EFFECTS OF STAND DENSITY AND FOLIAGE DYNAMICS ON TREE GROWTH OF SHORTLEAF PINE

(*Pinus echinata* Mill.)

By

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CHAPTER I

INTRODUCTION

Background

It is well known that thinning increases tree growth and redistributes stand growth. This activity improves environmental conditions for residual trees by reducing competition between plants and increasing the amount of available nutrients, water, and light (Daniel, Helms, and Baker 1979, Lavigne 1988, and Wittwer et al. 1996). Changes of site attributes due to thinning or other cultural activities such as fertilization and irrigation affects productivity of the stands by influencing foliage mass and/or area production, needle morphology, foliage light interception, the capability of the plants to allocate photosynthate to tree parts other than leaves and roots, and needle efficiency (Brix 1981a, Lavigne 1988, Law et al. 1992, Magnussen et al. 1986, Nemeth 1973, Valinger 1993, Vose 1988, Vose et al. 1994, and Wang et al. 1995).

Canopy foliage is limited by environmental site conditions such as water, nutrients, precipitation, and temperature (Brix 1981b, Grier and Running 1977, Linder et al. 1987, Snowdon and Benson 1992, and Vose et al. 1994). In particular, thinning has been found to increase tree and stand foliage mass by expanding the canopy toward open spaces, and together with site improvement by cultural treatments, an improvement in the photosynthetic rate per unit of foliage is expected (Brix 1983). According to Lavigne (1988) and Ginn et al. (1988), the amount of leaves per unit area decreases at the time of thinning application, but thereafter increases as time progresses. This statement is supported by Brix (1981b, 1983) in a thinned Douglas fir (*Pseudotsuga mensiesii* (Mirb) Franco.) stand.

Several studies have been applied trying to explain the relationship of changes in stand density to tree and stand growth, and tree and stand leaf biomass. Stemwood productivity is determined by the capability of leaf biomass to fix carbohydrates and the allocation to tree components. Carbon fixation and allocation depend on leaf biomass amount and its efficiency to intercept radiant energy and the conversion to chemical energy (Jarvis and Leverenz 1983 , Linder 1985). Law et al. (1992) found that stand basal area growth was directly related to the intercepted radiation, but individual tree growth was inversely related to radiation as stand density increased.

Stand and tree productivity is strongly related to leaf biomass amount (weight or area). The relationship between them is supported by the fact that foliage provides the surface across which photosynthetic gas exchange and transpiration occurs (Grier and Running 1977). Also, the amount, display, and duration of leaf biomass determine the quantity of intercepted radiation and the capability of photosynthesis, transpiration, and respiration processes to respond (Colbert et al. 1990, Vose and Allen 1988). The relationship between leaf biomass and forest productivity is supported by a variety of studies in conifer species such as Douglas-fir (Brix 1983), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Ford 1982), lodgepole pine ((*Pinus contorta* ssp. *latifoliada* (Engelm. exWats.) Critchfield)) (Lavigne 1988 and Pearson et al. 1984), jack pine (*Pinus* *banksiana* Lamb.) (Magnusen et al. 1986), loblolly pine (*Pinus taeda* L.) (Colbert et al. 1990, Dalla-tea and Jokela 1991, and Vose and Allen 1988), slash pine (*Pinus elliotti* var. *elliottii* Engelm.) (Colbert et al. 1990, Dalla-tea and Jokela 1991, and Nemeth 1973), radiata pine (*Pinus radiata* D. Don) (Mead et al. 1984, Snowdon and Benson 1992), and scots pine (*Pinus sylvestris* L.) (Cousen 1988, Valinger 1993).

Leaf area is an important characteristic of autotrophic ecosystems. Radiation interception, carbon fixation, carbon allocation, and water flux are highly dependent on it (Dalla-tea and Jokela 1991, Gholz 1982, and Grier and Running 1977). Leaf area index (LAI), an index that represents the amount of leaf area that occupies one square meter of soil surface (expressed as m^2m^{-2}), may be estimated as projected or all-sided leaf area index. Leaf area index is directly related to aboveground biomass production. Magnussen et al. (1986) derived a linear relationship between dry matter production and LAI for jack pine. He reported the relationship to be useful only for semistocked stands. Canopy foliage in overstocked stands will not allow increased production because respiratory losses and self-shading may be higher than the photosynthic gains. Comparable results were found by Vose and Allen (1988). They suggested that LAI is a good index of stocking because it integrates tree size, stand density, and site resources supply. In addition, Colbert et al. (1990) supported that LAI is useful to describe responses of cultural treatments and to compare stand leaf area responses between sites. However, Law et al. (1992) found that LAI varies between species, thus he proposed to use intercepted photosynthetically active radiation (IPAR) to compare stand growth efficiency between species.

In addition, growth efficiency (GE), defined as the amount of wood produced per unit leaf area or weight, incorporates the influence of photosynthetic efficiency and carbon allocation to tree parts (Stoneman and Whitford 1995). In general, foliage and roots have a higher priority than stemwood growth, but protective chemicals have lower priority than stemwood growth (Waring and Schlesinger 1985). Therefore, stemwood growth efficiency will be high when others tree parts have satisfied their carbon demand. Silvicultural activities such as thinning, fertilization, herbicides, and prescribed fires affect growth efficiency. Modification of site conditions affects leaf display and leaf production which in turn affects leaf efficiency and allocation of carbohydrates to tree parts (Brix 1981b, Mead et al. 1984, and Miller and Miller 1976). Vose and Allen (1988) found that nitrogen application increased LAI, but growth efficiency was reduced. The reduction in growth efficiency could be due to an increase in shading, respiration loss, or moisture stress due to an increase in leaf biomass amount. In contrast, Dalla-tea and Jokela (1991) reported that high levels of productivity are achieved through rapid leaf development due to increased absorption of photosynthetically active radiation in loblolly and slash pine.

Problem Statement

Leaf biomass dynamics and the contribution to stand and tree growth at different site and environmental conditions has been well documented for several conifer species such as Douglas-fir (Brix 1981b, Brix 1983), loblolly pine (Colbert et al. 1990, Hennessey et al. 1992, and Vose and Allen 1988), slash pine (Dalla-tea and Jokela 1991 and Colbert et al. 1990), Scots pine (Valinger 1993), and radiata pine (Linder et al. 1987, Mead et al. 1984, and Snowdon and Benson 1992). There has been little investigation on the effects of thinning on foliage development and the relationship of foliage to stand growth in shortleaf pine (*Pinus echinata* Mill.). Shortleaf pine is the most widely distributed southern pine and is the main softwood species in the Ouachita and Ozark Mountains of Arkansas, Missouri, and Oklahoma. In addition, most of the investigations related to LAI, needle biomass weight, and stand growth have overlooked mortality losses. Therefore, the derived relationships have been expressed either as net or survivor stand productivity, but little attention is focused on both components of production at the same time. Survivor growth is that on trees present at the beginning and end of a period (e.g. during a growing season). While, mortality is unsalvaged growth that counts negatively against survivor growth. Net growth is the resulting difference of survivor growth minus mortality (Smith et al. 1997).

Purpose of the Study

Based on the statement of the problem, the purpose of the present study is to investigate the effects of stand stocking density on stand leaf biomass production, LAI and growth efficiency as well as the relationship of stand leaf biomass and LAI to net and survivor stemwood growth.

Objectives of the Study

The present study is conducted to achieve the following objectives:

a) to monitor seasonal and annual needlefall patterns,

b) to assess the changes in stand needle biomass, LAI, and GE due to different stand densities and site conditions, and

c) to determine the relationship between stand needle biomass, LAI, GE, stand density, and stand growth.

Hypothesis

Based on responses to similar studies of conifer species other than shortleaf pine, I established the following hypotheses:

a) stand needle biomass, LAI, and GE are correlated to stand densities,

b) survivor and net stand stemwood growth are correlated to needle biomass and LAI, and

c) stand needle biomass, LAI, and GE are different due to different site conditions.

CHAPTER II

METHODOLOGY

Study Area

Location

The present study is conducted in natural shortleaf pine stands located in the Ouachita Mountains of northwestern Pushmataha County, Oklahoma. The study sites are located on industrial lands of the Georgia Pacific Corp. According to the USDA-SCS soil survey, site one (SI 17 m at age 50) and site two (SI 22 m at age 50) are included in the Carnasaw-Pirum-Clebit soil and Sherwood-Zafra associations, respectively. The soils are classified as well drained and deep, moderately deep, and shallow soils. The soil series are formed from sandstone and/or shale (Bain and Watterson 1979).

Climate

During the study period, total annual precipitation, recorded at Daisy Station in Atoka County, Oklahoma, ranged from 1308 (51.5 in) to 2243 mm (88.3 in) of rain. Annual precipitation was above the 30 year average, except for the last growing season of the study period in which it was near average. Average annual temperature, taken at McGee Creek Dam, at Atoka County, Oklahoma, was around 16^0 C (62^0 F) over the study period. The lowest monthly mean temperature registered during the winter was 3^0 C (37.4^0 F) and the highest during the summer seasons was 30^0 C (86^0 F) (NOAA 1989-1994).

Sampling Design

At the beginning of the study the stands were composed of 25-30 year-old natural shortleaf pine stands. At site one, nine square treatment plots of 0.16 ha (0.4 ac) were distributed among three blocks; a 0.04 ha (0.1 ac) measurement plot was established within each treatment plot. At site two, plot dimensions were 0.24 ha (0.6 ac) with a 0.08 ha (0.2 ac) measurement plot. Five 1 m^2 traps for litter fall collection were systematically distributed inside of the measurement plots. The sampling design was appropriate for applying a complete randomized block design to test for differences between treatments.

Treatments

The prescribed treatments were the application of three densities levels. The density levels were thinning to approximately 15 m^2ha^{-1} or 50 percent relative density (50 PRD) and 25 m^2ha^{-1} (70 PRD) and the unthinned control with approximately 35 m^2ha^{-1} (control). The stand stocking levels correspond to conditions defined in the stocking chart developed for shortleaf pine by Rogers (1983). The 50 PRD is classified as understocked, the 70 PRD corresponds to normal stocking, and the control is considered overstocked. Thinning treatments were applied prior to the 1989 growing season at site one and prior to the 1990 growing season at site two.

Variables

Stand Density and Stand Stemwood Growth.

Diameter at breast height (dbh) and number of trees per ha were the basic measurements used to calculate stand stocking. Stand density was measured as stand basal area and stocking as percent relative density.

Relative density was determined from equations used to prepare stocking charts for shortleaf pine developed by Rogers (1983). Annual stand basal area and relative density growth were determined from annual increments of individual trees. Annual basal area and relative density growth were expressed as survivor and net growth. Survivor growth is the annual basal area growth on trees that are alive at the beginning and end of the period. Net annual growth is the difference between standing basal area in two consecutive years. Wittwer et al. (1996) reported initial stand characteristics, quadratic mean diameter, and number of trees per unit area as well as survivor, and net basal area growth until the 1993 growing season for site one.

Total stemwood volume was estimated from Farrar and Murphy's (1987) taper equations for shortleaf pine using dbh, height, and crown-length measurements of individual trees. Total stemwood volume was estimated as inside bark stemwood volume.

Needlefall Estimation

Needlefall was collected beginning in September of 1990 for site one and 1991 for site two. Needlefall collection was made monthly during the Fall season and the first month of the winter, then needlefall was collected at least two times before the next peak leaf fall season started. Needlefall samples were collected and placed in paper bags and carried to the laboratory. Samples were ovendried for about 72 hr. at 65° C to constant weight and weighed to the nearest 0.01 g.

Because it was impossible to collect needlefall samples exactly the first day of each month, computational estimations were used to adjust the starting time of needlefall to the first day of each month. Similarly, it was necessary to estimate the amount of needlefall for the months in which collections were not made. The starting date for annual estimations was the first day of September and the ending date the last day of August. This date was based on the assumption that needlefall peak normally starts early in the fall season although climate may affect the starting time of needlefall as described for loblolly pine by Hennessey et al. (1992).

Needle Biomass Estimation

In addition, stand needle biomass by growing season was estimated from needlefall. Similar to other southern pines, shortleaf pine needles are retained on the tree for two growing seasons (Kinerson et al. 1974); therefore, the needles that fall in a given year are considered one year old and correspond to needles that were active during the previous and current growing season. Needles formed the current growing season are considered new and they fall during the Fall of the next year. Therefore, the sum of two consecutive years of needlefall was assumed to correspond to the amount of active needles during a growing season (Table 1). Needle biomass was estimated for four and five growing seasons for site two and one, respectively.

Stand All-sided Leaf Area Index Estimation

Stand all-sided LAI estimation was made using needlefall samples. Vose (1987) validated the use of needlefall to estimate LAI when he compared destructive sampling against a needlefall method. He found that there is a strong positive relationship between the two methods and the slope of the relationship is very close to unity. Needlefall samples for LAI estimations were selected from collections beginning in April of 1994 for both sites, four and five years following thinning application, respectively. Monthly selections were made from 1994 through 1996, except for the months when needlefall was not collected.

Table 1. Needlefall collection, needle biomass production, and growing season of needle biomass activity.

Needlefall Collection	Needle Biomass Production	Growing Season
(1990-1991)+(1991-1992)	1989 and 1990	1990
(1991-1992)+(1992-1993)	1990 and 1991	1991
(1992-1993)+(1993-1994)	1991 and 1992	1992
(1993-1994)+(1994-1995)	1992 and 1993	1993
(1994-1995)+(1995-1996)	1993 and 1994	1994

Estimation of all-sided LAI was based on specific leaf area (SLA) estimations. The first step to estimate SLA was to select randomly five complete fascicles from each 1 m^2 needlefall trap to obtain 25 fascicles per plot. From preliminary analysis, it was determined that shortleaf pine in the study sites had approximately 60% two-needle fascicles (Appendix A); therefore, three fascicles were selected from two-needle fascicles and two fascicles were selected from three-needle fascicles.

Since specific leaf area (SLA) is defined as the ratio between leaf area and needle weight (Hager and Sterba 1985), the second step was to determine total needle area (all-sided needle area) and ovendry needle weight. Total needle area was estimated using a leaf area measurement method for pine needles developed by Bingham (1983). It is a simple method that relies on the use of a low power magnifying lens with a scale arranged in such a way that it is seen through the lens. The projected diameter of the fascicles with two needles and chord of the fascicles with three needles was measured to the nearest 0.05 mm, length of the needles was measured to the nearest 0.5 mm with a standard metric rule. The leaf area per fascicle was calculated using the following equation (Bingham 1983):

$$A = 2RL(N+\pi)$$

where:

A= fascicle area,

R= average radius of needles,

L= average length of the fascicle,

N= number of needles per fascicle, and

π= 3.1416

Needlefall collected in 1994 and 1995 had previously been ovendried at 65^0 C before weighing while the 1996 samples had not been. There was concern that drying could affect the dimensions of the 1994 and 1995 sample material. A comparison of the effects of the drying on dimensional stability was completed using subsamples for two different monthly collections for 1996 from both sites. Paired subsamples subject to drying before measurement of needle length and radius were compared with those not dried before measurement. No significant differences were found and it was concluded that measurement of needle dimensions for estimating SLA could be made on the previously dried 1994 and 1995 samples.

SLA was estimated for each one of the sites, seasons, and years by block and treatment. Because only two or three monthly samples were available from January to August and monthly samples for September to December, the year was divided in two seasons. Comparisons showed no effect on SLA due to season during the year.

Stand all-sided LAI was estimated by multiplying the total annual leaf biomass per ha by mean annual SLA and converted to m^2m^{-2} units. Annual stand all-sided leaf area was estimated for each replicate plot. Similar to annual biomass, annual total stand LAI was calculated from the sum of two consecutive years of LAI. It was estimated for each site and treatment for 1993 and 1994 growing seasons.

Growth Efficiency Estimation

Growth efficiency (GE), defined as the ratio of net total stemwood volume growth produced per year to amount of stand leaf weight or area, was calculated for each treatment in both sites from stand needle biomass and stand LAI. GE_{NB} indicates GE estimations from needle biomass while GE_{LAI} indicates estimations from leaf area index. Four and five annual GE_{NB} estimations were made for stand needle biomass and two GE_{LAI} estimates were made for LAI.

Statistical Analyses

A complete randomized block design was used to estimate the analyses of variance in order to test for the effects of stand stocking densities on annual stand needlefall, annual stand needle biomass, stand all-sided LAI, and GE per year and site. When the analyses of variance were significant, comparisons of means were made using Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc.1988). Student t-test were applied to test for differences in annual needlefall, stand needle biomass, LAI, and GE between sites at the control level and to look for any significant difference in SLA between seasons.

In addition, regression analyses were applied to determine the tendency and the correlation between annual leaf biomass or all-sided LAI and stand basal area, net and survivor stand stemwood growth, stand relative density, net and survivor relative density growth, and net GE, respectively. Regression analyses were applied independently by site and year and by combining data from years and sites.

CHAPTER III

RESULTS

Study I. Needle Biomass

Needlefall

Seasonal Patterns

Monthly needlefall was not very consistent between years during the study period, although similar patterns were observed for all treatments within the same years. Peak needlefall mainly occurred in October, November, and/or December. Sometimes it was concentrated in one month and other years it was distributed over two or three months (figures 1 and 2). The start of needlefall was very variable. Sometimes it started during August and increased gradually over the next three months, but other times it started later with a single monthly peak needle fall during October or November.

On the other hand, seasonal patterns were very consistent over the study period on both sites. The heaviest needlefall amount always occurred during the fall season. The maximum and minimum amount of needlefall in control plots ranged from 2171 $kgha^{-1}$ to 3535 $kgha^{-1}$ at site one and from 2422 $kgha^{-1}$ to 3357 $kgha^{-1}$ at site two. Fall needlefall amount was around 60% of the total annual needlefall. Normally, a period of low

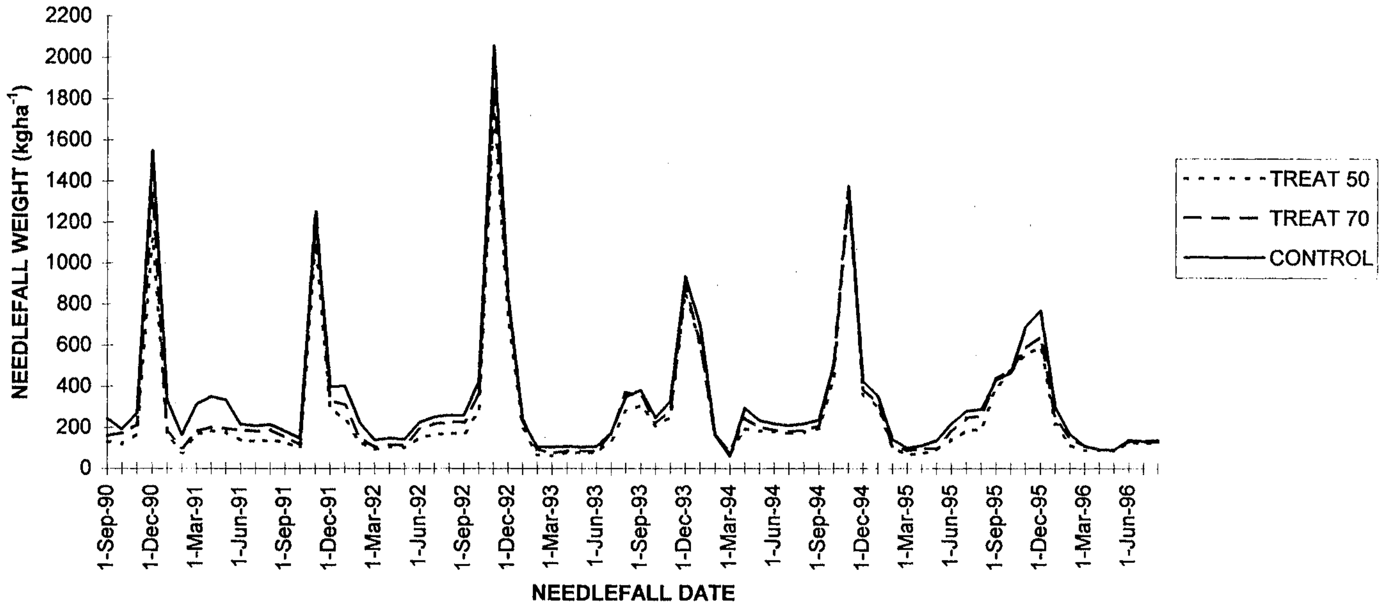

Figure 1. Monthly needlefall distribution at site one (SI 17 m at base age 50 yr.) over a six-year period.

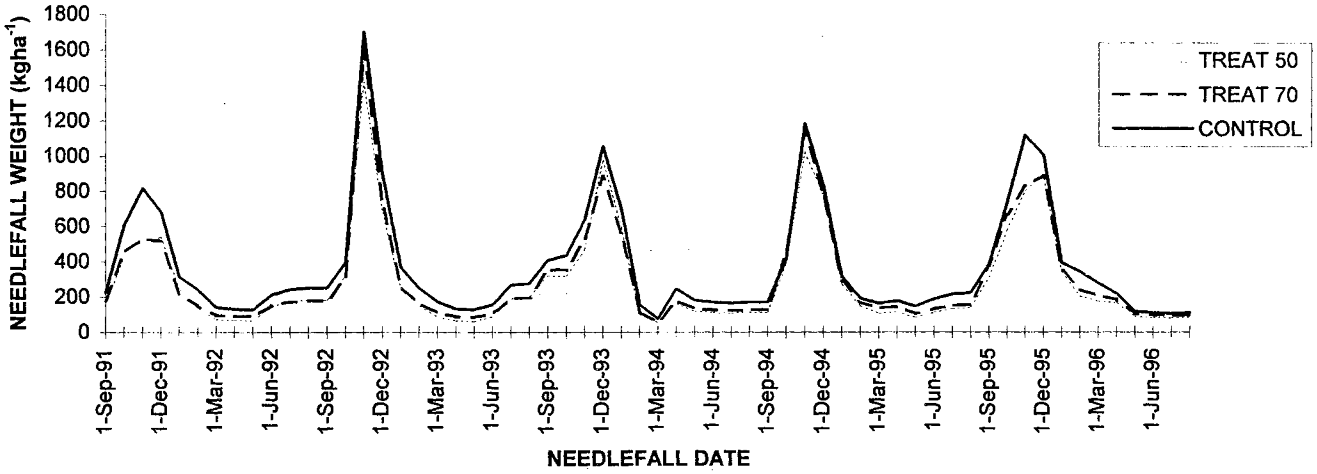

Figure 2. Monthly needlefall distribution at site two (SI 22 m at base age 50 yr.) over a five-year period.

monthly needlefall (January-August) was observed after the seasonal leaf fall occurred. It was very consistent between sites and treatments over the study period.

Annual Pattern

Annual needlefall varied between years, but the patterns between sites were similar. The lowest absolute needlefall amounts in site one occurred during the first and sixth year after thinning in all the treatments. In site two, the lowest amount was observed during the first year of the study period. The heaviest needlefall was observed during 1992-93 period in both sites and all the plots.

The effect on mean annual needlefall due to different densities in site one showed variable results for the six-year study period (table 2). Mean needlefall of unthinned plots was significantly different ($\alpha<=0.05$) from means of 50 PRD and 70 PRD treatments during the first year of the study period. Mean needlefall amounts for the second year and the fifth year were significantly different ($\alpha<=0.05$) among all the three treatments. In contrast, during the following two year periods (1992-1993 and 1993-1994) and the last period (1995-1996) annual needlefall showed no effects due to thinning. In spite of the varied mean annual needlefall responses due to thinning effects each year, needlefall was always greater in unthinned plots followed by the 70 PRD and the 50 PRD, respectively.

In contrast to site one, site two presented a consistent trend in mean annual needlefall response due to thinning (table 3). The control was always significantly different ($\alpha=0.05$) from the 50PRD and 70PRD treatments, but no significant difference

Table 2. Mean annual stand needlefall ($kgha^{-1}yr^{-1}$) by treatment in site one (SI 17 m at base age 50 yr.).

TREATMENTS	PERIOD[1]						MEAN
	1990-91	1991-92	1992-93	1993-94	1994-95	1995-96	
50 PRD	2722a[2]	2779a	3895a	3363a	3514a	2987a	3210a
70 PRD	3301a	3298b	4437a	3594a	3821b	3222a	3612b
CONTROL	4376b	3741c	4840a	3972a	4166c	3512a	4101c

[1] Correspond to September-August year period.

[2] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05).

Table 3. Mean annual stand needlefall ($kgha^{-1}yr^{-1}$) by treatment in site two (SI 22 m at base age 50 yr.).

TREATMENT	PERIOD[1]					MEAN
	1991-92	1992-93	1993-94	1994-95	1995-96	
50 PRD	2697a[2]	3696a	3446a	3396a	3807a	3408a
70 PRD	2831a	4017a	3532a	3762a	4130a	3654a
CONTROL	3988b	4987b	4394b	4211b	4913b	4499b

[1] Correspond to September-August year period.

[2] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05).

was found between the two thinning treatments. Comparing annual average needlefall amount for the overall five and six years, the unthinned treatment was significant different (p-value>0.05) from thinned treatments. Mean needlefall was only different between thinned treatments in site one, but not in site two.

The study in site one was established one year before that on site two; therefore, comparison of means were made at the control level for a five-year period. A non-significant difference between the sites (4046 vs. 4499 $kgha^{-1}yr^{-1}$, $\alpha=0.05$) was found.

Needle Biomass

Annual needle biomass was estimated as the sum of two continuous years of needlefall. It was assumed that new leaves were produced each spring and were active for two complete growing seasons (Kinerson et al. 1974). Therefore, the estimation of the annual needle biomass amount was based on new plus old needles (table 1, p. 12). The study on site one began one year before that on site two and needle biomass estimation was for five and four growing seasons, respectively.

Annual needle biomass amount varied between treatments every year, except for 1992 and 1993 growing seasons in site one for which treatments effects were not significantly different (table 4). Needle biomass was lowest at 50PRD and highest at the control level at both sites. The annual responses of needle biomass between thinned treatments were different on site one during the first, second and fifth year period. On site two, the response of stand needle biomass to thinned treatments in each one of the

Table 4. Mean annual stand needle biomass (kgha^{-1}yr^{-1}) by treatment in site one (SI 17 m base age 50 yr.) and site two (SI 22 m at base age 50 yr.).

SITE	TREATMENT	GROWING SEASON					MEAN
		1990	1991	1992	1993	1994	
	50 PRD	5501a[1]	6674a	7258a	6877a	6501a	6562a
ONE	70 PRD	6599b	7735b	8031a	7415a	7043b	7365b
	CONTROL	8117c	8581c	8812a	8138a	7678b	8265c
	50 PRD	-o-	6393a	7142a	6842a	7203a	6895a
TWO	70 PRD	-o-	6848a	7549a	7294a	7892a	7396a
	CONTROL	-o-	8975b	9381b	8605b	9124b	9021b

[1] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05). Mean comparisons are independently by site.

growing seasons was similar. The unthinned treatment was significantly different from both thinned treatments.

Analysis of mean annual stand needle biomass for the four and five year period showed a significant difference (α=0.05) between thinned and unthinned treatments at both sites. At site one, mean annual needle biomass was significantly different between thinned treatments, but at site two, the mean response of thinned treatments was not significantly different . The unthinned treatments produced the greatest stand needle biomass followed in descending order by the 70PRD and the 50PRD (table 4).

Because thinning treatments were done one year earlier in site one than in site two, differences due to year of thinning was confounded with site differences and comparisons between sites for thinned treatments were not possible. Thus, data from control treatments was used to compare effects between sites for a four-year study period. The analysis showed no significant difference in stand needle biomass amount due to differences in site productivity between the two sites.

Absolute amounts of stand needle biomass were very inconsistent between years. Site one was characterized by an increase in stand needle biomass from the first year to the third year of the study period in every treatment. The amount of stand needle biomass decreased during the fourth growing season to levels below the third but above the first and second growing seasons of the study period. The fifth growing season had a slightly higher amount than the first growing season.

Absolute amounts of stand needle biomass on site two increased from the first to the second growing season and from the third to the fourth growing season. The amount decreased in the third growing season to below the levels of the second season but above the levels of the first growing season. The fourth growing season needle biomass showed the greatest accumulation (table 4).

The ratio of needlefall on thinned plots to control on site one showed increases from 0.68 to 0.85 in the 50 PRD and 0.81 to 0.93 in the 70 PRD as the study period progressed (table 5). Ratios ranged from 0.71 to 0.79 for the 50 PRD and 0.76 to 0.87 for the 70 PRD treatments on site two. The first year of the study period site two exhibited higher ratios than site one, but ratios were lower at the end of the study period suggesting that thinned plots on site two invested relatively less carbohydrates in foliage development than site one. The maximum relative increase was observed from the first to the second growing season at both sites and each treatment, then the rate was lowered as time progressed. Ratio estimations would tend to reach one as canopy levels of thinned plots approached those of unthinned plots at both sites.

Stand Needle Biomass, Density, and Stocking Relationship

Decisions concerning forest density manipulation and evaluation of tree growth are normally made by using measures of density and stocking. Stand basal area, a quantitative measure of density, is the amount of vegetation expressed in square units per unit area (eg. m^2ha^{-1}). Percent relative density, a qualitative expression of stocking, is a percentage relative to the minimum density required to fully occupy the site (Smith 1986, Rogers 1983 and Baker et al. 1996). It is important to see how these two measures are related to stand attributes such as needle biomass which in turn are related to

Table 5. Ratio of stand needle biomass between thinned and unthinned treatments in site one (SI 17 m base age 50 yr.) and site two (SI 22 m at base age 50 yr.).

SITE	TREATMENT	GROWING SEASON				
		1990	1991	1992	1993	1994
	50 PRD	0.68	0.78	0.82	0.84	0.85
ONE	70 PRD	0.81	0.90	0.91	0.93	0.92
	CONTROL	1.0	1.0	1.0	1.0	1.0
	50 PRD	-o-	0.71	0.76	0.79	0.79
TWO	70 PRD	-o-	0.76	0.80	0.85	0.87
	CONTROL	-o-	1.0	1.0	1.0	1.0

physiological and ecological functions.

Regression analyses showed a strong linear correlation (p-value<0.001) between mean annual stand basal area and needle biomass for independent sites and pooled data. In particular, site two showed a very strong correlation ($R^2=0.91$). Although correlation estimations for site one and combined sites (figure 3) were lower than those for site two, they were also highly significant.

Generally, dense stands tend to reach a plateau in terms of stand density and needle biomass while understocked stands develop in basal area and needle biomass. In this study, unthinned areas presented narrower needle biomass and basal area development ranges than thinned areas. Shortleaf pine needle biomass production in unthinned plots ranged from 7678 to 9381 $kgha^{-1}yr^{-1}$ and in thinned plots needle biomass ranged from 5501to 8031 $kgha^{-1}y^{-1}$. Basal area in unthinned plots remained in the range of 38 to 45 m^2ha^{-1} while basal area in thinned plots ranged from 16.3 to 30.6 m^2ha^{-1}.

Percent relative density (PRD) was positively correlated to stand annual needle biomass. Since PRD is related to number of trees and basal area, it was expected to be correlated to needle biomass in the same way as stand basal area (figure 4). The coefficients of determination for PRD-needle biomass relationship for site one, two, and combined sites are 0.62, 0.90, and 0.65, respectively. The higher correlation between percent relative density and leaf biomass suggests it should be a useful parameter for manipulation of stand density and productivity.

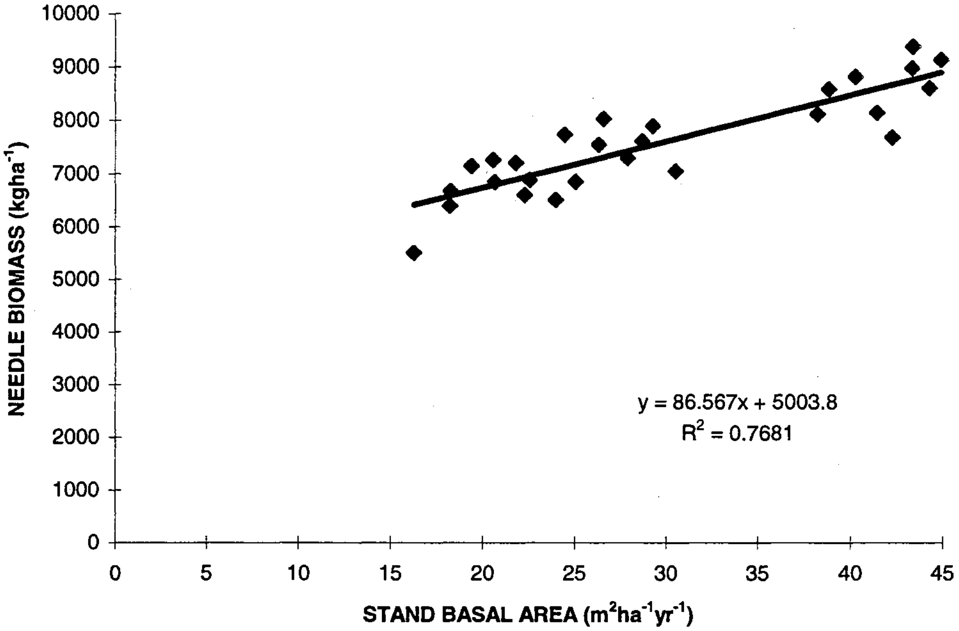

Figure 3. Stand basal area and mean annual stand needle biomass relationship for combined sites.

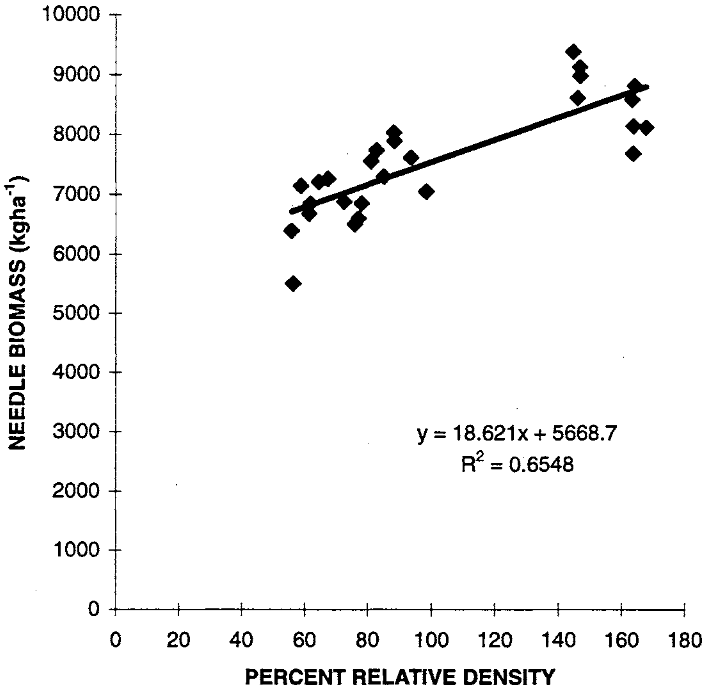

Figure 4. Percent relative density and mean annual stand needle biomass relationship for combined sites.

Stand Growth

Survivor and Net Basal Area Growth

Thinning effects on survivor basal area growth were not significantly different between all the treatments during the 1990 growing season at site one (table 6). However, during the 1991 growing seson, survivor growth of thinned treatments was significantly higher than that of unthinned treatment. During the last growing season of the study period, the 70 PRD treatment was significantly higher than the unthinned treatment.

At site two, survivor basal area growth was not significantly different among all the treatments, except for 1991 growing season (see table 6). During that growing season the control treatment was significantly higher than the 50 PRD treatment. The five-year mean survivor basal area growth was not significantly different among all the treatments in site one and two.

Net basal area growth of thinned treatments was significantly higher than net basal area growth of unthinned treatments in both sites, respectively (see table 6). Net basal area among thinned treatments was not significantly different. The lowest net basal area observed was 0.01 $m^2ha^{-1}yr^{-1}$ during 1991 growing season at the control level at site two. During that particular year, mortality was almost equal to survivor growth. Regardless of site and year, the lowest net basal area was at the control level because mortality frequently occurred in over-stocked stands. Survivor and net basal area growth was

Table 6. Annual stand basal area growth ($m^2ha^{-1}yr^{-1}$) for site one and site two.

SITE ONE

TREATMENT	GROWING SEASON					MEAN
	1990	1991	1992	1993	1994	
			Survivor Basal Area Growth			
50 PRD	1.82a[1]	1.98a	2.32a	1.98a	1.55ab	1.94a
70 PRD	1.89a	2.19a	2.21a	2.11a	1.84b	2.05a
CONTROL	1.80a	1.62b	2.12a	2.07a	1.28a	1.78a
			Net Basal Area Growth			
50 PRD	1.82a	1.98a	2.32a	1.98a	1.40ab	1.90a
70 PRD	1.89a	2.19a	2.14a	2.11a	1.84b	2.03a
CONTROL	0.79b	0.63b	1.43b	1.16a	0.82a	0.97b

SITE TWO

TREATMENT	1990	1991	1992	1993	1994	MEAN
			Survivor Basal Area Growth			
50 PRD	-o-	1.29a	1.18a	1.27a	1.15a	1.22a
70 PRD	-o-	1.54ab	1.26a	1.59a	1.36a	1.44a
CONTROL	-o-	1.74b	1.18a	1.45a	1.10a	1.37a
			Net Basal Area Growth			
50 PRD	-o-	1.29a	1.18a	1.27a	1.15ab	1.22a
70 PRD	-o-	1.54a	1.26a	1.59a	1.36a	1.44a
CONTROL	-o-	0.01b	0.04b	0.92a	0.61b	0.40b

[1] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05). Mean comparisons are independently by site and productivity measure.

similar for 50 PRD and 70 PRD treatments, respectively.

Net Stemwood Volume Growth

Periodic net volume growth ranged from 7.07 to 20.01 $m^3ha^{-1}yr^{-1}$ at site one and 12.27 to 17.09 $m^3ha^{-1}yr^{-1}$ at site two. At site one, net volume growth was not significant different among all the treatments, except during the last growing season (table 7). During that growing season 70 PRD treatment was significantly higher than the control treatment. The five-year mean annual volume growth was not significantly different between all the treatments. At site two, significant differences were only observed in 1992 growing seasons and for the mean four-year period. The 70 PRD treatment was higher than 50 PRD and control levels. Periodic mean annual volume increment over the study period was not significantly different among the sites.

Stand Needle Biomass and Stand Growth Relationship

Mean annual stand growth was measured in terms of basal area, percent relative density, and volume. Basal area and percent relative density were estimated as survivor and net growth and volume as net growth. Differences between survivor and net growth are due to mortality of trees, especially in overstocked stands. Net annual stand growth is the annual survivor growth minus mortality. This study involved stands with stocking ranging from understocked to overstocked plots; therefore, it was important to analyze

Table 7. Mean annual net volume increment ($m^3ha^{-1}yr^{-1}$) for site one and site two.

SITE	TREATMENT	GROWING SEASONS					MEAN
		1990	1991	1992	1993	1994	
	50 PRD	11.54a[1]	13.54a	17.31a	16.39a	8.79ab	13.41a
ONE	70 PRD	12.13a	15.81a	16.78a	20.01a	11.61b	15.37a
	CONTROL	10.26a	13.05a	15.62a	15.92a	7.07a	12.39a
	50 PRD	-o-	12.25a	12.36a	13.00a	13.48a	12.77a
TWO	70 PRD	-o-	14.69a	14.19b	17.09a	16.64a	15.65b
	CONTROL	-o-	12.25a	10.27c	15.83a	12.77a	12.80a

[1] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05). Mean comparisons are independently by site.

needle biomass and stand growth relationships with the productivity measures previously described.

Site one presented a weak quadratic relationship between net annual stand growth and needle biomass (R^2=0.28 and 0.47 P-value>0.1) for basal area and relative density, respectively (figures 5 and 6). In spite of the weak tendency, it was observed that net annual stand growth tended to increase at low canopy amounts, but decreased thereafter as needle biomass increased. The low coefficient of determination was attributed to the high variability of the observations. Maximum net annual stand growth was associated with needle biomass of approximately 6500 $kg \cdot ha^{-1} \cdot yr^{-1}$. This amount of needle biomass was related to a stand basal area of 25 $m^2 \cdot ha^{-1}$ and 80 PRD, approximately. Net annual stand growth declined dramatically when needle biomass exceeded 7500 $kg \cdot ha^{-1} \cdot yr^{-1}$. Negative net relative density growth was related to high stand needle biomass in the control plots. Negative net growth rates were due to mortality in control plots.

Basal area and relative density growth were a function of needle biomass at site two (R^2=0.83 and 0.77, p-value<0.001). Net stand growth (figures 7 and 8) tended to increase at low canopy amounts, but then as the canopy increased, net annual basal area and relative density growth decreased. Net annual growth reached its maximum at about 7000 $kg \cdot ha^{-1}$ of needle biomass. Relating needle biomass, basal area, and relative density, this amount of needle biomass is obtained when the stand reached approximately 70 PRD or 22 $m^2 \cdot ha^{-1}$ of basal area. Comparing this information against the stocking chart used for shortleaf pine (Rogers 1983), it is possible to see that maximum growth corresponds to the fully stocked range (between 60 and 100 PRD). Stands reached zero annual net

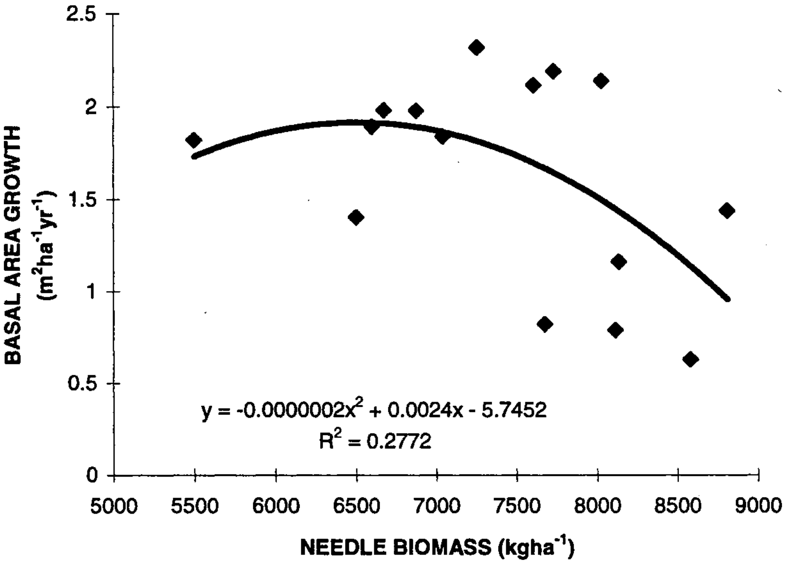

Figure 5. Mean annual net stand basal area growth and stand needle biomass relationship at site one (SI 17 m at base age 50 yr.).

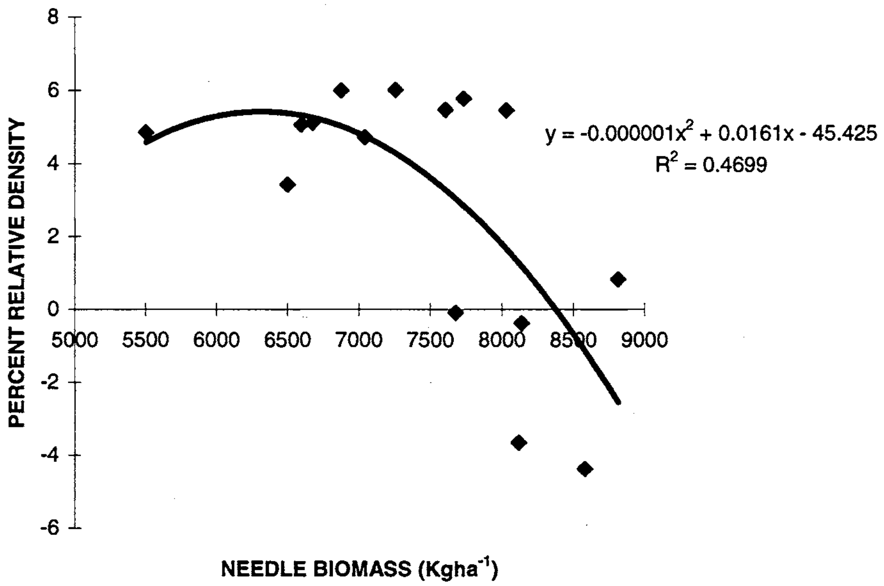

Figure 6. Mean annual net relative density increment and stand needle biomass relationship at site one (SI 17 m at base age 50 yr.).

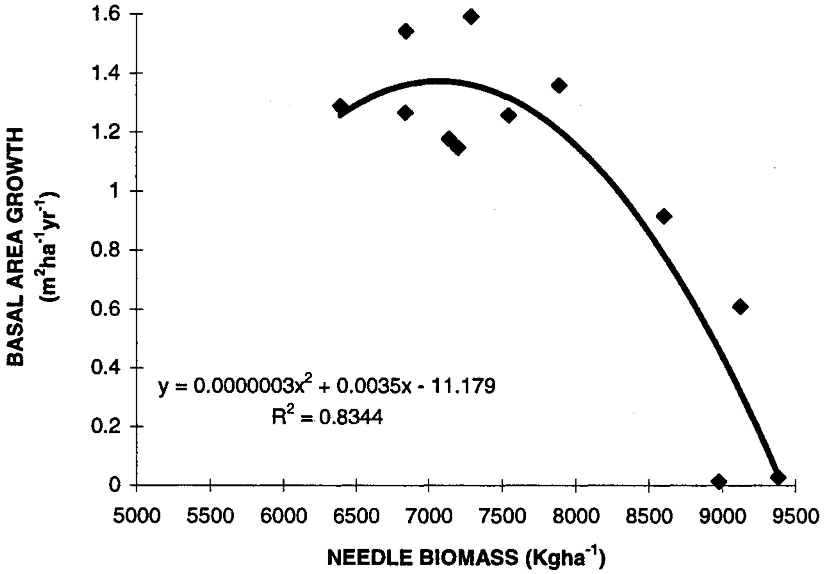

Figure 7. Mean annual net stand basal area growth and stand needle biomass relationship at site two (SI 22 m at base age 50 yr.).

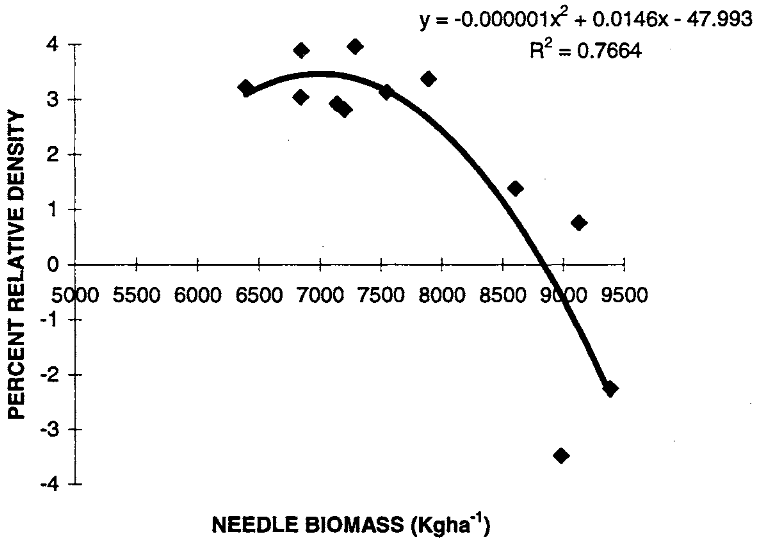

Figure 8. Mean annual net relative density increment and stand needle biomass relationship in site two (SI 22 m at base age 50 yr.).

basal area growth and negative net relative density growth at approximately 9000 kgha^{-1}yr^{-1} of needle biomass.

In addition, pooled data from both sites reflected the results obtained by independent analyses for each site. These analyses showed a weakly significant quadratic relationship with basal area (figure 9). The relationship of stand needle biomass to net annual basal area growth, and net relative density growth indicated similar coefficient of determination, (R^2= 0.49 and 0.50), respectively.

Figure 10 shows that there was not a strong relationship between needle biomass and survivor basal area growth. This was attributed to the fact that annual survivor basal area growth was not significantly different between treatments although needle biomass increased with density in both sites. Because of the high number of trees in unthinned stands, higher stand survivor growth might have been expected than in thinned treatments. However, annual tree growth is inhibited and tree mortality is increased by stressed site environmental resources reducing stand growth of unthinned treatments to levels of thinned treatments.

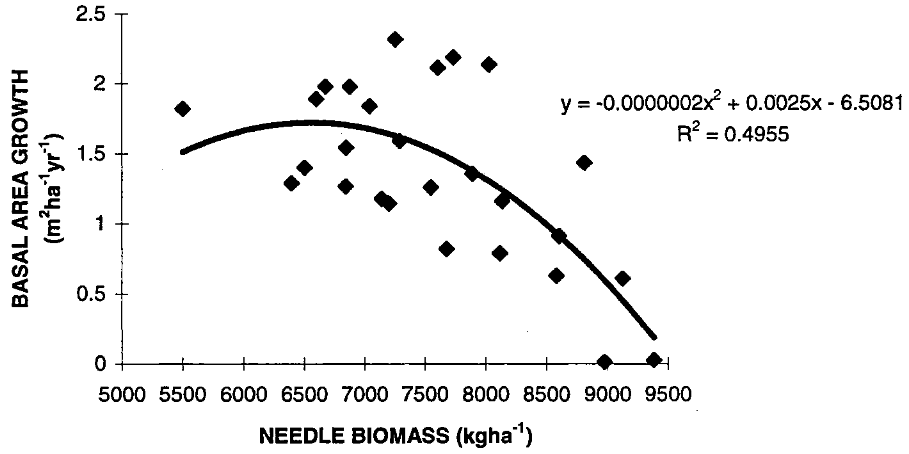

Figure 9. Mean annual net stand basal area growth and needle biomass relationship at combined sites.

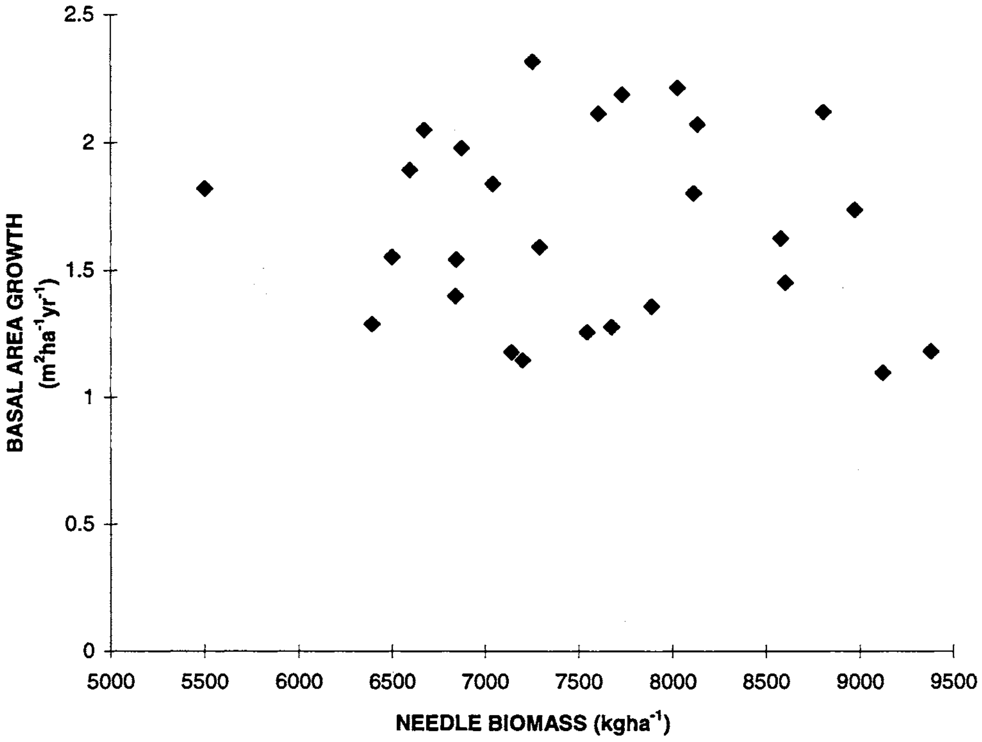

Figure 10. Mean annual survivor stand basal area growth and stand needle biomass relationship at combined sites.

Stand Needle Biomass, Density, and Growth Efficiency

Thinning modifies the stand environment by reducing competition and increasing availability of nutrients, water, and light per tree (Smith 1986). Studies in paper birch (*Betula, papyrifera* March.) showed that thinning influenced net photosynthetic rate, specific leaf area, interception of photosynthetically active radiation, water use efficiency, and nitrogen use efficiency (Wang et al. 1995). Site productivity regulates biomass production through its influence on foliage quantity and efficiency in carbon fixation, and carbon allocation (Kramer 1986). Therefore, stand growth is regulated by modifications of the physical environment, stand density and related changes in foliage quantity. Although thinning causes temporary reduction in foliage quantity, increased efficiency may result.

Net assimilation rate is defined as biomass production per unit of foliage. It includes photosynthetic and respiratory effects on dry matter production (Brix 1983). Therefore, net assimilation rate may be synonymous with growth efficiency (GE) and can be regarded as a measure of the efficiency of the foliage in wood production. GE accounts for the influence of photosynthetic efficiency and carbon allocation on stemwood growth (Stoneman and Whitford 1995).

Normally, GE has been analyzed utilizing LAI (m^2m^{-2}) as denominator, but in the case of this study stand needle biomass ($kgha^{-1}yr^{-1}$) was also used as a denominator. GE_{NB} analyses were related to needle biomass and stand density independently by site and by using the pooled data.

The analysis of net GE_{NB} means showed that thinned treatments were significantly greater than unthinned treatments for the five-year period at site one and for the four-year period at site two (table 8). Thinned treatments, were not significantly different on either site during growing seasons, except for the 1990 growing season at site one. GE_{NB} at the control level was significantly lower than thinned treatments during the first and second growing seasons of the study period at site one and site two and the last growing season at site one. Net GE_{NB} was not significantly different between sites for any of the treatment levels over the study period. Annual net GE_{NB} ranged from 0.92 to 2.64 m^3 of stemwood volume per metric tons of leaf biomass.

Stemwood volume net GE_{NB} had a significant quadratic relationship (p-value<0.10) with stand basal area and needle biomass. In particular, stronger coefficients of determination were obtained for site two than site one. Stand basal area explained 35%, 64%, and 40% of the growth efficiency variability for site one, two, and combined sites, respectively (figures 11, 12 and 13). Leaf biomass was not related to growth efficiency at site one, contrasting the high curvilinear relationship at site two (figure 14). The relationship with combined sites was significant at p-values =0.03 (figure 15). The lower correlation value was due to the additive variability by each one of the two sites.

Table 8. Mean net GE_{NB} (m^3 of stemwood volume per metric tons of foliage) estimations by site and treatment.

SITE	TREATMENT	GROWING SEASON					MEAN
		1990	1991	1992	1993	1994	
ONE	50 PRD	2.09a[1]	2.03a	2.32a	2.41a	1.35a	2.04a
	70 PRD	1.86b	2.05a	2.15a	2.64a	1.66a	2.07a
	CONTROL	1.27c	1.53b	1.78a	1.97a	0.92b	1.49b
TWO	50 PRD	-o-	1.93a	1.75a	1.93a	1.88a	1.87a
	70 PRD	-o-	2.16a	1.88a	2.35a	2.11a	2.12a
	CONTROL	-o-	1.41b	1.01b	1.84a	1.40a	1.44b

[1] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F test (SAS Institute Inc. 1988) (α=0.05).

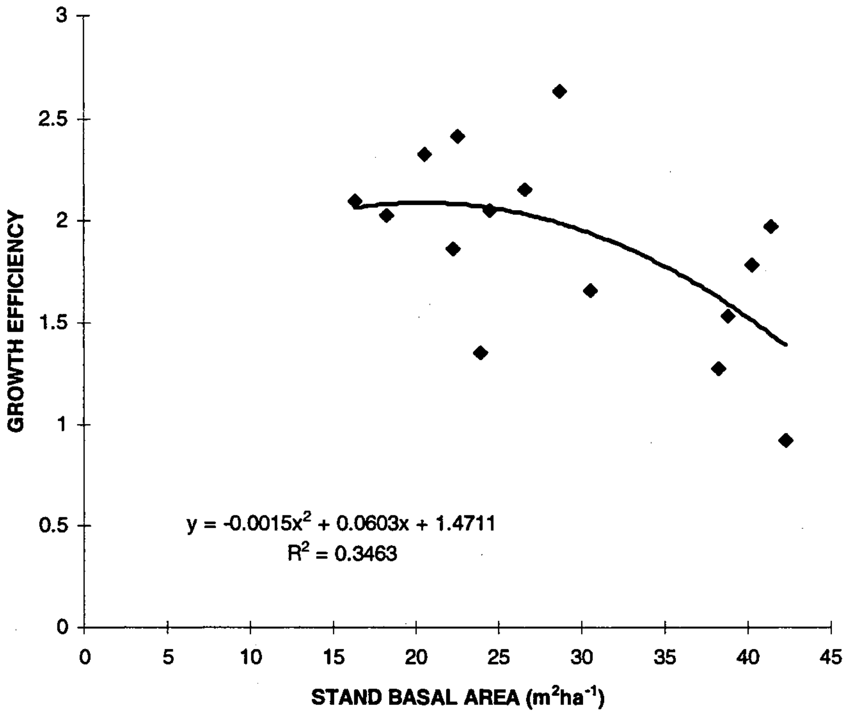

Figure 11. Net GE_{NB} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per metric tons of needle biomass) as a function of stand basal area at site one (SI 17 m at base age 50 yr.).

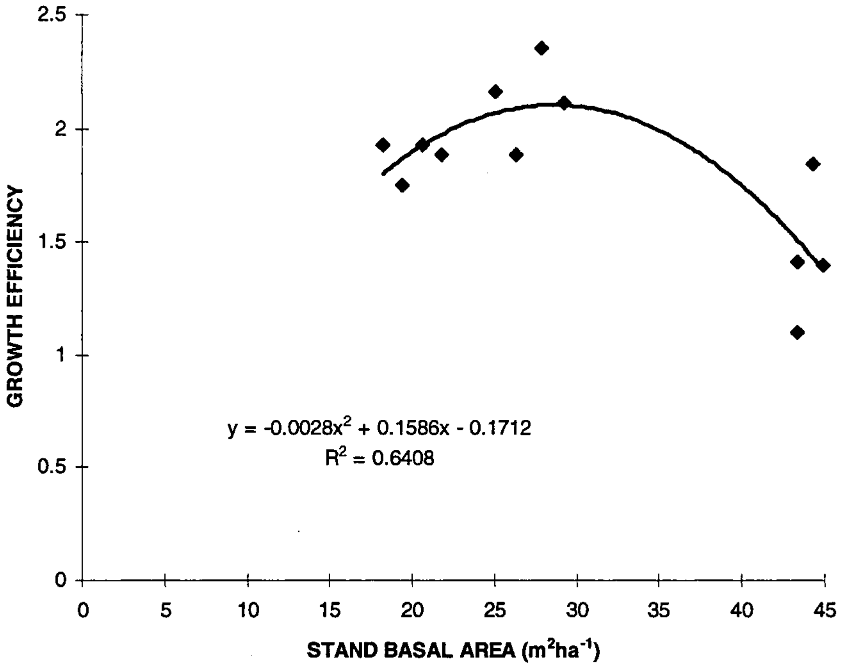

Figure 12. Net GE_{NB} ($m^2ha^{-1}yr^{-1}$ of stemwood volume per metric tons of needle biomass) as a function of stand basal area at site two (SI 22 m at base age 50 yr.).

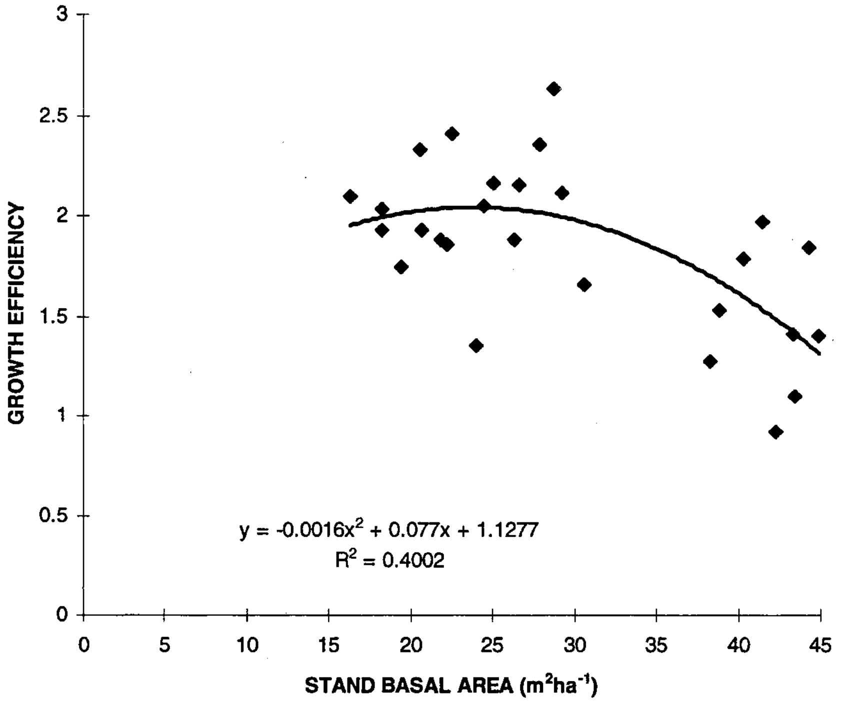

Figure 13. Net GE_{NB} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per metric tons of needle biomass) as a function of stand basal area at combined sites.

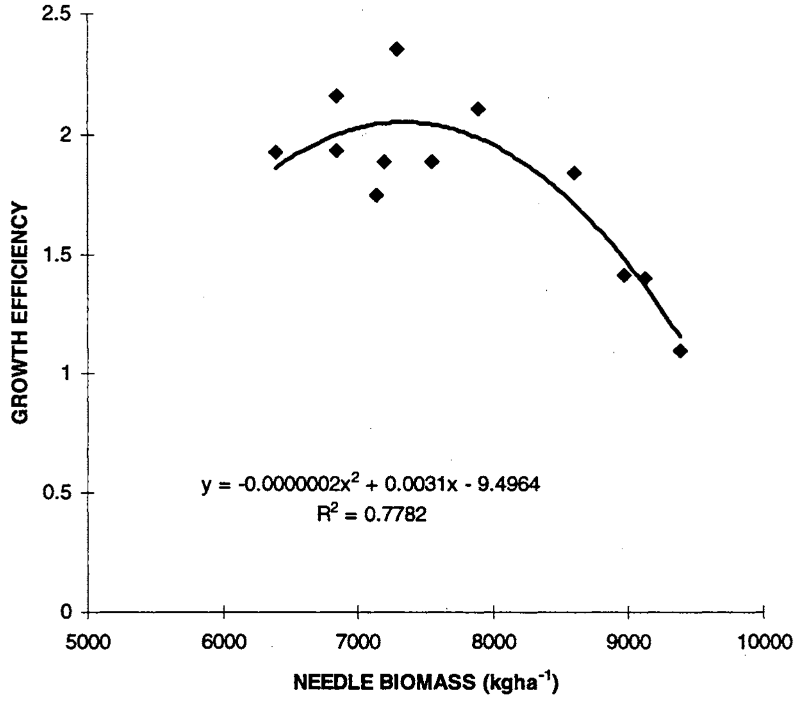

Figure 14. Net GE_{NB} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per metric tons of needle biomass) as a function of needle biomass at site two (SI 22 m at base age 50 yr.).

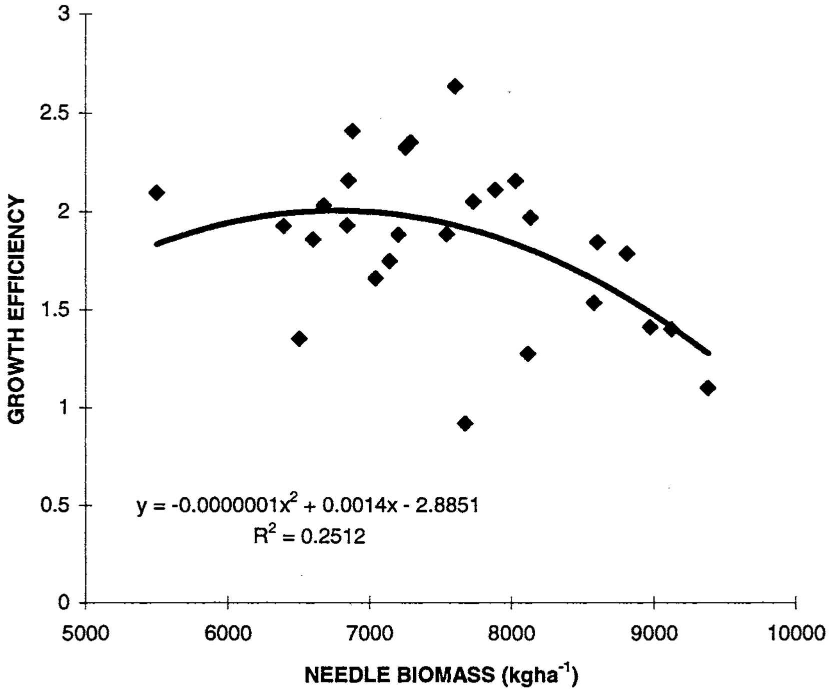

Figure 15. Net GE_{NB} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per metric tons of needle biomass) as a function of needle biomass at combined sites.

Study II. Leaf Area Index

Specific Leaf Area

Specific leaf area (SLA) was estimated for the period September-August to coincide with annual needle biomass production to estimate leaf area index (LAI). Mean annual all-sided SLA ranged from 109 cm^2g^{-1} to 114 cm^2g^{-1} over the three-year study period. SLA was not significantly different between seasons (table 9). Also, analyses of variance showed a non-significant difference between treatments by year and for the three-year study period at both sites (table 10).

Comparing our results to others studies, all-sided SLA of shortleaf pine was within the range determined for other southern pine species. For instance, Dalla-tea and Jokela (1991) estimated an all-sided SLA range between 111 and 129 cm^2g^{-1} and 96 and 110 cm^2g^{-1} in loblolly and slash pines, respectively. Also, Shelton and Switzer (1984) reported 89 to 144 cm^2g^{-1} all-sided SLA range in loblolly pine. For the same species, Blanche et al. (1985) found that all-sided SLA ranged from 60 to 140 cm^2g^{-1}. These results are supported by Vose and Allen (1988). They estimated projected SLA in loblolly pine to range from 38.9 to 60 cm^2g^{-1} equivalent to all-sided SLA=101 to 156 cm^2g^{-1}.

Hager and Sterba (1984) found that SLA of Norway spruce was not affected by thinning treatments. Also, Shelton and Switzer (1984) found little variation in SLA of loblolly pine over a diverse range of stand conditions and sites. They mentioned that the

Table 9. Mean specific leaf area (cm^2g^{-1}) by site, year, season, and treatment.

		YEAR PERIOD					
SITE	TREATMENT	1994		1995		1996	
		Jan-Aug	Sep-Dec	Jan-Aug	Sep-Dec	Jan-Aug	Sep-Dec
	50 PRD	111	112	106	111	112	112
ONE	70 PRD	111	112	108	115	113	112
	CONTROL	113	112	107	114	112	112
	50 PRD	112	111	113	110	117	117
TWO	70 PRD	108	110	110	110	114	114
	CONTROL	111	110	109	111	116	116

Table 10. Mean annual specific leaf area (cm^2g^{-1}) by site, year, and treatment.

SITE	TREATMENT	PERIOD (SEPT-AUG)			MEAN
		1993-94	1994-95	1995-96	
	50 PRD	111	109	111	111
ONE	70PRD	111	110	114	112
	CONTROL	113	109	113	112
	50 PRD	112	112	113	112
TWO	70 PRD	108	110	112	110
	CONTROL	111	109	114	111

variation found was not significant given the great diversity of stand conditions. In terms of seasonal variation, Vose and Allen (1988) found significant variation in SLA; however, Dalla-tea and Jokela (1991) reported little seasonal SLA variation in slash pine and loblolly pine (99 to 105 and 111 to 116 cm^2g^{-1}), respectively.

Most of the related studies agreed in that SLA varies with needle age and position within and among trees and stands. Current year foliage has higher SLA than older leaves (Dalla-tea and Jokela 1991 and Hager and Sterba 1984). Also, lower canopy leaves show the highest SLA. According to age and canopy positions, Shelton and Switzer (1984) ranked SLA as older-upper<older-lower<current-upper<current-lower. Variations in SLA with canopy position are due to differences in light exposure as an adaptation to maximize radiant energy harvest in a light limiting environment (Blanche et al. 1985, Del Rio and Berg 1979, and Kellomanki and Oker-Blom 1981). Branch bifurcation helps to reduce overlap and self-shading in loblolly pine; therefore, loblolly pine has higher SLA in lower canopy positions compared to slash pine (Dalla-tea and Jokela 1991).

Leaf Area Index

Leaf area index (LAI) and growth efficiency (GE) are important physiological tree parameters that explain annual stand increments. Leaf area, measured as LAI, is important for determining what is the contribution of stand leaf area to stand growth. In addition, GE_{LAI} is the ratio between periodic annual stemwood volume growth and LAI, thus it relates photosynthetic capacity of the leaves to carbon allocated to stemwood. Both parameters may be affected by stand stocking; therefore, the purpose of the present study was to estimate the effect of thinning and site qualities on LAI and net GE_{LAI}, and the relationship of LAI and stand density to annual stand growth and net GE_{LAI} three, four, and five years after thinning application in two different shortleaf pine site conditions.

Stand Density Effect on LAI

The greatest mean all-sided LAI was found in unthinned plots followed in decreasing order by the 70 PRD and 50 PRD for both sites and growing seasons. All-sided LAI varied between 7.2 m^2m^{-2} to 10.2 m^2m^{-2} (table No. 11). The lowest LAI was estimated in site one and the highest in site two. According to the analyses of variance, mean LAI was significantly different due to the effects of stand density in both sites and all growing seasons, except at site one in 1993 (p-value<0.03). At site one in the 1993 growing season the difference in LAI among density levels was not significant (p-value=0.08). In 1994, LAI of the control was significantly greater than the 50 PRD

Table 11. Mean stand all-sided LAI (m^2m^{-2}) by site, treatment, and year.

TREATMENT	SITE ONE		SITE TWO	
	1993[1]	1994[2]	1993[3]	1994[1]
50 PRD	7.6a[4]	7.2a	7.7a	8.1a
70 PRD	8.1a	7.9ab	7.9a	8.3a
CONTROL	9.1a	8.5b	9.5b	10.2b

[1] These dates correspond to four years after thinning application.

[2] This date correspond to five years after thinning application.

[3] This date correspond to three years after thinning application

[4] Columns followed by the different letter are significant different according Ryan-Einot-Gabriel-Welsch multiple F mean test (SAS Institute Inc. 1988) (α=0.05).

treatments in site one. Analyses of means estimated that mean LAI in unthinned treatments was always significantly greater, and mean LAI in 50 PRD and 70 PRD were not significantly affected by stocking densities (α=0.05) in both growing seasons at site two.

LAI, Density, and Growth Relationship

All-sided LAI and its relationship to stand density and annual stand growth was analyzed independently by site and growing season and by combining data from the two growing seasons and sites. Analyses of pooled data from the two sites were based on annual means of the treatments. Independent and pooled growing seasons analyses at each site were based on observations from each replicate plot. Both annual net and survivor growth were examined for relationships with LAI.

LAI was highly related to stand basal area at both sites. Pooled data from the two growing seasons reflected the results of independent annual estimates. Both sites indicated a linear relationship, but site two exhibited a stronger relationship than site one according to coefficients of determination (R^2=0.67 and 0.36, respectively) (Figures 16 and 17). However, the strongest linear relationship was obtained when mean treatment estimations of LAI and stand density were pooled (R^2=0.76) from the two sites and growing seasons (figure 18).

There was a quadratic relationship between LAI and net annual stand basal area growth the fourth and fifth year after thinning at site one and for the combined growing seasons at site two. The trend showed that net growth increased to a point, decreasing

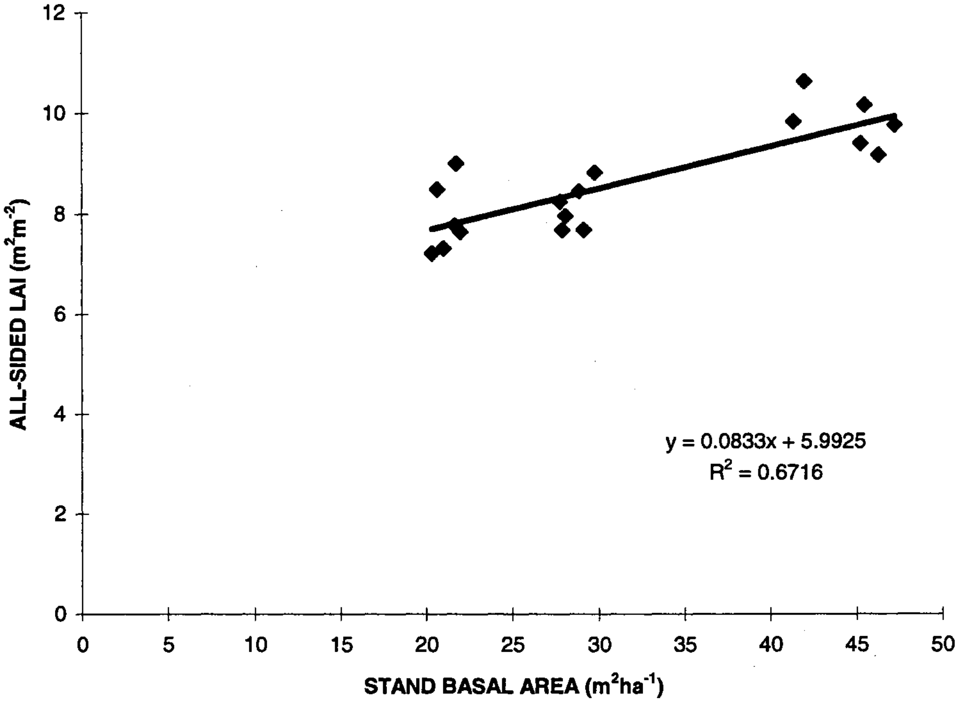

Figure 16. All-sided leaf area index and stand density relationship at site two (SI 22 m at base age 50 yr.).

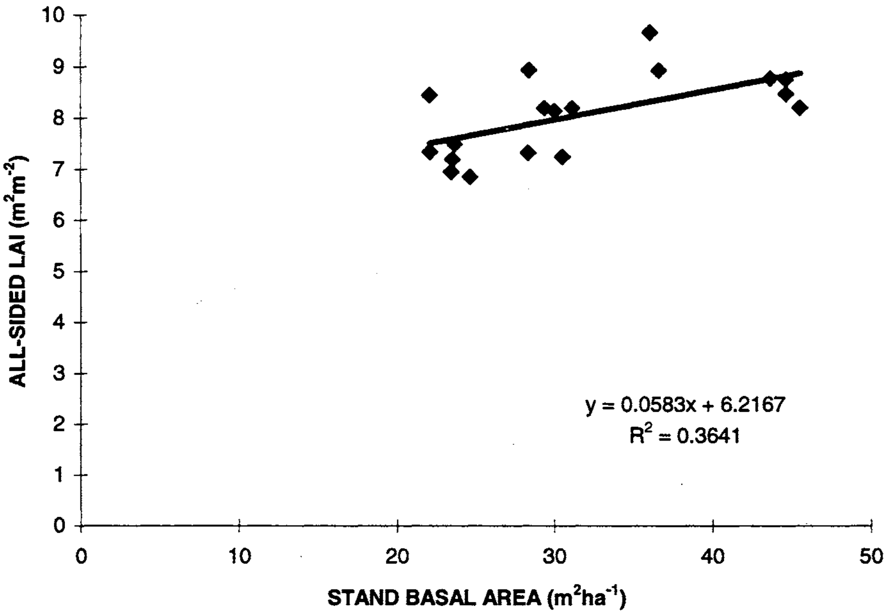

Figure 17. All sided leaf area index and stand density relationship at site one (SI 17 m at base age 50 yr.).

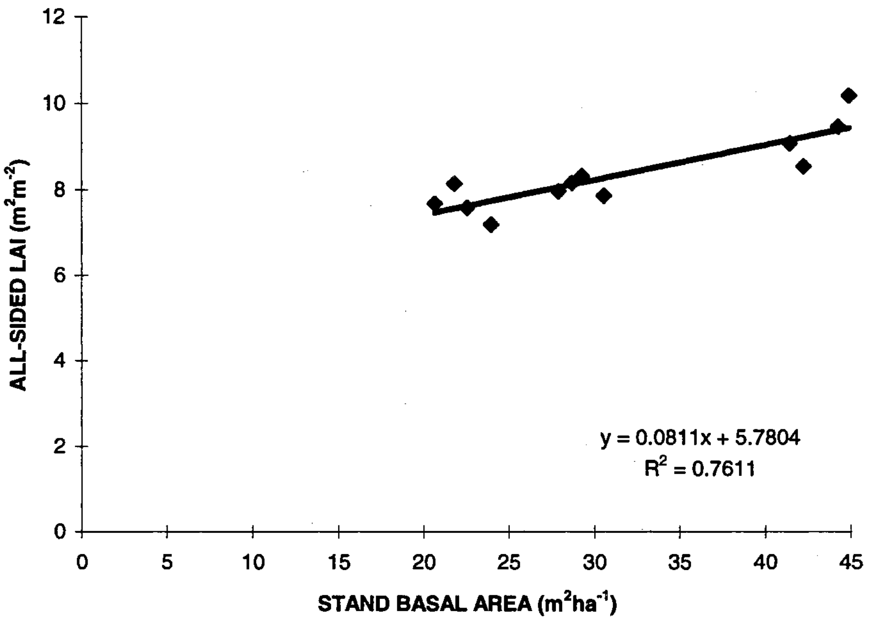

Figure 18. All-sided leaf area index and stand density relationship for combined sites and years. Data points are annual treatment means.

thereafter. Maximum annual stand basal area growth was found with different levels of LAI at each site. At site one maximum net annual stand basal area growth four and five growing seasons after thinning was related to LAI of 7.5 m^2m^{-2}, approximately. These relationships were supported by coefficients of determination of 0.49 and 0.58, respectively (figures No. 19 and 20). Because linear and quadratic tendencies were estimated in site two, the optimum growth related to LAI was not defined; however, the general trend was to decrease annual net stand basal area growth as LAI increased (figures No. 21). Since LAI was related to stand density, it was assumed that mortality occurred more frequently in stands with high LAI reducing net annual stand basal area growth as LAI increased.

A lack of a significant relationship was found between LAI and survivor stand basal area growth either for independent or pooled analyses in site one and two. The exception was a weak negative relationship observed in 1994 growing season in site one. LAI explained 21% of the stand annual survivor basal area growth variability in this growing seasons. In general, survivor stand annual basal area growth was maintained unchanged in spite of the increase in total LAI.

Stand Density Effects on Net GE_{LAI}

Net GE_{LAI} was not significantly different between treatments, except for 1994 growing season (table 12) at site one in which the control was significantly lower. At site two, the two year mean GE_{LAI} of 70 PRD treatment was significantly higher than the 50 PRD treatment and control. The lowest net GE_{LAI} was found in unthinned plots for both

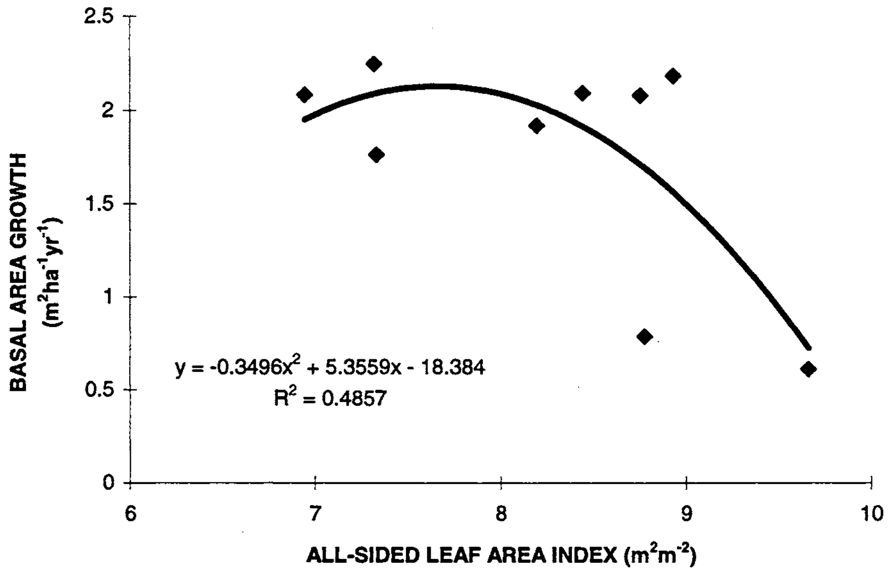

Figure 19. Mean annual net stand basal area growth and all-sided leaf area index relationship four growing seasons after thinning application at site one (SI 17 m at base age 50 yr.).

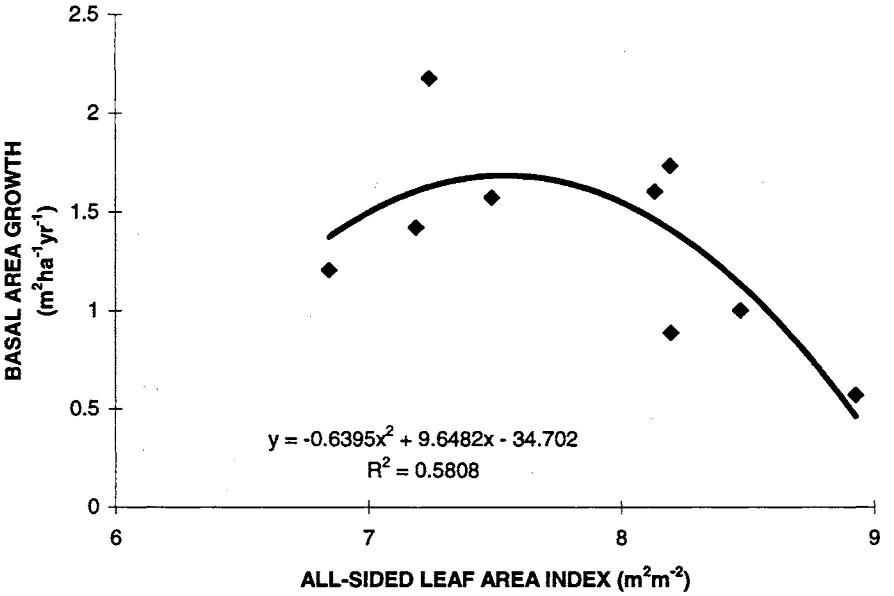

Figure 20. Mean annual net stand basal area growth and all-sided leaf area index relationship five growing seasons after thinning application at site one (SI 17 m at base age 50 yr.).

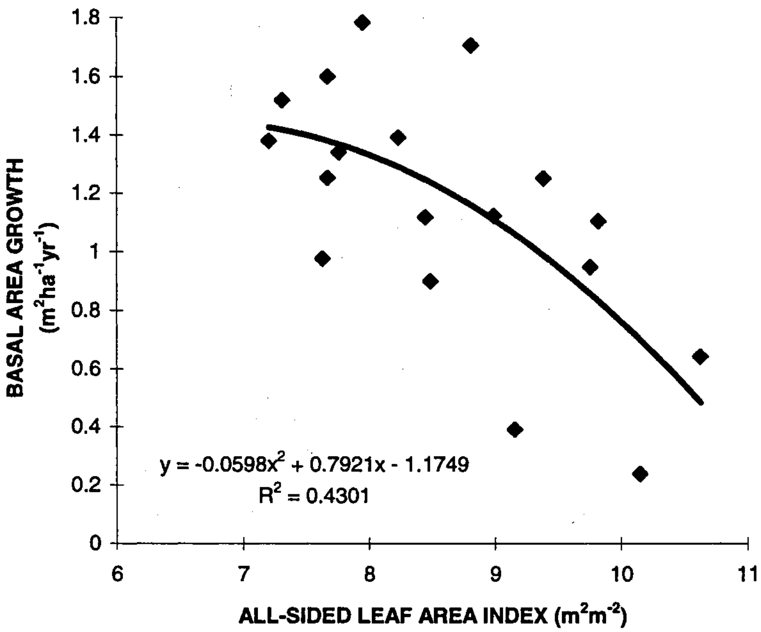

Figure 21. Mean annual net stand basal area growth and all-sided leaf area index relationship for combined growing seasons at site two (SI 22 m at base age 50 yr.).

Table 12. Mean net GE_{LAI} (m^3ha^{-1} of stemwood volume per a unit of LAI) by site, year, and treatment.

SITE	TREATMENT	GROWING SEASONS		MEAN
		1993	1994	
ONE	50 PRD	2.19a[1]	1.22a	1.71a
	70 PRD	2.47a	1.49a	1.98a
	CONTROL	1.78a	0.83b	1.30a
TWO	50 PRD	1.72a	1.67a	1.70a
	70 PRD	2.16a	2.00a	2.08b
	CONTROL	1.67a	1.26a	1.46a

[1] Columns followed by different letter are significant different according to Ryan-Einot-Gabriel-Welsch multiple F mean test (SAS Institute Inc. 1988)(α=0.05).
Mean comparisons were made independently by site.

growing seasons and sites. The range in net GE_{LAI} was between 0.83 and 2.47 m^3ha^{-1} of stemwood volume per each m^2m^{-2} of LAI. In spite of the lack of differences, net annual GE_{LAI} observed at the control was about two thirds of that at the 70 PRD at both sites. Net GE_{LAI} means were not different between sites at each treatment level.

LAI, Density, and GE_{LAI} Relationship

Net stand stemwood volume GE_{LAI} was significantly related to LAI. When mortality is subtracted from survivor stand growth, stand stemwood net GE_{LAI} is very low at high LAI. In particular, net GE_{LAI} analyses in site one showed linear and curvilinear tendencies in 1993 and 1994 growing seasons, respectively (figures 22 and 23). The coefficients of determination were 0.61 and 0.51 for each growing season. Analyses of site two showed a negative linear trend in both growing seasons (figures 24 and 25). The coefficients of determination explained 26% and 53% of the net stand stemwood GE_{LAI} variability, respectively. Combined data from both years reflected the negative linear tendency of independent growing season analyses (figure 26).

Previously, LAI was used as a surrogate of stand density, but it is also important to relate density, measured as basal area, directly to net GE_{LAI}. In 1993, the trend was undefined at site one, but in 1994, it showed a significant quadratic tendency. A lack of relationship between stand basal area and GE_{LAI} was observed when combined data from

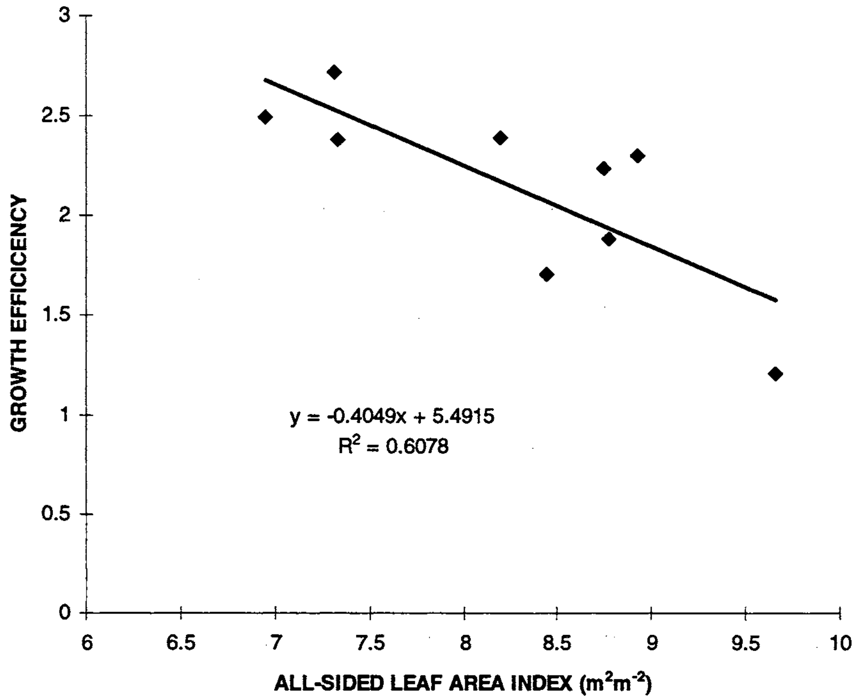

Figure 22. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and all-sided LAI relationship at site one four growing seasons after thinning application.

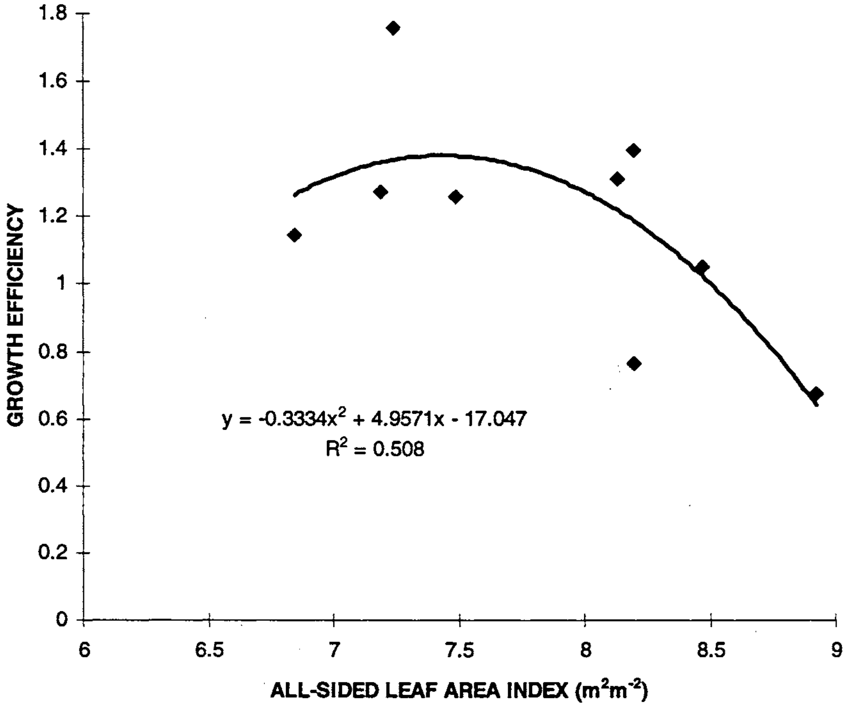

Figure 23. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and all-sided LAI relationship at site one five growing seasons after thinning application.

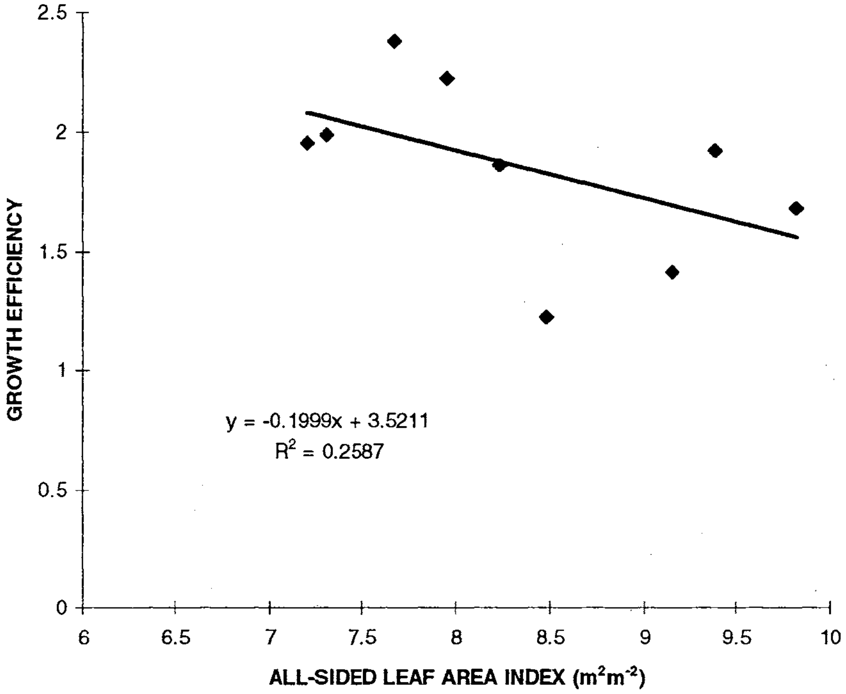

Figure 24. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and all-sided LAI relationship at site two three growing seasons after thinning application.

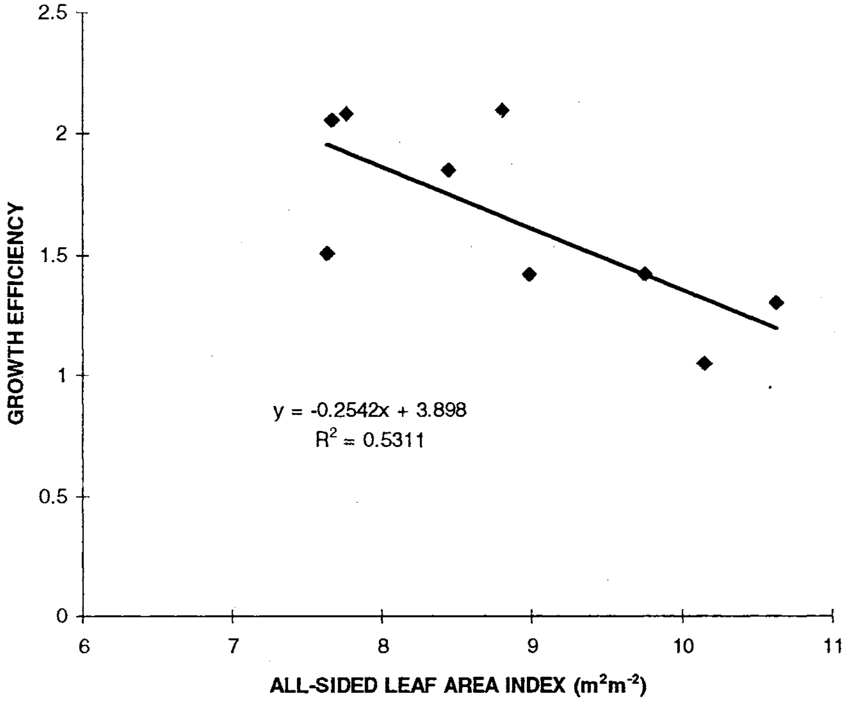

Figure 25. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and all-sided LAI relationship at site two four growing seasons after thinning application.

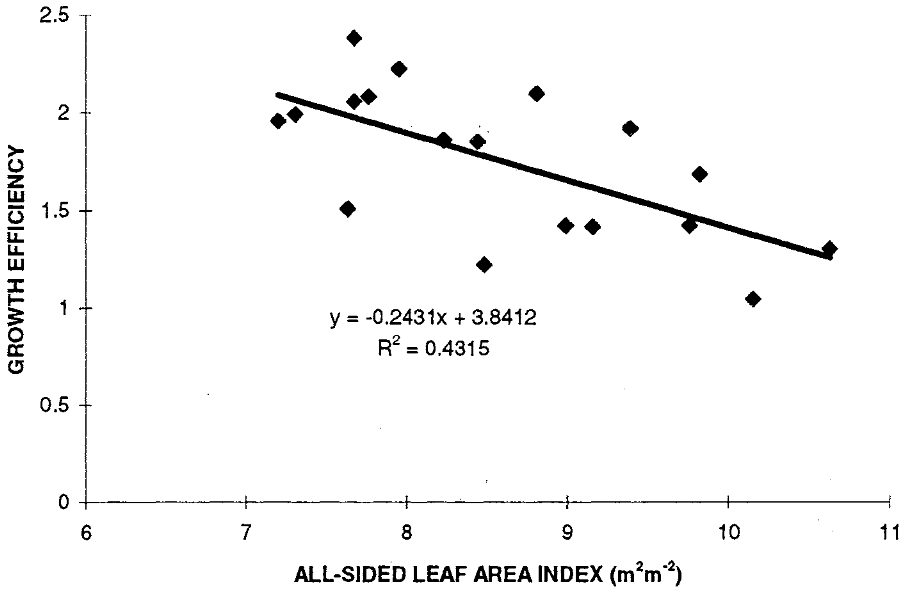

Figure 26. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and all-sided LAI relationship for combined growing seasons at site two.

site one was analyzed. Site two showed significant curvilinear tendencies independently for each growing season. The annual curvilinear tendencies were reflected when data from combined years was used. The general tendency was an increase to a point and then a decline in net GE_{LAI} as stand density increased (figure 27). Maximum net GE_{LAI} occurred approximately at a basal area of 30 m^2ha^{-1}, after that density level was reached net GE_{LAI} declined. A decline in stemwood GE_{LAI} as density increases probably indicates that most of the carbohydrates are allocated to priority uses by the trees to survive and that much photosynthate production is consumed by respiration.

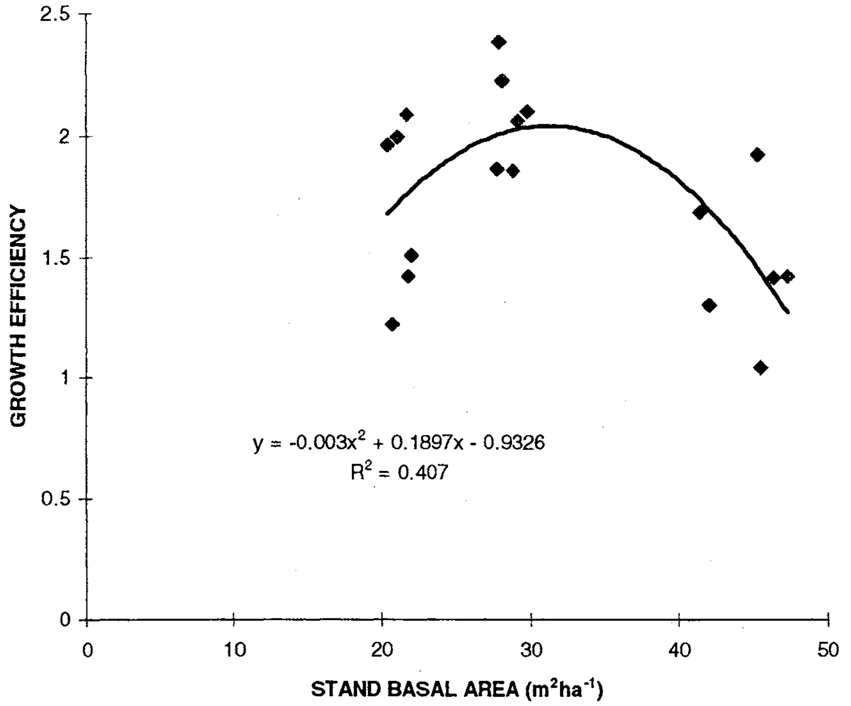

Figure 27. Net GE_{LAI} ($m^3ha^{-1}yr^{-1}$ of stemwood volume per m^2m^{-2} of LAI) and stand basal area relationship for combined growing seasons at site two.

CHAPTER IV

DISCUSION

Study I. Needle Biomass

Needlefall and Needle Biomass Patterns

General patterns of shortleaf pine seasonal needlefall agreed with previous research in a variety of species. Regardless of species, origin, age, site, and environmental differences, maximum needlefall always occurs in the fall season in the northern Hemisphere, although the starting time may vary because of the effect of climatic conditions. Crosby (1961) reported that about 60% of shortleaf pine litter accumulated in the fall season in 19 to 76 year-old stands in southeast Missouri. The remainder was equally distributed between winter, spring and summer seasons. Similarly, Dalla-tea and Jokela (1991), Lockaby and Taylor-Boyd (1986), and Van Lear and Goebel (1976) reported that most loblolly pine leaf fall occurred from October through December. Dalla-tea and Jokela (1991) estimated that between 50% and 70% of needlefall accumulated within the fall season. These patterns were very similar to those reported in our study in which about 60% of annual needlefall occurred in the fall.

Regardless of similar seasonal patterns, shortleaf pine needlefall quantity varied from year to year. Needlefall was variable within treatments through the study period, although annual needlefall changes were synchronized between treatments (see figures 1 and 2 and tables 6 and 7). From previous studies, it could be hypothesized that annual leaf production is partially related to differences in weather conditions such as precipitation. However, no relationship was observed between total annual and growing season precipitation and needle production in this study. Growing season precipitation and water balance seemed to be related to the next year's leaf production (see table 13). The above normal precipitation and surplus water balance present during the study period may have resulted in water balance not being the controlling factor in needle production. Under more severe water deficits, Hennessey et al. (1992) found that needle production of loblolly pine was related to water balance. Grier and Running (1977) indicated that leaf area increases as precipitation increases, but that the factors regulating leaf production are more complex than a simple relation to annual precipitation. Leaf biomass like leaf area has an upper production limit; therefore, beyond some precipitation limit additional increases in leaf area would not be expected.

Normally, thinning improves nutrients, moisture, and light availability, and these attributes are related to needlefall and needle production. For instance, fertilized and irrigated sites had improved needle formation and delayed monthly peak needlefall (Hennessey et al. 1992, Raison et al. 1992, and Snowdon and Benson 1992). Miller et al. (1976) found that corsican pine needlefall was delayed the first year after nitrogen application, but increased the following year. Dalla-tea and Jokela (1991) found that the interaction between fertilization and weed control improved needlefall of 6 year-old loblolly and slash pine about 1050% and 400%, respectively.

Table 13. Needle production in relation to precipitation and water balance.

GROWING SEASON	NEEDLE PRODUCTION ($kgha^{-1}yr^{-1}$)		PRECIPITATION (mm)[1]	WATER BALANCE (mm)
	(SITE ONE)	(SITE TWO)	(MAR-OCT)	Σ(PREC - EVAP) (Mar-Oct)
1989	4376	-o-	836	-28
1990	3741	3988	1130	262
1991	4840	4987	937	25
1992	3972	4394	1043	224
1993	4166	4211	924	-8
1994	3512	4913	707	-247

[1] Precipitation and pan-evaporation was taken from NOAA (1989-1994).

Stand needlefall in unthinned stands increases with stand age until needle production is limited by site resources. For instance, the highest loblolly pine (Dalla-tea and Jokela 1991) and slash pine (Gholz et al. 1985) needlefall was approached at age 15, approximately. Thinned stands also tend to reach maximum annual needle production through time. In this study, shortleaf pine showed a variable annual needle production, but the highest occurred in dense unthinned plots and thinned plots tended to approach the levels of the unthinned plots. However, after six growing season, needle production of unthinned plots was not attained by any thinned plots at each site. Comparatively, the highest annual shortleaf pine needle production (4987 $kgha^{-1}yr^{-1}$) was similar to slash pine (4453 $kgha^{-1}yr^{-1}$) and longleaf pine (4884 $kgha^{-1}yr^{-1}$), higher than radiata pine (3200 $kgha^{-1}yr^{-1}$) and lower than loblolly pine (5800 $kgha^{-1}yr^{-1}$)(Cromer et al. 1984, Gholz et al. 1985, Gresham 1982, Hennessey et al. 1992, and Trofymow et al. 1991).

Since stand annual needle biomass was estimated directly from annual needlefall, trends were very similar. Absolute values showed variable annual needle biomass patterns over the study period, but relative estimations showed a clear tendency to reach those amounts produced in unthinned plots over time (see table No. 5). By the end of the study period, the thinned plots had not reached the levels of the control plots. The 7678 to 9381 $kgha^{-1}yr^{-1}$ range in stand needle biomass observed in the unthinned control plots is near the range reported for other conifer species such as lodgepole pine, Douglas-fir, loblolly pine, and radiata pine (Keyes and Grier 1981, Mead et al. 1984, and Pearson et al. 1984).

Stand Needle Biomass and Density Relationship

Percent relative density may provide a better method of evaluating stocking levels than basal area, the most commonly used parameter. Since basal area includes the cross sectional area of physiological dead heartwood , it has less direct biological significance (Smith et al. 1997). Percent relative density incorporates stand basal area, number of trees and diameter, providing a better indication of site occupancy by trees and allows comparison of certain stand attributes with established norms (Wittwer et al. 1996).

Stand needle biomass clearly reflected stand basal area and/or percent relative density. There was a strong linear relationship between them, although differences were found between sites. Site two (high quality site) exhibited a stronger correlation than site one (low quality site) (R^2=0.91 vs. R^2=0.64). This was attributed to higher annual needle biomass variability in site one. Needle biomass increased as stand or stocking density increased up to 45 m^2ha^{-1} or 150 PRD, respectively. Although an asymptote showing the maximum stand needle biomass-stand density relationship point was expected, none was found in this study. Assuming that annual needlefall corresponded to annual needle production (Hennessey et al. 1992), annual stand needle production should increase with stand basal area until it reaches a maximum and then stand needle production should level off as overstocking develops. Nutrients, water, and light are insufficient to supporting needle growth beyond a certain maximum level. Also, as an acclimation process, self-shading at low crown positions may reduce needle dry weight, accelerating needlefall and reducing needle development (Magnussen et al. 1986).

Stand basal area, sapwood area, and diameter have been found to be strongly related to stand leaf biomass in several tree species (Blake et al. 1991, Gholz 1982, Hennessey et al. 1992, Loomis et al. 1966, and Wang et al. 1995). The sapwood area-stand needle biomass relationship shows stronger correlation and has a physiological explanation. Sapwood area is expected to be strongly correlated with foliar weight because water transport to the canopy is through the sapwood. Grier and Waring (1974) found that estimation of foliage from diameter at breast height is reliable for stands with small or relatively young trees, but not for irregular old stands. They found that leaf biomass in Douglas-fir, noble fir, and ponderosa pine was more closely related to sapwood area than diameter (R^2=0.97, 0.98, and 0.97, respectively). Similar results were found in Scots pine by Whitehead (1978). Long et al. (1981) added that a linear relationship occurred between sapwood cross-sectional area at a given height and the needle biomass above that height in Douglas-fir trees. Marchand (1984) found similar results in balsam-fir and red spruce when he related sapwood cross-sectional area at the base of the live crown to needle biomass.

Stand Needle Biomass and Annual Growth Relationship

Stand needle biomass was significantly related (p-value=0.05) to stand growth. However, the trends differed when net or survivor growth were related to stand needle biomass. Net annual stand growth increased to a maximum and then decreased as stand needle biomass increased. An increase in stand basal area with needle biomass represented the influence of radiation interception by leaf biomass while the decrease was attributed to the effect of tree mortality due to stressed environmental site resources (Vose and Allen 1988). High annual survivor growth of stands at high stand needle biomass was expected because of the greater number of trees. However, light could have influenced annual tree growth rate reduction in dense stands and improvement in thinned stands maintaining similar stand growth rates at all treatment levels (Waring et al. 1981). Since water balance (precipitation minus evaporation) was above normal, moisture availability may not have been considered a limiting factor in stand biomass production. Annual stand survivor growth remained unaltered in the range of stand needle biomass studied. Large amounts of stand needle biomass contribute little improvement in photosynthetically active radiation absorption. In heavily stocked stands, canopy structure is very dense and light can not penetrate to lower crown positions. Thinning improves canopy structure by reduction of clumpliness and foliage reflectance and transmitance (Dalla-tea and Jokela 1991). Net, and survivor periodic annual growth were similar among thinned stands, but net growth was substantially less than survivor growth in unthinned stands.

Stand needle biomass explained similar proportion of variation in growth when it was related to stand basal area growth and percent relative density. This was expected since stand basal area was strongly correlated with percent relative density. Values below zero are attributed to high occurrence of mortality in highly dense stands.

Study II. Leaf Area Index

LAI and Stand Density Relationship

LAI values in shortleaf pine stands were dependent on stand density and site, ranging from 7.2 $m^2 \cdot m^{-2}$ to 10.2 m^2m^{-2}. Low LAI corresponded to a low density and quality site, and high LAI values were related to overstocked stands. The lowest LAI in site one may be due to poorer environmental site conditions. In support of this, Grier and Running (1977) found that LAI is linearly related to site water balance. Brix (1983) reported that thinning and fertilization increased tree foliage in Douglas-fir. Similarly, Binkley and Reid (1984) found that fertilization increased stand leaf area in Douglas -fir. In addition, Vose and Allen (1988) said that stand LAI increased with fertilization in nitrogen deficient sites, and suggested that maximum LAI is restricted by moisture availability in loblolly pine sites. Therefore, LAI may increase only if the managed stands have less LAI than that allowed by moisture availability. Similar findings were reported by Colbert et al. (1990), and they added that the interaction of fertilization and weed control improved LAI development of loblolly and slash pine by 1210% and 290%, respectively. Lastly, Binkley et al. (1995) found that LAI and stand growth is restricted in old stands of lodgepole pine because of a decline in nutrient supply.

To compare all-sided LAI to projected LAI, all-sided LAI of shortleaf pine may be divided by a factor of 2.6 as indicated by Vose and Allen (1988) in loblolly pine. In general, all-sided LAI values estimated for shortleaf pine under site conditions in this study were comparable to several species. For instance, Vose (1987) reported projected

LAI range of 2.4 to 4.29 m^2m^{-2} (all-sided LAI=6.24 to 11.15 m^2m^{-2}) in loblolly pine. Colbert et al. (1990) estimated all-sided LAI as low as 1.2 and 1.9 m^2m^{-2} and as high as 15.7 and 7.4 m^2m^{-2} in loblolly and slash pine, respectively. In addition, Smith et al. (1991) reported projected LAI for lodgepole pine between 2.66 to 4.22 m^2m^{-2} (all-sided LAI=6.92 to 10.97 m^2m^{-2}). Similar to our study, these LAI were related to low and high density stands, respectively. Long and Smith (1992) reported a LAI range of 1.23 to 6.53 m^2m^{-2} in lodgepole pine. A similar LAI range was reported by Penner and Deblonde (1996) for jack and red pines. Magnussen et al. (1986) estimated a maximum projected LAI of 5.0 m^2m^{-2} for jack pine (all-sided LAI=13 m^2m^{-2}). Also, Nel and Wessman (1993), estimating LAI using canopy transmitance models, found similar values in a forest dominated by Engelmann spruce, subalpine fir, Douglas-fir and aspen.

Although stand basal area was well correlated to stand LAI, sapwood area appears to be better related to LAI. Whitehead (1978) estimated a linear relationship between cross sectional area of sapwood and foliage area in Scots pine. The coefficient of determination indicated that sapwood basal area explained 97% of the variability in foliage production. Marchard (1984) found that sapwood area had a high degree of correlation with LAI in balsam fir (R^2=0.96) and red spruce (R^2=0.93). In addition, Blanche et al. (1985) determined that sapwood cross sectional area at the base of the crown is better related to leaf area than that estimated at breast height and from diameter at breast height. Although, a variety of different regression models were tested, the linear model appeared to adequately predict leaf area in loblolly pine.

LAI and Stand Growth Relationship

LAI was significantly curvilinearly related to net stand basal area growth. Waring et al. (1981) described the same relationship in naturally established Douglas-fir stands. He estimated a maximum net basal area growth at projected LAI of 6 m^2m^{-2}. They agreed that net, but not gross, production falls to zero or below in very high LAI. Magnussen et al. (1986) mentioned that a positive linear relationship occurs only in semistocked stands when competition for environmental site conditions is favorable for developing full productivity and leaf area. In addition, Vose and Allen (1988) found that annual volume growth was linearly related to LAI in semistocked loblolly stands, but fully stocked loblolly stand approached an asymptote at projected LAI equal to 3.5 m^2m^{-2}. Other studies have described a positive linear tendency, but most of these studies have been based on destructive and individual tree measurements; therefore, mortality has been neglected as a component of the stand productivity (Binkley and Reid 1984, Lavigne 1988, Long and Smith 1992, and Penner and Deblonde 1996). The lack of relationship between survivor growth and LAI confirmed that mortality is a very important stand variable to take into account when overstocked stands are analyzed.

Mean annual growth of individual trees was higher in thinned than in control plots. The decline in individual tree growth in overstocked stands is not only a function of associated attributes of LAI such as light interception and shading, but is also associated with stressed environmental site resources due to high stand density (Colbert et al. 1990 and Vose and Allen 1988). Waring et al. (1981) mentioned that not only leaf area appears to have a direct effect on tree growth, but also other factors such as site moisture and nutrients are expected to interact with light interception and the shading effect of the canopy. Generally, dry matter production increases when intercepted photosynthetically active radiation increases, but stressed environments and structural canopy properties may influence light use efficiency (Dalla-tea and Jokela 1991). In addition, gains in intercepted radiation may be offset by higher maintenance respiration and water use by high stand LAI (Vose and Allen 1988). Also, increases in respiratory losses and shading conditions may outweigh gains in photosynthesis, thus increased production in overstocked stands with high LAI is not assessed (Magnussen et al. 1986).

LAI, Stand Density, and Growth Efficiency

Growth efficiency is an index that measures the amount of stemwood produced per unit leaf area or biomass. It accounts for the influences of carbon allocation to stemwood and photosynthetic efficiency and is a tool for evaluating silvicultural experiments (Binkley and Reid 1984, Brix 1983, and Stoneman and Whitford 1995). Net GE (measured as GE_{NB} or GE_{LAI}) was similar between the thinned treatments. Therefore, stand net GE was little affected by stand densities or LAI in the range of 15 to 30 m^2ha^{-1} or 7 to 9 m^2m^{-2}, respectively. In contrast, although not significantly different in some growing seasons, net GE in unthinned plots was lower because of mortality. On average, tree GE was higher in thinned stands, suggesting that tree carbon allocation and photosynthetic efficiency was higher in thinned plots. This seems logical since thinning removes less vigorous and efficient trees. Also, sufficient nutrients and moisture allow trees to develop in stemwood. When the relative carbon demands by roots and leaves are low, stemwood GE is normally high (Waring and Schlesinger 1985 and Brix 1983).

Net GE was related to LAI and stand density. In general, GE_{NB} increased to a maximum and then decreased and GE_{LAI}, after four growing seasons, decreased as stand density and LAI increased. Stoneman and Whitford (1995), Binkley and Reid (1984), and Waring et al. (1981) found a decrease in stand GE as density increased. Similar to our results Binkley and Reid (1984) found that stemwood GE-LAI correlation was lower than that of stemwood growth-LAI. Brix (1983) explained that an increase in foliage causes a decrease in light intensity in the lower crown position and this is a major reason for low GE in overstocked stands. Thinning improves needle production in the lower parts of the canopy and in combination with increased radiation interception tree growth and GE are improved. However, as the stands develop over time, the canopy foliage became dense decreasing light interception and stand growth and GE are reduced . Therefore, GE is dependent on foliage amount and photosynthetic efficiency of the leaves. According to Lavigne (1988), the non-productive biomass surface to foliage ratio may explain allocation patterns. Higher surface:foliage ratios consume more energy from respiration to maintain living tissues, reducing synthesis of new tissue. In the unthinned stands photosyntate production may be offset by maintainance respiration. In addition, Lavigne (1988) claimed that photosynthetic production was higher in unthinned balsam-fir plots, but at the tree level phosynthetic production was higher in thinned stands. In general, reduction of stand survivor GE may be due to increased shading, respiration, or stress in the environmental site resources (Colbert et al. 1990, Law et al. 1992, and Vose and Allen 1988).

From independent annual analyses, it is inferred that after four growing seasons LAI has reached its maximum positive influence in stemwood volume GE. Therefore, a silvicultural implication is to thin the stands below a basal area of 25 m^2ha^{-1} or LAI below 7 m^2m^{-2} to maintain a positive stemwood growth. Ecophysiological attributes are optimized to maximize stand growth under the densities described above at these particular sites.

CHAPTER V

CONCLUSION AND MANAGEMENT IMPLICATIONS

In summary, needlefall of shortleaf pine (*Pinus echinata* Mill.) followed a typical seasonal pattern. Normally, around 60% of the leaf fall occurred during the fall season. The remainder was distributed homogeneously during the remaining months. Annual needlefall was a function of stand stocking densities. It increased as stand stocking density increased. However, annual amounts by treatments did not increase consistently over time.

Annual needle biomass was affected by stand density, with higher stocking densities supporting higher needle biomass. Relative needle biomass amounts for thinned treatments showed that needle production tended to approach needle biomass amounts of unthinned plots as the study period progressed. Needle biomass was not significantly different between sites.

Although percent relative density may provide a better indication of site occupancy than basal area, it did not improve the relationship with stand needle biomass in this study. Both stand basal area and percent relative density were linearly related to stand needle biomass. Annual net basal area growth was related to needle biomass by a curvilinear trend. Thinned stands exhibited similar annual growth within a leaf biomass range of 5,500 to 8,000 kgha^{-1}, but growth of unthinned stand abruptly decreased above

8000 $kgha^{-1}$. Net GE_{NB} was curvilinearly related to needle biomass. Generaly, net GE_{NB} increased and then decreased as stand density increased.

All-sided LAI ranged between 7.2 to 10.2 m^2m^{-2}, respectively. LAI among thinned levels was not significantly different, but LAI was different from unthinned treatments. LAI increased as stand density increased. The LAI-stand net annual basal area growth relationship was expressed by a curvilinear trend. All-sided LAI was negatively related to net GE_{LAI}. Mean net GE_{LAI} was lower in unthinned plots, but differences were only significant in the 1994 growing season.

Needle biomass, LAI, and GE are three important variables that help to explain and determine potential stand productivity. For instance, from this study we can determine that the best growth is achieved when LAI is not above 7.5 m^2m^{-2} and the highest GE is found within stand density ranges of 25 to 30 m^2ha^{-1}. At this density leaf canopy optimize environmental site resources to produce wood. Above that point respiration maintenance overshadows photosynthetic gains. In addition, the highest annual basal area growth and GE occurred within the range suggested by Rogers' (1983) stocking chart for shortleaf pine. Optimum GE occurred at a LAI range of 7 to 7.5 m^2m^{-2} approximately, corresponding to stocking density ranges of 60% to 100% on Rogers' stocking charts. After that point, although stand needle biomass and LAI still increased, gross annual basal area growth and growth efficiency were constant because of the high number of trees, but at the individual tree level it decreased. Analyses of stand density and stand growth to LAI and GE relationships are important to determine maximum interaction of site environmental resources such as nutrients, moisture, and light. Thinning helps to release site environmental stresses by opening the canopy and redistributing site resources. Also, thinning reduces shade effects due to canopy structure reducing canopy respiration and water use by high LAI.

Undoubtedly, these three variables (stand needle biomass, LAI, and GE) are related to ecophysiological plant attributes such as light interception, photosynthesis, respiration, and transpiration and they play an important role in tree growth. Mortality occurs in overstocked stands as a consequence of stressed environmental site conditions that affect the balance between light interception, photosynthesis, respiration, and transpiration. Stand needle biomass, LAI, and GE reflected these effects on stand and tree growth.

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APPENDIX A. Number of two-needle, three-needle fascicles, and ratio of three-needle to two-needle fascicles in subsamples of pine leaf litter by treatment and block.

TREATMENT	BLOCK	TWO-NEEDLE FASCICLES	THREE-NEEDLE FASCICLES	RATIO
SITE ONE				
50 PRD	1	114	86	0.75
70 PRD	2	111	73	0.66
CONTROL	3	67	73	1.09
50 PRD	1	110	65	0.59
70 PRD	2	95	78	0.82
CONTROL	3	66	83	1.26
50 PRD	1	93	75	0.81
70 PRD	2	140	52	0.37
CONTROL	3	185	59	0.32
50 PRD	1	240	99	0.41
70 PRD	2	155	76	0.49
CONTROL	3	202	74	0.37
SITE TWO				
50 PRD	1	175	92	0.53
70 PRD	2	129	67	0.52
CONTROL	3	58	25	0.43
50 PRD	1	72	22	0.31
70 PRD	2	66	39	0.59
CONTROL	3	63	45	0.71
50 PRD	1	118	70	0.59
70 PRD	2	85	44	0.42
CONTROL	3	80	44	0.55
50 PRD	1	138	77	0.56
70 PRD	2	121	83	0.68
CONTROL	3	157	118	0.75
			MEAN	0.61

2

VITA

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