Maximum growth potential in loblolly pine: results from a 47-year-old spacing study in Hawaii

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Abstract: Growth, allocation to woody root biomass, wood properties, leaf physiology, and shoot morphology were examined in a 47-year-old loblolly pine (*Pinus taeda* L.) density trial located in Maui, Hawaii, to determine if stands continued to carry the high density, basal area, and volume reported at younger ages and to identify potential factors controlling expression of maximum growth potential. Basal area and volume were similar among spacings (square: 1.8, 2.4, 3.0, and 3.7 m) and averaged 93 $m^2 \cdot ha^{-1}$ and 1076 $m^3 \cdot ha^{-1}$, respectively, and were double the maxima reported for loblolly pine in its native range. Spacing had a significant influence on density, quadratic mean diameter, and height. Ring-specific gravity and percent latewood were similar among spacing treatments but values were high compared to mainland stands. Leaf light-saturated net photosynthesis, dark respiration, stomatal conductance, and quantum yield were comparable with values reported for loblolly pine in its native range. Foliar calcium concentrations, specific leaf area, and flush number were high in the Hawaii study. Higher carrying capacity in Hawaii may be related to a more favorable climate conducive to year-round leaf carbon gain, high nutrient availability, increased flushing, and less allocation to belowground mass.

Résumé : Nous avons étudié la croissance, l'allocation des ressources à la biomasse racinaire ligneuse, les propriétés du bois, la physiologie foliaire et la morphologie des pousses dans un peuplement de pin à encens (*Pinus taeda* L.) âgé de 47 ans situé à Maui, à Hawaii, et qui faisait partie d'une expérience de densité variable. Le but de l'étude était de déterminer si les peuplements continuaient de soutenir les valeurs élevées de densité, de surface terrière et de volume observées en jeune âge et d'identifier les facteurs qui pourraient être associés à l'expression de la croissance potentielle maximale. La surface terrière et le volume n'ont pas varié selon l'espacement (espacements carrés de 1,8, 2,4, 3,0 et 3,7 m) et ont respectivement atteint 93 m^2 ha^{-1} et 1076 $m^3 \cdot ha^{-1}$, en moyenne, ce qui correspond au double des valeurs maximales observées dans l'habitat naturel du pin à encens. L'espacement a eu un effet significatif sur la densité, le diamètre moyen quadratique et la hauteur des arbres. La densité du bois et le pourcentage de bois final étaient semblables parmi les traitements d'espacement, mais leurs valeurs étaient élevées comparativement aux peuplements continentaux. La photosynthèse foliaire nette sous une lumière saturante, la respiration à l'obscurité, la conductance stomatique et le rendement quantique avaient des valeurs semblables à celles qui ont été rapportées pour le pin à encens dans son habitat naturel. La concentration foliaire en calcium, la surface foliaire spécifique et le nombre de pousses étaient élevés dans l'étude hawaiienne. La plus forte capacité de support du milieu à Hawaii peut être reliée à un climat plus favorable qui est propice à un gain foliaire en carbone à longueur d'année, à une disponibilité élevée en nutriments, à une augmentation du nombre de pousses et à une plus faible allocation des ressources à la biomasse souterraine.

[Traduit par la Rédaction]

Introduction

Production rates of loblolly pine (*Pinus taeda* L.) in Hawaii, Brazil, Argentina, and South Africa indicate that full biological expression of growth potential in loblolly pine has not yet been attained in its native range in the southern United States (Jokela et al. 2004). Growth rates as high as 39 $m^3 \cdot ha^{-1} \cdot year^{-1}$ have been reported for second-rotation loblolly pine plantations in Brazil and Argentina, which is three times the volume increment of similar stands in the United States (Schultz 1999). In its native range, growth efficiency of loblolly pine usually declines and mortality increases once basal area surpasses a threshold of approximately 35 $m^2 \cdot ha^{-1}$ even with increased nutrient and water availability (Will et al. 2001; Albaugh et al. 2006). Maximum carrying capacity for closed-canopy loblolly pine stands in the southern United States is between 45 and 50 $m^2 \cdot ha^{-1}$ (Jokela et al. 2004). In contrast, basal area in a loblolly pine spacing study in Hawaii was 103 $m^2 \cdot ha^{-1}$ at age 34 (Harms et al. 2000). The most intensive management practices (weed control, irrigation, fertilization, and pest control) demonstrate that loblolly pine grown in the southern

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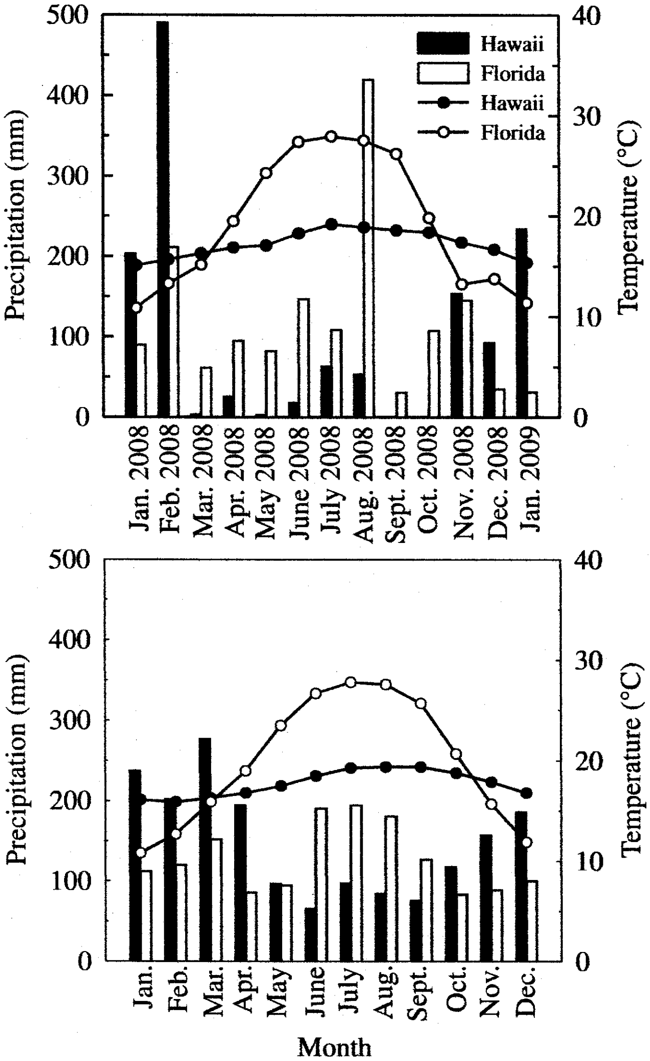
Fig. 1. Average 24 h temperature (lines) and precipitation (bars) by month recorded in Maui, Hawaii, and Tallahassee, Florida, during the year of the study and the 30-year averages.



United States can produce the high yields observed on favorable exotic locations, but only when stands are below maximum carrying capacity (Borders et al. 2004; Samuelson et al. 2004, 2008). In addition, it is unclear if greater productivity in exotic environments influences wood quality. Skolmen (1963) measured an average specific gravity (SG) of 0.42 for Hawaii-grown loblolly pine and concluded that because SG was lower than the 0.48 reported for loblolly pine in the southern United States (Mitchell and Wheeler 1959), wood of loblolly pine grown outside its native range may be structurally inferior.

Potential sources of greater carrying capacity in loblolly pine planted outside its natural range have been proposed but mechanisms remain unclear. Tripling of productivity on a 20-year rotation by loblolly pine planted in Brazil was attributed to a longer growing season, deeper and nutrient-rich soils, and lack of pathogens (Wallinger 2002). DeBell et al. (1989) attributed high basal area in a loblolly pine spacing study located in Maui, Hawaii (henceforth referred to as the Olinda Study), to favorable environmental conditions rapid growth of individual trees, a two-tiered canopy, and low competition-related mortality. Harms et al. (1994) proposed that low mortality and rapid growth in the same stands were a result of long crowns with high leaf area, high foliar nutrient concentrations, ample soil moisture, light penetration deep into the canopy, a long growing season, and lack of disease and pests. In addition, Harms et al. (1994) observed increases in flush number and needle length in loblolly trees in the Olinda Study and suggested that increased flushing was in response to climatic differences between sites. Lanner (1966) examined growth of 13 species from the United States mainland planted in Hawaii and described three characteristics of the Hawaiian climate that may account for greater growth. These factors were only a slight (2 h) change in day length from winter to summer, mild year-long temperatures, and high rainfall. Although the growing season in the southern United States is long and mild winter conditions facilitate photosynthesis, environmental conditions for year-round photosynthate production are likely more favorable in Hawaii. Because of environmental and site limitations, loblolly pine in the southern United States may be unable to support the leaf area or year-round positive leaf C gain needed to reach the high basal area and volume observed in exotic environments. Interactions between site factors and physiological processes that influence carrying capacity require further study.

The Olinda Study is located on the island of Maui, Hawaii, and was planted in 1961. To our knowledge, the Olinda Study is the only complete, replicated, long-term, experimental spacing study of loblolly pine in an exotic location in the world, making this a rare opportunity to (*i*) examine biological growth potential of loblolly pine at age 47 years, (*ii*) identify potential factors that influence carrying capacity and growth such as climate, leaf physiology, needle and shoot morphology, woody root allocation, and soil and foliar nutrients, and (*iii*) for the first time, assess wood quality properties of the Olinda Study trees.

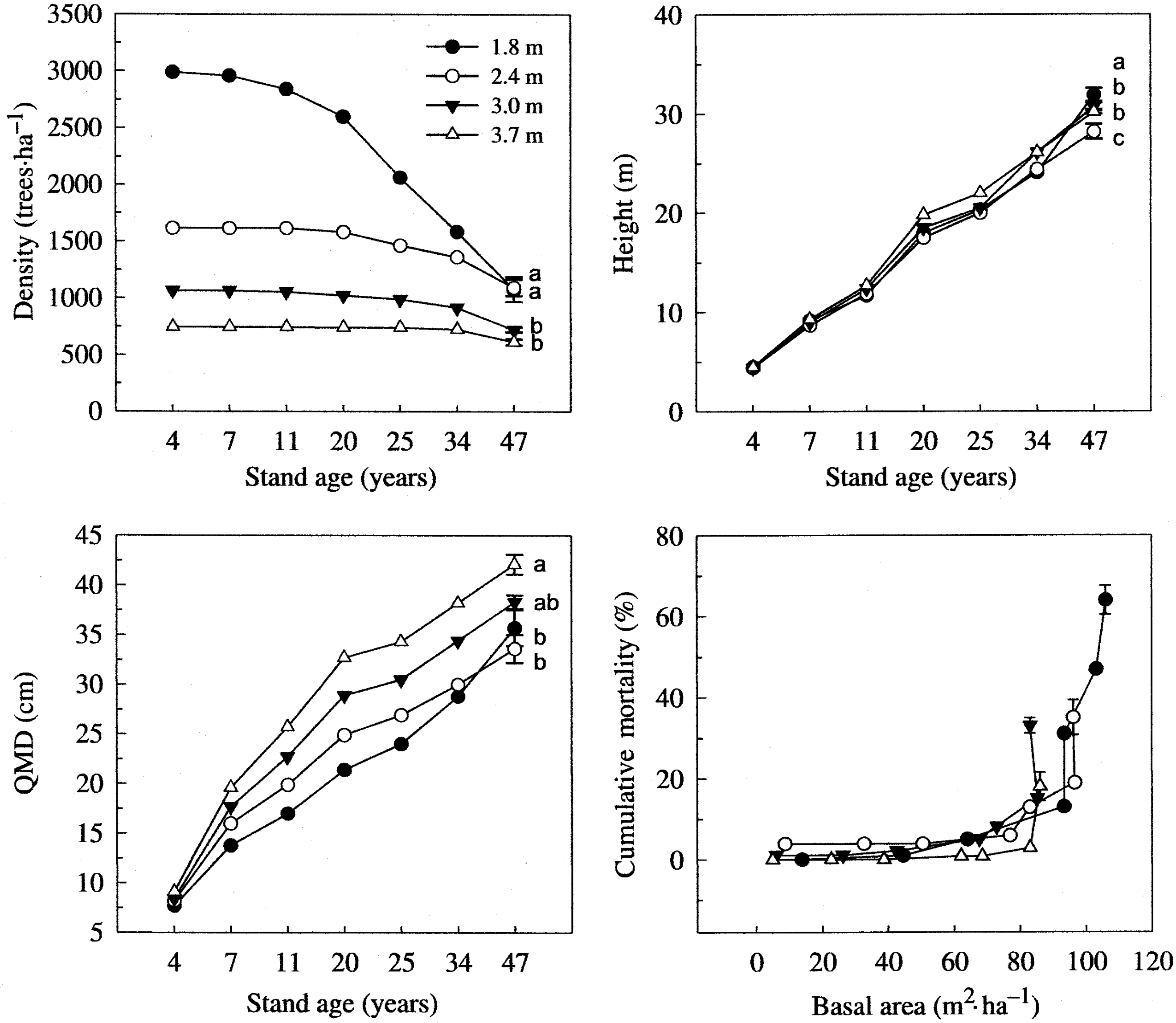
Materials and methods

Study site

The Olinda Study is located on Maui at latitude 20°49′N and longitude 156°17′W and at an elevation of 1120 m on the northwest slope of Haleakala. Soil is an Olinda loam with a 15 cm surface layer of dark red–brown granular loam over a 91 cm thick silty-clay loam subsoil in the subgroup Entic Dystrandepts (Whitesell 1970; Harms et al. 2000). Parent material is volcanic ash over andesite or basalt and soil pH is 6.2–6.4 (Whitesell 1970). Average site index at base age 25 years is 24 m (Harms et al. 2000).

Precipitation data for the Olinda site were available from a weather station in Olinda (coordinates: 20°48′N, 156°17′W; elevation 1259 m) located 1.8 km from the study site (www.ncdc.noaa.gov). The 30-year average annual rainfall for the area is 1793 mm (Fig. 1). Annual precipitation in 2008, during the study, was 1105 mm (Fig. 1). The rainy season in Maui runs from December through February and monthly rainfall in 2008–2009 was higher during this period. The closest station for temperature data was Kula Branch (coordinates: 20° 46′N, 156°19′W; elevation 930 m) located 6.5 km southwest from the site (www.ncdc.noaa.

Fig. 2. Influence of planting spacing on stand structural characteristics of loblolly pine (*Pinus taeda*) in Hawaii. Error bars at age 47 years are SEs. Different letters indicate significant (α = 0.05) differences between spacings at age 47. Data before age 47 were adapted from Harms et al. (2000). QMD, quadratic mean diameter.



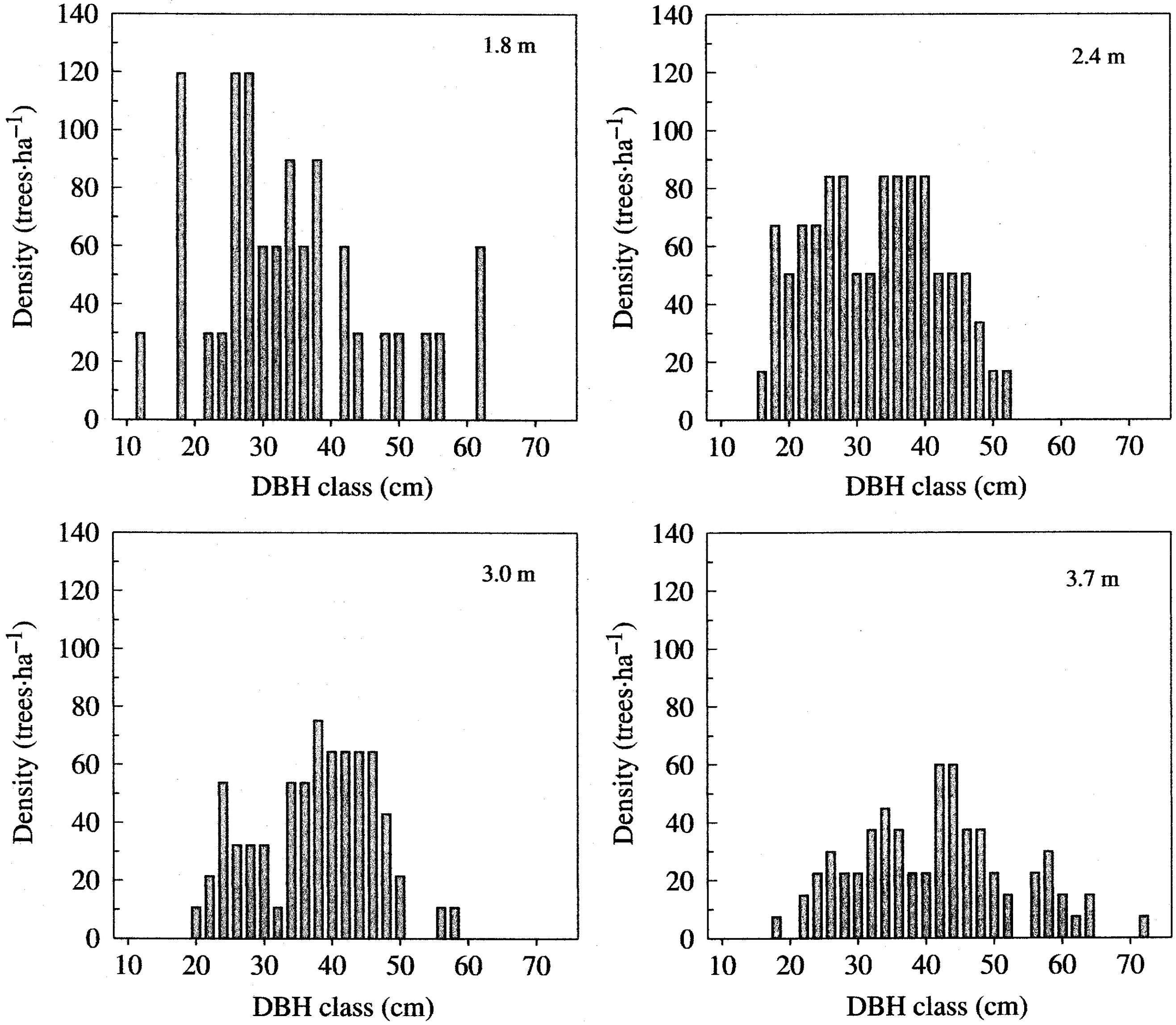
gov). The 30-year mean annual temperature is 17.7 °C with an average January temperature of 16.1 °C compared with an average July temperature of 19.3 °C (Fig. 1).

For comparison with a loblolly pine productivity study near Bainbridge, Georgia, that reported growth rates comparable with those of the Olinda Study early in stand development (Samuelson et al. 2008), weather data for Tallahassee, Florida (Tallahassee Regional Airport) (coordinates: 30°24′N, 84°21′W; elevation 16.8 m), are included (Fig. 1) (www.ncdc.noaa.gov). Temperature varied little across months at Olinda in contrast with pronounced seasonal patterns in temperature typical of the southern United States.

The 1.6 ha spacing trial was established in January 1961 by the USDA Forest Service and Hawaii State Division of Forestry and Wildlife on an old pasture. Forty years prior to study installation, the site was covered with the exotic, invasive shrub gorse (*Ulex europaeus* L.) (Whitesell 1970; Harms et al. 2000). Gorse is an opportunist legume species infesting the island of Maui and gorse infestations typically lower soil pH and concentrations of soil nutrients (Leary et al. 2006). The only record of vegetation management was given by Whitesell (1970) who described attempts to clear the gorse by repeated digging and burning. Whitesell (1970) reported that by 1961, an 8 cm thick layer of sod made up of the nonnative Kikuyu grass (*Pennisetum clandestinum* Hochst) common in pastures, nonnative rat-tail grass (*Sporobulus capensis* (Wild.) Kunth), and some gorse covered the site.

Seedlings were planted by digging a 30 cm deep hole and removing the sod at the planting spot. The study was designed using a Latin Square design with four replications. Each treatment plot was 0.11 ha with the central square 25-tree plot forming the measurement plot. Each measurement plot had a minimum of two buffer rows surrounding it. The

Fig. 3. Diameter at breast height (DBH) class frequency distributions for 47-year-old loblolly pine (*Pinus taeda*) planted at different spacings in Hawaii.



square spacing treatments were 1.8, 2.4, 3.0, and 3.7 m. One-year-old seedlings were purchased commercially and the seed source is unknown.

Two measurement campaigns were conducted. On 3–18 July 2008, plots were inventoried, coarse root biomass was measured with ground-penetrating radar (GPR), and leaf photosynthetic response to light was measured. Samples were collected for measurement of soil and foliar nutrient concentrations. During the second campaign on 13–21 January 2009, leaf light-saturated photosynthesis and stomatal conductance and shoot morphology were measured and wood core samples were collected for densitometry analysis.

Soil measurements

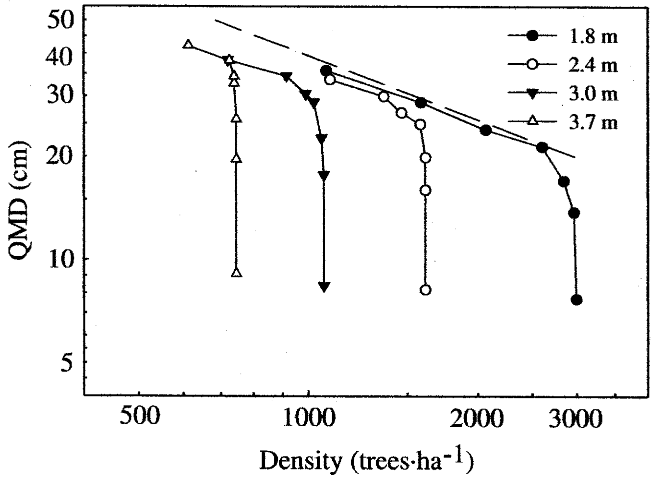
Soil bulk density was measured at two locations within each measurement plot, one adjacent to a tree approximately 30 cm from the bole and the second in the middle of an adjacent row. Samples were extracted from the top 8.5 cm of soil using a cylinder of known volume (172 cm^3) and then dried at 105 °C for 120 h and weighed. Data were pooled across location by plot.

Soil samples were collected to measure soil nutrient concentrations and organic matter at two depths, 0–15 and 15–30 cm, and at three subsample locations per plot positioned equidistant along a transect beginning adjacent to the tree and moving interrow between trees extending the length of the five-row measurement plot. Transect length varied with tree spacing treatment. Samples were pooled across location by depth and plot.

Stand inventory

An inventory was conducted in July 2008 on all 25-tree measurement plots. Diameter at breast height (DBH) (1.37 m) was measured on all living trees and the social class of all living trees was recorded. Total height was measured on one dominant, codominant, intermediate, and

Fig. 4. Stand trajectories for loblolly pine (*Pinus taeda*) in Hawaii planted at different spacings and plotted on a logarithmic scale. The broken line represents the limiting density boundary. Data before age 47 were adapted from Harms et al. (2000). QMD, quadratic mean diameter.



suppressed tree per plot with a laser hypsometer (TruPulse 200; Laser Technology, Inc., Centennial, Colorado) mounted on a tripod. Care was taken to ensure that measurements were taken at a distance equal to or greater than the height of the tree. Height of all trees in a plot was then predicted from DBH based on the height–DBH relationship from Arabatzis and Burkhart (1992) and Carlson et al. (2009):

$$[1] \quad \text{Height} = a \exp(b/\text{DBH})$$

where a and b are regression coefficients. Functions were fit by treatment ($n = 16$) and relationships between height and DBH were highly significant with $R^2 > 0.98$. Volume was estimated using height and DBH and equations from Burkhart (1977) selected by Harms et al. (2000) to calculate volume on the Olinda site from age 7 through 34. When the plantation was 26 years old, Harms et al. (2000) felled trees representing the range in DBH, measured stem volumes, and, based on paired t tests of differences between observed and estimated volumes, applied equations published by Burkhart (1977). Inventory data before age 47 were adapted from Harms et al. (2000) (means but not standard errors were available). The limiting density boundary reference line was obtained as described by Harms et al. (2000) using a quadratic mean diameter (QMD) of 25 cm and 2100 trees·ha^{-1} as the maximum density possible at that QMD estimated from the stand trajectory plot for the 1.8 m spacing and the Reineke equation (Reineke 1933) with a slope coefficient of 1.605.

Stem biomass at age 47 years was estimated using allometric equations based on DBH and height developed by Van Lear et al. (1986) for 41-year-old loblolly pine trees in a plantation in South Carolina. We did not estimate leaf or branch biomass because the relationship between branch or foliage biomass and height and DBH would likely vary between Olinda and mainland stands, based on work by Xu and Harrington (1998) with loblolly pine stands varying in tree and stand characteristics. No data on potential differences in stem taper between Olinda and mainland trees were available, so it is possible that differences in taper affected stem mass predictions.

Leaf area index was measured every 3 m along a transect positioned on the border of the first Latin Square row next to the access road using a plant canopy analyzer (LAI-2000; LI-COR Inc., Lincoln, Nebraska). Values were averaged by plot. Only the one row was measured due to topography and small plot sizes.

Coarse root biomass

Belowground coarse root biomass was separated into below-stump coarse roots and between-tree coarse lateral roots. References relating DBH to tap root or below-stump biomass are scarce, especially across multiple sites (i.e., Van Lear and Kapeluck 1995: one site, 15 trees). For our study, below-stump coarse root mass (kilograms per tree) was estimated using DBH (centimetres) from all live trees within the 25-tree measurement plots and applying the equation

$$[2] \quad \text{Below-stump coarse root dry mass} = [5647 - (1225 \times \text{DBH}) + (110 \times \text{DBH}^2)]/1000$$

This allometric equation ($R^2 = 0.93$) was developed by destructively sampling 1 m × 1 m (the depth depended on tap root length) pits at the base of 79 loblolly pines ranging in age from 6 to 49 years in Georgia, Mississippi, North Carolina, and South Carolina (Kurt Johnsen, unpublished data). Trees ranging from 3.7 to 36.5 cm DBH were excavated on a variety of soil textures (sandy, sandy loam, clay loam) and drainage classes (excessively well drained, well drained, somewhat well drained). Forty-nine percent of the surviving trees at the Olinda site fell within the range of diameters used to develop eq. 2. Although not ideal, the use of eq. 2 provided our best option for estimating below-stump coarse root biomass. However, we acknowledge that the unique soils at Olinda may have influenced tap root length.

Between-tree coarse lateral root biomass was estimated with GPR (Butnor et al. 2003, 2009). In well-drained, electrically resistive soils, GPR may be used to rapidly survey lateral roots, although the taproot directly beneath a tree cannot be measured by surface-based antennas (Butnor et al. 2003; Stover et al. 2007). The root survey had two parts: (1) linking radargrams directly to destructively sampled soil cores to correlate root reflectance with actual biomass (Butnor et al. 2003; Stover et al. 2007) and (2) collecting GPR data along series of parallel transects to get a representative sample on the 16 measurement plots, which was converted to mass of lateral roots per unit area with the correlation in part 1. The survey equipment, procedures, and postcollection processing techniques were similar to those presented by Samuelson et al. (2008), with the exception of the GPR unit, which was a SIR-3000 (Geophysical Survey Systems Inc., Salem, New Hampshire). A total of 48 calibration cores (three per plot) were collected to correlate GPR reflectance with lateral root mass. A series of parallel GPR survey transects spaced 0.3 m apart were laid out between the second and third rows of trees in the 25-tree measurement plot. Since the size of each measurement plot varied by spacing treatment (1.8, 2.4, 3.0, and 3.7 m), transect length was 9, 12, 15, and 18.5 m, respectively. GPR reflectance was well correlated with lateral root mass

Fig. 5. Influence of planting spacing on stand structural characteristics of loblolly pine (*Pinus taeda*) in Hawaii. Error bars at age 47 years are SEs. Mean annual increment is based on basal area or volume growth. Data before age 47 were adapted from Harms et al. (2000).

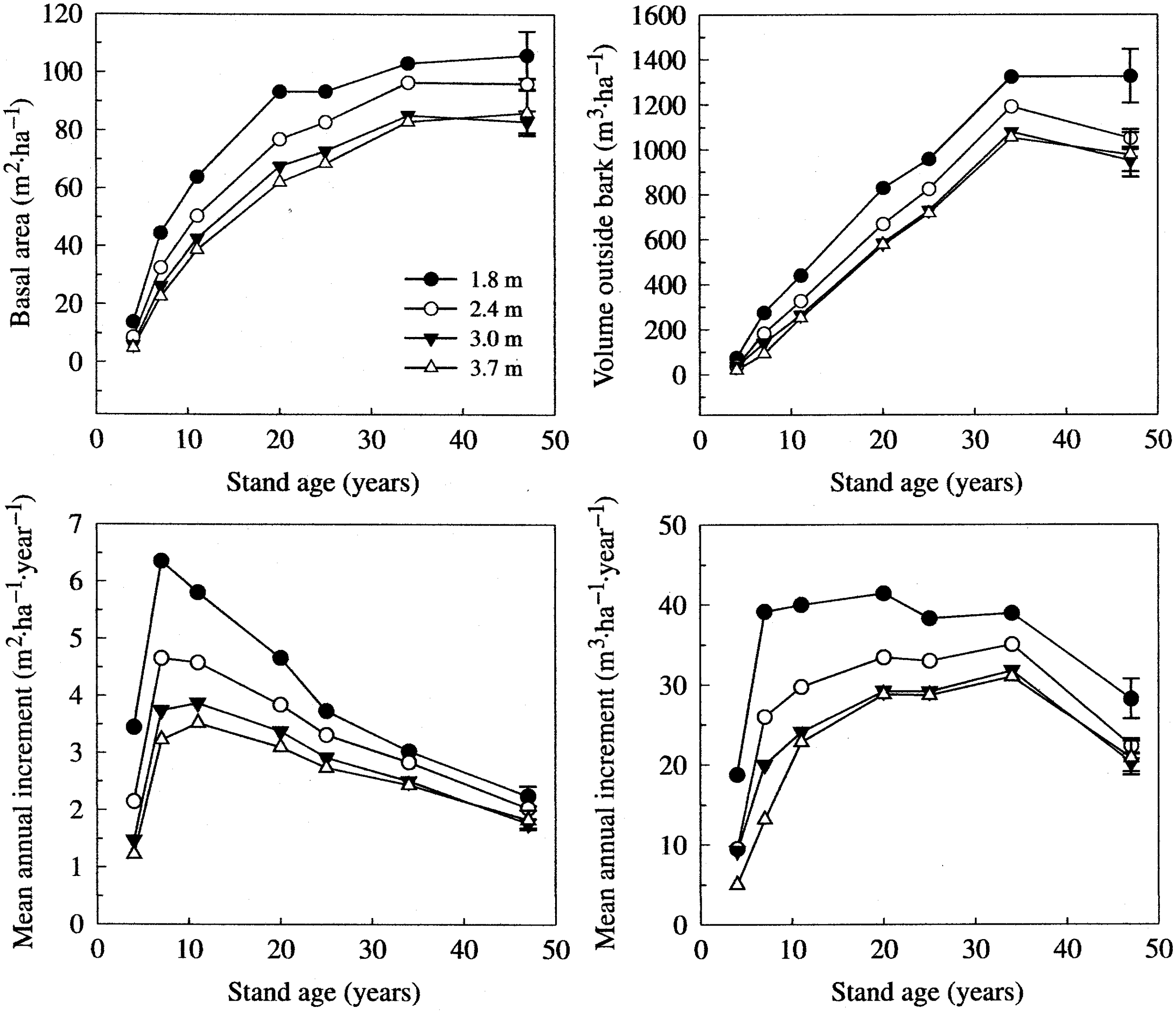


Table 1. Effects of planting spacing on biomass of 47-year-old loblolly pine (*Pinus taeda*) in Hawaii and associated ANOVA *p* values.

Spacing (m)	Stem (Mg·ha^{-1})	Between-tree coarse root (Mg·ha^{-1})	Below-stump coarse root (Mg·ha^{-1})	Total woody root (Mg·ha^{-1})	Root:total (%)
1.8	917.8±85.6	20.2±3.6	114.6±9.9	134.8±9.2	12.9±0.4
2.4	716.6±30.2	15.5±5.0	101.2±3.1	116.7±6.7	14.0±0.5
3.0	655.7±35.2	11.1±2.6	90.7±4.5	101.8±4.5	13.5±0.3
3.7	679.4±71.0	12.1±1.4	96.8±9.5	108.9±10.3	13.9±0.2
$p > F$	0.091	0.421	0.281	0.152	0.289

Note: Values are means ± SEs. Root:total, ratio of woody root mass to woody root mass plus stem biomass.

collected with soil cores ($R^2 = 0.80$) when fitted with a Weibull-type function taking the form

$$[3] \quad \text{Root mass per area} = a - b \times e^{(-c \times \text{GPR reflectance index}^d)}$$

where *a*, *b*, *c*, and *d* are regression coefficients.

Densitometry

Wood cores were removed at DBH with an increment borer from 10 trees per plot (per plot: seven cores 5 mm in diameter and three cores 12 mm in diameter) during the January 2009 sampling session for a total of 160 cores. Trees close to average plot diameters were selected from buffer

Table 2. Effects of planting spacing on whole-core densitometry and mean whole-core densitometry data across all rings and for the first 20 rings for 47-year-old loblolly pine (*Pinus taeda*) in Hawaii and associated ANOVA *p* values.

	Ring SG	Latewood SG	Earlywood SG	Percent latewood
Spacing (m)				
1.8	0.485±0.004	0.641±0.002	0.364±0.002 ab	43.76±1.19
2.4	0.499±0.010	0.648±0.002	0.364±0.003 ab	47.35±2.69
3.0	0.477±0.012	0.646±0.008	0.359±0.002 b	41.18±2.98
3.7	0.496±0.009	0.647±0.004	0.371±0.003 a	45.01±2.52
$p > F$	0.203	0.652	0.045	0.169
All ring numbers				
Mean	0.490	0.645	0.364	44.44
SD	0.044	0.028	0.022	10.06
Minimum	0.376	0.586	0.302	21.41
Maximum	0.613	0.724	0.425	75.52
Ring numbers 1–20				
Mean	0.470	0.638	0.358	39.76
SD	0.042	0.029	0.021	10.00
Minimum	0.352	0.574	0.299	14.99
Maximum	0.582	0.717	0.424	65.08

Note: Values are means ± SEs. Different letters indicate significant spacing effects at $\alpha = 0.05$. SG, specific gravity.

rows. Cores were kept under refrigeration to prevent warping and microbial growth until they could be processed in the laboratory. After an initial drying step (50 °C for 24 h), the cores were glued (Gorilla Glue, Cincinnati, Ohio) into yellow-poplar core holders, allowed to dry under ambient conditions, and then sawn into 2.3 mm thick strips, from pith to bark, leaving the transverse surface exposed and bordered by strips of yellow-poplar wood. Densitometery was performed using a Quintek Measurement Systems (Knoxville, Tennessee) X-ray densitometer with a resolution of 0.00001. SG measurements were determined at 0.06 mm intervals. A SG of 0.480 was used to differentiate between earlywood and latewood zones for each core. For the occasional instances where the earlywood or latewood zone could not be detected because of the limits of the sampling interval, any zero value for SG was not included in the averages determined for that particular ring number. Calibration of the densitometer was on a green volume and oven-dried mass basis. A few cores with defects (e.g., missing growth rings because of knots) that could not be compensated for by sample preparation were not used. Latewood, earlywood, and ring SG values and percent latewood were weighted by ring basal area to obtain a whole-core value for each tree sampled.

Leaf physiology

July 2008

A large sling-shot (BIGshot; SHERRILLtree Co., Greensboro, North Carolina) was used to propel a rope over a large branch in the upper canopy and then, by pulling on the rope, detach and fell the branch for leaf physiology measurements. One branch from the upper canopy of two trees was removed (two trees were sampled per plot). A secondary branch was cut off the felled branch and the cut end was recut underwater and kept in water for measurements. Leaf net photosynthetic response to light was measured immediately on attached foliage using two portable open gas exchange systems (LI-COR 6400; LI-COR Inc., Lincoln, Nebraska). Two fascicles from the most recent fully expanded flush were placed in each cuvette and light curves were initiated at a photosynthetically active radiation (PAR) level of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ followed by an eight-step reduction to 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR. Leaves were allowed to equilibrate for 5 min at each light level. Light response curves were measured at a cuvette CO_2 concentration of 400 ppm and at ambient temperature and ambient vapor pressure deficit (D). Leaf dark respiration (R_D), apparent quantum yield (Φ), light saturated net photosynthesis (A_{max}), the light compensation point (LCP), and maximum stomatal conductance (g_S) were calculated using nonlinear regression analysis described in Hanson et al. (1987). Gas exchange rates were calculated on a total needle surface area basis following Samuelson et al. (1992). One column of the Latin Square design was measured a day between 09:00 and 14:00. It took 4 days to complete the session.

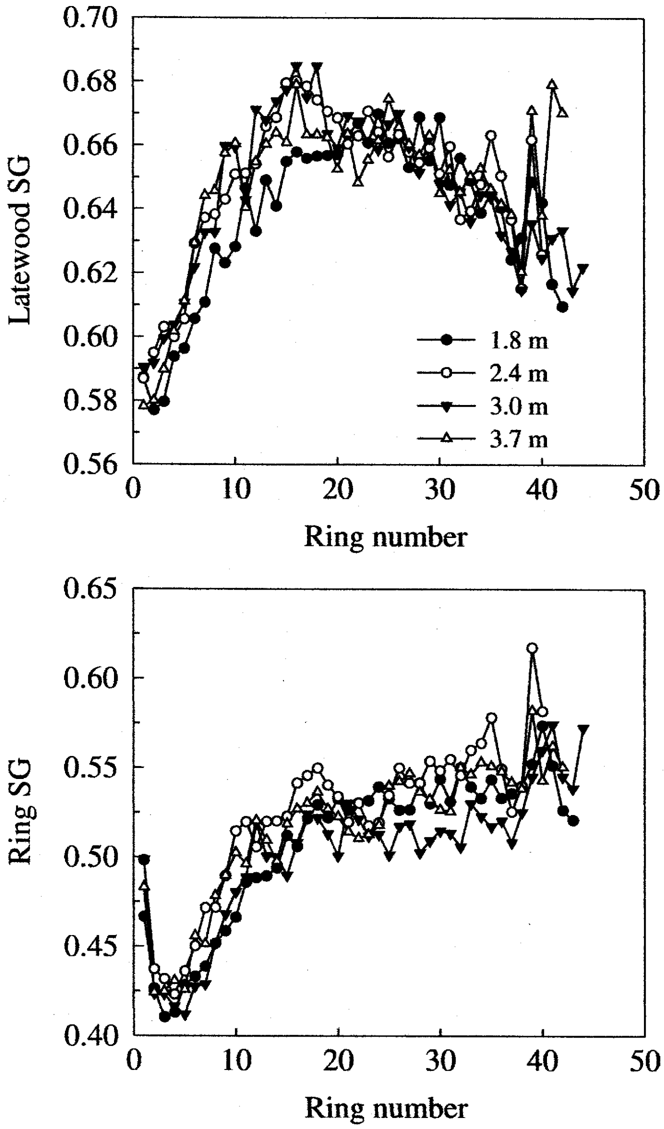
January 2009

Similar to the July 2008 measurements, one large branch from two trees per plot was detached from the upper canopy using the sling-shot. From each branch, three secondary branches were recut underwater and kept in water. Leaf A_{max} and g_S were measured on two needle age classes per secondary branch. Two detached fascicles from the most recently fully expanded flush and next older adjacent flush on each branch were measured within 3 min of detachment. Because it was unclear when flushes were produced, the younger flush was designated as 2 and the older flush as 1. Measurements were made at 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR, a CO_2 concentration of 400 ppm, and at ambient temperature and D.

Shoot morphology

Specific leaf area (SLA) was measured on the most recent

Fig. 6. Latewood specific gravity (SG), earlywood SG, ring SG, and percent latewood versus ring number for loblolly pine (*Pinus taeda*) planted at different spacings in Hawaii.



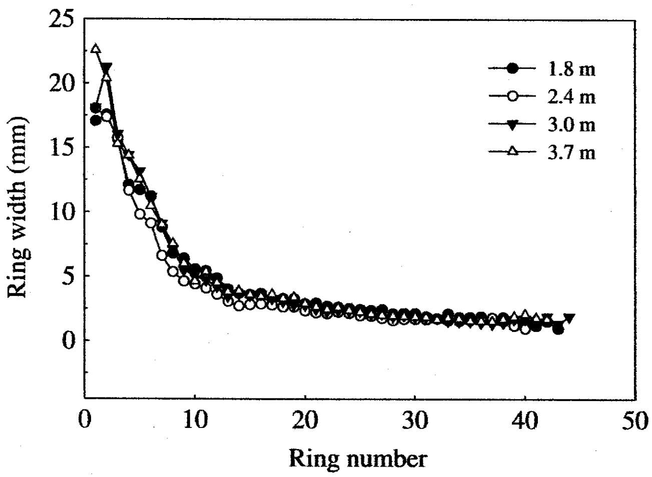
fully expanded foliage (flush 2) and the next adjacent older foliage (flush 1) in July 2008 and January 2009. Ten fascicles per flush were collected from branches used in physiology measurements. Foliage from one secondary branch per tree and two trees per plot was measured in July and foliage from three secondary branches per tree and two trees per plot was measured in January. Needle lengths and fascicle diameters were measured and total fascicle area was calculated following Samuelson et al. (1992). Needles were then oven-dried to a constant mass at 70 °C and SLA calculated as the ratio of total needle surface area to needle dry mass.

In January 2009, the number of flushes on three secondary branches from the one large sample branch per tree and two trees per plot was counted. Flushes were delineated by bud scale scars, the sterile-scale zone, and needled zone as described in Lanner (1966). Shoot length was determined for the three oldest flushes on each sample branch.

Soil and foliar nutrient analyses

Nitrogen and C analyses for both soil and foliage samples collected in July 2008 were performed with an EA Flash 1112 analyzer (ThermoFinnigan, Milan, Italy) at the USDA Forest Service Southern Research Station Laboratory in Research Triangle Park, North Carolina. Foliage samples collected for SLA (described above) were pooled by needle age and plot, dried at 70 °C, and then finely ground using a ball mill (Spex Sampleprep 8000; Spex CertiPrep, Metuchan, New Jersey) to a 0.2 mm particle size. The analyzer combusts powdered samples at 900 °C to assess total N and C contents (percentages). Twenty percent of all of the samples are duplicated to check the instrument's precision. One NBS standard and one CE Elantech Inc. (Lakewood, New Jersey) certified standard were used in each sample set to check the accuracy of the sample values. Sample sets were rerun if the coefficient of variation exceeded 5%.

Fig. 7. Ring width versus ring number for loblolly pine (*Pinus taeda*) planted at different spacings in Hawaii.



Soil organic matter content and micronutrient analysis were contracted to an independent laboratory (Spectrum Analytics, Washington Court House, Ohio). Samples for soil organic matter analysis were weighed and then ashed for 2 h at 360 °C. After cooling, the samples were reweighed and the percent mass loss with ashing determined. These values were compared with a regression equation to compute organic matter content (percentage) (Soil and Plant Analysis Council 1992). Soil and foliar samples for micronutrient analysis were processed with the Mehlich-III extraction (Soil and Plant Analysis Council 1992) and analyzed for P, K, Mg, and Ca using a TJA 61E inductively coupled plasma – atomic emission spectrometer (Thermo ElectronCorp., Waltham, Massachusetts).

Statistical analysis

The experimental design was a 4 × 4 Latin Square with a 25-tree center measurement plot. Measurements of leaf physiology and shoot characteristics and whole-core densitometry data were averaged across sample trees and plot averages were used in the analyses. The SAS standard Latin Square analysis of variance (SAS version 9.1; SAS Institute Inc., Cary, North Carolina) was used to test for spacing effects and, where appropriate, soil depth or needle age effects. Homogeneity of variance and normality assumptions were tested for each analysis. All variables were normally distributed with equal variances and no transformations were needed. Spacing effects on stand structure and growth were tested at age 47 years. In all tests, effects were considered significant at $\alpha = 0.05$, and when appropriate, Tukey's paired comparison procedure was used to determine differences between spacing treatments.

Results

Stand growth

At age 47, stand density was higher in the 1.8 and 2.4 m spacings than in the 3.0 and 3.7 m spacings. Average density in the two closest spacings was 1085 trees·ha^{-1} compared with an average of 667 trees·ha^{-1} in the two widest spacings (Fig. 2). The 1.8 m plots exhibited a steep increase in mortality relative to the other spacing treatments beginning at age 20, and by age 47, density was similar between the 1.8 and 2.4 m spacings (Fig. 2). Cumulative mortality by age 47 was 64% at a basal area of 100 m^2·ha^{-1} in the 1.8 m spacing compared with 18% and 80 m^2·ha^{-1} in the 3.7 m spacing (Fig. 2). Height at age 47 was greatest (31.9 m) in the 1.8 m spacing and least (28.2 m) in the 2.4 m spacing (Fig. 2). QMD was 42.1 cm in the 3.7 m spacing and greater than QMD in the 1.8 and 2.4 m spacings (Fig. 2). Size class frequency distributions indicated more trees in the larger diameter classes (>40 cm DBH) in the two widest spacings (Fig. 3). The 1.8 m plots retained a high number of small-diameter trees <30 cm DBH. The stand trajectories in the 1.8 and 2.4 m plots had reached the limiting density boundary at age 34 years, and by age 47, the trajectory line curved in all spacings (Fig. 4). The trajectories of the two widest spacings did not reach the limiting density boundary. Spacing effects on basal area ($p = 0.156$) and basal area increment ($p = 0.156$) were not significant at age 47 (Fig. 5). A trend ($p = 0.082$) towards greater volume ($p = 0.082$) and volume mean annual increment ($p = 0.082$) in the 2.4 m spacing relative to the 3.0 and 3.7 m spacings was detected (Fig. 5). Average basal area and volume at age 47 was 93 m^2·ha^{-1} and 1076 m^3·ha^{-1}, respectively. Leaf area index was 3.0 in the 1.8 m spacing, 3.2 in the 2.4 m spacing, 3.2 in the 3.0 m spacing, and 3.0 in the 3.7 m spacing (one plot per spacing was measured).

Spacing treatment had no significant influence on stem and coarse root biomass (Table 1). Stem mass was 742 Mg·ha^{-1} compared with a total of 116 Mg·ha^{-1} in coarse root biomass. Allocation to woody roots relative to stem plus woody root mass was not different between spacings and was 13.6%.

Densitometry

Whole-core earlywood SG was higher in the 3.7 m spacing than in the 3.0 m spacing, but spacing treatment had no significant effect on whole-core ring SG, latewood SG, and percent latewood (Table 2). Latewood SG increased from approximately 0.58 to 0.68 over the first 20 growth rings and then gradually declined thereafter whereas earlywood SG gradually increased over time (Fig. 6). Ring SG, which encompasses the proportions of earlywood and latewood in each ring, showed a brief decrease near the pith followed by an increase over the next 20 or so ring numbers (Fig. 6). Thereafter, ring SG reached a plateau. A similar plot profile was obtained for percent latewood (Fig. 6). Plots of the ring widths at each ring number indicated very rapid growth for all spacing treatments for the first 10 growth rings and then tapering off to a mean ring width of 1.6 mm for mature wood (Fig. 7). Over all spacing treatments, mean whole-core SG was 0.64 for latewood, 0.36 for earlywood, and 0.49 for ring SG (Table 2). Using only the data for the first 20 growth rings in the statistical analysis to represent younger stands, mean whole-core ring SG was 0.47 (Table 2).

Soil and foliar nutrients

Spacing had no significant influence on soil organic matter, bulk density, soil C content or C, N, P, K, Ca, and Mg concentrations (Table 3). Soil organic matter was 11.4% and

Table 3. Effects of planting spacing and soil depth on soil characteristics measured in July 2008 in 47-year-old loblolly pine (*Pinus taeda*) in Hawaii and associated ANOVA *p* values.

	Total C ($mg \cdot kg^{-1}$)	Total C ($Mg \cdot ha^{-1}$)	Total N ($mg \cdot mg^{-1}$)	Organic matter ($g \cdot kg^{-1}$)	P ($mg \cdot kg^{-1}$)	K ($mg \cdot kg^{-1}$)	Mg ($mg \cdot kg^{-1}$)	Ca ($mg \cdot kg^{-1}$)	Bulk density ($g \cdot cm^{-3}$)
Spacing (m)									
1.8	586.3±56.7	59.3±5.9	40.2±5.0	10.4±0.6	5.5±0.9	75.6±3.0	221±17.0	1164±128	0.57±0.02
2.4	607.6±54.0	61.7±6.8	34.0±3.1	12.1±0.9	4.6±1.2	78.1±8.0	315±32.3	1033±92.7	0.59±0.06
3.0	620.4±36.4	56.0±2.5	36.3±2.1	11.6±0.9	4.7±1.0	63.6±8.4	235±31.8	932±136	0.58±0.03
3.7	663.9±58.3	66.7±6.0	39.4±3.2	11.7±1.1	7.3±1.0	77.0±6.8	233±36.6	914±138	0.60±0.06
Depth (cm)									
0–15	699.2±27.9		43.2±1.8	10.8±0.5	7.6±0.7	84.3±3.2	280±14.8	1099±48.1	
15–30	539.9±31.9		31.8±2.2	12.1±0.7	4.1±0.5	64.1±4.7	223±26.8	923±112	
$p > F$									
Spacing	0.645	0.429	0.422	0.575	0.111	0.092	0.109	0.486	0.938
Depth	0.002		0.001	0.135	0.002	<0.001	0.06	0.173	
Spacing × depth	0.662		0.801	0.680	0.722	0.57	0.956	0.982	

Note: Values are means ± SEs.

bulk density was 0.58 $g \cdot cm^{-3}$. Soil C, N, P, and K concentrations decreased with depth. Soil C content for the 0–15 cm depth was 60.9 Mg $C \cdot ha^{-1}$.

Foliar N per unit leaf mass (N_M) or leaf area (N_A), and foliar P, K, Ca, and Mg concentrations were not significantly different between spacing treatments (Table 4). Foliar P and K concentrations and N_M were higher in the younger foliage and Ca and Mg concentrations were higher in the older foliage (Table 4).

Leaf physiology

Averaged across the four measurement days, hourly temperature and *D* during leaf gas exchange measurements were 23.7 °C and 0.9 kPa, respectively, in July 2008 and 19.3 °C and 0.8 kPa, respectively, in January 2009. The maximum *D* during measurements was 3.0 kPa in July and 1.8 kPa in January. Spacing treatment had no significant effect on A_{max}, g_S, R_D, Φ, and LCP measured in July 2008 or A_{max} and g_S measured in January 2009 (Table 5). Foliar A_{max} of the younger foliage (flush 2) was 3.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in July 2008 and 3.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in January 2009. Stomatal conductance of the younger flush was 35 $mmol \cdot m^{-2} \cdot s^{-1}$ in July 2008 compared with 113 $mmol \cdot m^{-2} \cdot s^{-1}$ in January 2009. In January 2009, A_{max} and g_S were higher in the younger foliage.

Shoot morphology

Spacing treatment had no significant influence on SLA in either sampling session, although a trend (p = 0.061) towards higher SLA in the widest spacing was noted in January 2009 (Table 6). A trend (p = 0.052) towards higher SLA in younger foliage in July 2008 was also observed. Fascicle lengths were similar among spacings.

The number of flushes measured in January 2009 was not significantly different between spacing treatments (Table 6). The maximum number of flushes was 6 and the average number of flushes was 3.8. Shoot lengths of the oldest three flushes did not vary significantly with spacing treatment and lengths were 6.6 cm in the oldest flush, 3.4 cm in flush 2, and 2.6 cm in the youngest flush.

Discussion

High stand densities commonly increase resource uptake, the efficiency of resource capture (mainly light), and growth early in stand development but, as observed in the Olinda Study, increasing mortality over time reduces production in stands with denser spacings (Will et al. 2005). For example, in a loblolly pine density study in South Carolina planted on the same spacings as Olinda, accelerated mortality and associated declines in volume were observed in the closer spacings as early as age 10 (Buford 1991). Similarly, in a 38-year-old loblolly pine density study in Louisiana also planted on the same spacings as the Olinda Study, Baldwin et al. (2000) reported a stem density of 817 $trees \cdot ha^{-1}$ in the 1.8 m spacing compared with 469 $trees \cdot ha^{-1}$ in the 3.7 m spacing and similar volume (473 $m^3 \cdot ha^{-1}$) between spacings. The limiting density boundary reference line for the Olinda Study indicated that by age 47, self-thinning and average QMD had progressed enough to demonstrate curvature in the trajectories in all plots, but tree survival and diameter

Table 4. Effects of planting spacing on foliar nutrient concentrations measured in July 2008 in 47-year-old loblolly pine (*Pinus taeda*) in Hawaii and associated ANOVA p values.

	P (mg·g^{-1})	K (mg·g^{-1})	Ca (mg·g^{-1})	Mg (mg·g^{-1})	N_M (mg·g^{-1})	N_A (g·m^{-2})
Spacing (m)						
1.8	1.17±0.06	4.61±0.45	2.46±0.29	1.37±0.12	12.4±0.4	0.74±0.03
2.4	1.31±0.08	5.60±0.55	2.70±0.32	1.06±0.11	13.0±0.3	0.74±0.04
3.0	1.24±0.07	5.21±0.62	2.44±0.30	1.22±0.11	12.8±0.5	0.72±0.02
3.7	1.25±0.08	5.23±0.55	2.75±0.32	1.25±0.77	12.4±0.6	0.67±0.02
Needle age						
1	1.12±0.04	4.11±0.25	3.25±0.16	1.31±0.08	11.7±0.2	0.71±0.02
2	1.36±0.04	6.25±0.24	1.99±0.10	1.02±0.05	13.7±0.2	0.72±0.02
$p > F$						
Spacing	0.445	0.280	0.582	0.617	0.135	0.407
Needle age	<0.001	<0.001	<0.001	0.017	<0.001	0.874
Spacing × needle age	0.936	0.556	0.424	0.933	0.283	0.831

Note: Values are means ± SEs. Needle age 2 is the most recent fully expanded foliage and needle age 1 is the next adjacent older foliage. N_M, foliar N concentration per unit leaf mass; N_A, foliar N concentration per unit leaf area.

growth, and thus stockability, remained high at Olinda relative to mainland stands. Basal area and volume accretion culminated near age 34 in all spacings and at basal areas ranging from 80 to 100 m^2·ha^{-1}. In contrast, the upper stocking level limit for loblolly pine in the southern United States is approximately 45 m^2·ha^{-1} (Jokela et al. 2004). By age 47, basal area ranged from 83 to 106 m^2·ha^{-1} and volume from 951 to 1326 m^3·ha^{-1} but neither was significantly different between spacings, possibly due to the small plots, low replication, and low statistical power. Volume at Olinda was much higher than values reported for stands on the mainland even under optimum resource availability. For example, Borders and Bailey (2001) summarized loblolly pine production on six research sites located in Georgia with stands ranging in age from 10 to 12 years and with densities of 741–1660 stems·ha^{-1}. They observed a maximum volume of 412 m^3·ha^{-1}, maximum basal area of 44 m^2·ha^{-1}, and maximum mean annual increment of 34 m^3·ha^{-1}. The Olinda stands carried an average basal area of 93 m^2·ha^{-1}, which was nearly double the maximum carrying capacity of stands on the mainland (Jokela et al. 2004). High basal area and very tall tree heights at Olinda compared with mainland trees resulted in exceptionally high estimates of stem biomass (742 Mg·ha^{-1}). For comparison, maximum standing stem biomass of highly productive unthinned loblolly pine stands on the mainland at a basal area of 45 m^2·ha^{-1} was 170 Mg·ha^{-1} (Jokela et al. 2004). It is unclear why height was significantly lower in the 2.4 m × 2.4 m spacing but may be a result of fewer taller trees >50 cm DBH.

Greater productivity in the Olinda Study compared with loblolly pine grown in its native range raises the concern of a possible negative impact on wood quality. Higher growth rates are generally associated with lower ring SG, but there are exceptions where growth rate and ring SG are poorly correlated and climate may have a greater influence on ring SG (Jokela et al. 2004). The wood quality for Olinda loblolly pine does not appear to be lower than on the mainland. Mean whole-core SG (0.49) was similar to the SG of 0.48 reported for loblolly pine in its native range (Mitchell and Wheeler 1959). Mean ring SG over the first 20 growth rings was 0.47, which is within the 0.44–0.61 range in ring SG (at a standard ring age of 10–11 years) reported for loblolly pine stands located throughout the southern United States (Jokela et al. 2004).

Not all exotic sites are as favorable to loblolly pine growth as the Olinda site. For example, 20-year-old loblolly pine grown on Molokai on a 3.7 m × 4.6 m spacing produced a volume of only 130 m^3·ha^{-1}, and the authors attributed greater growth at Olinda to better soils and higher annual rainfall (Buck and Imoto 1982). Olinda soils are of volcanic origin and considered very fertile and productive with a udic soil moisture regime (Soil Conservation Service 1984). In particular, soil Ca and Mg concentrations and organic matter were high relative to sites on which loblolly pine is often planted (Samuelson 1998; Kyle et al. 2005). At age 26 years, N_M, P, Ca, and Mg concentrations in Olinda foliage were considerably higher compared with mainland concentrations (Harms et al. 1994). The majority of foliar nutrient concentrations were similar between ages 26 (Harms et al. 1994) and 47 years with the exception of lower N_M at 47 years, but all nutrient concentrations were well above critical values for loblolly pine (Allen 1987; Colbert and Allen 1996). In loblolly pine, foliar Ca is considered satisfactory above 1.2–1.5 mg·g^{-1} (Dickens et al. 2003; Gregoire and Fisher 2004). Average foliar Ca concentration in Olinda trees was 2.6 mg·g^{-1} and nearly double the concentrations reported for mainland plantations. For example, foliar Ca ranged from 1.5 to 1.7 mg·g^{-1} in a 14-year-old loblolly pine stand in North Carolina fertilized with N, P, K, Ca, and Mg (Albaugh et al. 2008). Albaugh et al. (2008) also observed that Ca increases in foliage from fertilization were unexpectedly large relative to other nutrients and fertilized stands had greater volume growth per unit of Ca uptake than control plots. Kyle et al. (2005) attributed sustained growth up to age 33 in loblolly pine in response to fertilization at age 10 to added Ca, and foliar Ca was 1.7 mg·g^{-1} at age 33. Long-term decline in exchangeable soil Ca pools in response to short rotation timber harvests has been suggested as a source of lower productivity in southeastern forests (Huntington et al. 2000). The unique combination of fertile soils, minimal disturbance, mild temperatures, and adequate precipitation possibly reduced competition for belowground resources, thereby reducing allocation to woody roots. Two examples of allocation to belowground woody

Table 5. Effects of planting spacing on leaf physiological characteristics measured in July 2008 and January 2009 in 47-year-old loblolly (*Pinus taeda*) pine in Hawaii and associated ANOVA p values.

	July 2008					January 2009	
	A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	g_S ($mmol \cdot m^{-2} \cdot s^{-1}$)	R_D ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Φ ($\mu mol\ CO_2 \cdot \mu mol\ photon^{-1}$)	A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	g_S ($mmol \cdot m^{-2} \cdot s^{-1}$)
Spacing (m)							
1.8	3.8±0.5	43.2±7.3	0.43±0.06	30.6±4.1	0.015±0.001	3.4±0.2	117.3±11.0
2.4	3.3±0.4	33.4±3.8	0.36±0.06	26.9±2.6	0.015±0.002	2.9±0.1	101.3±10.0
3.0	2.9±0.4	31.0±5.0	0.43±0.07	29.1±5.0	0.017±0.001	3.4±0.2	127.9±11.0
3.7	3.1±0.3	31.0±2.8	0.37±0.73	32.2±2.6	0.014±0.001	3.0±0.2	106.8±10.0
Needle age							
1						2.9±0.1	101.0±6.6
2						3.4±0.1	125.6±7.3
$p > F$							
Spacing	0.182	0.095	0.732	0.772	0.445	0.133	0.333
Needle age						0.005	0.033
Spacing × needle age						0.700	0.917

Note: Values are means ± SEs. Needle age 2 is the most recent fully expanded foliage and needle age 1 is the next adjacent older foliage. A_{max}, light saturated net photosynthesis; g_S, stomatal conductance; R_D, dark respiration; LCP, light compensation point; Φ, quantum yield.

Table 6. Effects of planting spacing on shoot morphology measured in July 2008 and January 2009 in 47-year-old loblolly pine (*Pinus taeda*) in Hawaii and associated ANOVA p values.

	July 2008		January 2009					
	SLA ($cm^2 \cdot g^{-1}$)	Fascicle length (cm)	SLA ($cm^2 \cdot g^{-1}$)	Fascicle length (cm)	Number of flushes	Flush 1 length (cm)	Flush 2 length (cm)	Flush 3 length (cm)
Spacing (m)								
1.8	191.8±17.1	14.9±0.6	162.9±2.9	15.0±1.2	3.6±0.2	7.1±0.4	3.0±0.3	2.5±0.7
2.4	180.7±9.4	15.2±0.4	169.9±6.6	15.3±1.2	3.3±0.4	6.8±0.6	3.2±0.5	1.1±0.1
3.0	180.1±8.3	15.4±0.3	162.0±3.5	14.5±1.2	4.2±0.4	5.7±0.8	4.1±0.2	3.2±0.8
3.7	180.2±7.5	14.9±0.5	174.6±5.8	14.2±1.4	4.2±0.3	6.6±0.6	3.1±0.4	3.4±0.8
Needle age								
1	173.0±8.8	15.0±0.3	164.8±4.2	17.7±0.4				
2	193.4±5.4	15.3±0.3	169.9±2.8	11.8±0.5				
$p > F$								
Spacing	0.796	0.844	0.061	0.611	0.108	0.56	0.285	0.421
Needle age	0.052	0.479	0.164	<0.001				
Spacing × needle age	0.589	0.763	0.899	0.632				

Note: Values are means ± SEs. Needle age 2 is the most recent fully expanded foliage and needle age 1 is the next adjacent older foliage. Flushes are the three oldest flushes on a branch. SLA, specific leaf area.

mass as a percentage of total (woody root plus stem) mass in loblolly pine plantations are 26%–29% in 11-year-old stands (Samuelson et al. 2008) and 24% in 48-year-old stands (Van Lear and Kapeluck 1995). By comparison, 14% of biomass was allocated to roots versus roots plus stems in the Olinda stands, representing a distinct difference from the mainland. Pine stands grown in fertile soils may allocate less C to belowground net primary productivity than stands in nutrient-limited soils (Gower et al. 1994). However, soil C content was within the range reported for mesic to wet native montane forests in Maui (Schuur et al. 2001) and for Hawaiian dry tropical forest sites (Elmore and Asner 2006).

Leaf A_{max} was comparable with reports for loblolly pine on the mainland with similar N_A. Predicted A_{max}, based on relationships developed for loblolly pine in Florida, with an N_A of 0.7 $cm^2 \cdot g^{-1}$ was 3.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (McGarvey et al. 2004). High carrying capacity does not appear to be related to greater light use efficiency or higher photosynthesis rate relative to mainland trees but rather to a longer growing season. Leaf Φ was 0.015 $\mu mol\ CO_2 \cdot \mu mol\ photon^{-1}$ in upper canopy foliage of Olinda trees compared with the 0.017–0.031 $\mu mol\ CO_2 \cdot \mu mol\ photon^{-1}$ reported for young loblolly pine on the mainland (Samuelson et al. 2001). There appeared to be no winter decline in A_{max} but possibly seasonal precipitation and D related changes in g_S. Monthly precipitation and g_S were lower and maximum D was higher in July than in January but A_{max} was similar between dates. Average foliar R_D was 0.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and low compared with growing season values of 0.9–1.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for loblolly pine in Virginia (Samuelson et al. 1992) and 1.3–1.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for loblolly pine in Georgia (Samuelson et al. 2001). Foliar R_D is strongly related to temperature and represents a significant proportion, 30%–55%, of annual autotrophic respiration in loblolly pine (Maier et al. 2004). The range in average daily temperature was markedly lower at Olinda compared with temperatures typical of loblolly pine's native range. Nedlo et al. (2009) proposed that not only high temperatures but also greater temperature extremes reduce growth in loblolly pine through lack of full thermal acclimation of foliar R_D. The combination of high temperatures, high D, and limited soil water availability during the growing season has been shown to limit growth of other tree species relative to more favorable exotic environments (Waring et al. 2008).

Patterns in percent latewood support the hypothesis that greater ring SG at lower latitudes is in response to greater latewood formation favored by longer growing seasons and extended photosynthate production (Jokela et al. 2004). For example, our average whole-core percent latewood of 44.4 was higher than the range of 33.8–40.1 for loblolly pine sampled throughout the southern United States (Jordan et al. 2008). Plots of SG and percent latewood generally followed the same profiles as those reported for loblolly pine from the United States mainland (Hennessey et al. 2004; Martin and Jokela 2004; Clark et al. 2006; Mora et al. 2007; Jordan et al. 2008). Whole-core ring SG is influenced more by the latewood to earlywood ratio rather than earlywood and latewood SG (Clark and Saucier 1989; Tasissa and Burkhart 1998), which would account for higher whole-core SG in Olinda trees relative to Jordan et al. (2008) (0.49 for Olinda versus an average 0.46 for the mainland). The higher mean whole-core earlywood SG and a lower corresponding value for the latewood SG relative to Jordan et al. (2008) would appear to reflect a more moderated growth pattern resulting from a longer growing season. At the Olinda site, stem growth was possibly more even across the year rather than dominated by a surge of growth in the spring and slowing of growth in the fall related to temperature and water availability. Springtime water deficits on mainland sites are common and limit the growth of southern pines (Gholz and Boring 1991). Thus, earlywood SG may be higher and latewood SG may be lower and result in greater latewood formation, even in mature wood, in a manner analogous to that hypothesized for loblolly pine in its native range at lower latitudes (Jokela et al. 2004).

Leaf area index was not exceptionally high (3.0–3.2) relative to mainland plantations but the SLA of sun foliage appears to be higher in Olinda trees (183 $cm^2 \cdot g^{-1}$ in July and 167 $cm^2 \cdot g^{-1}$ in January) than in mainland trees. The SLA of sun foliage of loblolly pine was 112 $cm^2 \cdot g^{-1}$ in 9-year-old stands in Virginia (Samuelson et al. 1992), 73–90 $cm^2 \cdot g^{-1}$ in stands in Louisiana ranging in age from 9 to >34 years (Baldwin et al. 1997), 50–55 $cm^2 \cdot g^{-1}$ at canopy closure in loblolly pine in Texas (Chmura and Tjoelker 2008), 106–118 $cm^2 \cdot g^{-1}$ on good sites with stands ranging in age from 18 to 75 years (Shelton and Switzer 1984), and 122 $cm^2 \cdot g^{-1}$ in 11-year-old stands that were irrigated and fertilized (Samuelson et al. 2008). An intriguing thought is that higher SLA may be a morphological adjustment to intercept more diffuse radiation. An increase in the diffuse fraction of PAR has been shown to increase canopy photosynthesis (Mercado et al. 2009; Still et al. 2009), and typically, shade leaves have higher SLA than sun leaves (Bjorkman and Holmgren 1963) and are exposed to a higher diffuse fraction of irradiance (Still et al. 2009). The Olinda site is located on the northwestern leeward side of Haleakala and is subjected to high variability in diffuse radiation as a result of a tradewind inversion on the leeward side of Haleakala (Giambelluca and Nullet 1991). Cloud and fog zones begin at an elevation of approximately 1200 m and may shift rapidly with varying cloud conditions and down mixing of dry air through the inversion layer (Giambelluca and Nullet 1991).

Harms et al. (1994) observed increases in flush number and needle length of loblolly pine trees in the Olinda Study when compared with loblolly pine of similar age and spacing in South Carolina and suggested that increased flushing was in response to climatic differences between sites. Mature loblolly pine trees usually produce two or three flushes (Dougherty et al. 1994; Murthy and Dougherty 1997) but up to six flushes in 30- to 35-year-old trees were reported by Harrington (1991) on sites with optimal soil moisture. In the Olinda study at age 26, Harms et al. (1994) reported an average of three flushes with a range of two to four flushes whereas we tallied an average of 3.8 flushes with some trees producing as many as six flushes. The oldest flush was the longest and similar in shoot length to the same-age foliage in Harms et al. (1994). However, Harms et al. (1994) reported that the three flushes were of similar length in March. Given their shorter length, the flushes measured in January were likely initiated in December 2008 and considerable leaf expansion in the two younger flushes would need to occur from January to March, during the rainy season, to produce equal-length flushes. It is unclear if loblolly pine grown on Maui expresses true winter dormancy with a chilling requirement or if trees exhibit reduced flushing and shoot growth during the drier months. In addition, there has been no evidence of pests and diseases typically found in the native range of loblolly pine such as tip moth (*Rhyacionia frustrana* (Comstock)) and fusiform rust (*Cronartium fusiforme* Hedg. & Hunt ex Cumm.) (Schultz 1997) that can cause significant growth losses, although an aphid and various fungi have been found on loblolly pines in Hawaii (Hodges 1983; Schultz 1999).

In summary, stockability in the Olinda Study at age 47 remained much higher than maximum carrying capacity reported for mainland stands. DeBell et al. (1989) and Harms et al. (2000) stressed the need to better understand the importance of morphological and physiological factors associated with high levels of stockability in the Olinda Study. We recognize that plant and environmental factors associated with rapid early stand growth may be different from factors that we measured at age 47 years. Given that caveat, we propose that increased carrying capacity at the Olinda Study is related to (*i*) consistent year-round leaf C gain and reduced foliar R_D as a result of a moderate climate and less seasonal variation in temperature, which is also supported by increased percent latewood, (*ii*) high nutrient availability, in particular Ca, (*iii*) reduced C allocation belowground, and (*iv*) changes in shoot morphology, specifically high SLA and increased number of flushes relative to mainland stands. There was no evidence of lower wood quality compared with mainland loblolly pine stands.

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