



Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments

Eric J. Jokela^{a,*}, Philip M. Dougherty^{b,1}, Timothy A. Martin^{a,2}

^a*School of Forest Resources and Conservation, University of Florida, P.O. Box 110410, Gainesville, FL 32611-0410, USA*

^b*MeadWestvaco Co., P.O. Box 1950, Summerville, SC 29484, USA*

Abstract

Results from seven long-term experiments in the southern US were summarized to understand production dynamics of intensively managed loblolly pine plantations. Replicated studies that spanned a wide range of soil and climatic conditions were established (North Carolina—NC; Georgia—GA (three sites); Florida—FL; Louisiana—LA; Oklahoma—OK). All experiments received some combination of silvicultural treatments, including fertilizer application, understory competition control, irrigation, and thinning. Accumulation of stemwood biomass at age 15 years varied among sites and ranged from 70 Mg ha⁻¹ (NC) to 180 Mg ha⁻¹ (GA). All sites that received fertilizer and weed control applications were responsive to treatments, and growth responses ranged from about 2-fold (GA) to 3.5-fold (FL) at age 15 years. Variation in fertilizer responses among sites reflected differences in soil types, inherent site quality, and stages of stand development. Site carrying capacity, expressed as maximum basal area attained in closed canopy stands, was surprisingly consistent among sites and climatic conditions, reaching 45–48 m² ha⁻¹ under the most intensive silvicultural treatments. Across studies, competition-related mortality was initiated as stand basal areas approached 30–35 m² ha⁻¹, and annual stemwood biomass increment peaked as basal areas reached about 20–35 m² ha⁻¹. These data suggest that a regional maximum in stand density occurs for loblolly pine when regular fertilizer additions are made or inherent soil nutrient supply is high. Periodic density management will be required to minimize reductions in individual tree and net stand growth. Wood specific gravity at a standard ring age of 10–11 years varied both among sites and by treatment within sites, and ranged from approximately 0.45 (OK site) to 0.56 (GA sites). Maximum leaf area index (LAI) among sites varied from about 2.5 to 6.5. The relationship between stemwood biomass increment and LAI across sites was strong at LAI levels <3.0, but was considerably more variable at higher LAIs. Variation in stemwood increment at higher LAIs was substantially reduced, however, when extreme data points were removed; a logistic function explained 75% of the variation in stemwood increment across all sites. Differences in productivity among sites were not strongly related to site water balance. Taken together, these results support other work which suggests that soil nutrient availability is the dominant driver of loblolly pine productivity across its natural range. Future research should seek to better understand the mechanisms of nutrient demand, uptake and utilization efficiency in developing stands, as well as the factors controlling intraspecific tree competition.

© 2004 Elsevier B.V. All rights reserved.

Keywords: *Pinus taeda*; Production ecology; Leaf area index; Stemwood biomass; Wood specific gravity; Fertilization; Competition control

* Corresponding author. Tel.: +1-352-846-0890; fax: +1-352-846-1277.

E-mail addresses: ejokela@ufl.edu (E.J. Jokela), pmdough@meadwestvaco.com (P.M. Dougherty), tamartin@ufl.edu (T.A. Martin).

¹ Tel.: +1-843-851-4750; fax: +1-843-875-7185.

² Tel.: +1-352-846-0866; fax +1-352-846-1277.

1. Introduction

In the southern US, loblolly pine (*Pinus taeda* L.) is one of the most important commercial species, occupying more than 13 million ha (Schultz, 1997). Within its native range loblolly pine encompasses 15 southern and mid-Atlantic states from Delaware to Florida and west to southeastern Oklahoma (Fig. 1). Intensive management practices that include deployment of genetically improved seedling stock, mechanical and chemical site preparation, and fertilization are commonly used to increase forest productivity in plantation ecosystems throughout its range.

Applied and process-level research has been conducted over the last five decades with loblolly pine (Wahlenberg, 1946; Switzer et al., 1966; Lambeth et al., 1984; Teskey et al., 1987; Schultz, 1997; Mickler and Fox, 1998), yet our understanding of the effects of intensive management on stand development processes and production ecology are still

limited because few comprehensive, long-term experiments have been conducted that span the range from establishment to maturity. Elsewhere, when grown as an exotic, loblolly pine has exhibited significantly higher levels of production and stocking levels (e.g. Brazil, Hawaii, Australia, and South Africa) than that commonly observed within its native range (Burns and Hu, 1983; Schultz, 1997; Borders and Bailey, 2001). The causal mechanisms for these differences, however, are still poorly understood.

In this special issue of *Forest Ecology and Management*, the production dynamics of loblolly pine plantations were examined using seven long-term studies located in the southern US (North Carolina—NC; Georgia—GA; Florida—FL; Louisiana—LA; Oklahoma—OK). The diversity in study sites and associated soil–climate combinations provided a unique opportunity to examine production dynamics and the underpinning ecophysiological responses to a series of replicated silvicultural treatments. These analyses

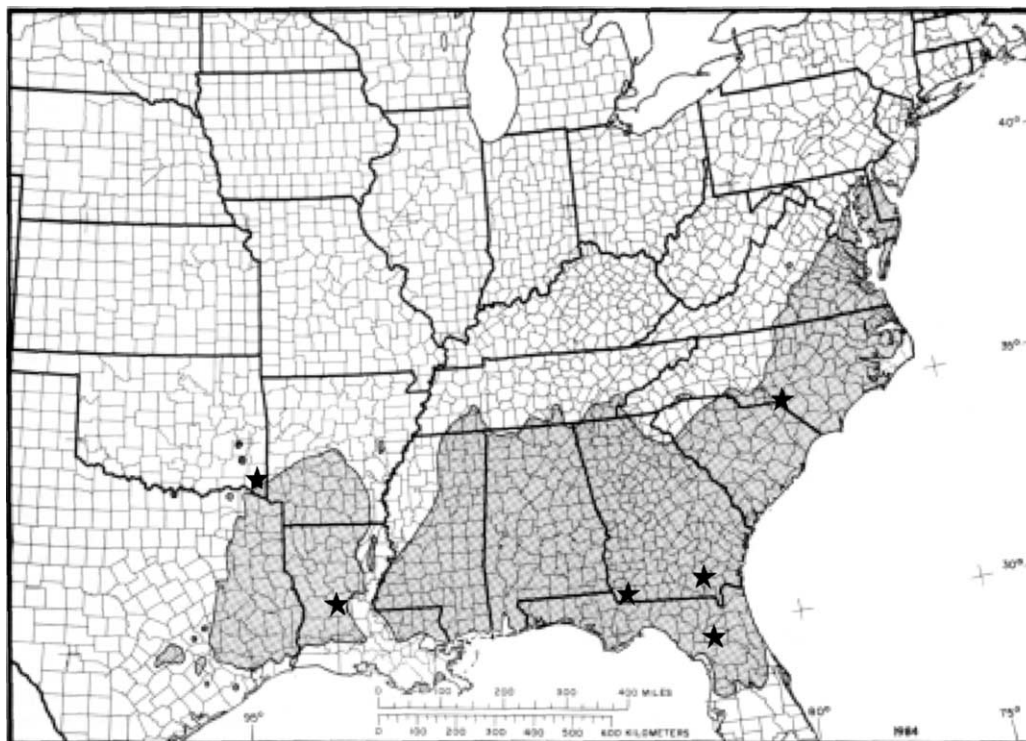


Fig. 1. Location of the seven long-term loblolly pine productivity experiments described in this paper (the star in southeastern Georgia represents two studies located in close proximity). The natural range of loblolly pine is indicated by the shaded region (Burns and Honkala, 1990).

have also contributed to understanding the plasticity of loblolly pine and to determining whether general relationships exist between production dynamics and stand attributes across its native range. Our goals in this synthesis are to provide forest scientists and practitioners with a more complete picture of growth and development processes, and to suggest new areas of research that could significantly advance our understanding of how to better optimize the productivity of native loblolly pine plantation ecosystems.

2. Study sites and data

Seven individual studies were established across the natural range of loblolly pine to examine factors that control and limit the productivity of managed stands (Fig. 1). These studies spanned a wide range of soil and climatic conditions (Table 1). For example, soils ranged from deep infertile sands in NC (Albaugh et al., 2004) and the lower Coastal Plain of FL and GA (Martin and Jokela, 2004; Borders et al., 2004) to deep alluvial soils located in the northwest extension of the loblolly pine range in southeastern OK (Hennessey et al., 2004). Climate among sites varied from 290 frost-free growing season days and little annual water deficits in FL, to 240 days in OK, with moderate to severe growing season water deficits occurring in 8 years out of the 17-year study period. Average annual precipitation levels varied among sites by about 30%, with the highest and lowest amounts received at LA (1560 mm) and OK (1205 mm), respectively.

Although experimental designs varied among locations, they all shared a common objective of using silvicultural manipulations (e.g. fertilizer additions, understory competition control, thinning) to enhance site productivity. Silvicultural treatments were diverse among studies, but included fertilizer applications at all sites except OK, understory competition control at most sites, irrigation at the GA-Irr and NC sites (Samuelson et al., 2004; Albaugh et al., 2004), and thinning at the LA and OK experiments (Hennessey et al., 2004; Sword Sayer et al., 2004).

Repeated inventory data in combination with site specific allometric relationships were used to generate stemwood biomass production estimates. Annual values of leaf area index (LAI) were determined from

either needlefall or gap fraction-based estimates (e.g. LAI2000; Li-Cor, Lincoln, NE), and were expressed as projected leaf area for the month with the highest LAI. The relationship between stemwood biomass increment and peak LAI was fitted using the SAS NLIN procedure (SAS Institute, 1992). Coefficients of determination for non-linear regressions were calculated as R^2 version 6 from Kvalseth (1985).

3. Results and discussion

3.1. Stemwood biomass accumulation

Accumulation of stemwood biomass was variable among study locations (Fig. 2). The GA-Wet and GA-Dry sites that received sustained weed control treatments and regular fertilizer additions were clearly the most productive, accumulating about 180 Mg ha⁻¹ of stemwood biomass at age 15 years compared to about 70 Mg ha⁻¹ at NC. These GA sites also had the highest levels of inherent site quality, as reflected in the growth rates of the unfertilized control plots (Fig. 2). From a climatic perspective, the OK site had the shortest growing season and most frequent growing season water deficits among locations. Variation in current annual increment was especially pronounced at OK. Yet, the unfertilized and unthinned control plots at this site accumulated as much stemwood biomass as the fertilized stands in LA and FL (through age 10 years), and about 67% as much dry matter as the intensively managed sites in GA.

Stemwood biomass increment among sites increased as the levels of stand basal area increased (Fig. 3). This relationship was asymptotic, with stemwood increments peaking at basal areas approaching about 20–25 m² ha⁻¹ at the FL and NC sites and 30–35 m² ha⁻¹ at the GA sites. Projected LAI also tended to peak at this level of stand density on fertilized sites (Albaugh et al., 2004; Martin and Jokela, 2004). Declines in stemwood increment at the FL site were especially pronounced beyond this level of density and likely reflected a combination of both increased intraspecific competition and nutrient limitations resulting from curtailment of the fertilizer treatments at age 10 years.

The overriding influence of soil nutrient availability on loblolly pine productivity was strongly evident

Table 1
 Characteristics of the experimental sites used in the synthesis analysis

Study designation	Geographical coordinates	Drainage class	Soil classification	Average annual precipitation (mm)	Frost-free days	Treatments	Monitoring period (year)	Authors
NC (North Carolina)	35°39'N–79°29'W	Somewhat excessively	Sandy, siliceous, thermic, Psammentic Hapludults	1220	225	Fertilization, irrigation	8–16	Albaugh et al.
FL (Florida)	29°40'N–82°20'W	Somewhat poorly	Sandy, siliceous, hyperthermic, Ultic Alaquods	1350	290	Fertilization, weed control	1–16	Martin and Jokela
GA-Wet (Georgia)	31°15'N–82°24'W	Somewhat poorly	Loamy, siliceous, thermic, Arenic Paleaquults	1300	265	Fertilization, weed control	3–15	Borders et al.
GA-Dry	31°15'N–82°24'W	Well	Loamy, siliceous, thermic, Grossarenic Plinthic Paleudults	1300	265	Fertilization, weed control	3–15	Borders et al.
GA-Irr	30°48'N–84°39'W	Well	Loamy, siliceous, thermic, Grossarenic Paleudults	1412	270	Fertilization, irrigation	1–6	Samuelson et al.
LA (Louisiana)	31°11'N–92°41'W	Moderately well	Fine-silty, thermic Plinthaquic Paleudults	1560	250	Fertilization, thinning	7–17	Sword Sayer et al.
OK (Oklahoma)	33°58'N–94°35'W	Somewhat poorly	Fine-silty, siliceous, thermic, Aquic Paleudults	1205	240	Thinning	9–24	Hennessey et al.

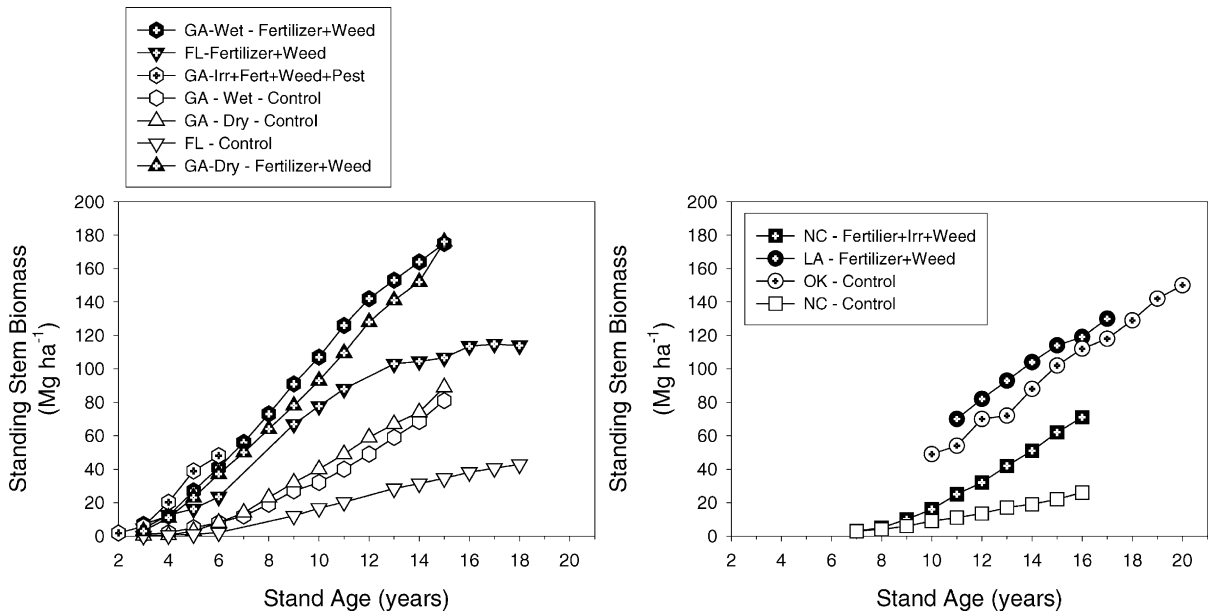


Fig. 2. Stemwood biomass accumulation for unthinned loblolly pine plantations subjected to a variety of silvicultural treatments in the southern US. Biomass values exclude bark for all studies except GA-Irr.

across the range of sites (Fig. 2). Forest fertilization, particularly with N and P, has been a common management practice used throughout much of the southern US since the 1970s (Allen, 1987; Jokela et al., 1991). At a common reference age (15 years), growth responses associated with the fertilizer and weed control treatments relative to the untreated controls ranged from about 2-fold (GA) to 3.5-fold (FL). The

wide range in variation in fertilizer responses among sites most likely reflected differences in soil types, inherent site quality, and stages of stand development as indicated by stand density. The NC site, although responsive to the fertilizer treatments (2.6-fold response), was the least productive overall, due in part to the xeric, sandy soils and timing of the treatments at this location (initiated at age 7 years). Annual fertilization and fertilization plus irrigation increased LAI and average nutrient concentrations at the NC site over time (Albaugh et al., 2004). However, productivity levels have never approached the more productive sites that received continuous management since planting (GA sites). These results reaffirm that soils in this region are nutrient impoverished and that correcting deficiencies early in the rotation (grand growth period) can significantly alter patterns of stand development and productivity.

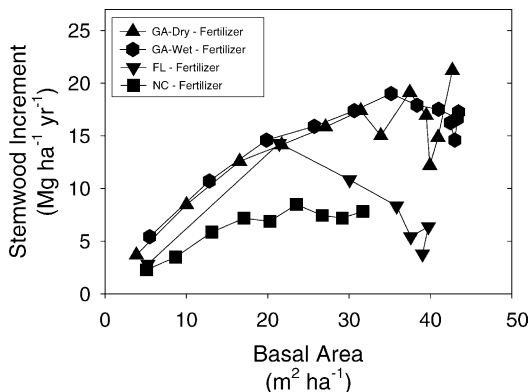


Fig. 3. Variation in stemwood biomass increment with stand basal area for selected silvicultural treatments in several unthinned, long-term loblolly pine productivity studies in the southern US.

As stand nutrient demands are commensurate with levels of production, maintaining adequate levels of soil fertility throughout the rotation will be necessary to ensure higher levels of productivity. For example, although nutrient mediated growth responses on the somewhat poorly drained Spodosols in FL were especially dramatic, levels of annual increment declined

sharply after curtailment of the fertilizer treatments at age 10 years. Re-fertilization at age 15 years was unsuccessful in elevating growth rates to previous levels observed at this site. The lack of decline in stemwood production for those sites having soils with a high apparent nutrient supply capacity (OK), or where fertilizer treatments were maintained (GA, LA) over time, provides an interesting set of challenges for both forest managers and scientists.

For managers, it will be important to determine the time frame over which nutrient management treatments can be used to sustain high rates of production. Activities that diminish the capacity of a stand to respond to nutrient additions and/or produce wood during the later stages of the rotation (e.g. due to high stand density) should be recognized and avoided. Further, these results suggest that nutrient management requires a rotation-long commitment to sustain both high levels of stand productivity and value. Without a sustained commitment to nutrient management, early investments in fertilization may result in increases in yields of lower value pulpwood, with limited production of higher valued products such as sawtimber.

From a biological perspective, additional research is needed to better understand the changes that occur in response to abrupt resource disturbances (i.e. addition or curtailment of nutrient treatments). From the FL results it is clear that LAI, foliar nutrient concentrations and productivity decreased rapidly and dramatically after fertilization ceased. Little is known, however, about how internal anatomy (xylem, phloem, and resource storage capacity), physiological processes, carbon allocation shifts, or root associates and soil microbial communities were impacted, and how long it takes these elements to reach new equilibria after resource treatments are reinitiated. It is likely that stand resilience in the face of chronic or abrupt resource disturbances will depend on the stage of development and the age of the stands being managed.

3.2. Site carrying capacity and tree mortality

Site carrying capacity, expressed as maximum basal areas attained in closed canopy stands, was surprisingly consistent among sites and climatic conditions (GA, FL, LA, OK). In general, basal area levels increased as the intensity of silvicultural treatments

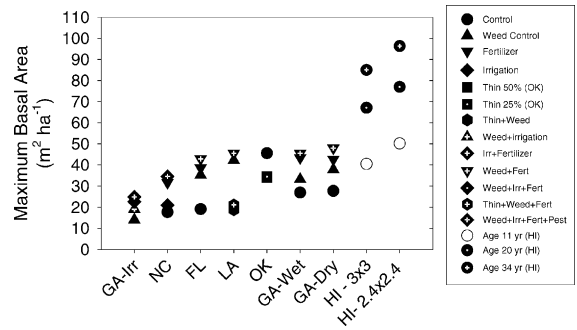


Fig. 4. Stand basal area for loblolly pine plantations managed under a variety of silvicultural treatments in the southern US. Measurements at each site coincide with the period of maximum stand basal area for the most intensive treatment. For contrast, data are included for loblolly pine stands grown in Hawaii (HI) at two spacings ($3 \text{ m} \times 3 \text{ m}$ and $2.4 \text{ m} \times 2.4 \text{ m}$) (Harms et al., 2000).

increased (Fig. 4). The productive GA-Dry site that received annual fertilizer additions and weed control treatments accrued the highest basal area ($48 \text{ m}^2 \text{ ha}^{-1}$) among locations (Fig. 4). Elsewhere, basal area levels approached a maximum of about $45 \text{ m}^2 \text{ ha}^{-1}$ before declining, including the OK control plots that were not thinned or fertilized. Basal area responses to the weed control only treatments tended to be lower than the fertilizer only treatments, and responses were most pronounced on those sites having inherently low soil fertility (e.g. FL; Fig. 4). The importance of competition for soil nutrients between pines and understory plants has been well established in this region. In nutrient-limited environments such as these, sustained control of understory competition can reduce nutrient deficiencies of pines, as do annual fertilizer applications (Colbert et al., 1990; Neary et al., 1990a; Jokela and Martin, 2000). However, it must be recognized that the long-term consequences of meeting nutrient requirements through fertilization versus understory vegetation control may be different, as understory plants can play a significant role in the storage and cycling of base cations (Hough, 1982).

The basal area data reported in this analysis suggests that a regional maximum in stand density occurs for loblolly pine when regular fertilizer additions are made or inherent soil nutrient supply is high. The lack of significant regional variation in upper stocking limits further suggests that genetic and climatic limitations (i.e. growing season precipitation deficits) may be less important than, for example, soil nutrient

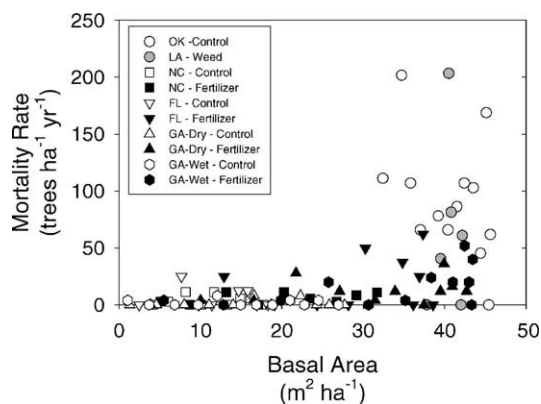


Fig. 5. Variation in tree mortality rate during development of stand basal area for selected silvicultural treatments in several long-term loblolly pine productivity studies in the southern US.

supply as factors influencing potential biological productivity and maximum basal area accretion.

Biomass increment in forest stands can be reduced when growing space requirements are not maintained. In these studies, competition-related mortality occurred well before the point where maximum basal area occurred. For example, accelerated competition-related mortality occurred within the range of 30–35 $\text{m}^2 \text{ha}^{-1}$ at almost all sites and treatments (Fig. 5). This was true for stands growing in areas with favorable water balance (GA, FL, LA), where fertilizers were applied (GA, NC, FL, LA), or with frequent growing season water deficits (OK). The rate of mortality among sites was highest in OK, although this site also had the highest initial planting density. This threshold of density-dependent mortality corresponded to about 60% of the maximum stand density index reported for loblolly pine (Dean and Baldwin, 1993).

For sites included in this analysis, most competition-related mortality occurred in diameter classes at or below the stand mean (i.e. lower crown classes). These trends are consistent with developmental patterns for single cohort stands (Oliver and Larson, 1996) and suggest that density management achieved either through regular thinnings conducted throughout the rotation, or altered initial planting densities, would be required to maintain adequate growing space to minimize mortality losses and reductions in annual production. It also appears from these data that intensive management practices such as fertilization would not be expected to alter the size–density combinations

above which competition-related mortality begins. Similar findings were reported by Dean and Jokela (1992) for slash pine (*Pinus elliottii* var. *elliottii*). Clearly, it will be important for forest managers and scientists to focus on how to better manage growing space requirements throughout the rotation. For example, a combination of thinning and fertilization treatments would represent a better management strategy than fertilization alone for increasing productivity and stand value. Once basal area levels exceed 35 $\text{m}^2 \text{ha}^{-1}$, growing space limitations, even in the presence of competition-related mortality, would likely limit fertilizer responses and the growth potential of the site.

In contrast to these results, research conducted with loblolly pine in Hawaii (DeBell et al., 1989; Harms et al., 1994, 2000) indicated that basal area levels could reach as high as 85–100 $\text{m}^2 \text{ha}^{-1}$. Competition-related mortality was considerably lower in Hawaii than in the southeastern US (DeBell et al., 1989), and it was hypothesized that higher solar radiation intensities and sun angles in Hawaii allowed greater retention of photosynthetically active leaf area that, in turn, facilitated enhanced survival and growth of lower crown class trees (Harms et al., 2000). For example, the doubling of productivity in Hawaii was associated with increased height (15%), diameter (25%), and number of trees surviving (16%) compared to the southeastern US (DeBell et al., 1989). It was also noted from these growth comparisons that foliar concentrations of N, P, Ca and Mg were considerably higher in Hawaii than South Carolina and that higher levels of nutrition may have contributed to higher rates of photosynthesis, stocking levels, and growth (Harms et al., 1994).

Mounting evidence from these and related studies conducted with loblolly pine, as well as other species, have shown that considerable variation in growth performance and stockability (maximum mean tree size–density relationships) can exist within a species, especially when grown outside of their native range (Ledgard and Belton, 1985; DeBell et al., 1989; Hermann and Lavender, 1999). Harms et al. (2000) reported that at age 20 years, loblolly pine plantations in Hawaii had 13% mortality at the limiting density boundary (2601 trees ha^{-1} and an averaged DBH of 21.4 cm) compared to 42% (1725 trees ha^{-1} and an averaged DBH of 18.5 cm) in the southeastern US. The physiological explanation for these differences

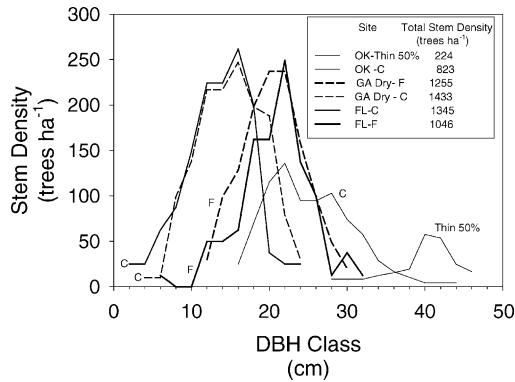


Fig. 6. Diameter distributions for loblolly pine plantations managed under a variety of silvicultural treatments from the Florida (age 13 years), Georgia Dry (age 14 years), and Oklahoma (age 24 years) long-term productivity studies. Total stand stem density for each site and treatment is provided in the legend.

are still poorly understood, but worthy of further investigation.

3.3. Diameter distributions

Diameter distributions are a revealing way to quantify the effects of site and management on stand dynamics, and the potential effect of these factors on the mix of product classes within the stand. Inherent site productivity, fertilizer treatments, and thinning treatments affected stand density and DBH distributions (representative sites shown in Fig. 6). The GA sites were inherently more productive than the FL sites, as shown by their higher cumulative stemwood biomass under control treatments (Fig. 2). This increased stemwood biomass accumulation resulted from both a higher mean DBH at the GA-Dry site (15.1 cm versus 13.5 cm at FL), as well as a greater number of trees in the larger DBH classes (Fig. 6). For the fertilized treatments, GA-Dry and FL had similar mean DBH (20.4 cm at GA-Dry versus 20.8 cm at FL), and almost identical distribution of trees in the larger size classes, but the GA-Dry site maintained a larger number of trees in the smaller size classes. The unthinned OK site had lower stem density and higher mean DBH (25.0 cm) than the FL and GA-Dry untreated stands; this was primarily attributable to the greater biomass accumulation and self-thinning (Fig. 6) that occurred in the older OK stands (24 years versus 14 years for GA-Dry and 13 years for FL).

The effects of the thinning treatment in the OK experiment were predictable and large, with the 50% reduction in BA with thinning at age 9 and 12 years producing decreased stem density (224 trees ha⁻¹ for thinned versus 823 trees ha⁻¹ unthinned), increased mean DBH (25.0 cm unthinned versus 39.5 cm thinned), and skewing of the DBH distribution toward the larger size trees (skewness 1.44 thinned versus 0.03 unthinned) by age 24 years. The resultant effects of thinning on the DBH distribution and product classes were dramatic. In the unthinned treatment, 23% of the trees would be classified as sawlogs (DBH ≥ 30 cm), while 96% of the trees in the 50% thinned treatment would fall in the sawlog class. In contrast, almost no stems had reached sawlog sizes in the younger, unthinned and fertilized GA-Dry and FL experiments (2 and 5% of stems with DBH ≥ 30 cm, respectively). Across the studies summarized here, stands established with 1400–2600 trees ha⁻¹ (GA, FL, LA, NC) produced little sawtimber even if they were fertilized annually over the time period of the study. These results underline the critical dual role of density management: avoiding density-related productivity declines and mortality (e.g. Figs. 3 and 5), and the shifting of site resources onto fewer, larger crop trees (Baldwin et al., 2000). In summary, the range of diameter distributions observed under the six study conditions suggests (1) that the most powerful tool we have to manage stem size is stand density manipulation and (2) that if stand density adjustments are made early in a sawtimber rotation (at establishment or an early thinning) then total yields (clearcut + thinning) will approach those of unthinned stands, while producing potentially large increases in wood value depending on market opportunities.

3.4. Ring specific gravity

Wood specific gravity at a standard ring age of 10–11 years (SG_{ring}) varied both among sites and by treatment within sites (Fig. 7). The OK site had the lowest SG_{ring} (0.44–0.46), followed by FL (0.48–0.54) and the two GA sites (0.53–0.58). The LA site had SG_{ring} ranging from 0.58 to 0.61, 29–36% higher than SG_{ring} at the OK site. In southern pine, geographic variation in SG_{ring} has been attributed to the ratio of latewood:earlywood in individual growth rings (Clark and Saucier, 1989). It is hypothesized that these

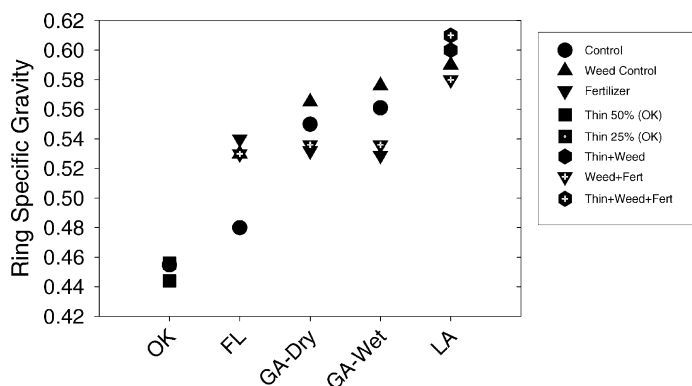


Fig. 7. Ring specific gravity for loblolly pine managed under a variety of silvicultural treatments in the southern US.

patterns are driven by latitudinal changes in growing season length, with rings having similar amounts of earlywood across locations, but greater amounts of latewood at lower latitudes, where longer growing seasons allow an extended period for latewood formation. The data in Fig. 7 generally support this hypothesis, with the OK site showing by far the lowest SG_{ring} , and the more southern sites showing higher SG_{ring} . Because SG_{ring} is also influenced by climatic factors, it should be considered that the results shown in Fig. 7 (from 1 year at each site) likely confound the effects of latitude with the effects of individual-year climate.

It is often assumed that treatments which increase growth rate will generally decrease SG_{ring} . In this set of studies, however, the patterns of treatment-induced variation in SG_{ring} varied by site. For example, control treatments tended to have intermediate values of SG_{ring} at the OK and GA sites, while the C treatment had lower SG_{ring} at the FL site. Plots receiving fertilizers, either alone or in combination with weed control, tended to have lower SG_{ring} at the GA and LA sites, while these treatments showed increased SG_{ring} compared to the controls at FL. It is possible that the previously mentioned effects of individual-year climate, as well as treatment effects on tree ontogeny (e.g. Jokela and Martin, 2000) and different genetic sources among sites may have obscured consistent responses of SG_{ring} to treatment.

3.5. Stemwood increment versus LAI

Many studies have shown strong relationships between leaf area and productivity in southern pines

(e.g. Vose and Allen, 1988; Dalla-Tea and Jokela, 1991; Albaugh et al., 1998; Burkes et al., 2003) and in other species (e.g. Long and Smith, 1992; Carlyle, 1998; Hinckley et al., 1999), although few have examined the commonality of these relationships across multiple sites and treatments. In this set of seven experiments, the relationship between stemwood increment and LAI was strong at LAI levels <3.0 , but at higher LAIs the relationship was more variable (Fig. 8A). For example, for plots with LAI between 3.0 and 5.0, values of stemwood increment ranged from $<1.0 \text{ Mg ha}^{-1}$ per year to almost 20.0 Mg ha^{-1} per year (Fig. 8A). The OK site was especially variable, showing the greatest range of any site for stemwood increment. When these data were screened to remove points with extreme reductions in stemwood increment at high basal areas (specifically FL and LA after age 13 years), the variation at higher LAI was reduced (Fig. 8B). A number of regression functions were fitted to the data, including linear, log-log, hyperbolic, and logistic. Analysis of fit statistics and residual plots suggested that the logistic model best described these data; this function explained 75% of the variation in stemwood increment in the screened data set (Fig. 8B; stemwood increment (Mg ha^{-1} per year) = $15.39 / (1 + e^{(2.90 - 1.13\text{LAI})})$, $R^2 = 0.747$).

Fig. 8B demonstrates that stemwood growth efficiency (stemwood production/LAI) at LAI > 3.0 is highly variable both among and within sites. Some of this variation may be attributable to differences in soil fertility, whether induced by treatments within sites or by differences in soil or climate among sites. Loblolly pine growth efficiency has been shown to respond

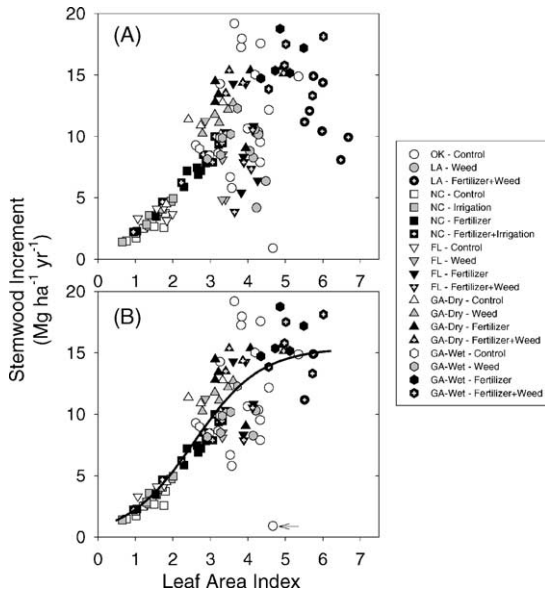


Fig. 8. Relationship between stemwood biomass increment and peak projected leaf area index for long-term loblolly pine productivity studies in the southern US. (A) All data. (B) Data screened to remove points showing extreme reductions in increment at high basal areas (specifically FL and LA after 13 years of age). Line shows a logistic function fitted through the data, excluding outlier indicated by arrow (stemwood increment (Mg ha^{-1} per year) = $15.39 / (1 + e^{(2.90 - 1.13\text{LAI})})$, $R^2 = 0.747$). The same function fitted through the data in (A) had $R^2 = 0.597$ (not shown).

positively to changes in soil nutrient supply (Albaugh et al., 1998), although this response is not universal. For example, Samuelson et al. (2001) saw no change in growth efficiency in fertilized and irrigated loblolly pine at the GA-Irr site, and Will et al. (2002) showed that fertilizer additions increased the ratio of stem biomass growth:LAI in 7-year-old loblolly pine stands, but decreased the ratio in 13-year-old stands.

Within- and between-site variation in climate is another likely source of variation in Fig. 8B. A number of studies have demonstrated that climate influences radiation use efficiency (McMurtrie et al., 1994; Runyon et al., 1994), and if radiation use efficiency varied with climate, it is likely that stemwood growth efficiency would follow. Soil water availability is a common limiting factor for forest productivity and we hypothesized that site water balance might explain some degree of variation in productivity across the loblolly pine range. Soil water balance parameters varied considerably across the wide geographical

range and long time intervals represented by these experiments. Annual precipitation ranged more than 200% across the full dataset, from a low of 590 mm (OK, age 24 years) to 1450 mm (NC, age 14 years). Calculated values of Thornthwaite potential evapotranspiration (PET), actual evapotranspiration (AET), and soil water deficit were similarly variable. In a few cases, individual outlying values of stemwood production could be associated with either unusually dry or wet conditions. For example, the very low value of stemwood production for the OK site (Fig. 8, 0.9 Mg ha^{-1} per year) was associated with an extreme drought year (age 23 years, 610 mm precipitation, 640 mm AET), while the highest value of stemwood PAI (Fig. 8, 19.2 Mg ha^{-1} per year) occurred during a wet year at the same location (age 14 years, 1140 mm precipitation, 720 mm AET). However, when the full range of data were analyzed, soil water balance parameters were not significantly correlated with annual stemwood increment. There was also no correlation of water balance parameters with the residuals of the stemwood increment versus LAI relationship shown in Fig. 8B, suggesting that changes in soil water availability were not the cause of the considerable variation in stemwood PAI at LAI values >3.0 .

A number of loblolly pine studies support the hypothesis that soil water availability is not the primary driver for productivity differences within its natural range (Hebert and Jack, 1998). Sampson and Allen (1999) modeled loblolly pine carbon dynamics under varying soil water-holding capacity and stand LAI conditions. From these simulations across the range of the species, these authors concluded that "LAI, rather than soil available water-holding capacity, may be more important in determining the long-term average productivity of loblolly pine on soils of median available water-holding capacity or greater". More detailed studies at the individual sites described in this paper show similar results. At the FL site, variation in canopy radiation use efficiency over a 10-year period was not correlated with a modeled index of soil water deficit (Martin and Jokela, unpublished data), while aboveground radiation use efficiency, LAI and growth were highly responsive to treatments which increased soil nutrient availability (Colbert et al., 1990; Jokela and Martin, 2000; Martin and Jokela, 2004). Irrigation treatments at both the NC and GA-Irr sites had a smaller effect on productivity

than fertilizer alone (NC, Albaugh et al., 1998), or the combination of fertilizer and irrigation (NC and GA-Irr, Albaugh et al., 1998; Samuelson et al., 2001). Previous work at the GA-Dry and GA-Wet sites showed strong LAI and growth responses to fertilizer in the absence of irrigation (Borders and Bailey, 2001; Will et al., 2002). Taken together, these studies suggest that soil nutrient availability is the dominant driver of loblolly pine productivity across its natural range. However, our understanding of the mechanisms that link soil nutrient availability to loblolly pine productivity is still in its early stages, and process-based predictions of forest productivity based on site nutrient status remain elusive.

3.6. Research needs

Researchers and practitioners alike have maintained considerable interest in developing management strategies that increase the productivity of loblolly pine stands in the southeastern US. Two-fold gains in productivity have been achieved over the last four decades using genetically improved seedlings for growth and disease resistance (McKeand et al., 2003), as well as ameliorative treatments such as fertilizer additions and understory competition control that increase soil fertility (Neary et al., 1990b; Sword et al., 1998; Borders and Bailey, 2001). The potential of achieving even greater levels of productivity and product value with loblolly pine exist in this region (Farnum et al., 1983; Sampson and Allen, 1999; Adegbidi et al., 2002).

The seven long-term studies reported here had no direct linkage in terms of experimental design. Each study addressed different objectives as the basis for understanding what controls productivity in loblolly pine ecosystems. Results from this synthesis, however, have highlighted several topics that require further investigation.

3.6.1. Nutrient demands, uptake, and utilization efficiency

These and other studies have reinforced the importance of soil nutrient availability for stemwood production across the native range of loblolly pine, particularly in intensively managed forest plantations (Colbert et al., 1990; Albaugh et al., 1998; Sword et al., 1998; Fox, 2000; Samuelson et al., 2001; Will et al.,

2002). To date, however, there is not a clear understanding of how soil processes, soil environment, root network development, and root network functioning interact to determine soil nutrient supply over an entire rotation for any site, much less across a wide range of soil–climate conditions. It is equally apparent that we need to better understand nutrient demand across the rotation for intensively managed plantations, particularly in a region where fertilizer additions are a common component of management prescriptions. This information is not only lacking for loblolly pine, but other commercial species as well. Improved genetics and culturing regimes that increase stand productivity are undoubtedly increasing tree and stand nutrient demands from the soil.

Our limited understanding of how nutrient uptake and utilization mechanisms influence forest productivity hampers the development of robust process-based models for forests in general (Landsberg, 2003). Nutrient supply, acquisition and utilization efficiency studies that explore these interactions from a community (tree, microbial, competing vegetation) standpoint are much needed. For example, recent studies have demonstrated that the forest floor is a strong sink for nitrogen (Richter et al., 2000), but little is known regarding the potential transformation of these materials into a utilizable nitrogen source throughout a rotation. In addition, because modern management systems are becoming more sophisticated in their selection and deployment of genetic materials, it is vital that we understand how species, family, and clonal variation influence these processes (Xiao et al., 2003).

3.6.2. Understanding mechanisms of intraspecific-tree competition

While nutrition management is paramount for keeping stand production potential high, it is apparent from these studies that rotation long stand density management will be essential for minimizing competition-related growth reductions and mortality losses, and to produce higher value, large dimension trees. In other words, the well established relationships between tree size and stand density (Dean and Baldwin, 1993) are apparently not altered by fertilizer additions within the natural range of loblolly pine. Better integration of our knowledge of fertilizer growth responses and stand development (e.g. leaf area, basal area) will be neces-

sary to optimize intensity, timing and frequency of fertilizer and thinning treatments. For example, we do not have sufficient information to determine whether the efficacy of fertilizer additions on growth is greater before or after a thinning treatment. We may need to further explore how community level factors such as nutrient immobilization by soil microbes or the relative nutrient sink strength of tree crown classes affects soil nutrient availability and tree nutrient acquisition.

3.6.3. *Species × hemisphere interactions studies*

Patterns of stand development and maximum size–density relationships appear to be consistent and relatively insensitive to levels of management intensity across the natural range of loblolly pine. However, when these same relationships are examined for this species when planted as an exotic the rules seem to change. For example, loblolly pine plantations in Hawaii collectively had greater maximum size–density boundaries, higher maximum basal area accrued over a range of spacings, and increased mean annual increments compared to rapidly growing plantations in the southern US (Harms et al., 2000). Similar findings have generally been noted for this species in Brazil, Hawaii, Australia, and South Africa (Burns and Hu, 1983; Schultz, 1997; Borders and Bailey, 2001). Taken together, these observations suggest that the genetic growth potential of loblolly pine is not being achieved within its native range. A detailed analysis that contrasts soil, climate, and tree ecophysiological characteristics in plantations in the southern US and the southern hemisphere could potentially provide great insight into the effects of genetic versus environmental controls on loblolly pine growth. Such a comparison might reveal whether large gains in productivity in the southern US could be achieved through additional silvicultural manipulations. Conversely, such an analysis may indicate that regional climate and site factors in the southern US limit the biological expression of species growth potential.

Because growth is a complex phenomenon that integrates site, climate, ecological, and genetic factors simultaneously, it will be advantageous to utilize process models for hypothesis generation and testing. In the near term, using a relatively simple process-based model such as 3-PG (Landsberg and Waring, 1997) to summarize, integrate and explore existing

data from this series of studies may help identify knowledge gaps and areas for research that were not apparent from the empirical analyses. In the longer term, application of this knowledge will require development of a model framework to predict stemwood biomass production as a function of stand and tree characteristics, resource supply (nutrients and water), and weather. Models that incorporate both tree function and site resource supply modules may be particularly useful, especially when they are linked to existing or modified growth and yield models which produce outputs or predictions in economically useful units (i.e. hybrid models, Baldwin et al., 1998). In the longer term, systems which use remotely sensed stand structural information to drive process-based production models within a geographic information systems framework are likely to become increasingly powerful and important tools for managing forest ecosystems at large spatial scales (Waring and Running, 1998; Landsberg, 2003).

Acknowledgements

This research was supported by the Florida Agricultural Experiment Station, and was approved for publication as Journal Series No. R-09872.

References

- Adegbidi, H.G., Jokela, E.J., Comerford, N.B., Barros, N.F., 2002. Biomass development for intensively managed loblolly pine plantations growing on Spodosols in the southeastern USA. *For. Ecol. Manage.* 167, 91–102.
- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* 44, 317–328.
- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192, 3–19.
- Allen, H.L., 1987. Forest fertilizers: nutrient amendment, stand productivity and environmental impact. *J. For.* 85, 37–46.
- Baldwin, V.C., Dougherty, P.M., Burkhart, H.E., 1998. A linked model for simulating stand development and growth processes of loblolly pine. In: Mickler, R.A., Fox, S. (Eds.), *The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment*. Springer-Verlag, New York, pp. 305–325.

- Baldwin, V.C., Peterson, K.D., Clark, A., Ferguson, R.B., Strub, M.R., Bower, D.R., 2000. The effects of spacing and thinning on stand and tree characteristics of 38-year-old loblolly pine. *For. Ecol. Manage.* 137, 91–102.
- Borders, B.E., Bailey, R.L., 2001. Loblolly pine-pushing the limits of growth. *S. J. Appl. For.* 25, 69–74.
- Borders, B.E., Will, R.E., Markewitz, D., Clark, A., Hendrick, R., Teskey, R.O., Zhang, Y., 2004. Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia. *For. Ecol. Manage.* 192, 21–37.
- Burkes, E.C., Will, R.E., Barron-Gafford, G.A., Teskey, R.O., Shiver, B., 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliotii* stands of different planting densities. *For. Sci.* 49, 224–234.
- Burns, R.M., Honkala, B.M., 1990. Silvics of North America, vol. 1, Conifers. Agriculture Handbook 654. USDA Forest Service, Washington, DC, p. 675.
- Burns, P.Y., Hu, S.C., 1983. Ecological and silvicultural factors associated with rapid growth of loblolly pine stands. In: Proceedings of the Second Biennial Southern Silvicultural Research Conference, Atlanta, GA, 4–5 November 1982, General Technical Report SE-24. USDA Forest Service Southeastern Forest Experiment Station, Asheville, NC, pp. 261–268.
- Carlyle, J.C., 1998. Relationships between nitrogen uptake, leaf area, water status and growth in an 11-year-old *Pinus radiata* plantation in response to thinning, thinning residue, and nitrogen fertiliser. *For. Ecol. Manage.* 108, 41–55.
- Clark, A., Saucier, J.R., 1989. Influence of initial planting density, geographic location, and species on juvenile wood formation in southern pine. *For. Prod. J.* 39, 42–48.
- Colbert, S.R., Jokela, E.J., Neary, D.G., 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. *For. Sci.* 36, 995–1014.
- Dalla-Tea, F., Jokela, E.J., 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. *For. Sci.* 37, 1298–1313.
- Dean, T.J., Baldwin, V.C., 1993. Using a density-management diagram to develop thinning schedules for loblolly pine plantations. Research Paper SO-275. USDA Forest Service Southern Forest Experiment Station, Asheville, NC, p. 7.
- Dean, T.J., Jokela, E.J., 1992. A density-management diagram for slash pine plantations in the lower Coastal Plain. *S. J. Appl. For.* 16, 178–185.
- DeBell, D.S., Harms, W.R., Whitesell, C.D., 1989. Stockability: a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern USA. *For. Sci.* 35, 708–719.
- Farnum, P., Timmis, R., Kulp, J.L., 1983. Biotechnology of forest yield. *Science* 219, 694–702.
- Fox, T.R., 2000. Sustained productivity in intensively managed forest plantations. *For. Ecol. Manage.* 138, 187–202.
- Harms, W.R., DeBell, D.S., Whitesell, C.D., 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. *Can. J. For. Res.* 24, 511–521.
- Harms, W.R., Whitesell, C.D., DeBell, D.S., 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. *For. Ecol. Manage.* 126, 13–24.
- Hebert, M.T., Jack, S.B., 1998. Leaf area index and site water balance of loblolly pine (*Pinus taeda* L.) across a precipitation gradient in east Texas. *For. Ecol. Manage.* 105, 273–282.
- Hennessey, T.C., Dougherty, P.M., Lynch, T.B., Wittwer, R.F., Lorenzi, E.M., 2004. Long-term growth and ecophysiological responses of a southeastern Oklahoma loblolly pine plantation to early rotation thinning. *For. Ecol. Manage.* 192, 97–116.
- Hermann, R.K., Lavender, D.P., 1999. Douglas-fir planted forests. *New For.* 17, 53–70.
- Hinckley, T.M., Keyes, M.R., Martin, T.A., Sprugel, D.G., 1999. Lessons from montane forests of the Pacific northwest. *Phyton* 39, 73–84.
- Hough, W.A., 1982. Phytomass and nutrients in the understory and forest floor of slash/longleaf pine stands. *For. Sci.* 28, 359–372.
- Jokela, E.J., Allen, H.L., McFee, W.W., 1991. Fertilization of southern pines at establishment. In: Duryea, M.L., Dougherty, P.M. (Eds.), *Forest Regeneration Manual*. Kluwer Academic Publishers, The Netherlands, pp. 263–277.
- Jokela, E.J., Martin, T.A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* 30, 1511–1524.
- Kvalseth, T.O., 1985. Cautionary note about R^2 . *Am. Statist.* 39, 279–285.
- Lambeth, C.C., Dougherty, P.M., Gladstone, W.T., McCullough, R.B., Wells, O.O., 1984. Large-scale planting of North Carolina loblolly pine in Arkansas and Oklahoma: a case of gain versus risk. *J. For.* 82, 736–741.
- Landsberg, J.J., 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. *Can. J. For. Res.* 33, 385–397.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- Ledgard, N.J., Belton, M.C., 1985. Exotic trees in the Canterbury high country. *NZ J. For. Sci.* 15, 298–323.
- Long, J.N., Smith, F.W., 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *For. Ecol. Manage.* 53, 53–64.
- Martin, T.A., Jokela, E.J., 2004. Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida, USA. *For. Ecol. Manage.* 192, 39–58.
- McKeand, S.E., Mullin, T.J., Byearam, T., White, T.L., 2003. Deployment of genetically improved loblolly and slash pines in the south. *J. Appl. For.* 101, 32–37.
- McMurtrie, R.E., Gholz, H.L., Linder, S., Gower, S.T., 1994. Climatic factors controlling the productivity of pine stands: a model-based analysis. *Ecol. Bull.* 43, 173–188.
- Mickler, R.A., Fox, S. (Eds.), 1998. *The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment*. Springer-Verlag, New York, p. 892.

- Neary, D.G., Jokela, E.J., Comerford, N.B., Colbert, S.R., Cooksey, T.E., 1990a. Understanding competition for soil nutrients—the key to site productivity on southeastern coastal plain spodosols. In: Gessel, S.P., Lacate, D.S., Weetman, G.F., Powers, R.F. (Eds.), Proceedings of the Seventh North American Forest Soils Conference. University of British Columbia Faculty of Forestry, Vancouver, BC, pp. 432–450.
- Neary, D.G., Rockwood, D.L., Comerford, N.B., Swindel, B.F., Cooksey, T.E., 1990b. Importance of weed control, fertilization, irrigation and genetics in slash and loblolly pine early growth on poorly drained spodosols. *For. Ecol. Manage.* 30, 271–281.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley, New York, p. 544.
- Richter, D.D., Markewitz, D., Heine, P.R., Jin, V., Raikes, J., Tian, K., Wells, C.G., 2000. Legacies of agriculture and forest regrowth in the nitrogen of old-field soils. *For. Ecol. Manage.* 138, 233–248.
- Runyon, J., Waring, R.H., Goward, S.N., Welles, J.M., 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Eco. Appl.* 4, 226–237.
- Sampson, D.A., Allen, H.L., 1999. Regional influences of soil available water-holding capacity and climate, and leaf area index on simulated loblolly pine productivity. *For. Ecol. Manage.* 124, 1–12.
- Samuelson, L.J., Stokes, T., Cooksey, T.E., McLemore III, P., 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. *Tree Physiol.* 21, 369–376.
- Samuelson, L.J., Johnsen, K., Stokes, T., 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to six years of intensive management. *For. Ecol. Manage.* 192, 59–70.
- SAS Institute, 1992. SAS Technical Report P-229 SAS/STAT Software: Changes and Enhancements, Release 6.07. SAS Institute Inc., Cary, NC, p. 620.
- Schultz, R.P., 1997. The Ecology and Culture of Loblolly Pine (*Pinus taeda* L.). Agriculture Handbook #713, USDA Forest Service, Washington, DC, p. 493.
- Switzer, G.L., Nelson, L.E., Smith, W.H., 1966. The characterization of dry matter and nitrogen accumulation by loblolly pine (*Pinus taeda* L.). *Soil Sci. Soc. Am. Proc.* 30, 114–119.
- Sword, M.A., Tiarks, A.E., Haywood, J.D., 1998. Establishment treatments affect the relationships among nutrition, productivity and competing vegetation of loblolly pine saplings on a Gulf Coastal Plain site. *For. Ecol. Manage.* 105, 175–188.
- Sword Sayer, M.A., Goelz, J.C., Chambers, J.L., Tang, Z., Dean, T.J., Haywood, J.D., Leduc, D.J., 2004. Long-term trends in loblolly pine productivity and stand characteristics in response to thinning and fertilization in the West Gulf Region. *For. Ecol. Manage.* 192, 71–96.
- Teskey, R.O., Bongarten, B.C., Cregg, B.M., Dougherty, P.M., Hennessey, T.C., 1987. Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine (*Pinus taeda* L.). *Tree Physiol.* 3, 41–61.
- Vose, J.M., Allen, H.L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *For. Sci.* 34, 547–563.
- Wahlenberg, W.G., 1946. *Loiblolly Pine: Its Use, Ecology, Regeneration, Protection, Growth and Management*. Duke University, Durham, NC, p. 603.
- Waring, R.H., Running, S.W., 1998. *Forest Ecosystems: Analysis at Multiple Scales*. Academic Press, San Diego, p. 370.
- Will, R.E., Munger, G.T., Zhang, Y.J., Borders, B.E., 2002. Effects of annual fertilization and complete competition control on current annual increment, foliar development, and growth efficiency of different aged *Pinus taeda* stands. *Can. J. For. Res.* 32, 1728–1740.
- Xiao, Y., Jokela, E.J., White, T.L., 2003. Growth and leaf nutrient responses of loblolly and slash pine families to intensive silvicultural management. *For. Ecol. Manage.* 183, 281–295.