Forest Ecology and Management 257 (2009) 2342–2349

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Specific gravity responses of slash and loblolly pine following mid-rotation fertilization

Kimberly R. Love-Myers [a,*], Alexander Clark III [b], Laurence R. Schimleck [a], Eric J. Jokela [c], Richard F. Daniels [a]

[a] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, United States
[b] USDA Forest Service, Southern Research Station, Athens, GA 30602, United States
[c] 353 Newins-Ziegler Hall, P.O. Box , University of Florida, Gainesville, FL 32611-0410, United States

ARTICLE INFO

Article history:
Received 15 December 2008
Received in revised form 24 February 2009
Accepted 17 March 2009

Keywords:
Fertilization
Mid-rotation
Wood density
Specific gravity
Wood properties
Loblolly pine
Slash pine

ABSTRACT

Wood quality attributes were examined in six stands of slash pine (*Pinus elliottii* Engelm. var. *elliottii*) and loblolly pine (*P. taeda* L.) in the lower Coastal Plain of Georgia and Florida. Several plots comprised each stand, and each plot was divided so that it received three fertilizer treatments: a control treatment with herbaceous weed control at planting and brush control at mid-rotation only (control); 45 kg ha^{-1} N + 56 kg ha^{-1} P + herbaceous weed control at planting and 224 kg ha^{-1} N + 45 kg ha^{-1} P + brush control at mid-rotation (fertilizer with N at planting); and 56 kg ha^{-1} P + herbaceous weed control at planting and 224 kg ha^{-1} N + 45 kg ha^{-1} P + brush control at mid-rotation (fertilizer without N at planting). Ring width, ring earlywood specific gravity (SG), ring latewood SG, whole ring SG, and ring percent latewood were measured on each of seven trees. Of these measurements, this study focused mainly on the properties related to SG. Examination of the rings showed that latewood SG was significantly lower in trees treated with fertilizers with and without N at planting in the two to three years following fertilization, but that latewood SG gradually returned to a level similar to the control. Fertilizer without N at planting may also have had a brief negative effect on earlywood SG following mid-rotation fertilization, but it was not as clear or lasting as the effect on latewood SG. Additionally, although slash and loblolly pine appear to differ in the developmental patterns of these SG properties, there were no significant differences in how these patterns interacted with treatment. This study demonstrated that fertilization treatments have similar short-term effects on the SG of slash and loblolly pines, particularly in latewood, but the trees will return to a SG pattern consistent with unfertilized trees within two or three years.

1. Introduction

Mid-rotation fertilization is a common silvicultural practice used in the management of slash (*Pinus elliottii* Engelm. var. *elliottii*) and loblolly (*P. taeda* L.) pine stands in the southeastern United States. Many studies have reported growth benefits associated with fertilizer additions (Pritchett and Comerford, 1982; Jokela et al., 1991). As a result, the number of stands being fertilized continues to grow rapidly. The North Carolina State Forest Nutrition Cooperative (NCSFNC), for example, reports that the annual area of southern pine plantations fertilized in 1990 was about 81,000 ha; this area increased to just over 485,000 ha in 2002 (Fox et al., 2007), which was largely the result of fertilizing intermediate-aged stands.

Strong increases in volume production have been documented with mid-rotation fertilization treatments (Jokela and Stearns-Smith, 1993). Recent results suggest that over 85% of the stands fertilized were responsive to additions of nitrogen (N) and phosphorus (P), and average growth gains were 30% (3.5 m^3 ha^{-1} yr^{-1}) over a six-year period following a one-time application of 224 kg ha^{-1} N and 28 kg ha^{-1} P; responses of over 7 m^3 ha^{-1} yr^{-1} were observed on some sites (FNC, 2006). Growth and yield models support the empirical conclusions of this study, as shown by Amateis et al. (2000), who demonstrated that trees can increase in both height and diameter in response to fertilization with N and P.

While fertilization can significantly improve volume growth, the forest products industry has recently become concerned that these fertilization methods may have negative effects on properties related to wood quality. Ring specific gravity (SG), latewood

* Corresponding author. Tel.: +1 706 542 7587; fax: +1 706 542 8356.
E-mail addresses: klove@warnell.uga.edu (K.R. Love-Myers), aclark@fed.us.gov (A. Clark III), lschimleck@warnell.uga.edu (L.R. Schimleck), ejokela@ufl.edu (E.J. Jokela), ddaniels@warnell.uga.edu (R.F. Daniels).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.03.031

and earlywood SG, percent latewood, microfibril angle (MFA), modulus of elasticity (MOE), and modulus of rupture (MOR) are generally of interest in this regard. SG and related properties are often given the most attention because of their ease of measurement, association with strength and stiffness of solid wood products (Nyakuengama, 1991), and relationship to the yield and quality of pulp (Morling, 2002). High SG is desirable for many products, including southern pine lumber, engineered wood products and composite panels, due to its positive relationship with wood stiffness and strength (Panshin and deZeeuw, 1980). High SG is also positively correlated with pulp yield (Panshin and deZeeuw, 1980). SG is often a good predictor of the properties of paper produced from the wood pulp. Higher SG wood tends to have longer tracheids with increased tear resistance and opacity; lower SG wood tends to have thinner walls and short tracheids that produce paper with good tensile, burst, fold, and sheet smoothness (Smook, 2002).

There are several studies that have examined the effects of mid-rotation fertilization on SG properties. Variable results have been reported, as responses to fertilization for any stand are the result of a complex series of interactions. As noted by Rojas (2005) site conditions at time of application, years since last application, climatic conditions after application and the nutrients used and their rates are all important. Water availability after application is particularly important in determining what the response will be like. For example, Nyakuengama et al. (2002) showed that the relationship between ring width and density depended on annual rainfall or seasonal rainfall. Choong et al. (1970) demonstrated that early-age fertilization of conifers (first and fourth years after establishment) did not significantly impact whole core SG properties. However, several studies reveal that the growth rings produced immediately following fertilization do experience a decrease in SG (Williams and Hamilton, 1961; Zobel et al., 1961; Mallonee, 1975; Morling, 2002). This effect was reported to last anywhere from two to five years, during which time the tree would gradually revert to a similar pattern as unfertilized trees (Morling, 2002; Nyakuengama et al., 2002). Clark et al. (2004) demonstrated that latewood SG showed a similar pattern in twelve-year-old loblolly pines following annual fertilization. Percent latewood within a ring also seems to decrease for several years following fertilization (Williams and Hamilton, 1961; Clark et al., 2004). There are, however, no reports stating that earlywood SG exhibits any particular pattern of decrease after fertilization.

Because the use of mid-rotation fertilization has increased so dramatically within the last two decades, it is important to understand the effects of this practice on various wood quality characteristics, such as SG. While mid-rotation fertilization has been proven to increase the overall quantity of wood, it is vital that it not result in an unexpected reduction of high-value products that can be made with that wood. Critical to this understanding is the need to learn whether the effects vary between different tree species or are similar across species. No previous studies have directly compared the effects of fertilization on wood quality between species under similar conditions. If different species have different wood quality responses to fertilization, it may be advantageous to wood producers to develop varying fertilization regimes for separate species based on a combination of growth and quality responses. Therefore, the objective of this study was to learn about and compare the effects of mid-rotation fertilization on SG in loblolly and slash pine in the years following fertilization.

The Cooperative Research in Forest Fertilization (CRIFF) G-series study established by the School of Forest Resources and Conservation at the University of Florida (Jokela et al., 2000) allowed for examination of the effects of mid-rotation fertilization on SG in both loblolly and slash pine. The CRIFF G-series study was originally designed to measure the effects of various fertilization regimes on growth properties of trees. This study also provides the opportunity to study the effects of various fertilization regimes on the wood properties of slash and loblolly pine.

2. Materials and methods

2.1. Origin of samples

This study was conducted on a subset of installations from the regional CRIFF G-series experiments. From this study, six stands were selected throughout the states of Georgia and Florida, based on the species and the fertilization treatments applied. The six stands were divided evenly between slash and loblolly pine. Although the soils in the stands varied, all stands used soil types that were consistent with each species' site requirements (Jokela et al., 2000). Table 1 summarizes the properties of each stand.

All stands were planted and fertilized between 1987 and 1989, and were approximately the same age at the time of mid-rotation fertilization (nine or ten years old). This study was unique in that the treatments used at planting and mid-rotation imitate actual operational management regimes. The three treatments used in this study included: the control group, with herbaceous weed control at planting and brush control at mid-rotation, 45 kg ha^{-1} N + 56 kg ha^{-1} P + herbaceous weed control at planting and 224 kg ha^{-1} N + 45 kg ha^{-1} P + brush control at mid-rotation, which is referred to as "fertilizer with N at planting", and 56 kg ha^{-1} P + herbaceous weed control at planting and 224 kg ha^{-1} N + 45 kg ha^{-1} P + brush control at mid-rotation, which is referred to as "fertilizer without N at planting". Note that the fertilizers with and without N at planting were identical treatments at mid-rotation and each administered both N and P at that time. The difference is only in the treatment received at planting, but by keeping these treatments separate rather than analyzing them together, it can be determined whether fertilization at planting influences the results of mid-rotation fertilization. All treatments were replicated three times at each site.

For each fertilizer treatment, increment cores (12 mm in diameter) were collected from twelve standing trees at breast height (1.37 m) in proportion to the diameter at breast height (DBH) distribution across the plot, resulting in a planned total of 108 cores from each stand. The increment cores were dried, glued to core holders and sawn into radial strips (12 mm tangentially, 2 mm longitudinally) using a twin-blade saw. One core sample was lost due to an unknown cause, possibly destroyed in the lab during

Table 1
Properties of six stands used in wood property analysis.

Location	Species	CRIFF soil group[a]	Planted and fertilized	Mid-rotation fertilization
Brantley Co., GA	Slash pine	D	1987	1997
Ware Co., GA	Slash pine	C	1988	1997
Nassau Co., FL	Slash pine	D	1989	1998
Putnam Co., FL	Loblolly pine	C	1987	1997
Flagler Co., FL	Loblolly pine	C	1987	1997
Glynn Co., GA	Loblolly pine	A	1988	1997

[a] Kushla and Fisher (1980).

sample preparation. Two more samples were lost during data collection. Therefore, a total of 645 core samples were used in the analysis. Radial growth and SG of earlywood and latewood of each annual ring for each radial strip was determined at 0.006 mm intervals using a direct-scanning X-ray densitometer (Quintek Measurement Systems™). Earlywood and latewood in each ring were distinguished using a SG threshold of 0.48. The densitometer was calibrated to express SG on a green volume and oven dry weight basis.

For each strip, rings for each of the four years following mid-rotation fertilization were analyzed for the effect of the fertilizer treatments on ring width, ring earlywood SG, ring latewood SG, whole ring SG, and ring percent latewood. This analysis was conducted to search for patterns in selected wood properties over time resulting from the mid-rotation fertilizer treatments.

2.2. Statistical analysis and model development

Statistical mixed effects models were used for the analysis of ring properties. The model in each case was a split-plot design, which was completely randomized at the whole plot level and a randomized complete block design with a nested blocking factor and subsamples on the split-plot level. To account for the individual years, the rings were analyzed as repeated measures on the subsamples. A separate analysis of variance (ANOVA) was performed on each factor of interest (ring width, earlywood SG, latewood SG, overall SG, and percent latewood in each ring).

Because of the structure of the experiment, several random effects had to be taken into account in addition to the fixed effects of the tree species and fertilizer treatment. For each observation, these random effects included the stand of origin and the plot of origin within the stand, as well as the tree from which the measurement came.

The model involved repeated measures on each tree, with one measurement for each response per ring. The responses of the rings associated with the four years following mid-rotation fertilization were measured (for example, if fertilization occurred in 1997, the rings were measured from 1998 to 2001). The ring from the year of fertilization was not used due to numerous factors outside the scope of this study that could have influenced the results in this year, including timing of fertilization and climatic variation. The relationship between the four rings could be considered either temporal or spatial because the measurements were taken over adjacent rings, which grew in sequential years. Because each tree generally contributed four measurements (one for each of the four years following fertilization), autocorrelation likely exists within each group of measurements from a single tree. To account for this, an autocorrelation structure among the repeated measures was included. Several different structures may be appropriate because of the combined temporal and spatial nature of the correlation. Structures that were tested included a first-order autoregressive temporal model, a spatial exponential model, a spatial linear model, a spatial Gaussian model, and a spatial power model. The final selection was based on the improvement made in the model using the Akaike Information Criteria (AIC). For ring width, a spatial Gaussian structure resulted in the lowest (most desirable) AIC. For earlywood SG, latewood SG, and ring SG, a spatial exponential model was chosen. For the percent latewood analysis, the most desirable model was the first-order autoregressive model.

A covariate was also included in the model, which was the appropriate measurement from the year prior to fertilization. For example, when the response was latewood SG, the covariate was the latewood SG from the ring formed in the year prior to mid-rotation fertilization. This adjusted for individual differences among trees—if a tree had low latewood SG prior to mid-rotation fertilization, it was likely to have low latewood SG after fertilization, and this helped separate the part of the effect due to the individual tree from the part due to the fertilization treatment.

The basic statistical model was:

$$y_{ijklmn} = T_i + S_{ij} + P_{ijk} + F_l + TF_{il} + e_{ijkl} + o_{ijklm} + \beta C + R_n + TR_{in} + FR_{ln} + TFR_{iln} + e^{*}_{ijklmn}$$

where T_i is the effect for tree species i; S_{ij} is the effect of the jth stand growing tree species i, and the error term for analysis of the tree species effect; P_{ijk} is the blocking effect of plot k within the jth stand of tree species i; F_l is the effect of fertilizer treatment l; TF_{il} is the interaction of tree species i with fertilizer treatment l; e_{ijkl} is the error from the differences between the experimental units (application of fertilizer l to plot k within the jth stand of tree species i) and the error term for the analysis of the fertilizer treatment and the interaction of the tree species and fertilizer treatment; o_{ijklm} is the random observational error resulting from tree m within the application of fertilizer treatment l to plot k within the jth stand of species i; R_n is the effect of ring n after mid-rotation fertilization; TR_{in} is the interaction effect of tree species i and ring n; FR_{ln} is the effect of fertilizer treatment l and ring n; TFR_{iln} is the three-way interaction effect of tree species i, fertilizer treatment l, and ring n; and e^{*}_{ijklmn} is the error resulting from measuring ring n on tree m within the application of fertilizer treatment l to plot k within the jth stand containing tree species i, and is the appropriate error term for analyzing the effect of the age of the ring relative to mid-rotation fertilization as well as all interactions involving that term. The covariate C is the appropriate measurement from the ring prior to fertilization.

All tests were conducted using the MIXED procedure available in SAS version 9.1 (SAS Institute Inc, 2004).

3. Results

For both latewood SG and ring SG, there was a significant response to the fertilizer treatments (Table 2). For all wood properties, there was a highly significant response to the ring number following mid-rotation fertilization; additionally, all wood properties showed significant interaction effects between tree species and ring number and between fertilizer treatment and ring number (Table 2). There was, however, no significant interaction between tree species and fertilizer treatment, which indicates that slash pine and loblolly pine reacted similarly to treatment. The interaction between tree species and ring number therefore indicates that the developmental patterns of all properties are different from year to year between slash and loblolly pine, but these pattern differences are natural and not related to the application of fertilizer.

Table 3 indicates that while average ring width following mid-rotation was expectedly larger in fertilized trees, latewood SG was significantly lower in trees treated with one of the fertilizer treatments with and without N at planting (0.7451 and 0.7401, respectively) compared to the control treatment (0.7602) only (P-value = 0.0069 and P-value = 0.0003, respectively). It also indicates that whole ring SG was significantly lower for fertilizer treatment without N at planting (0.5885) compared to the control treatment (0.6076) only (P-value = 0.0055).

Table 4a–e clarifies the interaction between the fertilizer treatments and ring number for each of the wood properties. Ring width was significantly higher for the fertilized trees (both with and without N at planting) than the control for two years following mid-rotation fertilization, which was not a surprising result given the previously mentioned research on growth responses to fertilization. There were also no significant differences in ring

Table 2
Analysis of variance for average wood properties at the ring level.

Property	Source[a]	Numerator d.f.	Denominator d. f.	*F*-value	*P*-value
Ring width	T	1	4.02	0.24	0.6485
	F	2	32.1	11.02	0.0002
	R	3	1313	202.19	<0.0001
	T*F	2	32.1	0.04	0.9642
	T*R	3	1313	2.62	0.0495
	F*R	6	1482	9.11	<0.0001
	T*F*R	6	1482	1.58	0.1482
Earlywood SG	T	1	3.92	2.00	0.2316
	F	2	30.5	0.92	0.4110
	R	3	1371	30.79	<0.0001
	T*F	2	30.8	0.42	0.6616
	T*R	3	1371	17.67	<0.0001
	F*R	6	1530	6.42	<0.0001
	T*F*R	6	1530	0.99	0.4336
Latewood SG	T	1	3.38	0.21	0.6714
	F	2	41.7	9.91	0.0003
	R	3	366	24.66	<0.0001
	T*F	2	41.7	0.67	0.5189
	T*R	3	366	6.51	0.0003
	F*R	6	477	5.70	<0.0001
	T*F*R	6	477	0.59	0.7392
Whole ring SG	T	1	3.93	0.35	0.5850
	F	2	35.8	5.58	0.0078
	R	3	1274	52.98	<0.0001
	T*F	2	35.9	0.34	0.7115
	T*R	3	1274	2.95	0.0318
	F*R	6	1447	6.73	<0.0001
	T*F*R	6	1447	0.45	0.8461
Percent latewood	T	1	3.93	0.04	0.8465
	F	2	32.4	1.41	0.2576
	R	3	1262	45.95	<0.0001
	T*F	2	32.5	0.35	0.7050
	T*R	3	1262	2.77	0.0405
	F*R	6	1429	3.08	0.0053
	T*F*R	6	1429	1.13	0.3433

[a] T = tree species, F = fertilization treatment, R = ring number; * indicates interaction.

width between the two fertilizer treatments in any year, which is verified by Fig. 1.

The earlywood SG of trees treated with fertilizer with and without N at planting were, in the majority of cases, not significantly different from the control treatment trees. However, there was evidence that treated trees may have experienced a brief drop in earlywood SG, since the first ring after mid-rotation fertilization with the fertilizer without N at planting had significantly lower earlywood SG (0.3383) than that of untreated trees (0.3545). Additionally, there was a significant increase in earlywood SG between a few subsequent years with treatments with and without N at planting, which was not detected for the control treatment. These trends are evident in Fig. 2.

Table 3
Estimated wood property means by fertilizer treatment, accompanied by Tukey's HSD pairwise comparisons.

Property	Fertilizer treatment		
	Control	With N at planting	Without N at planting
Ring width (m)	0.06842	0.07889a	0.09118a
Earlywood SG	0.3558a	0.3555a	0.3510a
Latewood SG	0.7602	0.7451a	0.7401a
Whole ring SG	0.6076a	0.5974ab	0.5885b
Percent latewood	62.54a	62.57a	61.21a

Treatments in each row with the same letter indicate no significant difference at $\alpha = 0.05$.

Table 4
(a–e) Estimated ring width, earlywood SG, latewood SG, whole ring SG, and percent latewood means by fertilizer treatment and ring number after mid-rotation fertilization, accompanied by pairwise comparisons with the Bonferroni adjustment.

Fertilizer treatment	Ring number			
	Ring 1	Ring 2	Ring 3	Ring 4
a. Ring width (m)				
Control	0.07751	0.06838a	0.06678a	0.06101b
With N at planting	0.09730c	0.08220d	0.07389a	0.06217b
Without N at planting	0.09873c	0.08310d	0.07431a	0.06751b
b. Earlywood SG				
Control	0.3545a	0.3558a	0.3569ac	0.3559a
With N at planting	0.3459ab	0.3522a	0.3595c	0.3646ac
Without N at planting	0.3383b	0.3469a	0.3577cd	0.3583ad
c. Latewood SG				
Control	0.7611a	0.7663a	0.7679a	0.7457c
With N at planting	0.7358d	0.7477b	0.7539ab	0.7429c
Without N at planting	0.7253d	0.7410bc	0.7487bc	0.7454c
d. Whole ring SG				
Control	0.5971	0.6140a	0.6162ac	0.6031ae
With N at planting	0.5687d	0.5958ab	0.6107bc	0.6142be
Without N at planting	0.5545d	0.5883b	0.6044c	0.6069ce
e. Percent latewood				
Control	59.98d	63.26a	63.71ab	63.21ac
With N at planting	57.63d	62.00ab	64.24b	66.43bc
Without N at planting	56.35d	61.05ac	63.51bc	63.92c

Treatments in the same column OR the same row in adjacent columns with the same letter indicate no significant difference at $\alpha = 0.05$; comparisons between treatments not in the same column or the same row in adjacent columns were not tested for significance.

Latewood SG demonstrated a clear drop after mid-rotation fertilization. Latewood SG in trees given fertilizer with N at planting remained significantly lower than the control treatment for two years following mid-rotation fertilization. For trees given fertilizer without N at planting, latewood SG remained significantly lower than the control treatment for three years following mid-rotation fertilization. There was a significant drop in latewood SG for the control treatment in year 4, which was also seen in trees fertilized with N at planting. Trees treated without N at planting did not experience a drop in latewood SG in this year, but latewood SG was still significantly low in year 3 for these trees; a significantly higher latewood SG would have been expected in this year. The fact that all treatments were affected indicates a factor outside of the study was most likely responsible for low latewood SG in this year, and this may be related to a drought in the southeastern United States that occurred in the fall of 2002, when the majority of trees would have been in their fourth year following mid-rotation fertilization. Fig. 3 demonstrates the drop in latewood SG for fertilized trees in the years immediately following mid-rotation fertilization, as well as the return to control levels in the subsequent rings.

Over the whole ring SG reductions are reflected in both earlywood and latewood, demonstrating a weaker version of the trend found in latewood SG. There was a significant drop in whole ring SG in trees treated with fertilizer with N at planting for one year when compared to the control, and for two years in trees treated with fertilizer without N at planting when compared to the control. Percent latewood did not demonstrate any significant trends, and neither fertilizer treatment showed a significant difference from the control in any year. Figs. 4 and 5 reflect these trends for whole ring SG and percent latewood, respectively.

Table 5a–e clarifies the interaction between tree species and ring number following mid-rotation fertilization. These tables demonstrate the differences in developmental patterns between the two species for these years. While no properties were

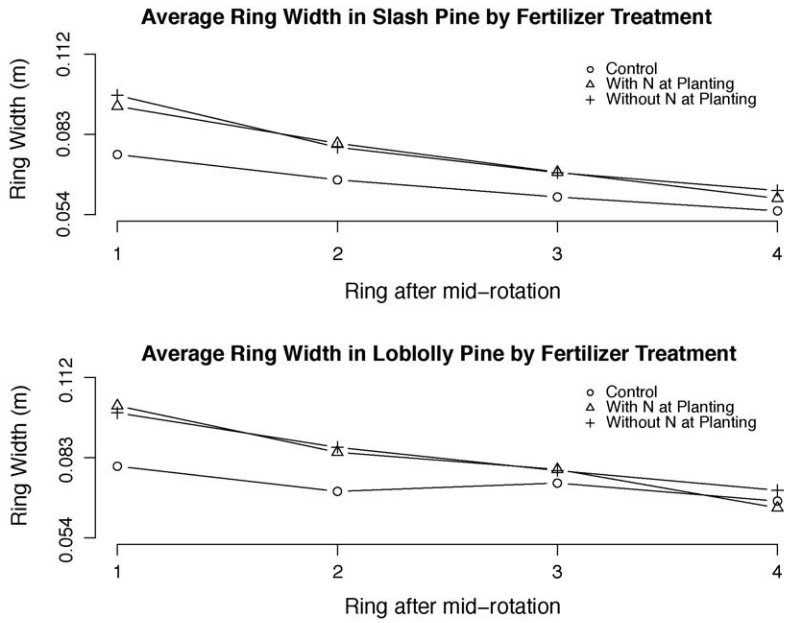

Fig. 1. Average ring width by tree species, fertilizer treatment, and ring number after mid-rotation fertilization.

significantly different in any given year between loblolly and slash pines, the patterns of variation (an increase or decrease) for all properties were different, which causes the interaction between tree species and ring number to be significant. This means that examining Figs. 1–5 can be especially helpful when understanding these differences. For example, slash pine experienced a significant increase in earlywood SG from ring 1 to 2 and ring 2 to 3 following mid-rotation fertilization. This did not occur in loblolly pine. Loblolly pine, on the other hand, experienced a significant increase in latewood SG between rings 1 and 2 following mid-rotation fertilization, and slash pine did not. Again, because there was no interaction between tree species and fertilizer treatment, it appears that this was a naturally occurring difference between slash and loblolly pine.

4. Discussion

This study examined response patterns in wood quality attributes following mid-rotation fertilizer applications in six loblolly and slash pine stands in the lower Coastal Plain of the southeastern U.S. There were several notable results. The study indicated that the effects of mid-rotation fertilization were temporary, and that treated trees had SG properties similar to those of untreated trees within two or three years. This is in agreement with previous studies (Posey, 1964; Ross et al., 1979), which have also suggested that the effects of fertilization on wood quality are transient in loblolly pine and yellow poplar in the southeastern United States; Nyakuengama et al. (2002) demonstrated similar transient effects in radiata pine (*Pinus radiata* D.

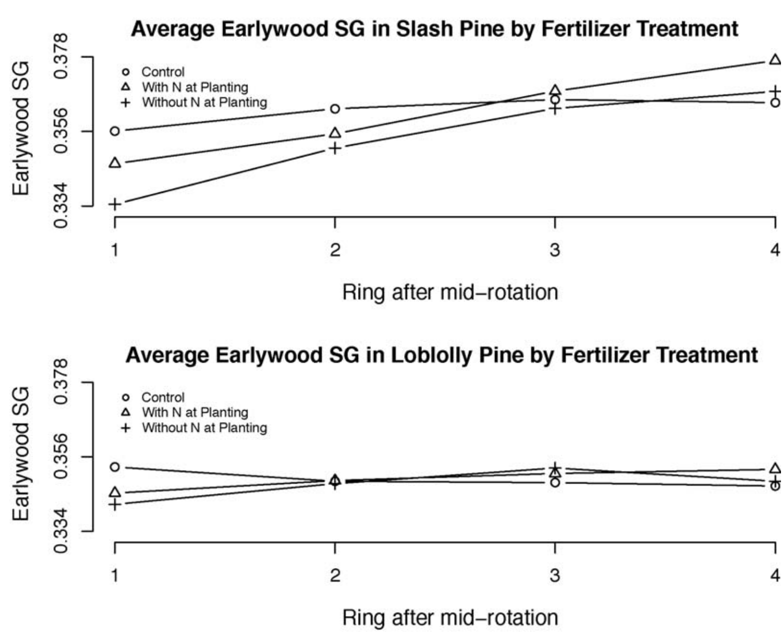

Fig. 2. Average earlywood SG by tree species, fertilizer treatment, and ring number after mid-rotation fertilization.

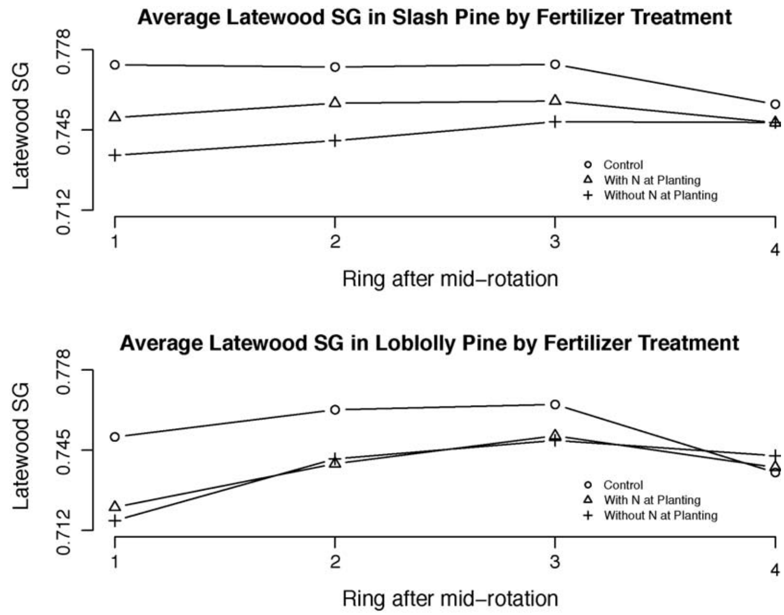

Fig. 3. Average latewood SG by tree species, fertilizer treatment, and ring number after mid-rotation fertilization.

Don) that lasted for five years following fertilization in south-eastern Australia.

There may have been a significant effect on earlywood SG for a short time after fertilization (perhaps two years) but the effect tended to be small and did not affect the overall earlywood SG in the four years following fertilization. Other studies have not reported similar findings, indicating that the effect is not large enough to be significant in smaller studies, or that it is unique to the particular trees used in this study due to geographic location or some other separating factor. It is also possible that the effect in this study was due to random chance, which does occur rarely in statistical analyses, and it may not appear if the study were repeated.

As in other studies, there was a significant effect due to fertilizer treatment in the four years following mid-rotation fertilization for latewood SG. Latewood SG was significantly lower in trees treated with fertilizer with N at planting in two rings following mid-rotation fertilization when compared to the control, and in three rings following mid-rotation fertilization for trees treated with fertilizer without N at planting. A combination of earlywood SG and latewood SG was seen in results for whole ring SG, which was not surprising. The results indicate there was no decrease in the percent latewood in any year following mid-rotation for fertilized trees, which implies the decrease in whole ring SG was due solely to the decrease in latewood SG rather than a lesser amount of higher density latewood. The finding that latewood SG and whole ring SG were significantly lower in fertilized trees agrees with the findings of Nyakuengama et al. (2002, 2003), who identified a decrease in density and wall thickness following mid-rotation fertilization in radiata pine. The effect of fertilization on latewood SG may be the result of reduced secondary wall thickening of latewood tracheids in the years immediately following treatment

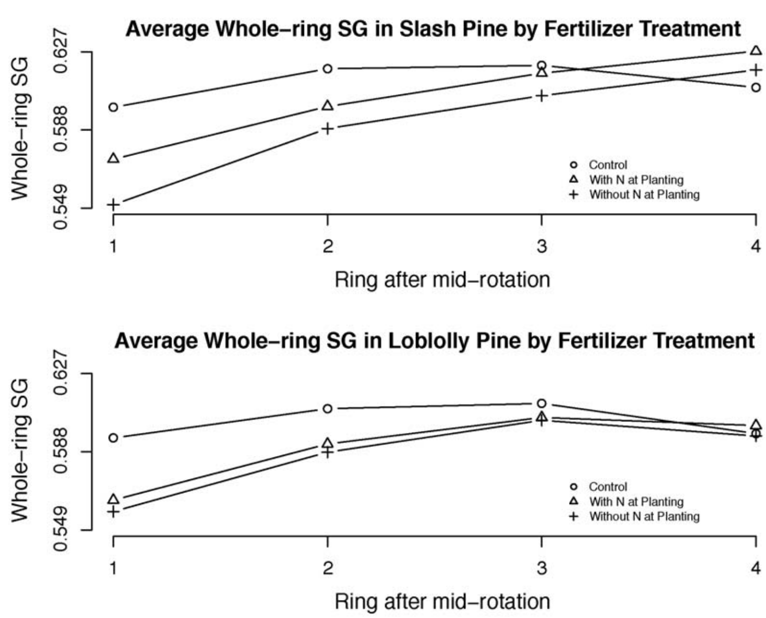

Fig. 4. Average whole ring SG by tree species, fertilizer treatment, and ring number after mid-rotation fertilization.

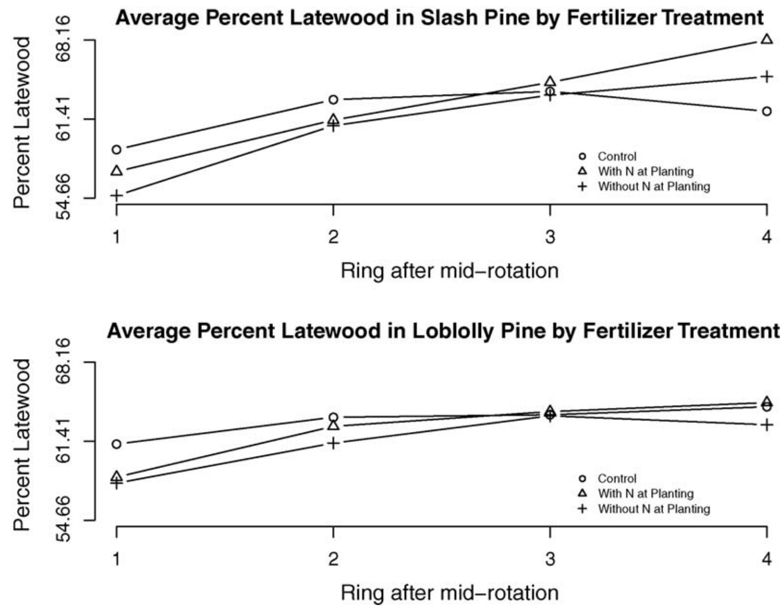

Fig. 5. Average percent latewood by tree species, fertilizer treatment, and ring number after mid-rotation fertilization.

(Clark et al., 2004; Nyakuengama et al., 2003). Some insight into the process of earlywood and latewood formation suggests the mechanisms behind this difference in fertilized trees.

A change in the balance of growth hormones, primarily auxins, is thought to be largely responsible for the transition from earlywood to latewood in loblolly pine (Megraw, 1985). These hormones are produced by the live crown of the tree and propagate down through the stem as the growing season progresses. In a mature tree the lowest levels of auxins are present in the lower portion of the tree, and this is related to smaller growth rings with a higher proportion of latewood compared to growth rings close to the live crown (Megraw, 1985).

Latewood formation has also been shown to correspond with the time in the season when height growth ceases and the needles that have formed during the growing season become mature, leading to a large increase in available photosynthate. This material is then available for secondary cell wall thickening, producing latewood cells rather than earlywood cells (Megraw, 1985). It has also been shown that while the amount of auxins available throughout the cambial region in Scots pine (*Pinus sylvestris* L.) is unchanged at this time, the radial distribution pattern within the cambial region is markedly changed during this period of transition (Uggla et al., 2001). Therefore, auxin availability and distribution in combination with the availability of photosynthate are the prevailing factors in the formation of earlywood or latewood.

It is recognized that increased foliar growth occurs following fertilization, with a subsequent increase in hormone (auxin) production and a reduction in the availability of photosynthate for secondary cell wall thickening (Larson et al., 2001). A study by Albaugh et al. (1998) showed that peak leaf area index (LAI) in fertilized loblolly pines doubled when fertilized primarily with N and P after four years of treatment, supporting the conclusion that fertilization increases foliar growth; this same study also indicated fertilization increases growth efficiency while reducing below-ground biomass allocation. Therefore, when SG is reduced in a ring post-fertilization, it indicates a combination of an increase in the number of cells being produced (in response to an increase in auxin) and a reduction in cell wall thickness (owing to less available photosynthate) has taken place. Results from the Nyakuengama et al. (2003) study of fiber properties in radiata pine agree with this conclusion, as there was an increase in the number of cells produced in the rings following fertilization but a decrease in cell diameter and wall thickness. Hence fertilization has either increased auxin production during the period of crown development, allowing cells to divide rapidly, or increased the length of time in which crown growth takes place, allocating photosynthate to be used in needle formation and growth rather than contributing to cell wall thickening, and delaying the change in auxin allocation patterns. In all likelihood, fertilization leads to some combination of increased auxin production and an extended crown formation period. Previous studies have indicated that fertilization can delay the start of the latewood formation period (Megraw, 1985).

Another result from this study is the relationship between the fertilizer with N at planting and the fertilizer without N at planting.

Table 5
(a–e) Estimated ring width, earlywood SG, latewood SG, whole ring SG, and percent latewood means by tree species and ring number after mid-rotation fertilization, accompanied by pairwise comparisons with the Bonferroni adjustment.

Tree species	Ring number			
	Ring 1	Ring 2	Ring 3	Ring 4
a. Ring width (m)				
Slash	0.08930a	0.07553b	0.06693c	0.05993d
Loblolly	0.09306a	0.08026b	0.07639c	0.06720d
b. Earlywood SG				
Slash	0.3457b	0.3564c	0.3654a	0.3697a
Loblolly	0.3468ab	0.3486ac	0.3507a	0.3495a
c. Latewood SG				
Slash	0.7522ab	0.7559a	0.7591a	0.7506c
Loblolly	0.7293b	0.7475a	0.7546a	0.7388c
d. Whole ring SG				
Slash	0.5745b	0.6023a	0.6138a	0.6181a
Loblolly	0.5723b	0.5964ab	0.6070a	0.5980a
e. Percent latewood				
Slash	56.86b	61.74a	63.92a	65.08a
Loblolly	59.11b	62.46a	63.73a	63.96a

Treatments in the same column OR the same row in adjacent columns with the same letter indicate no significant difference at $\alpha = 0.05$; comparisons between treatments not in the same column or the same row in adjacent columns were not tested for significance.

Although the two treatments did not result in significantly different wood properties in any year, the SG properties did differ in their relationship to control properties. While there was a significant difference in earlywood SG in the first year following mid-rotation fertilization between the control and the fertilizer without N at planting, this was not seen with the fertilizer with N at planting. Similarly, a significant difference in latewood SG between the control and the fertilizer without N at planting was seen for three years following mid-rotation, but this difference was observed for only two years for the fertilizer with N at planting. This indicates that in a larger study, a statistically significant difference may have been observed between the two fertilizer treatments. More research is needed, but because these treatments were identical at mid-rotation this may signify that the fertilizer delivered at planting could influence the wood quality differences after mid-rotation fertilization.

A further result from this study indicated that there was no significant difference in the way that slash and loblolly pine each respond to fertilization. Although there were differences in the way in which SG properties developed in slash and loblolly pine, the differences were not affected by fertilization. That is, application of fertilizer with or without N at planting to slash pine showed a reduction in SG characteristics (compared to the control treatment) that was similar in magnitude to the same treatment applications to loblolly pine. This implies that the results of studies of fertilization and SG characteristics for loblolly pine can likely be extrapolated to slash pine. This can expand many important experimental conclusions, for example, those of Antony et al. (in press) and Clark et al. (2004).

Acknowledgements

Thanks to the Wood Quality Consortium, University of Georgia, Athens, GA, USA for funding this project. Also thanks to the School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA for the use of the CRIFF G-series experiment data. Authors are indebted to the USDA-Forest Service, Athens, GA, USA for their valuable support in conducting this study. The wood samples were collected under an Agenda 2020 grant from the US Department of Energy.

References

Albaugh, T.J., Allen, L.H., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf area and above- and belowground growth response of loblolly pine to nutrient and water additions. Forest Science 44 (2), 317–328.

Amateis, R.L., Liu, J., Ducey, M.J., Allen, H.L., 2000. Modeling response to midrotation nitrogen and phosphorous fertilization in loblolly pine plantations. South, Journal of Applied Forestry 24, 207–212.

Antony, F., Jordan, L.C., Daniels, R.F., Schimleck, L.R., Clark III, A. Effect of mid-rotation fertilization on specific gravity of loblolly pine (*Pinus taeda* L.). Canadian Journal of Forest Research, in press.

Choong, E.T., Box, B.H., Fogg, J.P., 1970. Wood properties of young loblolly pine in response to cultural management. LSU Forestry Notes No. 88, Louisiana State University, LA.

Clark III, A., Borders, B.E., Daniels, R.F., 2004. Impact of vegetation control and annual fertilization on properties of loblolly pine wood at age 12. Forest Products Journal 54, 90–96.

Forest Nutrition Cooperative, 2006. Forest Nutrition Cooperative Synthesis. Available online at http://www.forestnutrition.org/synthesis.htm.

Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. Journal of Forestry 105, 337–347.

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, Dordrecht, The Netherlands, pp. 263–277.

Jokela, E.J., Stearns-Smith, S.C., 1993. Fertilization of established southern pine stands: effects of single and split nitrogen treatments. Southern Journal of Applied Forestry 17, 135–138.

Jokela, E.J., Wilson, D., Allen, J.E., 2000. Early growth responses of slash and loblolly pine following fertilization and herbaceous weed control treatments at establishment. Southern Journal of Applied Forestry 24, 23–30.

Kushla, J.D., Fisher, R.F., 1980. Predicting slash pine response to nitrogen and phosphorus fertilization. Soil Science Society of America Journal 44, 1303–1306.

Larson, P.R., Kretschmann, D.E., Clark, A., Isebrands, J.G., 2001. Formation and properties of juvenile wood in southern pines. General Technical Report FPL-GTR-129. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, 42 pp.

Mallonee, E.H., 1975. Effect of thinning and seasonal time of Nitrogen fertilization on the growth of pole sized loblolly pine. Thesis. Dept. of For. N.C. State University, Raleigh, N.C.

Megraw, R.A., 1985. Wood Quality Factors in Loblolly Pine. TAPPI Press, Atlanta, GA.

Morling, T., 2002. Evaluation of annual ring width and ring density development following fertilization and thinning of Scots pine. Annals of Forest Science 59, 29–40.

Nyakuengama, J.G., 1991. The physical and chemical properties of superior radiata pine (*Pinus radiata* D. Don) wood for thermo-mechanical pulping compared with standard radiata pine. B.Sc. Hons. Thesis. Dept. of For., Australian National University, Canberra, Australia.

Nyakuengama, J.G., Downes, G.M., Ng, J., 2002. Growth and wood density responses to later-age fertilizer application in *Pinus radiata*. IAWA Journal 23, 431–448.

Nyakuengama, J.G., Downes, G.M., Ng, J., 2003. Changes caused by mid-rotation fertilizer application to the fiber anatomy of *Pinus radiata*. IAWA Journal 24, 397–409.

Panshin, A.J., deZeeuw, C., 1980. Textbook of Wood Technology, 4th ed. McGraw-Hill Inc., USA.

Posey, C.E., 1964. The effect of fertilization upon wood properties of loblolly pine. Technical Report No. 22. School of Forestry, N.C. State University, Raleigh, N.C.

Pritchett, W.L., Comerford, N.B., 1982. Long-term responses of phosphorus fertilization on selected southern Coastal Plain soils. Soil Science Society of America Journal 46, 640–644.

Rojas, J.C., 2005. Factors influencing responses of loblolly pine to fertilization. Dissertation. Dept. of For. N.C. State University, Raleigh, N.C.

Ross, D., Buckner, E., Core, H., Woods, F., 1979. Nitrogen fertilization decreases yellow poplar wood density. Southern Journal of Applied Forestry 3, 119–122.

SAS Institute Inc., 2004. SAS/STAT User's Guide, Version 9.1. SAS Institute, Inc., Cary, NC.

Smook, G.A., 2002. Handbook for Pulp and Paper Technologists, 3rd ed. Angus Wilde Publications Inc., Vancouver.

Uggla, C., Magel, E., Moritz, T., Sundberg, B., 2001. Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in Scots pine. Plant Physiology 125 (4), 2029–2039.

Williams, R.F., Hamilton, J.R., 1961. The effect of fertilization on four wood properties of slash pine. Journal of Forestry 59, 662–665.

Zobel, B.J., Groggans, G.F., Maki, T.E., Henson, F., 1961. Some effects of fertilizers on wood properties of loblolly pine. Tappi Journal 44 (3), 187–191.