

Explaining growth of individual trees: Light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil

Dan Binkley^{a,*}, José Luiz Stape^b, William L. Bauerle^c, Michael G. Ryan^{d,e}

^a Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA

^b Department Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695-8008, USA

^c Department of Horticulture and Landscape Architecture, Colorado State University, Fort Collins, CO 80523, USA

^d Rocky Mountain Research Station, USDA Forest Service, 240W. Prospect, Fort Collins, CO 80526, USA

^e Affiliate Faculty, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Article history:

Received 27 March 2009

Received in revised form 22 May 2009

Accepted 28 May 2009

Keywords:

Eucalyptus clone

MAESTRA

Tropical plantation silviculture

Age-related decline

Competition

ABSTRACT

The growth of wood in trees and forests depends on the acquisition of resources (light, water, and nutrients), the efficiency of using resources for photosynthesis, and subsequent partitioning to woody tissues. Patterns of efficiency over time for individual trees, or between trees at one time, result from changes in rates photosynthesis and shifts in the relative partitioning to wood. We measured the production ecology (stem growth, light interception, and light use efficiency) to explain patterns of growth among trees within plots through stand development, and tested three hypotheses: (1) dominant trees have higher light use efficiency than subordinate trees; (2) lower variation in the size distribution of trees within plots allows higher light use efficiency; and (3) uniform stand structure and high light use efficiency reduce the age-related decline in tree growth. The experiment used clonal plantations of *Eucalyptus* at four locations in eastern Brazil. Irrigation and fertilization treatments ensured the major resource limitation for tree growth would be light supply. The influence of variation in the sizes of trees within plots was tested by comparing plots with all trees planted in a single day (uniform treatment) with plots where planting was spread over 80 days (heterogeneous treatment). Light interception per tree was simulated with the MAESTRA model. Across sites, treatments and whole-rotation stand development, dominant trees showed higher rates of stem growth, light interception, and light use efficiency than subordinate trees (supporting the first hypothesis). For example, dominant trees (80th percentile rank) at the end of the rotation grew four-times faster than suppressed trees (20th percentile rank), as a result of 2.1-fold greater light interception, and 1.8-fold greater stem growth per unit of light interception. In some cases, greater variation among tree sizes within plots led to lower efficiency of light use by average-size trees, providing mixed evidence for the second hypothesis. Greater uniformity of sizes of trees within plots did not substantially mitigate the decline in stem growth from mid-rotation to the end of the rotation, refuting the third hypothesis. The high efficiency of dominant trees underscores the marginal contribution of subordinate trees to total stand growth, and should spur further work on thinning to increase growth and lengthen rotations for dominant trees.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The supply rates of resources (light, water and nutrients) available to individual trees typically differ between trees and change through time, as a result of competition with other plants and differences in environmental conditions (such as soil nutrient availability). Entire stands may experience changes in resource supplies as a result of active forest management, climate trends,

and changes in soils. The factors driving these patterns can be examined by quantifying components of the production ecology equation (Monteith, 1977; Cannell, 1989; McMurtrie et al., 1994; Landsberg et al., 1996; Landsberg, 1997; Binkley et al., 2004):

Gross Primary Production

= Resource supply × Proportion of resource supply captured

× Efficiency of resource use (1)

When the focus is on the growth of stems (as in this paper), additional terms are included in the equation to account for partitioning of photosynthate to the growth of non-stem tissues

* Corresponding author. Tel.: +1 970 491 6519; fax: +1 970 491 6754.

E-mail address: Dan.Binkley@Colostate.edu (D. Binkley).

and respiration (Ryan et al., 1997). Stem increment is the gross primary production minus allocation to respiration and other tissues.

Over the past decade it has become clear that changes in resource use efficiency can account for substantial changes in stem growth of trees and stands. For example, Ryan et al. (2004) found that gross primary production declined by one-third from mid-rotation to late-rotation in a plantation of *Eucalyptus saligna* despite sustained high rates of resource supply and use; wood production dropped by more than half. Binkley et al. (2002) showed that dominant trees in this plantation produced twice as much wood per unit of light, water, and nitrogen as compared to subordinate trees near the end of the rotation. These results led to a general hypothesis that age-related decline in forest productivity resulted from increasing dominance among trees, and declining efficiency of resource use by subordinate trees (Binkley, 2004). The Brazil Eucalyptus Potential Productivity (BEPP) Project was designed to explore factors that determine the growth of individual trees and stands through an entire rotation (Stape et al., in review; Ryan et al., in review), and specifically to test the hypothesis that increasing dominance accounts for a substantial part of the age-related decline in stand growth.

The experiment reported in this paper had one overall objective, and three specific hypotheses. The objective was to apply the production ecology equation to individual trees, gaining insights on the key factors accounting for differences in stem growth among trees and across stand development. The three hypotheses (based on ideas from Binkley et al., 2002; Binkley, 2004) were:

1. Dominant trees have higher growth rates not only because of higher rates of light interception, but also because of greater growth rate per unit of light intercepted (light use efficiency). This would be a Type III pattern in Fig. 1; the development of a Type I or Type II pattern would refute this hypothesis.
2. Stands with lower variation in tree size distribution should show greater growth as a result of higher efficiency of light use by subordinate trees; increasing variation and dominance in a stand would suppress the efficiency of light use by subordinate trees, without increasing the efficiency of dominant trees. This would be supported if trees in the uniform stand structure treatment show higher light use efficiency than those in the heterogeneous treatment.
3. Greater uniformity in stand structure would lead to less age-related decline, as subordinate trees would lose less efficiency of light use in uniform plots. Hypothesis #2 would need to be supported, and the decline in stem growth between mid-

rotation and final-rotation growth rates would also need to be smaller in the uniform stand structure treatment to support this hypothesis.

Some of these ideas were tested for a single plot of *Eucalyptus saligna* at a single point in time (Binkley et al., 2002). We expanded the test of these ideas to four sites in eastern Brazil, with replicated treatments of stand structure and a total of 45 plots. The basic experimental design involved clonal plantations; one treatment minimized dominance among trees by planting all trees on the same day within a plot, and the other increased the development of dominance by staggering the planting time by up to 80 days for trees within each plot. At one location we compared clonal trees with seed-origin trees. Irrigation, intensive fertilization, and intensive weed control minimized (or removed) any limitation by these resources on growth throughout the rotation, leaving competition for light as the key resource issue.

2. Methods

2.1. Site descriptions

Our experiments on stand structure, age, and light use focused on the four BEPP sites (with a different clone in each location), described in detail in (Stape et al., in review). Briefly, the Aracruz site was at 19°49'S, 40°05'W near Aracruz in Espírito Santo, Brazil on an Ultisol with a clay content of 40%. Mean annual temperature during this rotation was 24 °C, with 1250 mm/yr precipitation. Trees were planted beginning in March 2001 at a 3.0 m × 3.0 m spacing and irrigated with an average of 2 mm/day to prevent water limitation. The Aracruz site showed the greatest response to irrigation and fertilization, increasing stem production by 51%.

The International Paper site was farther south and inland from the coast, at 22°21'S, 46°58'W near Mogi Guaçu in São Paulo, Brazil on an Oxisol with 40% clay content. Mean annual temperature through the rotation was cooler than the other sites (21.4 °C), with 1250 mm/yr precipitation. Trees were planted beginning in October, 2000 at a spacing of 3.0 m × 2.8 m, and irrigated with an average of 6 mm/day to prevent water limitation. Fertilization and irrigation at this site increased stem production by about 24%.

The Suzano site was located at 18°02'S, 39°52'W near Teixeira de Freitas in Bahia, Brazil on an Ultisol with about 25% clay. Annual mean temperature during this rotation was 24 °C, with 1363 mm/yr precipitation. Trees were planted beginning in December 2001, at 3.0 m × 3.0 m spacing and irrigated with an average of 5 mm/day to prevent water limitation. The irrigation and fertilization

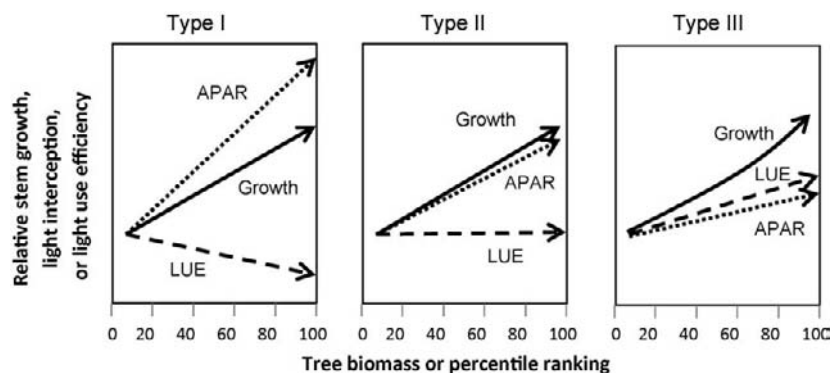


Fig. 1. Diagram of possible patterns among stem growth, light interception (APAR), and light use efficiency (LUE) as a function of increasing tree size within plots. We assume that larger trees in monoculture plantations will grow faster than smaller trees, and that APAR would also be higher for larger trees in all scenarios. The Type I pattern shows stem growth increasing (with increasing tree size within plots) less than the increase in APAR, resulting in a declining LUE. The Type II pattern shows the increase in growth is matched 1:1 with increases in APAR, with a constant LUE. The predicted Type III response shows that stem growth increases more than either APAR or LUE, so that both factors contribute to the greater growth by larger trees. Hypothesis #1 would be refuted by a Type I or II response, and supported by a Type III response.

treatment increased stem production by about 33% compared to the control treatment.

The Veracel site was located at 16°21'S, 39°34'W near Eunapolis in Bahia, Brazil on an Ultisol soil with about 35% clay content in the upper meter. Mean annual temperature during this rotation was 23.7 °C, with an average of 1440 mm/yr precipitation. Trees were planted beginning March 2001, at 3.0 m × 3.0 m spacing, and irrigated with an average of 3 mm/day to prevent water limitation. The Veracel site was the most productive in the BEPP Project, and its relative response to irrigation and fertilization was the smallest (about 20% greater stem yield than in the control treatment).

2.2. Experimental design, measurements, and modeling

The plots had 12 rows and 12 columns of trees (about 0.13 ha; 11 × 11 rows for Aracruz site), with the central 36 trees (about 325 m²) comprising the measurement plots. All trees within a plot were planted on the same day in the Uniform treatment. The Heterogeneous treatment was created by planting randomly one-third of planting spots in a plot on the first day, followed by another one-third of the trees planted 40 days later (in a staggered pattern among rows), and the final third planted 40 days after that. The basic design called for each treatment to have six replicate plots for each site, with three plots destructively sampled at mid-rotation, and three at final harvest. Three deviations from the basic design were: the Suzano site did not include a mid-rotation sampling; one block of the mid-rotation sampling at the International Paper was not irrigated (owing to limited irrigation capacity); and all the mid-rotation blocks at Veracel were not irrigated (owing to space limitations for the irrigation installation). We also included a seed-origin (*Eucalyptus grandis*) treatment at the end-of-rotation sampling at the International Paper site (described in detail by Boyden et al., 2008) to contrast seed-origin and clone-origin trees; seed-origin plantations show higher variation in tree growth rates within stands than clone-origin plantations (Binkley et al., 2002).

Tree growth was determined from measurement of breast-height diameter and height every 3 months, extrapolated to stem biomass (bark plus wood) with regression equations developed at each site (based on destructive sampling at mid-rotation and end-of-rotation, Stape et al., in review). We used stem increment over 9-month periods in this analysis, with mid-rotation ages of 17–26 months for Aracruz, 23–33 months for International Paper, and 18–27 months for Veracel. The end-of-rotation growth intervals spanned the intervals of 66–75 months for Aracruz, International Paper, and Veracel, and 63–72 months for Suzano.

The destructive harvesting at both periods involved ranking all 36 trees within a measurement plot from smallest to largest, with every fourth tree chosen for destructive sampling. All trees were measured for canopy radius in four directions. Each of the sample trees (25% of all trees) was measured for diameter, total height, height to the base of the live crown, and stem mass. The canopies were divided into thirds (based on height); for each third the average angle of leaf display was measured for 20 representative leaves, and then all leaves were stripped from all branches and weighed in the field. A subset of leaves from each third of each tree was returned to the lab for determination of fresh area (one-sided) and oven-dry mass. The leaf area per tree for the other 75% of trees in each plot was estimated with regression equations based on measured diameters and heights. Different equations for leaf area were developed from the destructive harvest for each site at each sampling period. Within a single site and sampling period, the leaf area equations worked well for both uniform and heterogeneous treatments (except for the end-of-rotation at the Veracel site, where separate equations were used for the stand structure treatments).

Individual tree light absorption was estimated with the MAESTRA model (Medlyn, 2004). Details of the three-dimensional

model for calculating absorbed photosynthetically active radiation (APAR) are described in detail by Wang and Jarvis (1990), Medlyn (1998), Grassi et al. (2002), and Bauerle et al. (2004). MAESTRA estimates mean intercepted solar radiant energy (per square meter of foliage) in the photosynthetically active and near infrared wave bands, using the radiative transfer model of Norman and Welles (1983) as a sub-model to account for radiation scattering, the proportion of direct and diffuse incoming radiant energy, and sun position.

We parameterized MAESTRA with the measured spatial coordinates and dimensions of trees within the 6 × 6 tree interior measurement plots. Given that MAESTRA represents the canopy with an array of ellipsoidal tree crowns, we accounted for the total leaf area (by canopy thirds) of simulated trees from the 36 trees comprising the measurement subplots, and two rows of neighboring trees. In the mid-rotation simulations, the two rows of neighboring trees were not included, so light interception (absorbed photosynthetically active radiation, APAR) may have been overestimated for trees on the edges of the plots. The extinction coefficients for both direct beam and diffuse radiation were accounted for by the zenith angle or angles of the sun. The path length of radiation was calculated with the model taking into account the distribution of leaf area, average leaf angle distribution, and foliage clumping. Direct and diffuse radiations were treated separately, where transmission of diffuse PAR was handled by the method developed by Norman (1979).

We applied a single incoming light regime for all sites and both periods to test our hypotheses, so our comparison of patterns within treatments would not be confounded by changes in environmental driving variables among sites and across time. The light regime was modeled for the month of September to represent an average condition; modeled light absorption per tree for September correlated very highly with modeled values for January and June. The use of September values for incident light influenced the magnitude of APAR (by 10–15%/day), but not the pattern among trees, treatments, or sampling periods. Our estimates of stem growth per MJ of APAR would not represent any single site and sampling period perfectly, but the relative comparisons (and hypothesis tests) of trees within plots, and treatments across sampling periods, are robust.

Light use efficiency (LUE, g/MJ) was defined as the average daily stem growth (g tree⁻¹ day⁻¹), across 9 months preceding destructive sampling divided by the modeled daily APAR (MJ tree⁻¹ day⁻¹). We examined the influence of tree dominance by ranking trees from smallest to largest within each site, treatment, and sampling period, and then tested for patterns between rank and tree growth, APAR, and LUE (Fig. 2). Individual trees were the focal units of this study. Within each site, a general linear model tested the effects of treatment (heterogeneous or uniform), tree rank (from smallest to largest), and time period (mid-rotation or end of rotation) (in SYSTAT 11, SYSTAT, 2004). The patterns of growth, APAR, and LUE in relation to tree rank (from smallest to largest) were plotted as best-fit lines (linear, quadratic, or power function) in SigmaPlot 8.0 (SPSS, 2002). A probability of a Type I error of 0.05 (one-tailed) was used for our hypothesis tests. Interactions among factors of treatment, rank, and time were significant for most of the comparisons, so we present results individually for these factors in all cases.

3. Results

3.1. Production ecology

The stands developed as expected, with notably higher variance in tree sizes in the heterogeneous treatment, and higher stand biomass (stem + bark) in the uniform treatment (Table 1).

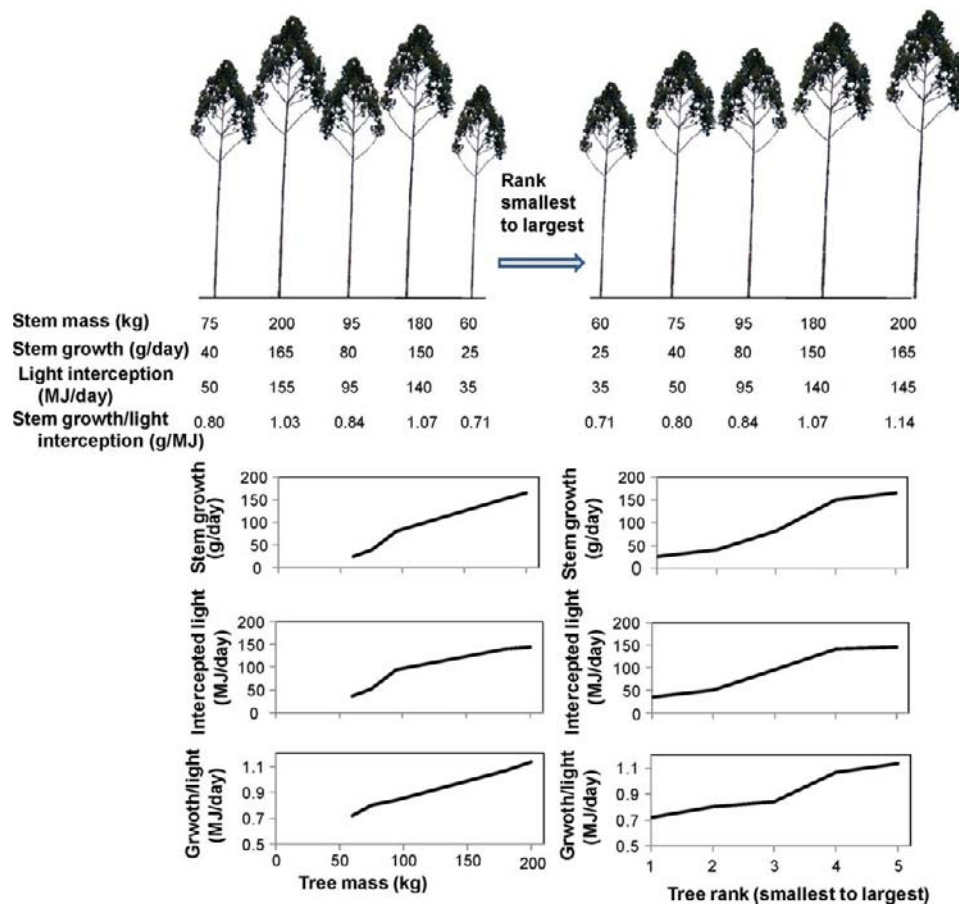


Fig. 2. The importance of tree dominance was evaluated by taking trees from each plot (left side of figure) and then ranking them from smallest to largest (right side of figure). Characterizing dominance by rank rather than size facilitated comparisons at different times in the rotations.

Accumulated stem mass spanned a 2-fold range at the end of the rotation, from about 100 Mg/ha at the Aracruz site to 200 Mg/ha at the Veracel site. The production ecology of the Aracruz site at the end of the rotation is illustrated in Fig. 3. The growth of individual trees increased substantially with increasing size of trees; doubling tree size from 100 to 200 kg led to a tripling of the average daily growth rate (Fig. 3A). The greater growth was matched with only a 75% increase in light interception (APAR), so the efficiency of light use (LUE) doubled. The pattern of increasing growth, APAR, and LUE by larger trees was consistent for both stand structure treatments (uniform and heterogeneous), for

both time periods (mid-rotation and end-of-rotation), and for all sites.

These trends in production ecology with tree size can be examined as a function of tree mass, or simply as a function of ranking of tree sizes within stands from smallest to largest (Fig. 3B). A 20th percentile tree (smaller than 80% of the trees in the plot) grew at a rate of about 10 g/day, compared with 140 g for an 80th percentile tree. The interception of light differed by a factor of almost 3, and LUE differed by a factor of almost 5. Using tree rank on the X axis allows for simple comparisons of the effects of tree sizes within stands, across stands of different age and biomass

Table 1

Tree diameter and height, and stand biomass at the beginning of each of the two 9-month sampling periods, and leaf area at the end of each site.

Site	Mid-rotation sampling				End-of-rotation sampling			
	Diameter (CV%) (cm)	Height (m)	Stem biomass (Mg/ha)	Leaf area index	Diameter (CV%) (cm)	Height (m)	Stem biomass (Mg/ha)	Leaf area index
Aracruz								
Heterogeneous	11.6 (36%)	14.3	19.4	4.2	16.7 (42%)	23.0	99	2.5
Uniform	13.0 (16%)	16.8	25.8	5.6	17.5 (27%)	25.9	111	1.4
International Paper								
Heterogeneous	13.4 (32%)	16.8	21.9	4.7	18.7 (31%)	27.1	147	3.0
Uniform	14.1 (16%)	18.7	30.0	5.0	19.5 (27%)	28.7	158	3.2
Veracel								
Heterogeneous	11.6 (25%)	15.2	15.2	4.7	20.5 (28%)	30.7	195	2.2
Uniform	13.3 (8%)	16.6	20.7	5.3	21.7 (15%)	32.3	207	3.7
Suzano								
Heterogeneous					18.1 (23%)	25.8	127	2.1
Uniform					18.4 (16%)	27.0	135	2.2

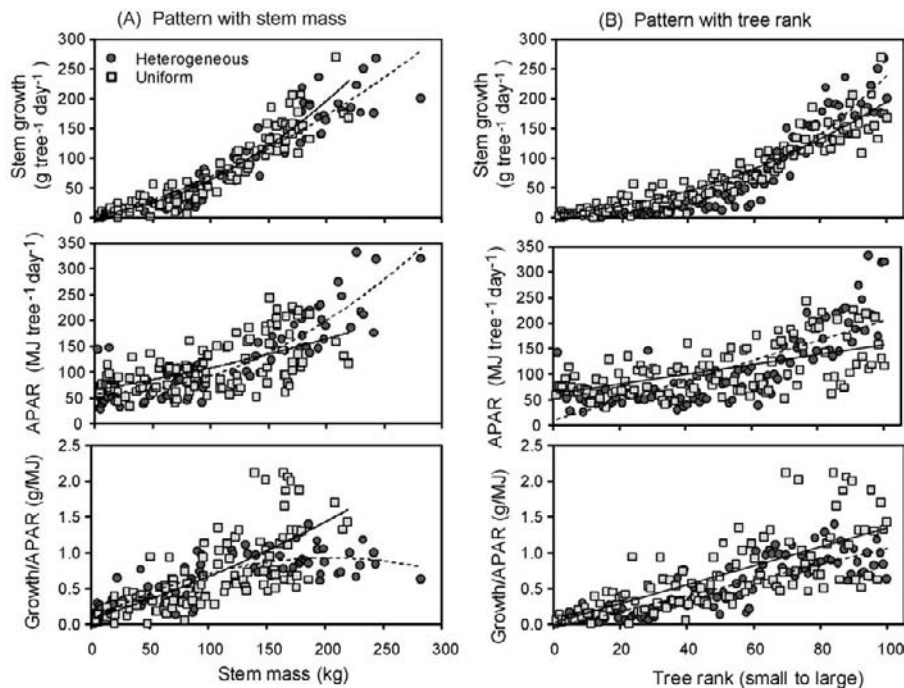


Fig. 3. Stem growth, light use (APAR), and efficiency of light use (LUE, stem growth/APAR) as a function of tree stem mass (A) and tree rank (B) for the Aracruz site at the end of the rotation. Larger trees, and higher ranking trees, showed higher values for all three dependent variables. The general patterns were consistent within sites for both independent variables; our hypothesis tests focused on Tree Rank to allow comparisons of mid-rotation and final-rotation sampling periods.

accumulation. The analysis of the other sites uses this tree-rank approach (Fig. 4).

The mid-rotation growth of individual trees was influenced more strongly by rank in the heterogeneous treatment than in the uniform treatment at Aracruz site (Fig. 4A). The influence of sample period (stand age) was also significant, as were interactions among main factors (Table 2), so our results are presented separately for each of the main factors. A 20th percentile tree in the heterogeneous treatment at the mid-rotation sampling at Aracruz showed almost no growth, compared with over 100 g/day in the uniform treatment. The 50th percentile trees grew about 40% better in the uniform treatment, but the 80th percentile trees showed similar growth rates (about 200 g/day) in the uniform and heterogeneous treatment. By the end of the rotation, the effects of stand structure on individual tree growth were less dramatic, as growth for all tree ranks declined. Light interception per tree differed more strongly among trees in the heterogeneous treatment at mid-rotation than in the uniform treatment, and this pattern remained strong through the end of the rotation. Light use efficiency increased with higher tree rank for both treatments and sampling periods. At mid-rotation, efficiency depended more strongly on rank in the heterogeneous treatment, but this treatment effect was much smaller by the end of the rotation.

Tree growth at the International Paper site at mid-rotation was also more regularly distributed among trees in the uniform treatment than in the heterogeneous treatment. The 20th percentile tree produced about 2/3 of the growth of the 80th percentile tree, compared with a four-fold difference for the 20th and 80th percentile trees in the heterogeneous treatment (Fig. 4B). The growth of the largest one-third of trees in both treatments remained high through the end of the rotation (in contrast to the Aracruz pattern), whereas the growth of the smaller half of the trees declined. Light capture per tree was particularly high for the largest trees at the end of the rotation for both treatments. Light use efficiency increased with increasing tree rank for both treatments at both periods of times, but treatments did not influence LUE patterns across the ranks at either time.

Growth was again more evenly distributed across tree rank at Veracel at mid-rotation in the uniform treatment, and the decline in tree growth by the end of the rotation was more pronounced in the heterogeneous treatment except for the very largest trees (Fig. 4C). Light interception per tree was greater for larger trees, and with a much stronger effect of tree rank in the heterogeneous treatment. The differences between the two sampling times were smaller than at the other sites (though still very significant). Light use efficiency depended strongly on tree rank for both treatments and sampling periods, with the 80th percentile tree showing more than twice the wood growth per unit of APAR as the 20th percentile tree.

The patterns for these three sites were averaged (Fig. 4D) to provide a grand, overall illustration of the effects of stand structure and age. The largest trees increased in growth and light interception from the mid-rotation to the final-rotation sampling. All size classes of trees declined in LUE by the end of the rotation, though large trees remained more efficient than mid-rank and small trees.

Tree-rank influenced stem growth at the end of the rotation at the Suzano site, but the effect of stand structure treatments was not quite significant ($P = 0.07$, one-tailed test; Fig. 5A). Light interception per tree depended strongly on rank and moderately (and significantly) on stand structure treatment. The efficiency of light use increased only moderately with tree rank in both treatments (and the treatment effect was not significant).

The comparison of clonal trees and seed-origin trees at the International Paper site showed no effect of genetic origin on tree growth as a function of tree rank (Fig. 5B). For any given tree rank, APAR tended to be about 10–15% greater for seed-origin trees, but the trend was not significant. The combination of equal growth and higher APAR produced a trend of lower LUE for seed-origin trees, but again this pattern with tree rank did not differ significantly between genetic origins.

3.2. Hypothesis tests

Our first hypothesis was supported for all sites: dominant trees showed both greater light capture and efficiency (a Type III pattern

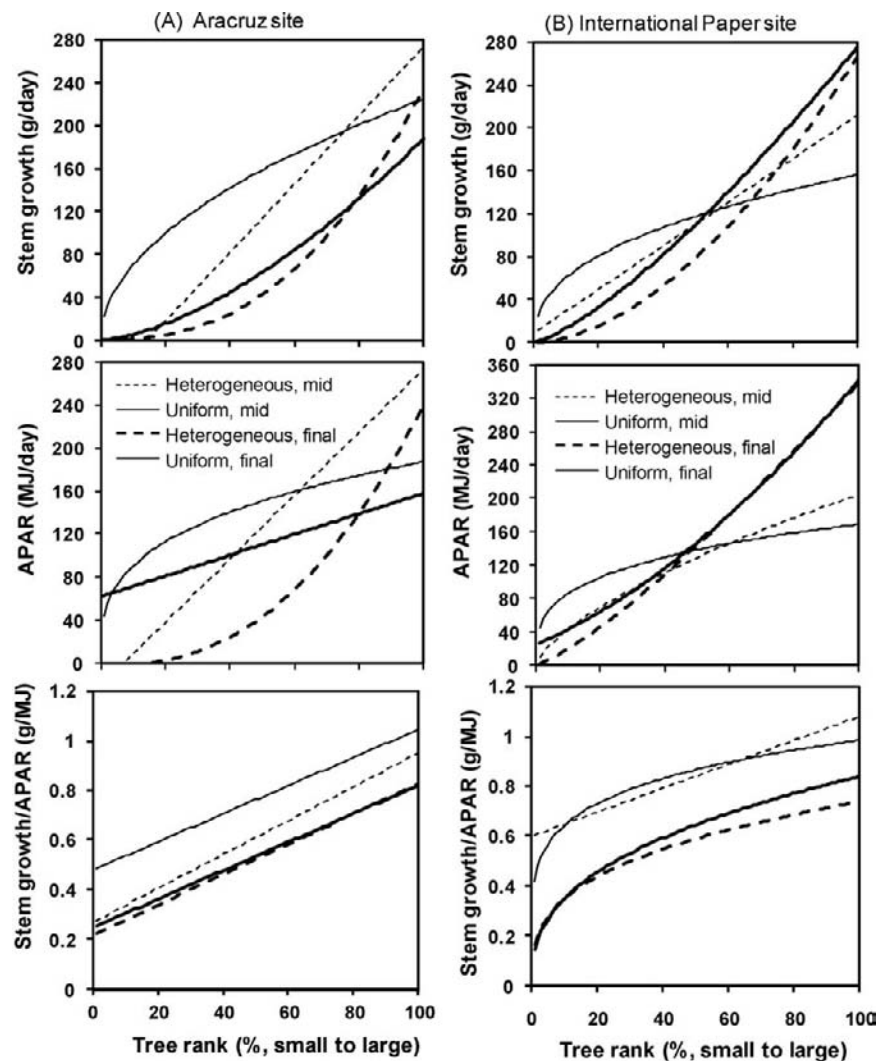


Fig. 4. Stem growth, light use (APAR), and efficiency of light use (LUE, stem growth/APAR) for the four sites. All three factors increased with tree rank across the four sites, but treatment (uniform or heterogeneous stand structure) and sampling period had variable effects (and interactions). See Table 2 for significance of factors. (A) Aracruz site, (B) International Paper site, (C) Veracel site, and (D) Average trends for three sites averaged together (all factors were significant, as well as all interactions). Larger trees grew faster, mid-rotation trees grew faster than trees at the end of the rotation, and trees in uniform plots grew faster than trees in heterogeneous plots (except for the very largest 10–25% of the trees). Larger (higher rank) trees captured more light, with the effect of tree rank increasing over time. Larger trees had higher light use efficiencies, and trees in uniform plots had higher LUE than heterogeneous trees, except for the largest 20% of trees at mid-rotation.

in Fig. 1) for both treatments and sample periods. Overall, higher growth of dominant trees was driven by roughly similar contributions of greater APAR and greater LUE.

We also hypothesized that the uniform treatment would show greater growth as a result of higher LUE by subordinate trees. This was supported, except for a lack of influence of stand structure on LUE at the International Paper site. We conclude that uniformity may typically influence LUE, but that more investigation would be needed to understand situations where this did not apply (such as the International Paper site).

Our final hypothesis was that greater uniformity in stand structure would lead to less age-related decline because high uniformity would sustain higher LUE. This hypothesis was not supported, as the heterogeneous treatments did not show a consistently greater decline in LUE.

4. Discussion

Overall, larger trees within stands grew more wood because they intercepted more light, and because they produced more stem mass per unit light. These patterns are consistent with the stand-

level patterns reported by Ryan et al. (in review), where stand-level stem growth and gross primary production declined with declines in APAR and LUE. The decline in efficiency of the subordinate trees was a major factor driving the stand-level decline.

A tree with high leaf area might be expected to intercept less light per unit of leaf area (MJ/m^2) because of self-shading by leaves within the same canopy. Similarly, small trees might be expected to intercept less light per unit of leaf area because shading by larger trees substantially reduces incident light. Across all sites, treatments, and sampling periods, both of these expectations would be wrong. The MAESTRA simulation of light interception per leaf area related linearly (with near-zero intercept) with leaf area for all plots, as illustrated in Fig. 6 for the International Paper site. Larger trees captured just as much light per unit leaf area as mid-size trees, and canopies of small trees were not substantially shaded by neighbors. The simulated capture of light per unit leaf area increased between mid-rotation and final-rotation by an average of 45% across all sites (compare Fig. 6A and B). A variety of factors could explain the pattern. The mid-rotation canopies were slightly deeper (9 m) than the final-rotation canopies. We explored possible explanations with some exploratory runs of the MAESTRA

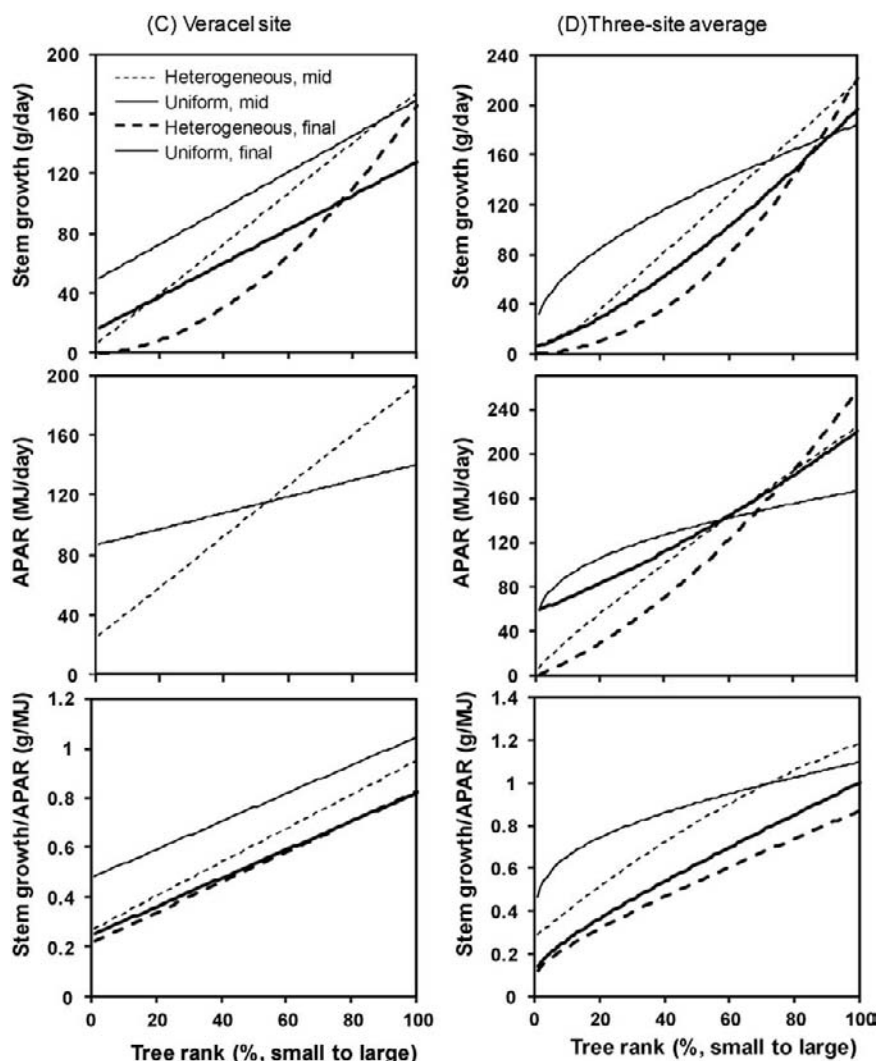


Fig. 4. (Continued).

model. Light capture per unit of leaf area increased by 10–25% for simulated canopies of constant leaf area but increasing canopy depth. The angle of leaf display had relatively little influence on estimated light interception per unit leaf area; changing leaf angle from 35° to 53° changed light capture by only 6%. We conclude that the primary factor accounting for increased light interception per leaf area in the older trees was an overall reduction in stand leaf area (Stape et al., in review), but this inference needs more detailed examination and experimentation. Nonetheless, our work indicates that within a single stand at a single point in time, a

Eucalyptus tree that has twice the leaf area of another tree should be expected to intercept twice as much light.

Higher LUE by dominant trees could result from higher rates of photosynthesis, or lower allocation to other sinks such as respiration and belowground production. We did not assess photosynthetic rates in this experiment, but O'Grady et al. (2008) reported that dominant *Eucalyptus globulus* trees had about twice the rates of light saturated photosynthesis as compared to suppressed trees. In this case, the differences in photosynthetic capacity were largely explained by canopy height rather than

Table 2

The effect of tree rank was significant ($P < 0.05$ indicated by "X"; otherwise "0" indicates $P > 0.05$) for individual tree growth, light interception (APAR), and light use efficiency (LUE) for all four sites. Interactions with stand structure and sampling period were also significant in many cases, indicating that the overall effect of single factors was often confounded by other factors.

Factor	Aracruz			International Paper			Suzano			Veracel		
	Growth	APAR	LUE	Growth	APAR	LUE	Growth	APAR	LUE	Growth	APAR	LUE
Tree rank	X	X	X	X	X	X	X	X	X	X	X	X
Stand structure (uniform or heterogeneous)	X	X	X	X	X	0	0	X	0	X	X	X
Sample period (mid-rotation or final-rotation)	X	X	0	X	X	X	–	–	–	X	X	0
Rank × structure	X	X	X	X	X	0	0	X	0	X	X	0
Rank × period	X	X	X	X	X	0	–	–	–	X	X	0
Period × structure	X	X	X	X	X	0	–	–	–	X	0	0
Rank × period × structure	X	X	X	X	X	0	–	–	–	X	X	0

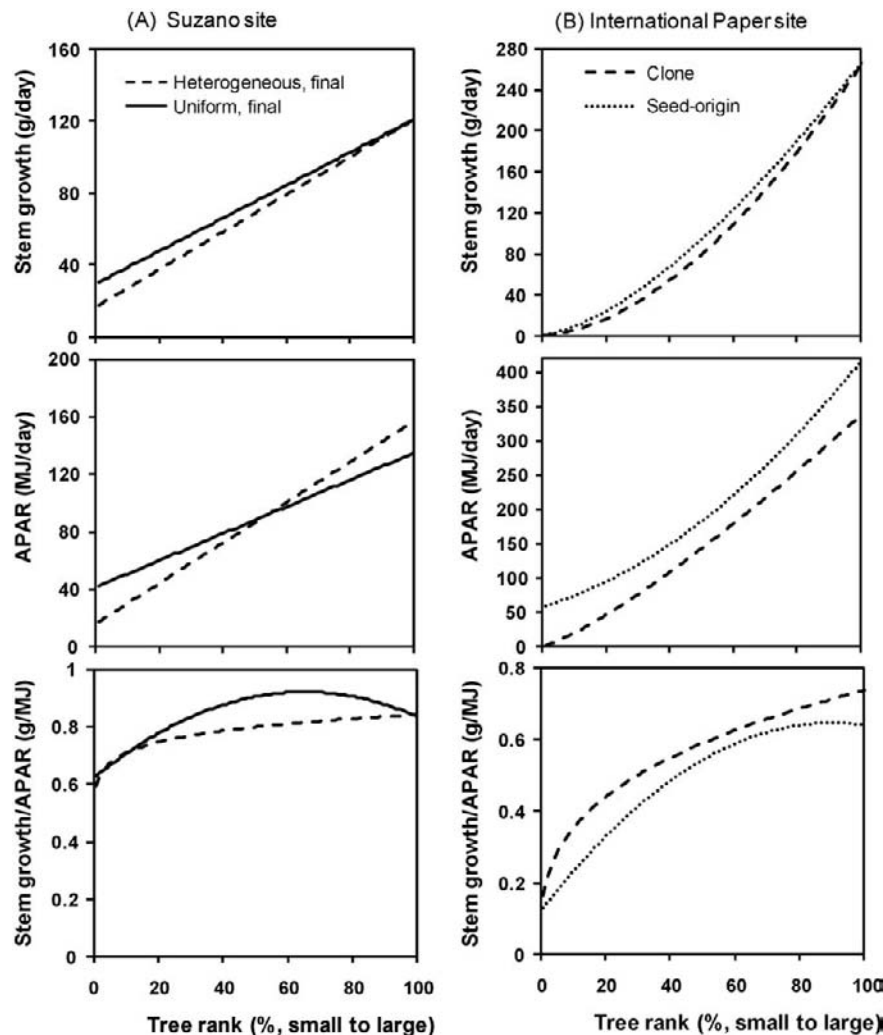


Fig. 5. (A) End-of-rotation patterns for Suzano site; tree rank was a significant factor for stem growth, APAR, and LUE, whereas treatment and treatment $\times$ rank were significant only for APAR. (B) End-of-rotation for seed-origin vs. clonal trees at the International Paper site; larger trees showed higher growth, APAR, and LUE than smaller trees, for both seed-origin and clonal trees. Seed-origin trees showed the same growth (relative to tree rank) as clonal trees (top), but tended to intercept more light ($P = 0.12$; middle), leading to a non-significant trend ($P = 0.33$) of lower LUE for seed-origin trees than for clonal trees.

dominance *per se*. Dominant trees also showed higher rates of dark respiration from leaves, though the suppressed trees showed twice the ratio of respiration:photosynthetic capacity in summer.

Ryan et al. (in press) measured leaf and stem respiration at the Aracruz site as part of the larger BEPP Project, and they found that

stem respiration was about 1/3 greater for trees in the heterogeneous treatment. However, the actual size of the respiration flux was too small to account for a large portion of the difference in stem growth. More work is needed on actual photosynthesis and respiration among trees within plots to determine the general effects of stand heterogeneity on stem respiration.

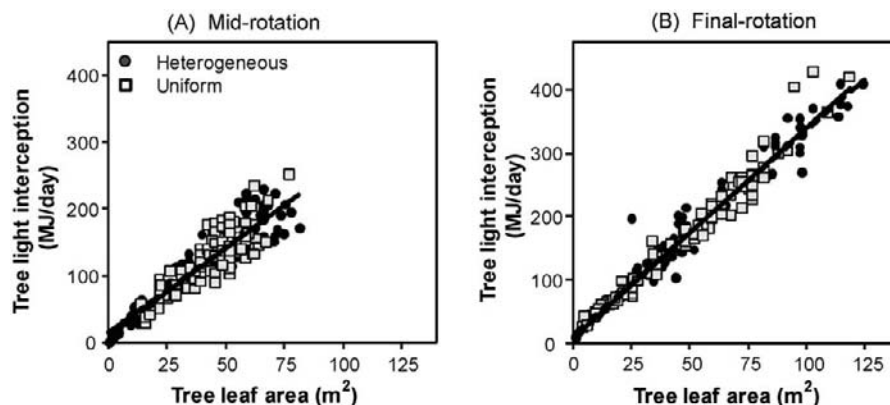


Fig. 6. MAESTRA simulations of APAR related strongly with individual tree leaf area in all sites, treatments, and sampling periods. The patterns from the International Paper site showed no effect of stand structure treatment on the relationship, but final-rotation trees absorbed more light per unit of leaf area than mid-rotation trees.

Allocation to belowground production might differ substantially between dominant and subordinate trees, both in terms of $\text{g m}^{-2} \text{yr}^{-1}$ and proportion of total Gross Primary Production. However, we have no clear idea why allocation should depend on dominance status of trees within a plot when water and nutrient supplies are ample. Differences in belowground allocation among trees within a plot would be particularly difficult to measure, but intensive experimentation might be warranted given the very large importance of patterns of LUE.

Fernandez and Gyenge (2009) also emphasized that differences in efficiency of resource use between large and small trees may be important, even when dominance is not strongly developed in a stand. They suggested that changes in efficiency of resource use could follow differences in rates of acquisition of resource by individual trees; declines in efficiency of resource use may result from declines in acquisition of resources. In our experiment, the only changes in light capture would have resulted from competition from neighbors, so the patterns in LUE were not related to changes in resource supply rates at a stand level.

Trees that intercepted more light used the light more efficiently, consistent with general trends reported at the stand level by Binkley et al. (2002, 2004). Other studies have also shown that increasing use of resources is not associated with declining efficiency of resource use. West and Osler (1995) found that growth of individual *Eucalyptus regnans* trees increased with increasing (modeled) APAR, with a slope near 1.0. Albaugh et al. (2004) showed that improved nutrition of loblolly pine (*Pinus taeda*) was associated with higher stem growth per unit leaf area, indicating likely increases in LUE with increased rates of resource use. Will et al. (2001) found that differences in APAR accounted for most of the variation in growth among loblolly pine stands, but LUE did tend to increase slightly with increasing APAR. Henderson and Jose (2005) examined responses of three hardwood species to nitrogen fertilization, and in all cases the increases in aboveground net primary production resulted from substantial increases in both light capture (higher leaf area) and LUE (calculated with Beers Law). du Toit (2008) reported that site preparation treatments that led to 25–35% increases in net primary production resulted about equally from increases in APAR and LUE.

The patterns in stem growth, APAR, and LUE in this experiment showed a variety of statistical interactions with tree rank, treatment, stand age, and site. These interactions indicate that removing nutrient and water limitations does not remove all variation among sites, stand structure, and age. Some of the interactions may have resulted from genetic differences among the clones in resource use efficiency, but little is known about how genetics influences individual-tree efficiency of resource use within stands. Boyden et al. (2008) modeled growth of trees in the heterogeneous clonal-tree plots and the seed-origin plots at the International Paper site. They concluded that stem growth (from 44 to 54 months) was more sensitive to neighboring trees where the neighbors were genetically identical to the focal tree. Our analysis of the same experiment 2 yr later showed a trend toward greater APAR in the genetically variable (seed-origin) treatment. Trees in clonal plantations have very regular canopies, with somewhat limited abilities to change crown morphology in response to neighboring crowns. The greater flexibility in crown shapes that developed in the seed-origin plots may have allowed for greater occupancy of the available canopy space, allowing greater flexibility in an individual tree's response to competing neighbors.

Three notable implications for silviculture arise from this work. The subordinate trees intercepted less light and used it less efficiently than dominant trees; thinning regimes that concentrated resource use on larger trees should be particularly effective in *Eucalyptus* plantations. The value of concentrating resource use

on fewer, larger trees may be even more important where water and nutrient supplies limit growth in addition to APAR (also noted by West and Osler, 1995). The second implication is that the age-related decline in stand growth results disproportionately from declining growth, resource use, and efficiency of resource use by subordinate trees. The dominant *Eucalyptus* trees retained high LUE at the end of the rotation, and lengthened rotations would likely show sustained, high growth rates in these trees. The final implication is that highly uniform stands are likely to grow best, as a result of both higher APAR and higher LUE. All of these features warrant further investigation, including the effects of thinning and spacing on LUE; patterns in older stands; and patterns resulting from interactions of limiting supplies of water, nutrients, and light.

Acknowledgements

We thank the hundreds of colleagues involved in the Brazil *Eucalyptus* Potential Productivity (BEPP) Project, and the staff in the Institute for Forest Research (IPEF) at the ESALQ campus of the University of Sao Paulo. J.L. Stape was sponsored by CNPq 306561/2007. In particular, we thank Sebastiao Fonseca and Rodolfo Loos (Aracruz), Jose Mario Ferreira (IPBR), Sergio Silva and Rodrigo Hakamada (Veracel), and Jose Luiz Gava (Suzano).

References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manag.* 192, 3–19.
- Bauerle, W.L., Bowden, J.D., McLeod, M.F., Toler, J.E., 2004. Modeling intra-crown and intra-canopy interactions in red maple: assessment of light transfer on carbon dioxide and water vapor exchange. *Tree Physiol.* 24, 589–597.
- Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. *For. Ecol. Manag.* 190, 265–271.
- Binkley, D., Stape, J.L., Ryan, M., 2004. Thinking about resource use efficiency in forests. *For. Ecol. Manag.* 193, 5–16.
- Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H., Fownes, J., 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* 5, 58–67.
- Boyden, S., Binkley, D., Stape, J.L., 2008. Competition among *Eucalyptus* trees depends on genetic variation and resource supply. *Ecology* 89, 2860–2867.
- Cannell, M.G.R., 1989. Light interception, light use efficiency and assimilate partitioning in poplar and willow stands. In: Pereira, J.S., Landsberg, J.J. (Eds.), *Biomass Production by Fast-Growing Trees*. Kluwer Academic Publisher, Dordrecht, pp. 1–12.
- du Toit, B., 2008. Effects of site management on growth, biomass partitioning and light use efficiency in a young stand of *Eucalyptus grandis* in South Africa. *For. Ecol. Manag.* 255, 2324–2336.
- Fernandez, M.E., Gyenge, J., 2009. Testing Binkley's hypothesis about the interaction of individual tree water use efficiency and growth efficiency with dominance patterns in open and close canopy stands. *For. Ecol. Manag.* 257, 1859–1865.
- Grassi, G., Meir, P., Cromer, R., Tompkins, D., Jarvis, P.G., 2002. Photosynthetic parameters in seedlings of *Eucalyptus grandis* as affected by rate of nitrogen supply. *Plant Cell Environ.* 25, 1677–1688.
- Henderson, D.E., Jose, S., 2005. Production physiology of three fast-growing hardwood species along a soil resource gradient. *Tree Physiol.* 25, 1487–1494.
- Landsberg, J.J., Gower, S.T., Roy, J., 1996. Applications of Physiological Ecology to Forest Management. Academic Press, San Diego.
- Landsberg, J.J., 1997. The biophysical environment. In: Nambiar, E.K., Brown, S.A. (Eds.), *Management of Soil, Water, and Nutrients in Tropical Plantation Forests*. ACIAR Monograph 43, Canberra, pp. 65–96.
- McMurtrie, R.E., Gholz, H.L., Linder, S., Gower, S.T., 1994. Climate factors controlling productivity of pine stands: a model-based approach. In: Gholz, H.L., Linder, S., McMurtrie, R.E. (Eds.), *Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis*. *Ecol. Bull.* 43, 173–188.
- Medlyn, B.E., 1998. Physiological basis of the light-use efficiency model. *Tree Physiol.* 18, 167–176.
- Medlyn, B., 2004. A MAESTRO retrospective. In: Mencuccini, M., Grace, J., Moncrieff, J., McNaughton, K.G. (Eds.), *Forests at the Land-Atmosphere Interface*. CAB International, Wallingford.
- Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. *Philos. Trans. R. Soc. B* 281, 277–294.
- Norman, J.M., 1979. Modification of the Aerial Environment of Plants. ASAE, St. Joseph, MI.
- Norman, J.M., Welles, J.M., 1983. Radiative transfer in array of canopies. *Agron. J.* 75, 481–488.

- O'Grady, A.P., Worledge, D., Wilkinson, A., Battaglia, M., 2008. Photosynthesis and respiration decline with light intensity in dominant and suppressed *Eucalyptus globulus* canopies. *Func. Plant Biol.* 35, 439–447.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 213–262.
- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. *Ecol. Mon.* 74, 393–414.
- Ryan, M.G., Stape, J.L., Binkley, D., in review. Whole-rotation production ecology in the Brazil Eucalyptus Potential Productivity Project. *For. Ecol. Manag.*
- Ryan, M.G., Cavaleri, M.A., Almeida, A.C., Penchel, R., Senock, R.S., Stape, J.S., in press. Wood CO₂ efflux and foliar respiration for *Eucalyptus* in Hawaii and Brazil. *Tree Physiol.*
- SPSS, 2002. Sigmaplot 8. 0 for Windows. SPSS Science, Chicago.
- Stape, J.L., Binkley, D., Ryan, M.G., Fonseca, S., Loos, R., Silva, S., Hakamada, R.E., Takahashi, E.N., Silva, C.R., Ferreira, J.M., Lima, A.M., Leite, F.P., Andrade, H., Branco, G.C., Gava, J.L., Alves, J.M., in review. Influence of water, nutrient and stand structure on wood production in the eight sites of the Brazil Eucalyptus Potential Productivity Project. *For. Ecol. Manag.*
- SYSTAT, 2004. SYSTAT 11.0. SPSS Science, Chicago.
- Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model—MAESTRO. *Agric. For. Met.* 51, 257–280.
- West, P.W., Osler, G.H.R., 1995. Growth response to thinning and its relation to site resources in *Eucalyptus regnans*. *Can. J. For. Res.* 25, 69–80.
- Will, R.E., Barron, G.A., Burkes, E.C., Shiver, B., Teskey, R.O., 2001. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. *For. Ecol. Manag.* 154, 155–163.