

Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina

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Stand structure and crown architecture of loblolly pine (*Pinus taeda* L.) spacing trials in Hawaii and South Carolina were examined for attributes that would explain markedly different stockabilities (stand density per mean stand DBH), respectively, 1740 and 850 trees/ha at a quadratic mean stand DBH of 25 cm. In plots spaced at 2.4 × 2.4 m, these stockabilities produced 604 m³/ha at age 25 in Hawaii, and 297 m³/ha in South Carolina. Data collected in these stands indicate that stockability differences were associated with differences in tree size-class structure, crown length, and leaf area. Both stands were characterized by a two-tiered height structure, but the crown bases of trees in the subdominant class in Hawaii extended 1–2 m below the bases of the crowns of the dominant height class. In the South Carolina stands the crown bases of both height classes were at the same level. Green crown lengths in Hawaii were 4–7 m longer than in South Carolina, and the associated crown leaf area of 63.9 m² was five times greater. The differences in stockability was attributed to the Hawaiian site and climate, which provide a long growing season, high solar radiation, high sun angle, favorable temperatures, and a favorable soil moisture regime and foliage nutrient status, and to a lack of significant insect and disease pests. The influence of genotype on stockability was not testable with these data.

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La structure de peuplement et l'architecture de la cime du pin à encens (*Pinus taeda* L.) dans des essais d'éclaircies à Hawaii et en Caroline du Sud ont été examinées pour des attributs qui pourraient expliquer différentes densités relatives (densité du peuplement par le DHP moyen du peuplement), respectivement 1740 et 850 arbres/ha à un DHP moyen quadratique du peuplement de 25 cm. Dans les placettes dont l'espacement est de 2,4 × 2,4 m, ces densités relatives ont produit 604 m³/ha à 25 ans à Hawaii et 297 m³/ha en Caroline du Sud. Les données récoltées de ces peuplements indiquent que les différences de densité relative sont associées aux différences dans la structure des classes de dimensions, la longueur de cime et la surface foliaire. Les deux peuplements sont caractérisés par une structure à deux étages, mais la base des cimes dans la classe subdominante à Hawaii s'étend de 1 à 2 m sous la base des cimes des arbres dominants. Dans les peuplements de la Caroline du Sud, la base des cimes des deux classes de hauteur est au même niveau. Les longueurs de cime verte à Hawaii sont de 4 à 7 m plus longues qu'en Caroline du Sud, et la surface foliaire de 63,9 m² était cinq fois plus grande. Les différences de densité relative sont attribuées au site hawaïen et au climat, d'où une saison de croissance plus longue, un rayonnement solaire élevé, un angle d'incidence élevé, des températures favorables, un régime d'humidité du sol et un statut nutritif du feuillage favorable et une absence significative d'insectes et maladies. L'influence du génotype sur la densité relative n'a pu être testé avec ces données.

[Traduit par la rédaction]

Introduction

Stockability was introduced as a concept by DeBell et al. (1989) to describe the tree size – stand density relationships that exist in stands that are realizing their maximum productivity. The significance of stockability to productivity and forest management was evaluated and illustrated with data from loblolly pine (*Pinus taeda* L.) spacing trials and genetic studies. In this report we focus on identifying tree and stand attributes associated with the stockability differences observed in a subset of those data.

Stockability expresses the tolerance of a forest system to crowding and to competition for resources that results from increasing stand density. It is defined as the maximum num-

ber of trees that can be grown at a given rate or to a given size, and is determined by genotype and environment (climate, site, and management practices). Stockability can be assessed quantitatively by any of several size–density measures. These include (i) maximum mean size–density relationships, (e.g., Reineke's (1933) stand density index, and the self-thinning rule (Yoda et al. 1963)); (ii) size–density combinations above which competition-related mortality begins (e.g., Reukema and Bruce's (1977) *D*-max line); and (iii) size–density combinations above which growth rate of individual trees is reduced below some specified level.

Stand productivity can be viewed as a function of (i) growth of individual trees and (ii) the stockability of the system. Most silvicultural and research efforts to increase productivity have centered on increasing individual tree growth

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TABLE 1. Topographic and climatic factors at the Hawaii and South Carolina plantation locations

	Hawaii	South Carolina
Latitude	20°49'N	34°37'N
Elevation above sea level (m)	1140	172
Aspect	NW	S
Slope	10–20%	0–5%
Precipitation (mm) ^a		
Annual	1143	1247
March–September	485	763
Air temperature (°C) ^b		
Mean annual	17	15
January	15	5
July	18	26
Solar radiation (MJ/m ²) ^c		
Annual potential	10 428	9133
March–September	6 843	6241
Photoperiod (h) ^d		
Maximum (June)	13.4	14.5
Minimum (December)	10.9	9.8
Solar altitude (degrees) ^e		
Maximum (mid-May to mid-July)	90	75
Minimum (mid-November to mid-January)	50	35

^aHawaii, Taliaferro (1957); South Carolina, National Oceanic and Atmospheric Administration (1989).

^bHawaii, data on file at the Pacific Southwest Forest and Range Experiment Station, Honolulu, Hawaii; South Carolina, National Oceanic and Atmospheric Administration (1989).

^cBuffo et al. (1972); Reifsnnyder and Lull (1965), corrected for slope, aspect, and elevation.

^dList (1951), Table 171.

^eList (1951), Table 170.

as measured by an increase in size or quality. Little apparent effort has gone into developing means for increasing productivity by increasing the number of trees per unit area that can be grown to a given size, i.e., stockability. Most earlier and current literature suggests that stockability is relatively constant for a species; that is, the slope and intercept of the size–density relationship (or self-thinning line) that defines it do not differ by genotype within a species or over a wide range of environmental and management conditions (Reineke 1933; Daniel et al. 1979; Westoby 1984; Long 1985). Supposedly, genetic and cultural manipulations to improve growth affect the time required for the crop to attain some fixed limiting density asymptote or line but do not change its slope or intercept.

Recent studies in loblolly pine show that the notion of constant stockability for a species can be questioned. Data presented by DeBell et al. (1989) show that differences in stockability accounted for most of the twofold difference in basal area and volume production observed between plantation spacing trials in Hawaii and the southeastern United States. Significant differences in stockability also have been shown with site-index class (Strub and Bredenkamp 1985) and seed source (Buford 1989; Schmidting 1988). Perala and Cieszewski² report that stockability of aspen stands is affected by mean July air temperature. The stockability differences evident in these reports suggest that growth enhance-

ments need not be limited to improving individual tree growth during the early stages of stand development. Substantial gains in productivity may be achievable at the stand level if the nature and causes of stockability differences are better understood.

Our objectives in this research were to gain insight into stand and environmental components of stockability and to identify essential elements of high-stockability systems. Our approach was to compare the stand structure and crown architecture in loblolly pine spacing trials in Hawaii and South Carolina that exhibit marked differences in stockability. Stockability of these stands, expressed as the number of trees per hectare at a quadratic mean stand diameter of 25 cm, was 1740 for the Hawaii planting and 850 for the South Carolina planting. These values were estimated from the data using the stand model of Lloyd and Harms (1986). The effect of this difference in stockability on productivity was an approximate doubling of per-hectare volume yield at all spacings in Hawaii at age 25 years (DeBell et al. 1989).

Materials and methods

The plantations

The Hawaii spacing trial was established in 1961 in the Olinda Forest Reserve on the island of Maui on abandoned pasture land (Whitesell 1970, 1974). The site is situated at 1140 m above sea level on the leeward side of east Maui. The field layout consists of four square spacings (1.8, 2.4, 3.0, and 3.7 m) planted in a 4 × 4 Latin square design. Each plot is 0.11 ha in area, with the 25 trees in the center forming the measurement sample. All plots had two or more exterior isolation rows. Diameters of all sample trees were measured at plantation ages 4, 7, 11, 20, 25, and 26 years; heights of all sample trees were measured at ages 4, 7, 11, and 26 years, and on a nine-tree subsample at ages 20 and 25 years. Average site index is 24 m (base age 25 years).

The South Carolina trial was established in 1957 on the Calhoun Experimental Forest in the Piedmont near the town of Union (Balmer et al. 1975; Harms and Lloyd 1981). The site lies at 172 m above sea level. This study was planted on an abandoned cotton field in a randomized block design with four replications of the same four spacings employed in the Hawaii trial. Each plot is 0.24 ha in area, with 64 trees in the center forming the measurement sample. Each plot had two or more isolation rows. A subsample of trees was measured for height and diameter at ages 5, 7, and 11 years; all trees were measured at 15, 20, 25, and 30 years. Average site index is 21 m (base-age 25 years). Seed origin of the planting stock in both trials is unknown.

The environment

The prevailing climate at the study sites is summarized in Table 1. Seasonal variation in selected environmental factors is graphed in Fig. 1. The climatic differences between Hawaii and South Carolina are associated with the effects of latitude on the amount, duration, and intensity of solar radiation. Ten percent more radiation falls annually on the Hawaii plantation than on the South Carolina plantation. There is only a 2.5-h difference in daily photoperiod between the longest and shortest days in Hawaii versus a difference of 4.7 h in South Carolina. The daily noon sun angle during the growing season is 90° in Hawaii, but it is never more than 75° in South Carolina. Mean air temperature varies 3°C from summer to winter in Hawaii and is favorable for growth throughout the year; in South Carolina the variation is 21°C, and length of the growing season averages 220 days.

Annual precipitation in Hawaii is 8% less than in South Carolina, and the March–September period tends to be drier in Hawaii

²D.A. Perala and C.J. Cieszewski. Stockability, growth, and yield of the circumboreal aspens (*Populus tremuloides* Michx., *P. tremula* L.). Submitted for publication.

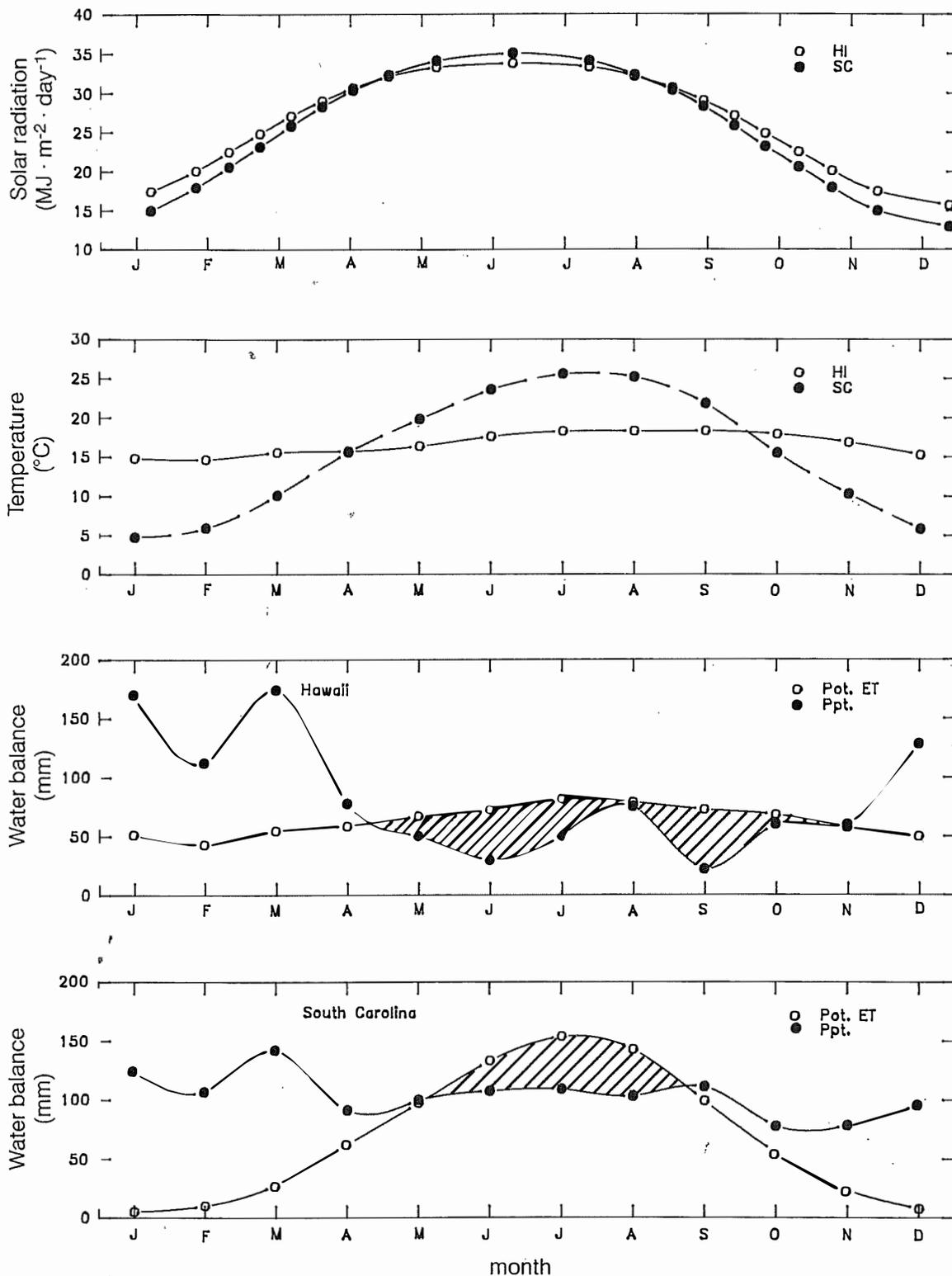


FIG. 1. Annual variation in potential radiation, mean air temperature, precipitation (Ppt.) and potential evapotranspiration (Pot. ET) in Hawaii (HI) and South Carolina (SC). Periods of potential water deficits are indicated by crosshatching. Potential evapotranspiration was calculated according to Thornthwaite and Mather (1957).

than in South Carolina. Both locations are subject to summer water deficits when the potential evapotranspiration exceeds rainfall. The period of water deficit begins earlier and lasts longer in Hawaii, where it extends from April into October, than in South Carolina, where it extends from June through August, but the deficit is relieved during August in Hawaii (Fig. 1). Although the period of water deficit is shorter in South Carolina, it may be

more severe there than in Hawaii because air temperatures are much higher (Fig. 1).

Soils

The soil on the Hawaii site is an Olinda loam in the subgroup Entic Dystrandepts. Typically the surface layer is a dark reddish-brown granular loam about 15 cm thick. The subsoil is a dark

reddish-brown and yellowish-red subangular blocky silty clay loam about 91 cm thick. This soil developed in volcanic ash over andesite or basalt. It is slightly acid (pH 6.0–6.2) in both the surface layer and subsoil (Foote et al. 1972; Whitesell 1974). Olinda soil is well drained, with a moderately rapid permeability.

The South Carolina soil is an Appling sandy loam (clayey, mixed, thermic, Aquic Hapludults). Typically the surface layer is a grayish brown sandy loam about 20 cm thick. The subsoil is a brownish yellow sandy clay loam grading to a light yellowish brown and light gray clay loam about 117 cm thick. The soil is strongly acid (pH 4.5–6.0 in the surface and 4.5–5.5 in the subsoil). It is moderately well drained, slowly permeable, and formed in residuum weathered from mixed acid and basic crystalline rocks (Camp et al. 1975).

Methods

The basic stand measure that defines stockability is the maximum number of trees per unit area that can be grown to a given size, independent of age. We assumed that the physical structure of stands and morphological characteristics of tree crowns of stands at or near the limiting density would provide a basis for evaluating tree and stand level features associated with high stockability. Self-thinning in these plantations had progressed sufficiently long in the 1.8-m spacing plots so that by age 25 distinct limiting size–density boundary lines had become evident (DeBell et al. 1989). With the exception of the 3.4-m spacing plots in Hawaii, all of the spacing plots at both sites had been actively self-thinning for 5 or more years.

To evaluate the overall performance of the plantations, we summarized the averages of the tree and stand variables for each of the four spacings at age 25. To evaluate stand structure, we first calculated size-class frequency distributions for diameter on 2-cm intervals and for height on 1-m intervals, using age-25 data from the South Carolina plots, and age-26 data from the Hawaii plots (a complete height sample was not measured at age 25). Tree heights were measured to the nearest 1 ft (1 ft = 0.305 m) with an Abney level; diameters were measured with a steel tape to the nearest 0.1 cm at breast height (DBH; at 1.37 m). We constructed frequency diagrams of height and diameter from these data after converting the height measurements to meters. We further defined stand structure as an arbitrary two-tiered canopy in which the 200 tallest trees per hectare were assigned to the dominant crown class and the remaining trees were placed in the subdominant crown class. The characteristics summarized for each of these stand fractions were trees per hectare, mean DBH, total height, height to the base of the green crown, and length of the green crown. Analysis of variance procedures were used to test differences between crown classes.

The growth rates of trees and stands depend on the trees' ability to produce and display photosynthetically active leaf surface (Kramer and Kozlowski 1979; Landsberg 1986), and the efficiency with which photosynthate is converted into cellulose and other components of tree biomass. For this study we chose to measure crown structure and leaf area as the most readily quantifiable attributes of photosynthetic capacity. In March 1987, when the Hawaii planting was 26 years old, 10 trees from the 2.4-m spacing were felled for analysis. To select the samples, the data were divided into ten diameter classes each having an equal number of trees. One sample tree was taken from the midpoint of each class. Two or three randomly selected trees were tagged in each of the four replicate plots of the spacing to make up the sample of 10; DBH of each was measured and marked, after which they were felled for analyses. In April 1988, the same procedures were followed on the South Carolina planting, which was then 31 years old. Spring shoot elongation had not yet begun at either location at the time of sampling.

The following field and laboratory procedures were used at both locations. The sample trees were cut at a stump height of 15 cm and measured for total height and height to the base of the live crown. The live crown was cut into thirds and further sec-

tioned into approximately 1-m lengths. A ring count was made at the base of the crown to determine its age.

In each third of the green crown the number of live branches was recorded and two of them were randomly selected for measurements. The sample branches were stripped of their needles and weighed to the nearest gram on spring or portable platform scales. The six sample branches were then cut into small pieces and bulked for the tree. A grab sample of about 400 g was bagged and placed on ice in a portable cooler for later oven drying at the laboratory. The needles stripped from the sample branches were weighed to the nearest gram and bulked for the crown. A grab sample of about 200 g was bagged and put on ice with the branch subsamples.

Samples of the previous year's shoot growth flushes were collected from the ends of branches in the upper crown section of each tree, placed in plastic bags, and put on ice for later measurement. An attempt was made to obtain two samples from each growth flush from each tree, but this was not always possible because breakage and scattering of the branches when the trees were felled sometimes made it difficult to identify flush age of the shoots. Needle samples also were obtained for subsequent nutrient analyses. These samples consisted of fully expanded fascicles from the initial flush on the past growing season. They were collected from all sides of the upper crown and placed in precooled plastic bags and put on ice. The coolers containing the stem, crown, and needle subsamples were transported to the laboratory for analysis.

The branch and foliage subsamples were reweighed in the laboratory and oven-dried to a constant weight at 100°C. Dry weight to green weight factors were calculated for each component of each tree and used to estimate branch and foliage dry weights for each third of the crown from the weights previously taken in the field.

A subsample of 25 green fascicles was removed from the bulked crown foliage samples for needle area measurements. The projected area of each needle was determined with an optical area measuring device (LI-COR Inc., Lincoln, NE 68504). The needles were then oven-dried. Area to weight factors were calculated from the 25 fascicles and used to estimate total crown needle area of each tree from crown foliage dry weight estimates. The fascicle data were further analyzed and summarized to produce estimates of per-fascicle dry weight and specific leaf area (leaf area per unit dry weight) for each location.

The grown flush samples were measured to determine length of the green (needle-bearing) portion of the shoot of each flush, the number of fascicles for each flush, and the average fascicle length for each flush. The measurements were averaged and tabulated by tree for each location.

Needle samples collected for nutrient analyses were oven-dried to constant weight at 65°C, ground to 40 mesh in a Wiley mill, and stored at –15°C until analyzed. Subsamples were used for chemical assays as follows: N by a modified micro-Kjeldahl procedure (Nelson and Sommers 1973); P by the molybdovanadate procedure (Jackson 1958); and metals by atomic absorption (Perkin-Elmer Corp. 1976). Foliar nutrients were calculated as a proportion of dry foliage weight (percentage or ppm).

The crown weight data were summarized by position in the crown and total crown to give average number of branches, branch and foliage dry weight, and leaf area for each location. The maximum age of the live crown of each tree was assumed to be equal to the number of annual rings observed at the base of the crown.

Results and discussion

Stand characteristics and productivity

The primary tree and stand level attributes of the spacing trials at age 25 years are summarized in Table 2. The increase in survival percentage and tree size with increase in spacing, and the increase in basal area and volume yield

TABLE 2. Tree and stand characteristics of 25-year-old loblolly pine trials planted in Hawaii (HI) and South Carolina (SC)

	Spacing (m × m)							
	1.8×1.8		2.4×2.4		3.0×3.0		3.7×3.7	
	HI	SC	HI	SC	HI	SC	HI	SC
Trees per hectare								
Planted	2990	2990	1683	1683	1077	1077	746	746
Surviving	2063	1611	1463	1235	1003	936	739	628
Percent	69	54	87	74	93	87	99	84
Mean DBH (cm)	24.1	17.8	27.2	20.6	30.5	23.4	34.3	27.2
Mean height (m)	19.8	18.1	19.9	19.3	20.5	19.4	21.7	19.8
Basal area (m ² /ha)	94.4	41.8	84.9	43.1	73.2	41.1	68.2	37.0
Volume (m ³ /ha)	677	279	604	297	534	289	526	262

NOTE: Each value is the average of four replicate plot means. The plantings were established and measured using Imperial units; the values shown are approximate metric equivalents.

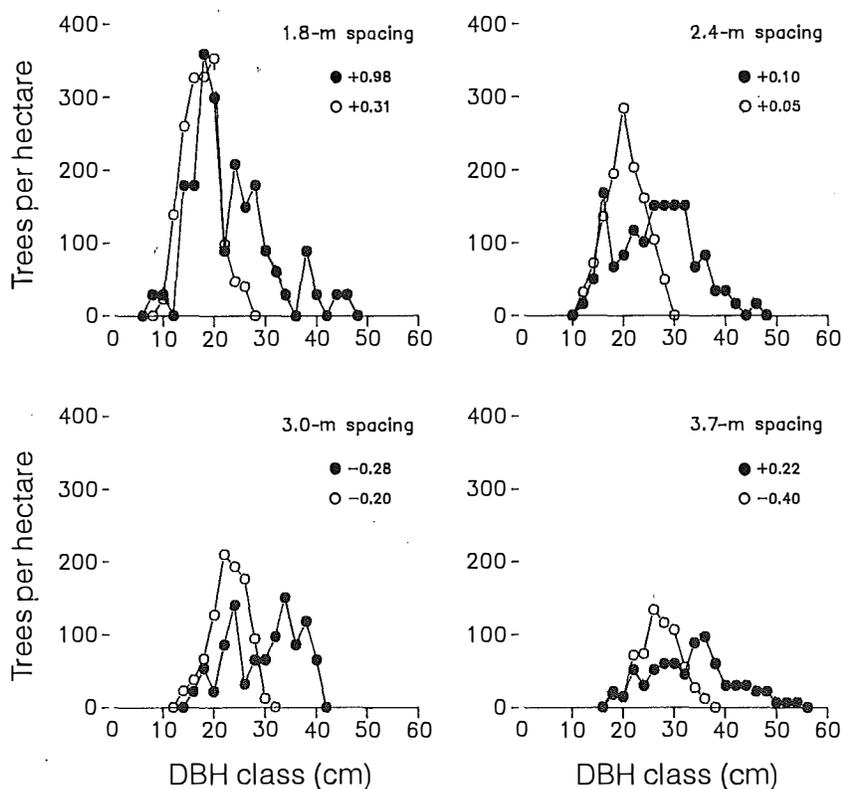


FIG. 2. Diameter-class frequency distributions and coefficients of skewness in loblolly pine spacing trials in Hawaii (age 26, ●), and South Carolina (age 25, ○).

with decrease in spacing reflect the often observed and well-documented influence of growing space on growth (Sjolte-Jorgensen 1967).

The 3-m difference in site index between locations accounts for some of the differences in growth and productivity shown in Table 2, but data from published yield tables indicate that the effect of the difference is relatively small: yield table calculations for planted stands in the southeastern United States with an initial spacing of 2.4 × 2.4 m show that at 25 years the volume yield of a site index 24 stand is 22% greater than yield of a site index 21 stand (Hafley et al. 1982). The data in Table 2 for the 2.4 × 2.4 m spacing show that the yield in Hawaii was 103% greater than

the South Carolina yield. Averaged over all four spacings the volume-yield difference was 108%. Another indication that site index was not a major factor is that the effect on stand density normally associated with site-index differences is absent. Number of trees per unit area in fully stocked stands of the same age tends to be less on high sites than on low sites because of more rapid stand development (Smith 1962), but 6–15% more trees survived in the higher site index Hawaii plantings than in the lower site index South Carolina plantings at the same initial spacings.

The data in Table 2 also illustrate the size–density relationship that distinguishes the high-stockability stands in Hawaii from the low-stockability stands in South Carolina.

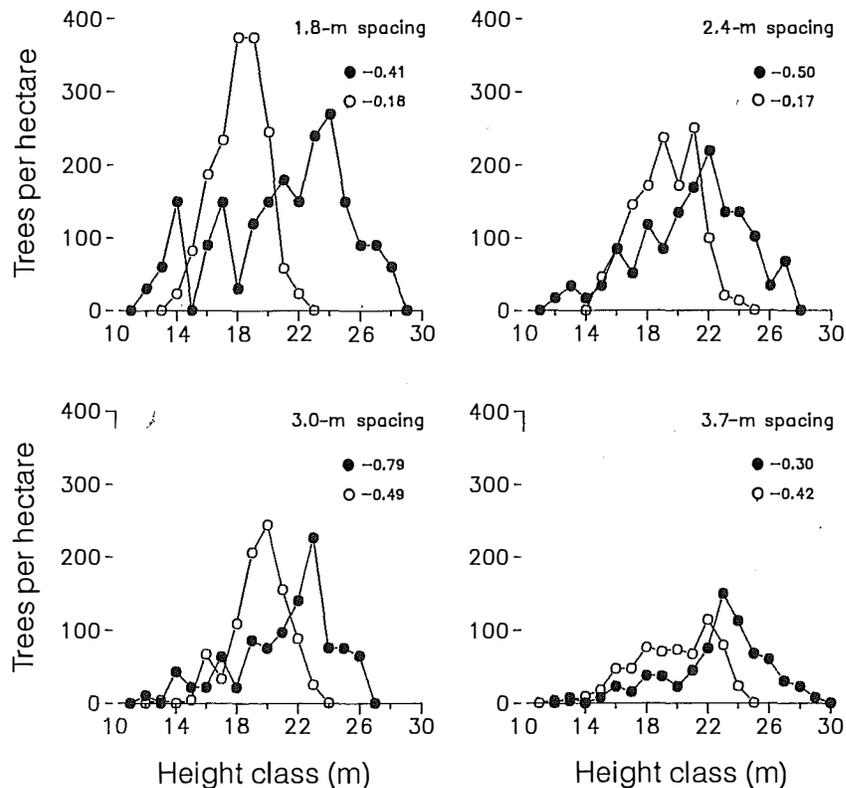


FIG. 3. Height-class frequency distributions and coefficients of skewness in loblolly pine spacing trials in Hawaii (age 26, ●), and South Carolina (age 25, ○).

For any of the spacings, the surviving number of trees and the average mean stand diameter are always greater in Hawaii than in South Carolina.

Stand structure

The diameter and height relationships within and between stands were evaluated by examining the size-class frequency distributions (Figs. 2 and 3). Both diameter and height distributions are asymmetrical. In the case of diameter, five of the eight distributions tended to be positively skewed, tailing off to the right as is typical of well-developed, even-aged stands (Assmann 1970). Distributions for the 3.0-m spacing plots at both locations and the 3.7-m spacing plots in South Carolina were negatively skewed (Fig. 2). Each of the South Carolina diameter distributions had a single peak. The Hawaii distributions were quite variable, but most of them were bimodal. There was a large difference in the spread of the size classes between locations. For the same spacings, there were from 6 to 11 more 2-cm diameter classes in Hawaii than in South Carolina. However, within a location, all spacings tended to have the same number of classes. In Hawaii there were 18–20 classes at each spacing except the 3.0-m spacing, which had only 13 (possibly an artifact of the 25-tree plot size). There were 9 or 10 classes at each spacing at the South Carolina site. The smallest diameter class tended to be the same at both locations for any one spacing, and the Hawaii plots did not retain any more smaller trees than the South Carolina plots retained. Rather, the Hawaii plots grew more larger trees (Fig. 2).

All of the height-class distributions were negatively skewed, tailing off to shorter trees to the left, also a characteristic of even-aged stands (Assmann 1970) (Fig. 3). However, at all spacings the distributions peaked one or more classes

higher in Hawaii than in South Carolina, and the number of classes was greater in Hawaii at both extremes.

Stand structure expressed in terms of the 200 tallest trees per hectare versus the remainder of the stand provided additional insight into stand differences between locations. Table 3 summarizes mean values for stand parameters by crown-class fraction and spacing for Hawaii and South Carolina. Because more trees survived in Hawaii across all spacings, the Hawaii plots had more trees in the subdominant crown-class fraction than did the South Carolina plots. On a percentage basis both locations had similar proportions of trees in the same stand fraction, with South Carolina plots having a few percent more trees in the dominant stands and a few percent less in the subdominant stands than had the Hawaii plots. The proportion in the dominant stand fraction progressively increased a few points with increasing spacing at both locations.

Variance analyses of the data for the total stand indicate that tree spacing significantly affected DBH and green crown length at both locations, but not total tree height or height to the base of the green crown (Table 3). The significant effect of spacing on crown length is difficult to reconcile with the nonsignificant effect on height; possibly it is an artifact of the data. Differences among means in Table 3 were compared using Duncan's new multiple-range test (Steel and Torrie 1960). Variance analyses of the stand fractions indicate the mean values of each of the stand parameters were significantly larger in the dominant than in the subdominant stand fraction across all spacings at both locations, except for the height to the base of the green crown in South Carolina. In South Carolina the base of the subdominant canopy was located an average of 0.7 m below the base of the dominant canopy, a nonsignificant difference. In Hawaii,

TABLE 3. Stand structure of loblolly pine stands planted at different spacings in Hawaii and South Carolina

	Stand fraction	Spacing (m×m)			
		1.8×1.8	2.4×2.4	3.0×3.0	3.7×3.7
Hawaii					
Trees/ha (%)	Dominant	200 (10)	200 (14)	200 (20)	200 (27)
	Subdominant	1804 (90)	1231 (86)	803 (80)	531 (73)
	Total	2004 (100)	1431 (100)	1003 (100)	731 (100)
Mean DBH (cm)	Dominant	36.8 ^{ab}	34.3 ^b	36.6 ^{ab}	41.4 ^a
	Subdominant	21.8 ^e	25.6 ^{cde}	28.6 ^{cd}	31.1 ^c
	Total	23.3	26.8	30.5	33.9
Total height (m)	Dominant	25.6 ^a	24.6 ^a	24.6 ^a	25.8 ^a
	Subdominant	20.5 ^b	20.4 ^b	20.6 ^b	21.8 ^b
	Total	21.0 ^x	21.0 ^x	21.4 ^x	22.9 ^x
Height to base of green crown (m)	Dominant	16.6 ^a	14.5 ^a	15.6 ^a	15.9 ^a
	Subdominant	14.8 ^b	13.1 ^b	14.0 ^b	14.1 ^b
	Total	15.0 ^x	13.3 ^x	14.3 ^x	14.6 ^x
Green crown length (m)	Dominant	9.0 ^a	10.1 ^a	9.0 ^a	9.9 ^a
	Subdominant	5.6 ^d	7.3 ^{bc}	6.6 ^{bcd}	7.4 ^{bc}
	Total	6.0 ^x	7.7 ^{yz}	7.1 ^z	8.3 ^y
South Carolina					
Trees/ha (%)	Dominant	200 (12)	200 (16)	200 (21)	200 (32)
	Subdominant	1411 (88)	1035 (84)	736 (79)	428 (68)
	Total	1611 (100)	1235 (100)	936 (100)	628 (100)
Mean DBH (cm)	Dominant	21.4 ^c	24.2 ^{bc}	26.0 ^b	29.5 ^a
	Subdominant	17.4 ^e	20.1 ^{de}	22.6 ^d	25.9 ^b
	Total	17.8	20.6	23.4	27.2
Total height (m)	Dominant	20.3 ^a	21.2 ^a	21.2 ^a	21.4 ^a
	Subdominant	17.9 ^b	19.0 ^b	18.9 ^b	19.0 ^b
	Total	18.1 ^x	19.3 ^x	19.4 ^x	19.8 ^x
Height to base of green crown (m)	Dominant	15.5 ^a	17.3 ^a	17.3 ^a	14.8 ^a
	Subdominant	15.4 ^a	16.6 ^a	16.1 ^a	14.1 ^a
	Total	15.4 ^x	16.7 ^x	16.4 ^x	14.3 ^x
Green crown length (m)	Dominant	4.8 ^{ab}	3.9 ^b	3.9 ^b	6.6 ^a
	Subdominant	2.5 ^d	2.4 ^d	2.8 ^d	4.9 ^c
	Total	2.8 ^x	2.7 ^x	3.0 ^x	5.5 ^y

NOTE: Each value is the average of four replicate plot means. Values are from the Hawaii planting at age 26 and from the South Carolina planting at age 25. The values for the Hawaii data differ from Table 2 because the 1-year difference in age. Means within a parameter not followed by the same letter (a-e) are significantly different ($P = 0.05$); total stand was tested by separate ANOVA; values not followed by the same letter (x, y, z) are significantly different ($P = 0.05$).

however, the difference was significant, the base of the crowns of the subdominant canopy extending 1.5–1.8 m below the base of the dominant canopy (Table 3). In Hawaii the trees in the subdominant stands were 4–6 m shorter than the dominant trees; in South Carolina the subdominant trees were only 2.2–2.4 m shorter. It is evident from these data that a distinct two-tiered canopy had developed at both locations. In Hawaii, however, the lower layer extended from below the dominant canopy base up into the dominant canopy, while in South Carolina, the crown bases of both crown classes were within a meter of being at the same level.

Crown structure

In the plots in Hawaii, the pine foliage appeared thick and dark. Little sunlight reached the forest floor, and there was almost no understory vegetation. In the South Carolina plots, pine crowns appeared thin and the foliage sparse; sunlight filtered through and there was a woody understory of numerous sweetgum stems (*Liquidambar styraciflua* L.).

TABLE 4. Characteristics of loblolly pine trees sampled across diameter classes in 2.4-m spacing plots in Hawaii (HI, age 26 years) and South Carolina (SC, age 31 years)

	Plantation	Mean	Range
Total height (m)	HI	21.9	16.4–25.0
	SC	21.3	18.7–23.0
Height to crown (m)	HI	13.1	9.5–16.4
	SC	15.4	12.4–18.0
Live crown length (m)	HI	8.8	7.0–11.6
	SC	5.9	3.7–7.0
Crown ratio	HI	0.41	0.33–0.53
	SC	0.28	0.18–0.33
Crown age (years)	HI	13.8	11–17
	SC	13.5	8–17
Stem diameter (cm)	HI	28.6	14.5–44.5
	SC	22.0	16.8–28.7
Stem volume inside bark (m ³)	HI	0.69	0.09–1.72
	SC	0.34	0.15–0.56

TABLE 5. Tree crown parameters for loblolly pine trees sampled across diameter classes in 2.4-m spacing plots in Hawaii (HI) and South Carolina (SC)

	Plantation	Lower crown		Middle crown		Upper crown		Total crown	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Number of branches	HI	12.5	5-24	19.7	11-30	21.0	8-33	53.2	27-79
	SC	6.9	3-12	10.8	5-17	13.5	7-18	31.2	23-40
Weight of branches (kg)	HI	15.1	0.8-63.6	14.7	1.3-33.8	5.4	0.4-12.2	35.2	3.3-105.3
	SC	5.6	0.7-16.5	5.4	1.2-14.9	2.1	0.1-4.4	13.1	2.2-30.3
Weight of foliage (kg)	HI	3.9	0.1-19.6	6.0	0.4-13.4	5.0	0.3-8.8	15.3	0.8-40.3
	SC	1.5	0.3-5.0	2.5	0.6-4.3	1.8	0.2-2.9	5.7	1.1-10.9
Leaf area (m ²)	HI	16.4	0.2-82.0	25.2	1.5-56.1	21.1	1.3-36.8	63.9	0.4-168.4
	SC	3.3	0.6-11.0	5.4	1.2-9.5	4.0	0.4-6.4	12.7	2.5-24.2

TABLE 6. Shoot growth - flush characteristics of loblolly pine trees sampled in Hawaii (HI) and South Carolina (SC)

	Plantation	n	Mean	Range	
Number of flushes	HI	10	3.0	2-4	
	SC	9	2.1	1-4	
Green shoot length (cm)					
	First flush	HI	5	7.3	5.5-9.3
	SC	9	17.7	10.5-23.5	
	Second flush	HI	10	8.8	2.2-13.0
	SC	8	6.4	2.7-13.5	
	Third flush	HI	8	8.9	3.8-12.5
	SC	1	5.2	—	
Fascicle length (cm)					
	First flush	HI	5	21.9	20.0-25.0
	SC	9	15.4	12.7-18.0	
	Second flush	HI	10	19.5	15.0-22.5
	SC	8	12.0	8.5-16.2	
	Third flush	HI	8	15.6	10.5-19.0
	SC	1	15.0	—	
Internode length (mm) ^a					
	First flush	HI	5	1.4	1.1-1.9
	SC	9	1.7	1.2-2.3	
	Second flush	HI	10	1.8	0.8-2.4
	SC	8	1.1	0.8-1.4	
	Third flush	HI	8	1.5	0.9-1.8
	SC	1	1.3	—	

^aDistance between adjacent fascicles.

Light levels in the stands were not measured, but these observations are well supported by the data from the sample trees (Tables 4 and 5). Average height of the sample trees at both locations was about the same, though the range was greater in Hawaii than in South Carolina. The Hawaii trees were 5 years younger than the South Carolina trees but averaged 6.5 cm larger in diameter and had twice the volume of the South Carolina trees. The crowns of the South Carolina sample trees were shorter than those of the Hawaii trees and had pruned to greater heights from the ground. The South Carolina trees also had the smaller ratio of crown length to total tree height (Table 4). Although the 5-year difference in age may account for some of these differences, the average crown ratio for the South Carolina planting as a whole, had already reduced to only 29% when measured at age 20 (Harms and Lloyd 1981). Age of the oldest living branches, based on the number of rings in the stem at the base of the live crown, averaged about 14 years at each

location, so the overall structure of the crowns spanned the same age range. We have therefore assumed that the 5-year difference in tree age is not a significant factor in interpretation of the crown data.

The Hawaii sample trees had more live branches, foliage, and leaf area in total, as well as within the separate portions of the crowns (Table 5). Per branch, the Hawaii trees supported an average of 287 g of needles with an area of 1.2 m². The corresponding values for the South Carolina trees are 184 g and 0.40 m². In both locations, branches in the middle third of the crowns carried the most foliage: 39% of the total for the trees in Hawaii and 44% of the total for the South Carolina trees. The upper crowns carried 33 and 32% of the foliage in Hawaii and South Carolina, respectively, and the shaded lower third carried 25 and 26% of the foliage in Hawaii and South Carolina, respectively. The Hawaii trees had 68% as much foliage in the lower crown as the South Carolina trees carried in the entire crown. The vertical distribution of foliage in the crowns of these trees was characteristic of the pattern reported for loblolly pine (Kinerson et al. 1974; Vose 1988) and does not appear to have been influenced by location. Branching is also similar in the two locations: the Hawaii trees had 6.1 branches per unit of crown length and the South Carolina trees had 5.3. Per unit of crown length, the Hawaii trees carried an average of 1.74 kg/m of foliage and the South Carolina trees 0.97 kg/m.

Shoot and needle characteristics

The annual shoot growth cycle of loblolly pine begins in late February or early March when temperatures becomes favorable and continues into September or October (Wahlenberg 1960). Lanner (1966) observed this growth pattern in the trees of the Hawaii plantation when they were 3 years old. Most needles produced in one growing season are retained until near the end of the second, but a few are often retained until early in the third (Wahlenberg 1960). The sample trees at both locations had only a scattering of 2-year-old needles, so no attempt was made to distinguish age when the samples were collected.

The flush data for the sample trees are summarized in Table 6. The Hawaii pines produced an average of 3 flushes: two trees produced 2, and one tree produced 4. The South Carolina pines produced an average of 2.1 flushes. One tree produced 1 and another 4. Average green lengths of the three flushes on the Hawaii pines ranged from 7.3 to 8.9 cm. On the South Carolina trees, the length of the foliated portion of the first flush averaged almost 18 cm, but the second

TABLE 7. Needle characteristics of loblolly pine trees sampled in Hawaii (HI) and South Carolina (SC)

	Plantation	Mean	Range
Fascicle dry weight (g)	HI	0.13	0.08–0.18
	SC	0.14	0.12–0.17
Fascicle area (cm ²)	HI	5.3	3.88–6.36
	SC	3.0	2.13–3.74
Specific leaf area (cm ² /g)	HI	40.9	33.61–54.40
	SC	21.7	17.43–26.91

NOTE: Values are averages of 25 fascicles per tree.

flush averaged only 6.4 cm in length. The single third-flush sample was 5.2 cm long. These lengths do not represent current height growth since the shoots were collected from branches of the upper crown and only the green, foliated length was measured.

Loblolly pine shoot growth is sensitive to environmental conditions, and it is likely that the year-round uniformly warm temperatures and relatively constant day length in Hawaii (Fig. 1) favor continuous production of photosynthate and production of uniform shoot flushes. In the South Carolina Piedmont, the rate of photosynthesis is much reduced in winter during periods of freezing temperatures, and the length of the spring flush depends primarily on environmental conditions at the time of bud formation and the amount of reserve carbohydrates produced in the previous growing season (Kramer and Kozlowski 1979). Subsequent flushes depend on current photosynthate production and tend to be progressively shorter as the growing season advances.

Needle fascicles on the first two flushes were between 6 and 7 cm longer on the Hawaii pines than on the South Carolina pines (Table 6). At both locations needle length was greatest for the first flush and tended to decrease for succeeding flushes. Internode length (distance between adjacent fascicles) was somewhat variable but similar among flushes and between locations, ranging on average from 1.1 to 1.8 mm (Table 6).

Needle characteristics of the 25-fascicle sample taken from each tree are summarized in Table 7. Average dry weight per fascicle did not differ appreciably by location and fell within the range of values reported by Shelton and Switzer (1984) for loblolly pine. Fascicle area and specific leaf area, however, did vary by location. For the same dry weight, the projected area of fascicles from the Hawaii pines was 1.8 times greater than the area of fascicles from the South Carolina pines, chiefly because the needles of the Hawaii pines were longer than those of the South Carolina pines. The specific leaf area of the fascicles from the South Carolina trees was about half that reported in the literature, but that of the Hawaii fascicles was comparable (Dalla-Tea and Jokela 1991; Vose and Allen 1988; Shelton and Switzer 1984). The statistical significance of the differences between needle characteristics at the two locations could not be tested, nor were data collected to evaluate within-crown variation. However, the maximum and minimum values for leaf area, and for specific leaf area, did not overlap between locations, which suggests that observed differences in the area-related characteristics were real. The sensitivity of shoot and needle growth to past and current environment precludes a more detailed analysis of the differences observed from this single sample.

TABLE 8. Foliar chemical concentrations in needles of loblolly pine trees sampled across diameter classes in the 2.4-m spacing plots in Hawaii and South Carolina

	Hawaii		South Carolina	
	Mean	Range	Mean	Range
Macronutrients (%)				
Nitrogen	1.73	1.47–1.97	1.06	0.89–1.19
Phosphorus	0.14	0.11–0.18	0.10	0.09–0.12
Potassium	0.38	0.34–0.42	0.39	0.32–0.53
Calcium	0.42	0.22–0.60	0.18	0.10–0.24
Magnesium	0.18	0.10–0.23	0.06	0.03–0.08
Micronutrients (ppm)				
Sodium	41.5	220–604	17	12–25
Copper	1.4	0.5–2.5	2.3	2.0–3.4
Zinc	22	11–30	22	19–28
Manganese	179	102–211	361	254–450

Means and ranges for eight nutrients and Na in needles of the 10 sample trees from the 2.4-m plots at each location are shown in Table 8. Concentrations of N, P, Ca, Mg, and Na were substantially higher in needles from the Hawaii site; K, Cu, and Zn levels were similar for the two locations; and Mn concentrations were more than twice as high in needles from the South Carolina site. Nitrogen and P levels are approximately 70 and 40% higher, respectively, in Hawaii foliage, and presumably are a factor in the dark coloration of the foliage in Hawaii. The mean concentrations of N in Hawaii are higher than any we have seen reported for loblolly pine past the sapling stage in the United States and are much higher than the generally agreed upon critical level of 1.10% (Allen 1987). Phosphorus levels in Hawaii were also substantially higher than the critical level of 0.10% for loblolly pine (Allen 1987). Similarly, levels of Ca and Mg in Hawaii averaged two and three times higher, respectively, than levels of these nutrients in the South Carolina stand. Critical levels for these nutrients are 0.12 and 0.07% respectively (Allen 1987). The similarity between K levels in the foliage at both locations may be due to the fact that this element is readily leached and thus does not accumulate. The higher Mn levels in South Carolina are probably related to the higher acidity of the South Carolina soils. Also, Mn levels tend to be negatively correlated with N levels. The high Na levels (415 ppm) in Hawaii probably reflect the insular environment, in which periodic deposition of Na is associated with frequent storms.

It appears from these data that the trees in Hawaii, despite their very rapid growth, are under little or no nutrient stress. However, nutrients may be growth limiting in South Carolina; N and Mg were slightly below critical levels there, and other macronutrients were at or a little above critical levels (Table 8).

Nitrogen and Mg are important constituents of chlorophyll (Kramer and Kozlowski 1979). Although we did not measure chlorophyll concentrations, numerous studies have demonstrated a strong positive correlation between N and chlorophyll levels. Thus, assuming higher chlorophyll levels with higher N concentrations, the actual photosynthesis factory in Hawaii is likely to be even larger than indicated by leaf weight alone. Presumably, foliage of the Hawaii trees contains much more chlorophyll than does foliage of the South Carolina trees. Also, the Hawaii trees, with their

higher specific leaf area, would display their chlorophyll more effectively than would the South Carolina trees.

Environmental relations

The environmental conditions in Hawaii evidently favored the development of large, deep, highly productive crowns that were able to maintain growth of the trees in densely stocked stands. In South Carolina, the trees had smaller crowns, the canopies were sparse, and the nutrient-poor site supported fewer trees. While genotypic differences may be involved, the differences in quantity and quality of the crowns and foliage do not appear to be the result of altered crown architecture. Crown age, number of branches produced per unit of crown length, number of annual growth flushes, and distribution and age of foliage retained are all typical of loblolly pine crown architecture and were similar at the two locations.

In Hawaii, high sun angles and greater solar radiation intensity result in deep penetration of light into the canopy and help promote the development of large, heavily foliated crowns (Janke and Lawrence 1965). The light climate in South Carolina is quantitatively and qualitatively less favorable for crown growth. It is well documented that leaf structure and photosynthetic capacity are sensitive to the light environment (Kramer and Kozlowski 1979; Kozlowski et al. 1991), and thus we assume that the needle and crown differences that were measured result at least in part from developmental responses to the light regimes within the canopies at each location.

Air temperature is also an important factor. Like other conifers, loblolly pine will photosynthesize whenever air and soil temperature and soil moisture are suitable (Kramer and Kozlowski 1979); photosynthesis probably takes place year-round in Hawaii. Although there is no true cold dormancy in Hawaii, the formation of latewood and annual cessation of shoot growth indicate that the trees experience annual rest periods. Local weather conditions are consistent with the occurrence of such rest periods: at the elevation and aspect of these plots there are, typically, diurnal temperature differences of 8–10°C, with minimum temperatures as low as 5°C and maximums of 23°C during the months of December to February. The dormant period may also be initiated by the reduced photoperiod in the fall and winter months (Fig. 1) (Zahner 1968).

A significant temperature effect on stockability was reported by Perala and Cieszewski (see note No. 2) in a wide ranging analysis of stockability of aspen (*Populus tremuloides* Michx. and *Populus tremula* L.) stands. They found that for each 10% increase in mean July temperature, stockability of aspen was reduced by 5%. In our data, the increase in mean July temperature (Table 1) from 18°C in Hawaii to 26°C in South Carolina was associated with a 51% decrease in stockability, an 11.6% reduction per 10% increase in temperature.

Site-specific differences below ground also influenced the growth and development of these stands. There were differences in available soil volume, water-holding capacity, and, by inference from needle tissue nutrient concentrations, available soil nutrients. We did not measure soil properties, but the published soil descriptions indicate that soil moisture conditions were more favorable in Hawaii than in South Carolina. A representative profile of the Olinda soil series has an available water capacity of about 5 cm in the surface 30 cm, and the Appling series has an available water capac-

ity of about 3.6 cm in the surface 30 cm. This suggests that the Hawaii soils could support a larger transpiring surface, i.e., larger crowns, than the drier South Carolina soils.

A factor that could not be studied but one that can substantially influence growth is the genetic makeup of the trees at the two locations. Another factor important to growth is the presence of disease and insect pests. None were observed in Hawaii, and their absence could have had a positive impact on productivity of the plantations. The only observed pest in South Carolina was fusiform rust (*Cronartium quercuum* f.sp. *fusiforme*) cankers on 6% of the stems.

Conclusions

This study of the stockability of loblolly pine stands in Hawaii and South Carolina has shown that there are specific differences in stand structure and crown architecture associated with the observed differences in stockability. Furthermore, these differences are seen to be a function of the effects of the environment on tree growth and development. A distinguishing feature of the high stockability Hawaii stands was a two-tiered crown-class structure with a subdominant stand having green crowns extending up into the main canopy from below the base of the canopy of the dominant stand, thereby increasing occupancy of the canopy space with functioning crowns. The trees in Hawaii were characterized by long crowns with high foliage biomass and leaf area that had developed in association with high solar radiation intensities and high sun angles that allow light penetration deep into the canopy. Growth was further enhanced by the favorable temperature regime and soil moisture conditions. In this environment, trees in the subdominant position were able to maintain a positive carbon balance sufficient for survival and growth. In South Carolina, site and environmental conditions did not favor development of deep crowns. Annual solar radiation in South Carolina is only 10% less than in Hawaii, but the angle of the sun is lower and less light penetrates into the canopy. The growing season is shorter, soil moisture can be limiting in the summer, and summer temperatures are much higher, favoring high transpiration and respiration rates. These conditions limit crown development by reducing net photosynthesis in the poorly lit lower parts of the crowns. Trees in the lower crown classes that could not maintain a positive carbon balance would soon be eliminated from the stand. Although crown characteristics and the amount of foliage produced in Hawaii and South Carolina differed substantially, the basic architecture of the crowns was the same in both locations.

These observations are based on only two examples of stands with markedly different stockabilities. On other sites different stand and tree characteristics and other environmental factors may be important or limiting influences on stockability. Genetic characteristics are also certainly of fundamental importance. However, it seems apparent that as a minimum requirement to achieve high stockability, trees must have photosynthetically efficient crowns that maintain positive growth in densely stocked stands regardless of their canopy position, i.e., in low- as well as high-light conditions, and also must have efficient root systems able to compete for water and nutrients.

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