spacing at ages 7 and 11 years (Whitesell, 1970, 1974), a third evaluates stand productivity and stockability differences between loblolly pine in Hawaii and the southeastern US at Age 25 years (DeBell et al., 1989), and a fourth examines tree, stand, and environmental components of growth and stockability at Age 26 years (Harms et al., 1994).

In this paper, we examine the Hawaii data for the broader, overall, effects of initial spacing on the temporal patterns of stand growth and development through a full rotation. Survival, height and diameter growth; basal area and volume growth and yield; and stand structural characteristics from the time of establishment to Age 34 years are reported. To put the growth of this plantation in perspective, we compare the various components of its development with a southeastern US ‘standard’ derived from a loblolly pine yield model (Hafley et al., 1982).

2. Methods

The spacing trial was established in 1961 as a research study in the Olinda Forest Reserve on the island of Maui (Whitesell, 1970). The site is 1140 m asl, on the northeast side of east Maui at latitude 20°49’ N. The mean air temperature on Maui is 14°C and varies 3°C from summer to winter; average annual rainfall is 1143 mm with a wet winter and spring and a relatively dry summer (Harms et al., 1994). Growth is possible throughout the year. The soil is Olinda loam, in the subgroup Eutic Dystrandepts. Typically, the surface layer is a dark reddish-brown granular loam ca. 15 cm thick over a dark reddish-brown and yellowish-red subangular blocky silty clay loam subsoil. This soil developed in volcanic ash over andesite or basalt. It is slightly acid (pH 6.2–6.4) in both the surface layer and subsoil. Olinda soil is well drained, with a moderately rapid permeability (Foote et al., 1972). Average site index of the plantation is 24 m (base Age 25 years).

The field layout of the plantation consists of four blocks each with four square spacings: 1.8, 2.4, 3.0, and 3.7 m, planted in a randomized 4 × 4 Latin square design. Each plot is square, 0.11 ha in area, with the 5 × 5 rows in the center forming a 25-tree measurement sub-plot. All sub-plots had two or more exterior isolation rows. At the time of planting, the ground cover was a 3-inch sod layer of kikuyu grass (Pennisetum clandestinum Hochst.), rattail grass (Sporobolus cernuus [Wild.] Kunth), and gorse (Ulex europaeus L.). The grass was heavily grazed just before planting. The sod was removed at each planting spot, and holes 30 cm deep were dug for the seedlings. Planting stock was 1–1 nursery-grown seedlings of unknown seed source origin. The 21 trees that died during the first year were replaced.

Measurements were made at ages 4, 7, 11, 20, 25, 26, and 34 years. Diameter at breast height (DBH,
3. Results

3.1. Stand development

The major stand attributes of the Olinda plantation are summarized in Table 1. Early development of the plantation was described by Whitesell, 1970, 1974. He observed that the tree crowns had closed in the 1.8 m spacing by the fourth year at an average stand height of 4.5 m, by the seventh year in the 2.4 m and 3.0 m spacings, at an average stand height of 8.8 m, and that they were nearly closed in the 3.7 m spacing by the 11th year, when the average stand height was 12.7 m. Length of the green crown in the 1.8 m spacing decreased from 64% of tree height at ages 7 to 29% at Age 26, and from 81% to 36% in the 3.7 m spacing during the same period.

3.1.1. Survival and mortality

Mortality in the Olinda plantation was density related; no causes other than competition for growing space were identified, i.e., except for minor mortality after planting, losses were confined to trees in the suppressed and intermediate crown classes, and number of trees dying varied directly with initial density (Long and Smith, 1984; Oliver and Larson, 1990). Self-thinning began earliest and trees died in greatest numbers in the 1.8 m spacing, but losses did not become substantial until after Age 20 (Fig. 1 and Table 1). By Age 34 an average of 47% of the trees in the 1.8 m plots had died, and although mortality had begun to occur in the 2.4 m and 3.0 m plots, only 19% and 15%, respectively, had died by the 34th year. Less than 3% of the trees in the 3.7 m plots had died by the 34th year (Table 1). Survival curves from the yield model predictions for plantations in the Southeast show the same trends and relationships to spacing as in Hawaii, but self-thinning begins at much younger ages in all spacings, and the rates of mortality, and the absolute numbers of trees lost are greater, resulting in a pronounced divergence of the curves from the Olinda data (Fig. 1). By Age 34 years, predicted mortality in the Southeast is 67% in 1.8 m spacings, 47% in 2.4 m spacings, and 30% and 18%, respectively, in 3.0 m and 3.7 m spacings. At both locations, the survival curves were progressively declining and converging as a result of self-thinning. At Age 34, the curves of the closest and widest spacings for the
Table 1
Means for stand components of the Olinda plantation, Maui, Hawaii, at age of measurement a, b

<table>
<thead>
<tr>
<th>Spacing (m)</th>
<th>Plantation age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Number surviving (trees per ha)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>2990</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>1615</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>1066</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>746</td>
</tr>
<tr>
<td>Cumulative mortality (%)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>0.0</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>3.9</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>1.1</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>0.0</td>
</tr>
<tr>
<td>Height (m)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>4.5</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>4.4</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>4.4</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>4.5</td>
</tr>
<tr>
<td>Quadratic mean diameter at breast height (cm)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>7.7</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>8.2</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>8.4</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>9.1</td>
</tr>
<tr>
<td>Basal area per ha (sq m)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>13.8</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>8.6</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>5.9</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>4.9</td>
</tr>
<tr>
<td>Total volume per ha (cu m outside bark)</td>
<td></td>
</tr>
<tr>
<td>1.8 x 1.8</td>
<td>75</td>
</tr>
<tr>
<td>2.4 x 2.4</td>
<td>38</td>
</tr>
<tr>
<td>3.0 x 3.0</td>
<td>37</td>
</tr>
<tr>
<td>3.7 x 3.7</td>
<td>20</td>
</tr>
</tbody>
</table>

a Each value is the average of four replicate plot means.
b Trees per ha planted: 1.8 m = 2990; 2.4 m = 1680; 3.0 m = 1078; 3.7 m = 746.

Southeast were 363 trees/ha apart, while the Olinda curves were still 860 trees/ha apart.

3.1.2. Height
Spacing had no significant effect on average stand height, although trees in the 3.7 m spacing were consistently taller than those in the closer spacings as early as the 7th year (Harms et al., 1994). By Age 25 average height of the 3.7 m spacing was 22 m, 2 m taller than the other spacings. At Age 34 average heights of the 3.0 and 3.7 m spacings were equal and both these spacings were 2 m taller than the two closest spacings (Table 1 and Fig. 1).

We selected the site index curve needed to drive the yield model from among several published curves (Golden et al., 1981; Pienaar and Shiver, 1980; Smalley and Bower, 1971). None of the curves were entirely satisfactory, but this was to be expected since height growth patterns are known to be sensitive to the particular edaphic and environmental factors present
on a site, and the conditions at Olinda differ substantially from the conditions found in the Southeast. Qualitative comparisons of the site index models against the observed data indicated that the model of Smalley and Bower (1971) most closely approximated the height growth characteristics of the Olinda plantation and therefore was chosen to drive the yield model. The average height growth patterns of the Olinda plantation and the estimated average height-age curves for plantations in the Southeast are displayed in Fig. 1. The curves show that height growth of the Olinda plantation was reduced after about Age 11 relative to the Southeast, and remained below the Southeast curves as age increased. The 3.7 m Olinda spacing, however, fell within the range of the Southeast curves throughout the period of observation.

3.1.3. Diameter

Differences among spacings in mean stand diameter were evident four years after planting, when trees in the 3.7 m spacing were already 18% larger in DBH than in the 1.8 m spacing (Table 1) and Whitesell (1970). The relative growth advantage of the wider spaced trees had increased to 52.8% by the 20th year, dropping back to 32.6% at the end of the 34th year. During the nine years between ages 11 and 20 the 3.7 m spacing grew 7.0 cm, 59.1% more than the 1.8 m spacing which grew 4.4 cm. During the nine years between ages 25 and 34 growth of the 3.7 m spacing was only 3.9 cm, 18.7% less than the 1.8 m spacing which had grown 4.8 cm. This may be an indication that competition in the 3.7 m spacing had become more intense with time relative to the 1.8 m spacing, which had developed a substantial degree of differentiation among trees, i.e., the coefficient of variation of mean DBH at Age 34 was 37.8% in the 1.8 m spacing versus 26.6% in the 3.7 m spacing. The spacing effect on diameter is further demonstrated by the divergence of the DBH growth curves. From the 4th to the 20th year, divergence increased progressively with increase in spacing, but from the 20th through the 25th year growth of the three widest spacings declined while growth of the 1.8 m spacing increased. From the 25th through the 34th year, growth increased again except for the 2.4 m spacing which, for no apparent reason, continued its decline (Fig. 1).

The yield model estimates of DBH (Fig. 1) indicate lower overall diameter growth rates for the Southeast. The difference between Olinda and the Southeast for any one spacing tended to be greater at all ages than the difference between that spacing and the next wider or closer spacing within the same location. Furthermore, the difference in DBH between locations increased as spacing increased. At Age 25, average stand diameters in Hawaii were 2.9–5.9 cm larger than for the same spacings in the Southeast.

The relative response of diameter growth of loblolly pine in the Southeast to increased spacing is of the same order of magnitude as in the Olinda spacings.
The maximum growth advantage of 3.7 m spacings over 1.8 m spacings was 39.7% at Age 20, dropping to 27.3% at Age 34. Between ages 11 and 20, 3.7 m spacings were estimated to grow 7.6 cm, 43.4% more than 1.8 m spacings which were estimated to grow 5.3 cm. Between the ages of 25 and 34, 3.7 m spacings were estimated to grow 3.3 cm, 18.2% less than the 1.8 m spacings which were estimated to grow 3.9 cm.

3.1.4. Stand growth trajectories

The relationship between mean DBH and stand density describes a trajectory that is characteristic of developing even-aged stands. As trees grow, stands advance through various stages along a typical path that ultimately attains a self-limiting maximum mean tree size–density boundary along which the stands then grow (Harms, 1984; Long and Smith, 1984; Oliver and Larson, 1990). The limiting density boundary can be equated to the self-thinning rule of Yoda et al. (1963) or the stand density index of Reineke (1933). Stand trajectories for the Olinda plantation and plantations in the Southeast are plotted in Fig. 2. The limiting density boundary reference line for Olinda was obtained by using a quadratic mean DBH of 25 cm and 2100 as the maximum (limiting) number of trees per ha possible at that DBH, estimated from a plot of the DBH–density data from the 1.8 m spacing. The line was located on the graph using the Reineke (1933) equation with a slope coefficient of 1.605, which Hasenauer et al. (1994) determined to be applicable to loblolly pine plantations in the southeastern US. The reference line for the Southeast was calculated using a mean DBH of 25 cm and 1150 trees/ha, the average of the values for maximum number of trees reported for coastal plain and Piedmont sites by Hasenauer et al. (1994). Our assumption in placing these reference lines was that the slope of the limiting density line was the same for both Olinda and the Southeast.

The difference in levels of the reference lines is a function of the higher stockability of the Olinda plantation as discussed by DeBell et al. (1989). They used the maximum mean tree size–density boundary line as a measure of stockability which they define as the maximum number of trees that can be grown to a given size under a particular set of conditions (DeBell et al., 1989; Harms et al., 1994)

Fig. 2. Mean stand DBH-density trajectories in relation to spacing for the Olinda plantation (filled symbols), and for plantations in the southeastern US (open symbols). Ages (years) are shown for the DBH-density pairs plotted for each location. Estimated limiting density boundaries are shown for Olinda (dash), and for the Southeast (solid).

Following stand establishment, and for a period of years that varied with initial spacing, the trajectories rose vertically as trees grew in diameter (Fig. 2). As competition intensified and self-thinning commenced, the trajectories began to curve, the curvature increasing as the trajectories approached closer to the limiting density boundary. Self-thinning and mean DBH growth had progressed sufficiently by Age 20 to place the 1.8 m spacing trajectory at Olinda and the 1.8 m and 2.4 m spacing trajectories in the Southeast at their respective limiting density boundaries (Fig. 2). At Age 20, the mortality at the limiting density boundary at Olinda was 13% and there were 2603 trees/ha remaining with a mean DBH of 21.4 cm; the corresponding mortality in the Southeast was 42% with 1725 trees/ha remaining with an associated mean DBH of 18.5 cm. Self-thinning and diameter growth had not progressed enough by Age 34 in the 2.4, 3.0, and 3.7 m spacings at Olinda for their trajectories to have reached the limiting density boundary. In the
Southeast, the 3.0 m but not the 3.7 m trajectory had reached the limiting density boundary.

3.1.5. Size-class differentiation

Stand differentiation, which results from differential growth among the component trees (Oliver and Larson, 1990), was examined by evaluating DBH size-class frequency distributions by 5 cm class widths. Frequency distributions at Age 34 are graphed by spacing and location in Fig. 3 to show percentage of trees per ha present in a spacing above a minimum diameter class. The Olinda spacings fall into two groups, with the smaller trees in the 1.8 m and 2.4 m spacings and the larger trees in the wider spacings. Southeastern US plantations show a uniform progression across spacings, due probably to the internal structure of the yield model. The greatest difference between the Olinda plantation and the Southeast is in the absolute range of diameter classes. There is a 5 cm difference in the minimum diameter class between locations—10 cm for Olinda and 15 cm for the Southeast, but the maximum diameter class for the 3.7 m spacing at Olinda is 60 cm as compared to 40 cm for the same spacing in the Southeast. The smaller minimum diameter and greater range in tree size at any one spacing at Olinda further reflects greater tolerance of that system to crowding.

3.2. Stand productivity

3.2.1. Basal area

Net basal area per ha and mean annual basal area increment (MAI) at Olinda were greatest at the 1.8 m spacing to Age 34, and progressively less at successively wider spacings (Table 1, Figs. 4 and 5). Basal area increased continuously but at a gradually reducing rate throughout the 34 years of record. However, between the ages of 20 and 25 there was a period of substantial reduction in the rate of increase in all spacings, but most notably in the 1.8 m spacing in which the change was almost flat (Fig. 4). There was an initial rapid increase in basal area and associated MAI across all spacings. The differences in basal area among spacings widened until about Age 20, after which the rate of increase declined and the differences among spacings decreased. MAI culminated between ages 4 and 7 years in the two closest spacings and between ages 7 and 11 in the widest spacings, decreasing thereafter and beginning to converge (Fig. 5).

Basal area accumulation patterns in southeastern US plantations are similar to Olinda, but at lower absolute levels, through Age 11. Basal area MAI in the Southeast culminates later than at Olinda: at about Age 11 at 1.8 m spacings and between 11 and 20 at the wider spacings (Fig. 5). Between ages 11 and 20 years, the basal area accumulation and MAI curves for the 1.8 m spacing begin to fall below the 2.4 m spacing, and by Age 34 have crossed the curves for the wider spacings so that at Age 34 there is less basal area at 1.8 m spacing than at the 3.7 m spacing (Figs. 4 and 5). After Age 20, the basal area curves of all spacings are flattening and converging. By Age 34 curves of all spacings in the Southeast have converged to a point where they are within 3.5 m²/ha of each other in basal area and within 0.1 m²/ha/year in MAI. This was not the case at Olinda: at Age 34 years, curves of the Olinda spacings were still 20.1 m²/ha in basal area and 0.6 m²/ha/year in MAI from convergence, although
they appeared to be in the early stages of drawing together (Figs. 4 and 5).

The convergence and crossing-over of basal area and volume curves for different spacings have been observed in other loblolly pine spacing studies, in natural and planted loblolly pine stands, and for other conifers (Beford, 1991; Liegel et al., 1985; Harrison and Daniels, 1988; Hatley et al., 1982). The phenomenon is probably due to a physiological inability of trees at older ages in closely spaced stands to rapidly take advantage of growing space released by mortality to increase their growth. With continuing mortality this can result in a net loss in basal area.

3.2.2. Volume
Volume yields increased with decreasing spacing, with the greatest differences among the three closest spacings (Fig. 4). The 3.0 m and 3.7 m spacing yields were similar throughout the period of measurement, as was volume MAI after Age 20 (Fig. 5). Unlike basal area, however, the yield curves for volume showed an essentially linear and parallel increase, to Age 34.
There was no indication of convergence or a yield maximum (Fig. 4). Growth rate of the 1.8 m spacing was consistently greater than the wider spacings, but was essentially flat after Age 7. There was a period of reduced growth between ages 20 and 25 similar to that shown in the basal area curves. MAI of the 1.8 m spacing attained an apparent maximum at Age 20, decreasing to Age 25, and increasing slightly thereafter to Age 34. Growth rates of the other spacings had not culminated, the curves having taken on a broad, flat, and slightly increasing form (Fig. 5). The reduction in volume and basal area growth of the Olinda plantation between ages 20 and 25 was probably a consequence of intense competition that developed as the stands approached and, in the case of the 1.8 m spacing, reached the limiting density boundary (Fig. 2). The severity of competition is reflected in the substantial increase in mortality during this period (Fig. 1). The growth recovery after Age 25 is probably a result of growth increases of the surviving trees as they occupied the space released by the trees that died.

Volume yield and MAI for the Southeast have patterns similar to the basal area trends. Growth and yield both converge by Age 34, and the curves for the 1.8 m spacing cross the wider spacings by Age 20 (Figs. 4 and 5). Volume MAI culminates later than basal area: the two closest spacings reach maximum volume growth at about Age 20, the 3.0 m spacing at Age 25, and the 3.7 m spacing probably at about Age 34.

Net volume and basal area and volume yields for the Olinda plantation and the Southeast at Age 34 are compared in Table 2. Both volume and basal area accumulations are greatest at the 1.8 m spacing at Olinda, and least at this spacing in the Southeast. Moreover, maximum yields at Olinda of the most productive spacing (1.8 m) were about twice the maximum yields of the most productive spacing (3.0 m) in the Southeast at this age.

4. Discussion

Experimental studies of the influence of initial spacing on tree growth and plantation development have a long history (Sjolte-Jorgensen, 1967). In particular, the responses of loblolly pine trees in the southeastern US to initial spacing have been investigated and well documented in numerous spacing trials (Arnold, 1978; Harms and Lloyd, 1981; Owens, 1974; Shephard, 1974; Sprinz et al., 1979), and yield studies (Buford, 1991; Clutter et al., 1984; Halley et al., 1982) among others. The patterns of tree and stand responses to initial spacing in Hawaii are consistent with spacing effects observed in the Southeast as depicted by the Halley et al. (1982) yield model in Fig. 1. However, the nature of the responses differ substantially in magnitude. This was evident in the 1.8 m spacing at the limiting density boundaries where the difference between Hawaii and the southeastern US amounted to 62% more trees surviving and a 15% greater diameter at Age 34 years. This translates into 114% more basal area and 140% more volume (Table 2). When averaged across the four spacings, basal area and volume yields of the Olinda plantation at Age 34 were almost double (1.8 x) the yields in the Southeast.

It is evident from the data that the critical factors accounting for differences in yield between Olinda and the Southeast are tree survival and diameter growth. Tree height was not a factor because site index was a constant. The nature of the effects can

Table 2

<table>
<thead>
<tr>
<th>Item</th>
<th>Spacing (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.8 × 1.8</td>
</tr>
<tr>
<td></td>
<td>Olinda   SEUS</td>
</tr>
<tr>
<td>Trees per ha</td>
<td>1585      976</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>103.1     48.2</td>
</tr>
<tr>
<td>Total volume, c.f. (m³ ha⁻¹)</td>
<td>1324      552</td>
</tr>
</tbody>
</table>

* SEUS yields are from Halley et al. (1982) for site index 80 (24 m) base Age 25.
be seen by comparing stand development trajectories for the two locations (Fig. 2). The trajectories show that loblolly pine trees on the Olinda site were slow to thin relative to the Southeast but yet were able to continue to increase their diameters under conditions of crowding and competition that cause significant self-thinning and growth reduction in stands of comparable spacings and site index in the southeastern US. The result is that for each of the four spacings the mean DBH attained for a given number of surviving trees was always greater for the Olinda plantation. Since yield is the product of mean tree size and number of trees per unit area, the net effect of this was the nearly twofold yield differences observed.

Explanations for the high stockability of the Olinda plantation have been proposed by Harms et al. (1994) based on a study of the crown architecture of the trees and the structure of the stands at Age 26. They found a two-tiered crown-class structure with a sub-dominant stand having live crowns that extended from below the live crown base of the dominant stand well up into the main canopy. This served to increase the occupancy of the canopy space with functioning leaf area. The Olinda trees also had long crowns with high foliage biomass and leaf area. The development of these characteristics was attributed to the high solar radiation intensities and high sun angles at the latitude of Hawaii that allow penetration of sunlight deep into the canopy. In this light environment trees in the lower crown classes were able to retain their foliage and maintain a positive carbon balance sufficient for survival and growth in the densest stands. Growth rates were further enhanced by a long growing season, favorable temperature regime and soil moisture conditions, and a lack of disease and insect problems. In comparison, from measurements in a similar plantation in the Piedmont of South Carolina, they found crown development and growth to be limited by a less favorable light climate, a shorter growing season, and more stressful temperature and soil moisture conditions (Harms et al., 1994).

5. Conclusions

The Olinda trial serves to emphasize two important points. First, that the growth potential of loblolly pine is far greater than is apparent from growth records on plantations in the southeastern US, a fact long since established by its performance at other locations in the sub-tropics. The data show that the growth of even unimproved stock when grown in very favorable environments, such as found in Hawaii, can double that which is currently being achieved in managed plantations in its natural range. (Burns and Hu, 1983; DeBell et al., 1989; Schulz, 1997).

Second, to capture the growth potential of loblolly pine, research must identify and quantify the specific tree, and stand physiological, and environmental factors that are responsible for the high survival rates and accompanying high diameter growth rates evident in the Olinda plantation at the high levels of competition that are not tolerated in plantations of the same spacing in the Southeast. And, conversely, research must identify the site-specific factors that are limiting to loblolly pine in the Southeast. Of the environmental and site factors thought to be responsible for the high stockability of the Olinda site by Harms et al. (1994), i.e., high sun angle, high solar radiation intensity, long growing season, favorable soil conditions, high foliage nutrients, and freedom from pests, most are not naturally present in non-limiting amounts in the Southeast. However, the potential for loblolly pine to respond to favorable environments suggests that improvement in productivity should be possible. That improvement is possible is supported in a recent report by Piensar and Shiver (1993). Their data show that at Age 8, yield of genetically-improved loblolly pine planted on marginal agricultural cropland in the Georgia Piedmont was more than doubled by the simple expedient of complete control of the herbaceous competition during plantation establishment. It is evident from the Olinda plantation data that efforts to enhance the growth of loblolly pine should target research to improving productivity by discovering methods for increasing numbers of trees per unit area that can be grown to a desired size.

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