

Age-related Decline in Forest Ecosystem Growth: An Individual-Tree, Stand-Structure Hypothesis

Dan Binkley,^{1,2,*} José L. Stape,^{1,4} Michael G. Ryan,^{1,3} Holly R. Barnard,^{1,3} and James Fownes^{5,6}

¹Department of Forest Sciences, Colorado State University, Ft. Collins, Colorado 80523, USA; and ²Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, Colorado 80523, USA; ³USDA Forest Service, Rocky Mountain Research Station, 240 W. Prospect Avenue, Ft. Collins, Colorado 80523, USA; ⁴Department of Forest Sciences, University of São Paulo, Piracicaba, SP, CNPq Brazil; ⁵College of Tropical Agriculture and Human Resources, University of Hawaii, Manoa, Hawaii 96822, USA; and ⁶Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003, USA

ABSTRACT

Forest growth is important both economically (yielding billions of dollars of annual revenues) and ecologically (with respect to ecosystem health and global carbon budgets). The growth of all forests follows a predictable general trend with age. In young forests, it accelerates as canopies develop; it then declines substantially soon after full canopy leaf area is reached. The classic explanation for the decline in growth invoked the increasing respiration costs required to sustain the larger masses of wood characteristic of older forests. Direct measurements of respiration have largely refuted this hypothesis, and recent work has focused on stand-level rates of resource supply, resource use, and growth. We developed and tested a hypothesis at the scale of individual trees (in relation to stand structure) to explain this declining stand-level rate of stem growth. According to our hypothesis, changes in stand structure allow dominant trees to sustain high rates of growth by increasing their acquisition of resources and using these resources

efficiently (defined as stem growth per unit of resource used); smaller, nondominant trees grow more slowly as a result of their more limited acquisition of resources and a reduced rate of growth per unit of resource acquired. In combination, these two trends reduce overall stand growth. We tested this hypothesis by comparing growth, growth per unit of leaf area, and variation among trees within plots in two series of plantations of *Eucalyptus* in Brazil and by estimating individual-tree rates of growth and use of light, water, and nutrients in a plantation of *Eucalyptus saligna* in Hawaii. Our results supported the individual-tree hypothesis. We conclude that part of the universal age-related decline in forest growth derives from competition-related changes in stand structure and the resource-use efficiencies of individual trees.

Key words: Forest growth; *Eucalyptus* plantations; ecosystem production; growth decline; resource use.

INTRODUCTION

One of the most universal patterns in the growth of forests is a humped trend in stem production through stand development. Forest growth in-

creases after stand initiation, peaks near the time when maximum leaf area is attained, and then declines substantially. This pattern has been recognized for centuries (see the overview in Assmann 1970) and has been the subject of research in production ecology for decades (compare Möller and others 1954; Kira and Shidei 1967). The classic explanation for the postpeak decline has invoked a

Received 19 February 2001; accepted 19 June 2001.
*Corresponding author; email: dan@cnr.colostate.edu

combination of declining stand-level growth (gross primary production) and an increase in stemwood respiration (lowering net primary production). This elegant model has become legendary in forest ecology textbooks (compare Kimmins 1997; Barnes and others 1998). However, two recent reviews and a workshop all concluded that the available evidence does not support the stem-respiration explanation (Gower and others 1996; Ryan and others 1997; Gower and McMurtrie 1999).

What then does explain the universal decline in forest growth after peak leaf area is reached? Most previous and current work on this question has focused on the scale of stand-level patterns, such as hectare-level stem growth, net primary production, leaf area, and belowground production. In this paper, we propose that part of the answer may lie at the scale of single-tree patterns of stand structure, with changes in these individual-tree trends summing to provide the classic stand-level decline in stem growth.

The increasing use of resources by dominant trees is a well-known feature of forest stand development (compare Assmann 1970; Oliver and Larson 1996; Smith and Long 2001), and changes in stand structure have been thought to lead to reductions in stand-level growth because dominant trees, which use large proportions of a stand's resources, are inefficient at growing wood. In the past, direct measurements of single-tree rates of resource use were difficult, and inferences were often based on ideas about the ground area projection of canopies or a holistic notion of growing space (compare Assmann 1970; Oliver and Larson 1996; Smith and Long 2001).

In contrast, we propose that changes in stand structure contribute to declines in stand-level growth by increasing differences in the efficiency of resource use (defined as wood production per unit of resource use) between dominant and nondominant trees. We hypothesized that prior to maximum leaf area, all trees obtain resources and have high rates of production per unit of resource used. As competition for resources intensifies, the dominant trees continue to use large quantities of resources, typically increasing their proportional share of resource use at the expense of nondominant trees. Further, the dominant trees with high supplies of resources should use those resources more efficiently than nondominant trees to produce stem growth. This trend could be universal because older forests are typically comprised of dominant and nondominant trees. Moreover, heavily thinned forests that contain only dominant trees have lower densities of trees per hectare that may have lower

rates of wood production owing to lower resource use (such as lower light interception).

We tested this hypothesis with three case studies of fast-growing plantations of *Eucalyptus* trees. These plantations follow the same trends in stem growth as forests in temperate zones, typically reaching a maximum rate of stem growth when stem biomass is on the order of 40–60 Mg/ha. Tropical growing conditions and intensive management allow these plantations to reach peak growth about 10 times faster than the rate generally observed in temperate forests (Ryan and others 1997).

Our hypothesis test had three components. First, a circumstantial test compared growth in stands of *Eucalyptus* in Brazil that originated either from seed or from clonal propagation techniques. If the clonal stands showed a higher growth rate and more uniform growth among stems, it would indicate that differences in stand structure may contribute to stand-level differences in production, as predicted by both the classic forestry literature and our hypothesis. Conversely, a lack of difference in growth between these different stand structures would indicate that stand structure plays only a minor role in changes in stand-level growth over time and that some ecophysiological factor that scales with tree size is more important (Ryan and others 1997). The second case examined within-stand patterns in stem growth and leaf area of individual trees in Brazil; our hypothesis would be supported if the dominant trees showed higher rates of stem growth per unit leaf area than smaller ones. Our third case was similar to the second, except that we used direct estimates of resource use (rather than leaf area) in a 1-year-old and a 5.5-year-old stand in Hawaii.

METHODS

Case 1: Growth and Variance within Clonal and Seedling Plots in Brazil

We compared stemwood growth rates and within-plot variability of tree sizes in 22 experiments (by International Paper do Brasil) within 100 km of Mogi-Guacu (22°21'S, 46°58'W) in São Paulo State, southeastern Brazil. These experimental trials were designed to evaluate the growth performance of a range of *Eucalyptus* clones. We used these experiments to examine differences in production and variance in stem sizes between clonal stands and seedling-origin stands. The trials were planted from 1988 to 1994 on highly weathered, deep (more than 2.5 m) Oxisols (clay content from 18% to 50%) or Entisols (clay content from 3% to 15%).

Table 1. The Initial Stand-level Characterizations and the Parameters of the Relationships between the Woody Mass (W, kg), Foliage Leaf Area (LA, m²), and Diameter at Breast Height (D)

Site No.	Soil ^a (Clay)	Age at Start of Current Year (y)	Wood Mass (Mg/ha)	Leaf Area Index (m ² /m ²)	Current Wood Increment (Mg ha ⁻¹ y ⁻¹)	Wood Regression Coefficients		Foliage Regression Coefficients	
						a _w	b _w	a _f	b _f
1	O (12)	5.5	54.6	2.8	5.5	0.090	2.572	0.089	2.311
2	U (12)	6.5	70.6	2.8	14.0	0.083	2.602	0.080	2.257
3	O (13)	6.6	86.7	3.4	7.6	0.152	2.408	0.146	2.058
4	U (6)	5.5	87.3	3.9	2.4	0.125	2.469	0.157	2.076
5	U (10)	5.5	106.1	3.4	17.8	0.124	2.516	0.037	2.547
6	U (21)	5.5	91.1	3.1	17.5	0.250	2.216	0.159	1.980
7	U (14)	5.8	180.8	4.8	24.2	0.123	2.502	0.001	3.935
8	U (12)	5.5	202.6	5.0	2.7	0.111	2.551	0.011	2.855
9 ^b	E(5)	5.6	84.2	2.7	17.6	0.067	2.734	na	na
10	U (4)	6.5	77.2	2.6	4.1	0.176	2.355	0.002	3.596
11	E (4)	7.3	148.4	4.0	15.2	0.269	2.193	0.017	2.697

^aO (Oxisol), U (Ultisol), E (Entisol), and clay (%) at 30-cm depth

^bSite 9 used the foliage allometric of site 10 (closest site).

(W = a_wD^{b_w}, LA = a_fD^{b_f})

Mean annual temperature is 21.2°C. Rainfall reaches 1350 mm, concentrated between October and March. Plots were established with a completely randomized block design. There were three (one trial) or four (21 trials) replicate plots, with tree spacings of either 3 × 3 m (441-m² plots) or 2.5 × 3 m (368-m² plots). From the 7 × 7 rows of trees in each plot, the diameters and heights of the central group of 5 × 5 trees and the individual volume were estimated by the age-specific allometric equation. For example, the equation for 6–8-year-olds was:

$$\text{Stem Volume} = 0.00005447 \text{ DBH}^{1.921157} h^{0.950581} \quad (r^2 = 0.99, n = 202)$$

where stem volume is in cubic meters, DBH is diameter in centimeter at 1.3-m height, and height (h) is in meters. The plot total volume was then scaled to hectares based on the plot area. At each site, these experiments tested the performance of between four and 29 clones of *E. grandis*, *E. saligna*, *E. urophylla*, and *E. grandis* × *urophylla*. Each experimental site also included seed-origin treatments that used high-performance *E. grandis* seedlings grown from seeds collected from carefully selected mother trees on a Seed Production Area in the region (ex-Coff's Harbour, Australia). Complete pest and weed control were applied in all experiments, and all plots received fertilizer (30 kg N

ha⁻¹, 70 kg P ha⁻¹, and 30 kg K ha⁻¹) at the time of planting.

Case 2: Within-Plot Patterns in Wood Growth per Unit Leaf Area in Brazil

The second set of plantations in Brazil (by Copener Florestal Ltd.) consisted of 11 stands of *Eucalyptus grandis* × *urophylla* in mixed clonal plantations (30–50 clonal cuttings randomly mixed in the nursery) within a 50-km radius of Entre-Rios (11°58'S, 38°07'W) in Bahia State in northeastern Brazil (Table 1). We predicted that larger trees would have higher rates of wood production per unit of leaf area than smaller trees within the same stands.

The stands were established as permanent inventory locations covering the breadth of regional soils and climate. The soils are highly weathered and deep (more than 2 m) Ultisols, Oxisols, and Entisols. Annual precipitation varies from 900 mm (inland) to 1400 mm (near the coast). Mean temperature is 25.5°C (Stape and others 1997). All forests were planted at 3.5 m × 2.6 m spacing. They were given an initial fertilization of 12 kg N ha⁻¹, 41 kg P ha⁻¹, and 13 kg K ha⁻¹, and chemicals were applied to control leaf-cutting ants and weeds.

In each stand, a circular inventory plot of 471 m² was measured in 1996–97 and again 1 year later, keeping track of individual tree development. After the last measurement, nine trees in each stand were harvested; these trees represented three size classes

(mean diameter, plus one standard deviation, and minus one standard deviation). At harvest time, the forests were between 6.3 and 8.3 years old (rotation ages). For each tree, the biomass and leaf area were determined from quantitative subsamples. Woody biomass (stem+bark+branch) was estimated by stand-specific allometric equations ($W = a_w \text{DBH}^{b_w}$) for all trees within the stand. Site-specific allometrics were also established for leaf area per tree ($LA = a_f \text{DBH}^{d_f}$). All equations were fitted using the Gauss-Newton nonlinear method (SYSTAT 2001) (Table 1). At the stand level, the summation of the individual trees' growth was divided by the plot area to estimate current annual wood increment and leaf area index.

Case 3: Resource Use and Wood Growth in Hawaii

The Hawaii experiment was part of a larger investigation into the ecophysiology of declining growth rates. Annual precipitation averages more than 4000 mm at this site, and well-drained, deep (more than 2 m) Andisol soils provide a consistently large supply of water. We examined growth and resource use in two 30×30 m plots of *Eucalyptus saligna* trees (grown from seeds) at 3×3 m spacing. The main plot was 5.5 years old at the time of harvest in September 1999, and rapid growth had been fostered by complete weed control. Fertilization four times yearly comprised a total (over 5.5 years) of $1260 \text{ kg N/ha}^{-1}$, 540 kg P/ha^{-1} , $1040 \text{ kg K/ha}^{-1}$; in addition, a complete set of other nutrients was given once yearly (Binkley and Resh 1999). Prior to harvesting at 5.5 years of age, the 21 trees in the center 225-m^2 subplot were measured for diameter at breast height (DBH, 1.3 m) and canopy extent in four directions. The other plot was 1 year old at the time of harvest in September 1999 and had been treated in the same way as the older plot.

We used Granier-type sensors (Granier 1987) to measure water flux for all 21 trees in the 5.5-year-old plot and for 13 trees in the 1-year-old plot. In both plots, water flux was measured for 13 days (calendar days 237–250 of 1999). Sensor probes were constructed of pairs of 20-mm-long, 1.65-mm-diameter stainless steel needles. A pair of sensors was inserted 8–15 cm apart at a height of 15 cm (younger plot) or 2 m (older plot) (Barnard 2000). Natural temperature differences between the probes within an individual tree were less than 0.1°C . In three trees, two sensors were placed opposite each other at the same height to test for within-tree differences in estimated water flux; flux estimates differed by up to 11% within trees. Temperature differences of all sensors were recorded

every 15 sec and stored as 15-min means with a 2/x datalogger (Campbell Scientific Instruments, Logan, UT, USA). Water use per tree was extrapolated linearly to an annual basis from the 13 measurement days. This scaling should be robust in relation to water use among trees, although the actual annual rate may be somewhat inaccurate. Given the high precipitation and lack of any evidence of water limitation in these plantations, we believe that the annual extrapolation is reasonable.

Trees were cut down, and each canopy was divided into thirds based on height. All leaves in each canopy third were stripped and weighed in the field. A subsample from each third of each canopy was returned to the lab for the determination of specific leaf area and oven-dried weight. The canopy subsamples were ground and analyzed for nitrogen (N) concentration by combustion furnace.

Stem growth in the 5.5-year-old plot was calculated using a biomass regression equation developed from trees at this site:

$$\text{Stem Mass} = 0.06619 \text{ DBH}^{2.5001} \\ (r^2 = 0.99, n = 56)$$

where stem mass is wood+bark in kilograms, and DBH is diameter in centimeters at 1.3-m height (M. G. Ryan D. Binkley, J. Fownes, unpublished). Stem growth in the 1-year-old plot was determined by weighing the entire stem in the field and converting to oven-dried mass based on the moisture content of a subsample from each tree.

Leaf area over the development of the 5.5-year-old stand was measured every 2–3 months with a LICOR LAI-2000 (Licor, Inc., Lincoln, NE, USA). Periodic calibration was based on the destructive harvesting of trees to establish allometric relationships between diameter and leaf area. We corrected the LAI-2000 measurements so that they matched the allometric estimates and applied this correction to all LAI-2000 measurements between harvests.

To test the hypothesis, we determined the leaf area at the time of harvest for each tree (rather than by allometry). We used the MAESTRO model (Wang and Jarvis 1990) to estimate light absorbed by individual tree canopies for each tree in the 5.5-year-old plot. MAESTRO simulates light absorption for an individual tree crown using crown-specific information on crown dimensions and height, leaf area, and position with respect to other trees, and species or site-specific values of crown shape, leaf area distribution, and leaf angle. We measured the center of each canopy to the nearest 0.5 m, crown radii in four orthogonal directions (parallel and perpendicular to tree rows), tree

height, and crown length. We simulated light absorption for a 15-day period in August 1999 that had a mixture of sunny and cloudy days and used a more recent version of the program code (MAESTRA; B. E. Medlyn, University of New South Wales, Australia, <http://www.ed.ac.uk/~bmedlyn/maestra/>).

The model was forced with data for incoming photosynthetically active radiation measured with a sensor located in a clearing approximately 200 m east of the stand. The model predicted that the stand would intercept 90% of incoming photosynthetically active radiation, nearly identical to the 88% interception measured over several days in September 1999 with a Decagon Accupar Ceptometer (Model PAR-80; Decagon Devices, Pullman, Washington). The average daily interception of light was extrapolated to an annual estimate by multiplying by 365 days. This simple approach probably overestimates the actual light intercepted per tree because of seasonal patterns in incoming light and leaf area, but it should be sufficient for comparisons among trees within the stand, and it does provide units for a comparison with annual stem growth.

Nitrogen use was indexed as the N content of the canopies, extrapolated from the measured fresh weights of the canopies and the N concentrations in the subsamples, as determined on a NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy).

RESULTS

Case 1: Growth and Variance within Clonal and Seedling Plots in Brazil

The prediction that clonal stands would grow more rapidly than seed-origin stands was supported by the data from the 22 clonal trials (Figure 1). Clone-origin treatments averaged 17% faster growth than seed-origin trees (32.6 vs 27.8 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$, paired t -test, $P < 0.01$). The mean for the clones at each location is an average of the four to 29 clones comprising the trial at a given location, and some of these clones performed poorly. If only the better half of the clones in each trial were examined, then the clone-origin treatments would show an average 32% faster growth than the seed-origin trees (36.8 versus 27.8 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$). We speculate that the greater growth in the clonal stands was the result of a more uniform stand structure and consistent efficiency of resource use among individual trees, whereas the remarkably higher growth rate of the better half of the clonal types resulted from both a

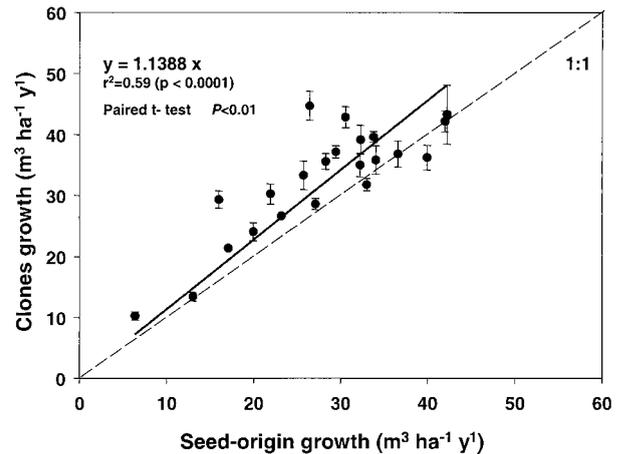


Figure 1. Stem growth (mean annual increment) was substantially higher for clonal stands ($33 \text{ m}^3 \text{ha}^{-1} \text{y}^{-1}$) than for stands grown from *Eucalyptus* seedlings ($28 \text{ m}^3 \text{ha}^{-1} \text{y}^{-1}$). Each site had from four to 29 clones (average, 14) for comparison with plots grown from seedlings of carefully selected mother trees. Bars represent one standard error of the mean of the clones.

uniform stand structure and superior genotypes. Separating these confounded effects of stand structure and genotypes could have important operational and strategic consequences.

The clonal stands showed lower variation in stem volumes, as predicted. The coefficients of variation (CV, the standard deviation divided by the mean) in stem volumes for the 22 experiments averaged 50% for *E. grandis* seed-origin trees, as compared with 30% for the clones (Figure 2). For both types of stands, variance increased with stand age, indicating increased dominance and suppression within the stands.

Case 2: Within-Plot Patterns in Efficiency of Wood Growth per Unit Leaf Area in Brazil

Wood growth per unit of leaf area increased dramatically with increasing tree size within stands in eight of 11 stands in Brazil (Figure 3). Across these eight stands, wood growth per unit of leaf area increased by almost threefold with an increase in tree diameter from 10 to 20 cm, and the largest 25% of the trees produced 50% more stem growth per unit of leaf area than the other 75% ($P = 0.001$). The three stands that showed no trend in stem growth/leaf area across tree diameters were the least productive. The difference in wood growth per unit of leaf area among trees within stands increased with increasing stand production; a doubling of stand increment was associated with a dou-

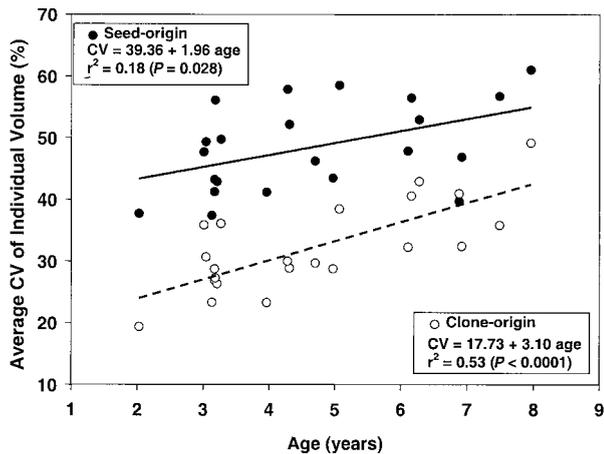


Figure 2. Stem volume for *Eucalyptus* plots grown from seed in the 22 experiments at São Paulo State was substantially more variable (CV = coefficient of variation) among stems within plots for seedling-origin plots than for clonal plots.

bling in the slope of the relationship (within stands) between diameter and wood growth per unit of leaf area. Overall, the more productive sites showed greater differentiation in efficiency among trees. Bigger trees were more efficient than smaller trees in the same stands, and this difference in efficiency increased as stand productivity increased.

Case 3: Resource Use and Wood Growth in Hawaii

At 5.5 years, the trees averaged 21.6 m in height (range, 8.0–29.2 m), with a stand leaf area index of 5.1 and a total stem biomass of 96.4 Mg/ha⁻¹. Stem wood production in this plot peaked at about 2.5 years of age (Figure 4) and declined by about 50% by year 5. Leaf area remained high after the peak in stem growth, so the decline in stem growth was related to a decrease in the efficiency of stem growth per unit leaf area at the stand level. The decline in stem growth generally followed the trend in stand-level leaf area, and the stand-level efficiency of stem growth per square meter of leaf area declined from about 0.47 kg/m⁻² in years 1 and 2 to 0.30 kg/m⁻² in year 5.

The patterns in case 2 were based on individual-tree leaf area, since no estimates were available for individual-tree light interception. The trend in light interception per unit of leaf area (based on the MAESTRA model and calibrated by the field data) declined exponentially with increased tree diameter ($r^2 = 0.39$, $P < 0.01$). Whereas a 10-cm-diameter tree averaged 1.6 MJ APAR/m⁻² of leaf area, a

20-cm tree intercepted 1.0 MJ APAR/m⁻² of leaf area. This lower rate of light interception per unit of leaf area resulted from greater self-shading within canopies of larger trees. This trend indicates that the relationships between stem growth per unit of leaf area in case 2 would likely be a conservative estimate of the trend in stem growth per unit of light intercepted, since the larger trees (that is, those with more leaf area) should have had lower light interception per unit of leaf area.

In the 5.5-year-old plantation, trees with higher light interception, greater canopy N content, and more water use had higher rates of stem growth per unit of resource use (Figure 5). The largest 25% of the trees accounted for 45%–50% of the total plot use of light, water, and N, but they contributed a disproportionate 60% of the total plot wood growth. The efficiency of wood growth per unit of resource used was about twice as great for the top 25% of trees than for the other 75%, supporting the individual-tree hypothesis.

At the time of harvest, trees in the 1-year-old plot were 6–8 m tall and had 10.7 Mg of stem/ha⁻¹ and a leaf area index of 5.25. The difference in efficiency between the top 25% and lower 75% of the trees (Figure 6) was about one-third the difference found for the 5.5-year-old trees, which is consistent with the increasing variance among trees found over time in case 1 from Brazil. The 5.5-year-old trees were also more efficient than the 1-year-olds in growing wood per unit of leaf area or resource, which would be expected since the canopy of the younger plot was notably smaller early in the year.

DISCUSSION

Implications from the Literature

Only a few studies have examined the relationships between growth and resource use on an individual-tree basis within forests. When Kaufmann and Ryan (1986) estimated individual tree growth as a function of potential light absorption, they concluded that suppressed understory trees may be as efficient as dominant trees. Roberts and others (1993) argued that leaf area efficiency (stem growth per unit of leaf area) should be higher among non-dominant trees in stands with low leaf area and many gaps in the canopies. They expected that in stands with higher leaf area and greater canopy stratification, intermediate trees would have higher leaf area efficiencies than either suppressed trees (which received too little light) or dominant trees (which could not fully utilize all the intercepted light).

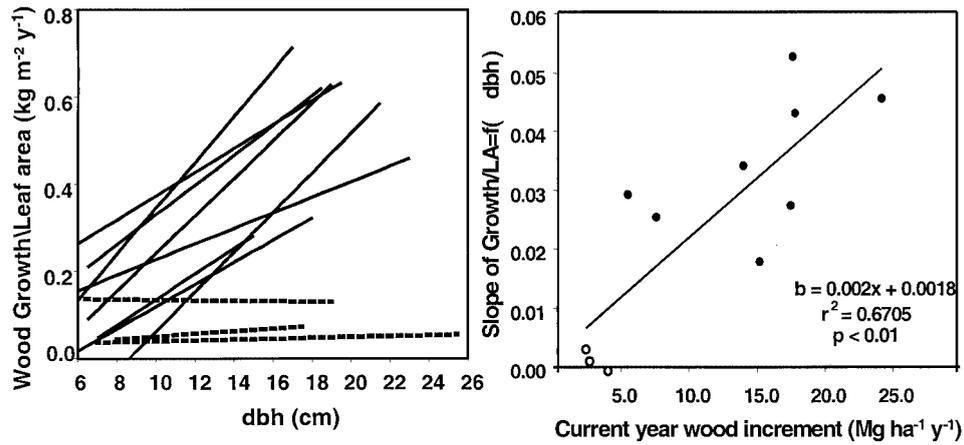


Figure 3. Wood increment per unit of leaf area among trees within 11 stands (*left*) (solid lines significant at $P < 0.01$; dashed lines $P > 0.1$) and slope of the relationship within stands as a function of current stand increment of wood (*right*) (open circles are slopes for the nonsignificant relationships; solid circles are for the significant relationships from the left figure).

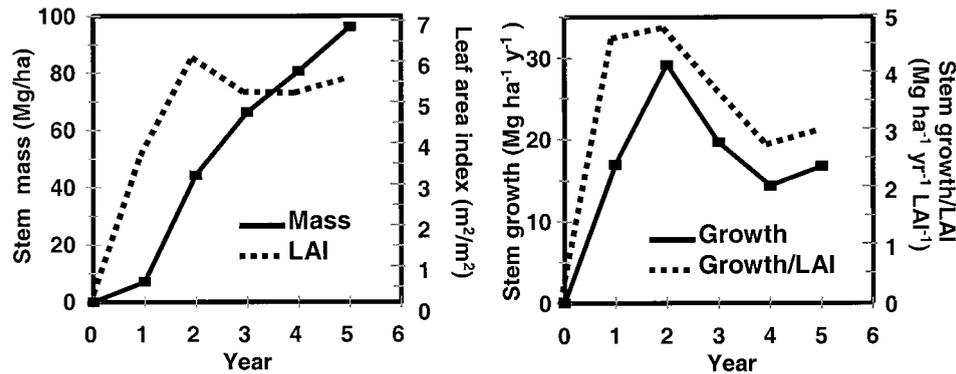


Figure 4. Accumulation of stem mass and leaf area (*left*) and stem growth and stem growth per unit of leaf area (*right*) for the *Eucalyptus saligna* plot in Hawaii.

O'Hara (1988) had the strongest empirical evidence to test for individual tree patterns within stands. Using the sapwood area of Douglas-fir stems as a surrogate for leaf area, he found that stem volume growth per unit of sapwood area was higher for trees with more sapwood area. Trees with twice the sapwood area showed about 65% more stem growth per unit of sapwood area. The differences in growth per unit of sapwood area were strongest in an unthinned control plot, where dominant trees produced twice as much wood per unit of sapwood area as intermediate trees. Stands that had been thinned four times over the 64 years of stand development showed only a 15%–30% greater growth per unit of leaf area in dominant trees.

These findings are consistent with our individual-tree hypothesis. The thinning treatments reduced the variance in tree sizes within O'Hara's (1988)

stands and reduced the range in stem growth per unit sapwood area. In a related paper that focused on stand-level patterns, O'Hara (1989) showed that two pairs of stands with similar basal area and sapwood area differed in volume increment per unit of sapwood area as a result of different tree densities; the pair with 20%–30% more trees showed an approximately 20%–30% greater increment in stem volume per unit of sapwood area. However, confounding differences in stand density and structure (particularly canopy structure) make it difficult to test ideas about the effects of stand structure on the efficiency of individual trees. O'Hara (1996) also reported higher rates of stem volume increment per unit of leaf area in older cohorts within multicohort stands of ponderosa pine (*Pinus ponderosa*), providing more direct support for the individual-tree hypothesis (although the trend in dominance was confounded by trends in tree age).

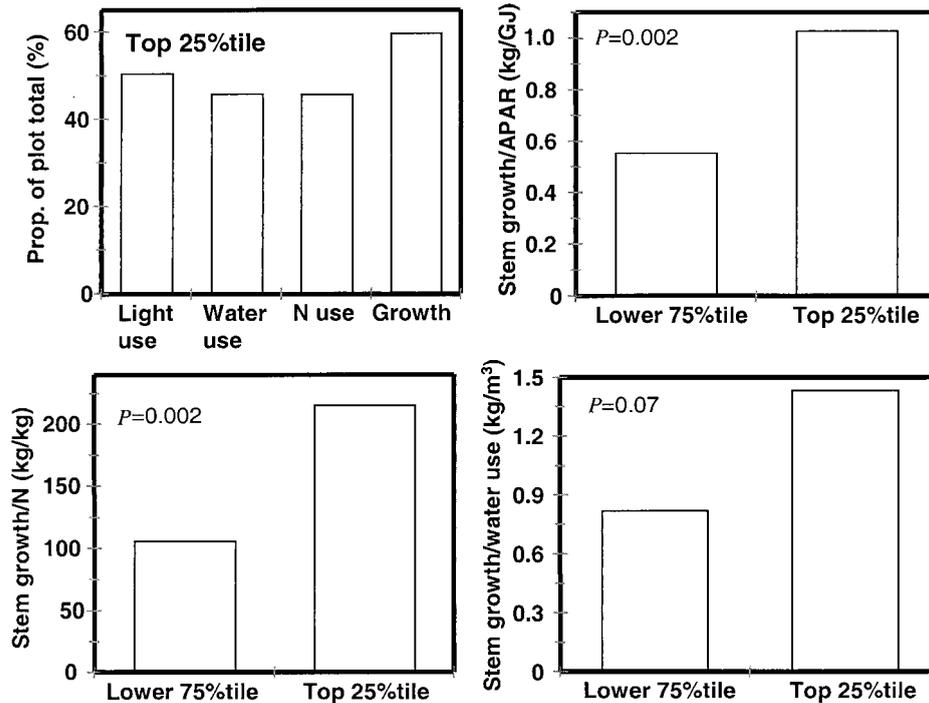


Figure 5. The largest 25% of the trees in the 5.5-year-old plot in Hawaii (case 3) used 45%–50% of the light, water, and nitrogen in the plot, but they contributed 60% of the plot stem growth (*top left*). The largest 25% of the trees were about twice as efficient in producing wood per unit of light (*top right*), nitrogen (*bottom left*), and water (*bottom right*).

Smith and Long (2001) also proposed that changes in stand structure and the efficiency of individual trees over time may explain the universal pattern of stand-level decline in production, but their proposition differs from our individual-tree hypothesis. They concluded that stand-level declines in growth were an “emergent property” at the “population level” that could not be derived from individual-tree physiological processes or the sums of individual-tree features. In the studies presented here, differences in tree population structure were not relevant, since we examined individual trees and stands at single points in time (and no stands had suffered much mortality since planting). Smith and Long (2001) asserted that the progressive redistribution of a constant amount of foliage into fewer, larger crowns should decrease the efficiency of dominant trees at the same time that competitive suppression decreased the efficiency of nondominant trees. In contrast, our hypothesis emphasizes the declining efficiency of nondominant trees, together with a sustained, high efficiency in dominant trees.

Implications of the Hypothesis for Patterns in Forest Growth

The evidence presented here supports the single-tree/stand-structure hypothesis that suppressed

trees have less wood production per unit of resource use. But what are the ecophysiological processes that underlie this pattern? The simplest explanation might be altered carbohydrate allocation. Perhaps the suppressed trees fix as much carbon (C) per unit of resource used, but they also allocate more C to the production of other tissues (such as roots) or to respiration. Alternatively, the rate of C fixation per unit of resource use could be lower, as a result of lower photosynthetic capacity or performance in suppressed trees. Lower photosynthetic capacity (essentially, the amount of active carboxylating enzyme) or performance (total diurnal photosynthesis) in suppressed trees would imply a lower rate of C uptake for the same level of use of light, N, and water than is observed in dominant trees. Direct experimentation is needed, and the design of these experiments may need to recognize that the optimal “strategy” for a suppressed tree might be persistence (until a canopy dominant tree dies) rather than maximum current C gain.

Stand leaf area declines in most forests some time after reaching a maximum at a relatively early point in stand development (Gower and others 1996; Ryan and others 1997). In cases where leaf area and total light interception at the stand level do not decline (as in case 3 from Hawaii), the single-tree

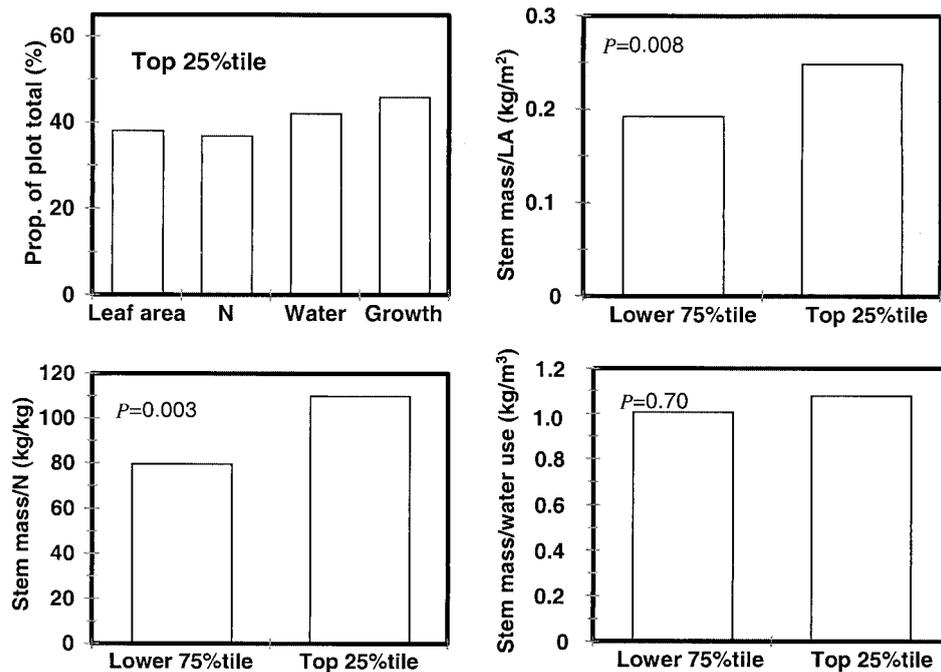


Figure 6. The largest 25% of the trees in the 1-year-old plot in Hawaii (case 3) accounted for 35%–45% of the leaf area, water use, and N use (*top left*), but they contributed 45% of the stem mass (= growth for the 1st year). The largest 25% of the trees were 29% more efficient at producing wood per unit of leaf area (*top right*), 38% more efficient at producing wood per unit of N in the canopy (*bottom left*), and equally efficient at producing wood per unit of water used.

hypothesis predicts that the efficiency of wood production per unit of leaf area declines as the stand differentiates into well-illuminated trees and shaded trees. Poorly illuminated lower canopy leaves on dominant (young) trees would therefore grow more wood than poorly illuminated upper canopy leaves on suppressed (older) trees. This condition could be the result of differences in the allocation of photosynthate in suppressed trees (where the best leaves are shaded) and dominant trees (where most leaves are illuminated). We are not confident that shaded leaves “know” if they are on suppressed or dominant trees, but a recent shading experiment (of individual branches and whole trees) with mountain birch (*Betula pubescens*) showed remarkably strong differences in leaf retention based on the overall illumination status of the canopy (Henriksson 2001). This issue of growth per unit of leaf area (and resource use) needs to be investigated at multiple scales (branch, individual tree, and stand) to determine the extent to which stand-level rates depend on the structure of trees and stands.

Combined with these earlier studies, our work demonstrates that individual trees may vary substantially in stem growth per unit of resource use, and this differentiation in growth efficiency may be accentuated

in stands with the largest variance in tree sizes. Does this pattern of individual trees and stand structure explain the age-related decline in ecosystem production? Perhaps, but more direct tests are needed. We are currently developing a more rigorous test of the individual-tree hypothesis that will compare the total C budgets and resource use of a full rotation of clonal plantations of *Eucalyptus* with different structures (uniform tree sizes and heterogeneous tree sizes for the same clone). If our individual tree hypothesis is supported by this test, it may explain a large portion of the age-related decline in stem growth but not the entire decline. Ryan and others (1997) suggested that age-related declines may derive from a suite of factors, and such important factors as declining nutrient supply clearly reduce productivity in some cases. We think that differentiation of stand structure leads to an overall reduction in the efficiency of producing wood per unit of resource used and that other factors (such as declining nutrient supply) may then amplify this hypothesized universal trend.

The individual-tree hypothesis also has implications for ecosystems that are comprised of more than one species. Surprisingly few experiments have documented the total ecosystem production in monocultures and mixed-species forests; in most cases, monocultures of the faster-growing species

grow more than mixed-species forests (Kelty 1992; Cannell and others 1992). This general trend is also consistent with the individual-tree hypothesis for age-related growth declines. The dominant species should be more efficient in producing wood per unit of resource used, and any resource use by less efficient, nondominant trees should lower total ecosystem growth. The two possible exceptions to this prediction would be situations where the suppressed species could utilize resources that were unavailable to the dominant species. For example, a suppressed species that could grow at light levels below those that could be used by the dominant species might be able to marginally increase ecosystem production (Cannell and others 1992). The second exception would be mixtures that included N-fixing species. These mixtures might show greater growth rates than monocultures as a result of an increased N supply combined with high efficiency of resource use of the non-N-fixer (Binkley 1992; Kaye and others 2000).

ACKNOWLEDGMENTS

This research was funded by the National Science Foundation (DEB93-06356 and DEB97-08521), and J.L.S. collaboration was supported by the CNPq–Conselho Nacional de Desenvolvimento Científico e Tecnológico of the Ministry for Science and Technology of Brazil (201144/97-2). We thank Breandan O’Laoithe, Eoin Kyne, D. White, S. White, and C. Giardina for assistance in the field and lab; Belinda Medlyn for assistance with the MAESTRA program; Fabio Brun, International Paper do Brasil S.A., and Jose Augusto Ribeiro, Copener Florestal, Ltd., for help with the data collection; J. Pastor, K. O’Hara, F. W. Smith, and two anonymous reviewers for insights that served to improve the manuscript; C. Giardina, and R. Senock for overall collaboration on the Hawaii project; and Mauna Kea Agribusiness for providing the opportunity for our work on the Hawaii plantation. D.B. and M.G.R. are also grateful to R. H. Waring and D. Perry for leading our interest to the study of the ecophysiology of stand growth.

REFERENCES

- Assmann E. 1970. The principles of forest yield study. Oxford: Pergamon Press.
- Barnard HR. 2000. Testing the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna* MS [thesis]. Colorado State University, Fort Collins.
- Barnes BV, Zak DR, Denton SR, Spurr S. 1998. Forest ecology. New York: Wiley.
- Binkley D. 1992. Ecology of mixtures of N₂-fixing and non-N₂-fixing tree species. In: Cannell M, Malcolm D, Robertson PA, editors. Ecology of mixed species stands. Oxford: Blackwell Scientific. p 99–123
- Binkley D, Resh SC. 1999. Rapid changes in soils following Eucalyptus afforestation in Hawaii. Soil Sci Soc Am J 63:222–5.
- Cannell M, Malcolm D, Robertson PA, editors. 1992. Ecology of mixed species stands. Oxford: Blackwell Scientific.
- Gower ST, McMurtrie RE. 1999. An analysis of the age-related decline in aboveground net primary production; potential causes and stand-to-global scale implications. Santa Barbara (CA): NCEAS, University of Santa Barbara.
- Gower ST, McMurtrie RE, Murty D. 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol Evol 11:378–82.
- Granier A. 1987. Mesure du flux de seve brute dans le tronc du Douglas par une nouvelle methode thermique. Ann Sci For 44:1–14.
- Henriksson J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. Oecologia 126: 482–6.
- Kaufmann MR, Ryan MG. 1986. Environmental, physiographic, and stand effects on individual tree growth in subalpine forests. Tree Phys 2:47–59.
- Kaye JP, Resh SC, Kaye MW, Chimner RA. 2000. Nutrient and carbon dynamics in a replacement series of Eucalyptus and Albizia trees. Ecology 81:3267–73.
- Kelty MJ, editor. 1992. The ecology of mixed species forests. Dordrecht (The Netherlands): Kluwer.
- Kimmins JP. 1997. Forest ecology. New York: Prentice-Hall.
- Kira T, Shidei T. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap J Ecol 17:70–93.
- Möller CM, Müller D, Nielsen J. 1954. Graphic representation of dry matter production in European beech. Forstl Forsoegsvaes Dan 21:327–35.
- O’Hara KL. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. For Sci 42:1–34.
- O’Hara KL. 1989. Stand growth efficiency in a Douglas fir thinning trial. Forestry 62:409–18.
- O’Hara KL. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can J For Res 18:859–66.
- Oliver CD, Larson BC. 1996. Forest stand dynamics. New York: Wiley.
- Roberts S, Long JN, Smith FW. 1993. Canopy stratification and leaf area efficiency: a conceptualization. For Ecol Manage 60:143–56.
- Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–62.
- Smith FW, Long JN. 2001. Age-related decline in forest growth: an emergent property. For Ecol Manage. 1–3: 175–181.
- Stape JL, Gomes AN, Assis TF. 1997. Estimativa da produtividade de povoamentos monoclonais de *Eucalyptus grandis* x *urophylla* no Nordeste do Estado da Bahia-Brasil em função das variabilidades pluviométrica e edáfica. In: Proceedings of the IUFRO Conference on Silviculture and Improvement of Eucalypts, 24–29 August 1997, Salvador. EMBRAPA/CNPQ, Colombo, Brazil. p 192–8, total pages 417p.
- SYSTAT. 2001. SYSTAT 8.0. Chicago: SPSS Science.
- Wang YP, Jarvis PG. 1990. Description and validation of an array model—MAESTRO. Agric For Meteorol 51:257–80.