Chapter IV

Testing for Dominance/Suppression Relationships in Loblolly Pine Plantations

Introduction

Two conceptual models of the role of competition in the dynamics of size structures have been proposed (Weiner 1985, Weiner and Thomas 1986). The first assumes that competition acts on all individuals equally or in direct proportion to their size. Competition is assumed to be *two-sided* and described as *resource depletion*. In the second model competition is thought to be disproportionate to plant size. Large plants usurp resources at the expense of smaller plants. This type of competition is termed *one-sided* and is categorized as *resource pre-emption*. In the most extreme form of one-sided competition, smaller individuals would exhibit no competitive influence on larger neighbors.

Tests for the most appropriate model have been based on the analysis of size distribution parameters and the distribution of relative growth rates across a density gradient and through time. Under the resource depletion model, it is assumed that competition acts to reduce the relative growth rates of all competing plants by the same proportion (Weiner 1985). This proportional reduction in growth rates results in a reduction in the variance of growth rates which leads in turn to a decrease through time in skewness and in size inequality. Under the resource pre-emption model, it is assumed larger plants are able to usurp more than their proportional share of resources. In the presence of intra-specific competition, size inequality should increase through time (Weiner and Thomas 1986) and relative growth rates should be positively correlated with size (Ford 1975, Cannell *et al.* 1984, Schmitt *et al.* 1987).

Evidence for the existence of dominance/suppression relationships in even-aged monocultures has been reported from designed experiments with annual species and from analysis of unreplicated field trials with various tree species (Ford 1975, Cannell *et al.* 1984, Perry 1985, Brand and Magnussen 1988, Larocque and Marshall 1993). There are no published reports of testing for dominance and suppression in managed even-aged plantations from replicated field trials. Analysis of size inequality and the relative growth rate/size relationship across a density gradient and how this relationship changes through time would provide a powerful test of the existence of dominance and suppression competitive relationships and may be of utility in improving growth and yield models.

Data and Methods

Data from the Coop and Calhoun spacing studies were used to examine the time trend of size inequality and the relationship between relative growth rate and tree size. On these studies individual-tree measurements began prior to crown closure; when intra-specific competition is often assumed to begin, and continued beyond the time of crown closure. Analysis of stand development trends across the density gradient suggest the presence of competition across all densities.

Following Hunt (1978, 1982) we used functional growth analysis to estimate relative growth rates. Relative growth rates for dbh were estimated from a set of equations used to describe the relationship between dbh and age. For most trees with at least four measurements over time, the Richard's model (Richard 1959) described the dbh time trend extremely well:

$$d = \alpha[1 - e^{(-\beta(A))}]^{\theta}$$

where α, β, and θ are parameters to be estimated from the data and A is stand age. The unknown coefficients were estimated via the Marquardt algorithm as implemented in SAS (1990). For the two spacing studies, 3,015 of the total 3,322 trees were fit to the Chapman-Richard's function.

Where the Chapman-Richards model provided a poor description of the data (based on graphical analysis), or where there were less than four observations per tree, a second or first degree polynomial model was fitted to the data. Between the two datasets, sixty-two trees died after their first measurement. As these trees represented small suppressed individuals, their relative growth rate for that age was set to zero in this analysis.

Analysis of the impact of mid-rotation thinning on the relationship between relative growth rate and size was based on the Coop Thinning study. Nineteen of the plots suffered extreme insect or weather related damage (greater than 10% annual mortality from insects or weather) over at least one remeasurement interval. Data from that interval and subsequent measurements of these plots were dropped from this analysis.

There were more than 63,000 individual-trees in this study and many trees with less than 3 remeasurements. Functional analysis was not feasible with these data and relative growth rate was estimated via classical analysis as the mean over a measurement interval. Mean relative growth rate over each measurement interval was computed as:

$$(\bar{r}) = \frac{\ln(d_2) - \ln(d_1)}{t_2 - t_1}$$

where d_i is the dbh at time i and t_i is the age at time i. Trees that died before the second measurement were assigned a relative growth rate of zero. Linear interpolation was used to estimate the dbh associated with the estimated growth rate. Similarly, stand-level attributes were estimated for the midpoint of each measurement interval.

The general trend between relative growth rate and size for a given cohort was summarized as the slope of a fitted line. A resistant line, which is useful for exploring the linear relationship between two variables, was used to estimate the slope of the relationship (Hoaglin *et al.* 1983). Resistance to occasional extreme values is obtained by splitting the data into three groups and using median values within each group to estimate the slope and intercept of the line. These slopes were used to quantify changes in this relationship over time and across densities. Size was expressed as individual-tree dbh relative to the median dbh for the cohort. We also examined the relationship between absolute dbh and scaled dbh where dbh was scaled between 0 and 1.

The correlation between the slope coefficient and arbitrary classes of the crown projection index (CPI) and of crown ratio were used to relate the point where the correlation between relative growth rate and size switches from negative to positive to measures of crown closure. The impact of thinning on the slope coefficients was assessed via paired t-tests.

Testing for Dominance/Suppression

Analysis and Results

a. Size Inequality

For the Coop spacing data the average Gini coefficient for each location was plotted over age (Figure 4.1) and analyzed via an Analysis of Contrasts (Tables 4.1 to 4.4). Analysis at location 1 was based on ages 5- through 11-years as some plots were dropped due to severe ice-storm damage.

At all locations there is strong evidence that averaged over time, density influences the degree of size inequality (p-values < 0.01 for location 1, p-value $= 0.02$ at location 2, p-value = 0.04 at location 3, p-value = 0.08 at location 4). At a given age, size inequality increases with increasing density.

Linear and curvilinear trends in size inequality vary with location. At locations 2 and 4 there is a general tendency for inequality to decline over time (p-value < 0.01 at location 1, p-value = 0.02 at location 4). However, much of this decline occurs between ages 5- and 10-years and at location 4 the trend varies with initial density (p-value = 0.02). There is no evidence of a linear component to the temporal trend at locations 1 and 3.

At location 1, the quadratic effect varies with initial density (p-value=0.06). There is strong evidence of a quartic component to the time trend (p-value = 0.01). At location 2 there is no evidence the temporal trend varies with density but there is a high degree of curvature in the trend as indicated by the significant quadratic, cubic, and quartic trends (p-values < 0.01).

At location 3, the quadratic trend again varies with initial density (p-value < 0.01). This interaction results from a steep decline in inequality from age 11- to 14-years on the 4 x 4 spacing. Overall, there is strong evidence of a cubic trend (p-value = 0.01). At location 4, the quadratic trend also varies with initial density (p-value = 0.02) and there is a high degree of non-linearity in the overall time trend (p-value = 0.02).

For the Calhoun Spacing study (Figure 4.2 and Table 4.5), there is strong evidence (p-value = 0.01) of a spacing effect averaged over time. The strong (p-value =< 0.01) quartic time effect is consistent with the observation that size inequality initially declines, then increases before finally leveling off or decreasing again. The lack of evidence for any interaction between time effects and spacing suggests this pattern holds for all four treatments.

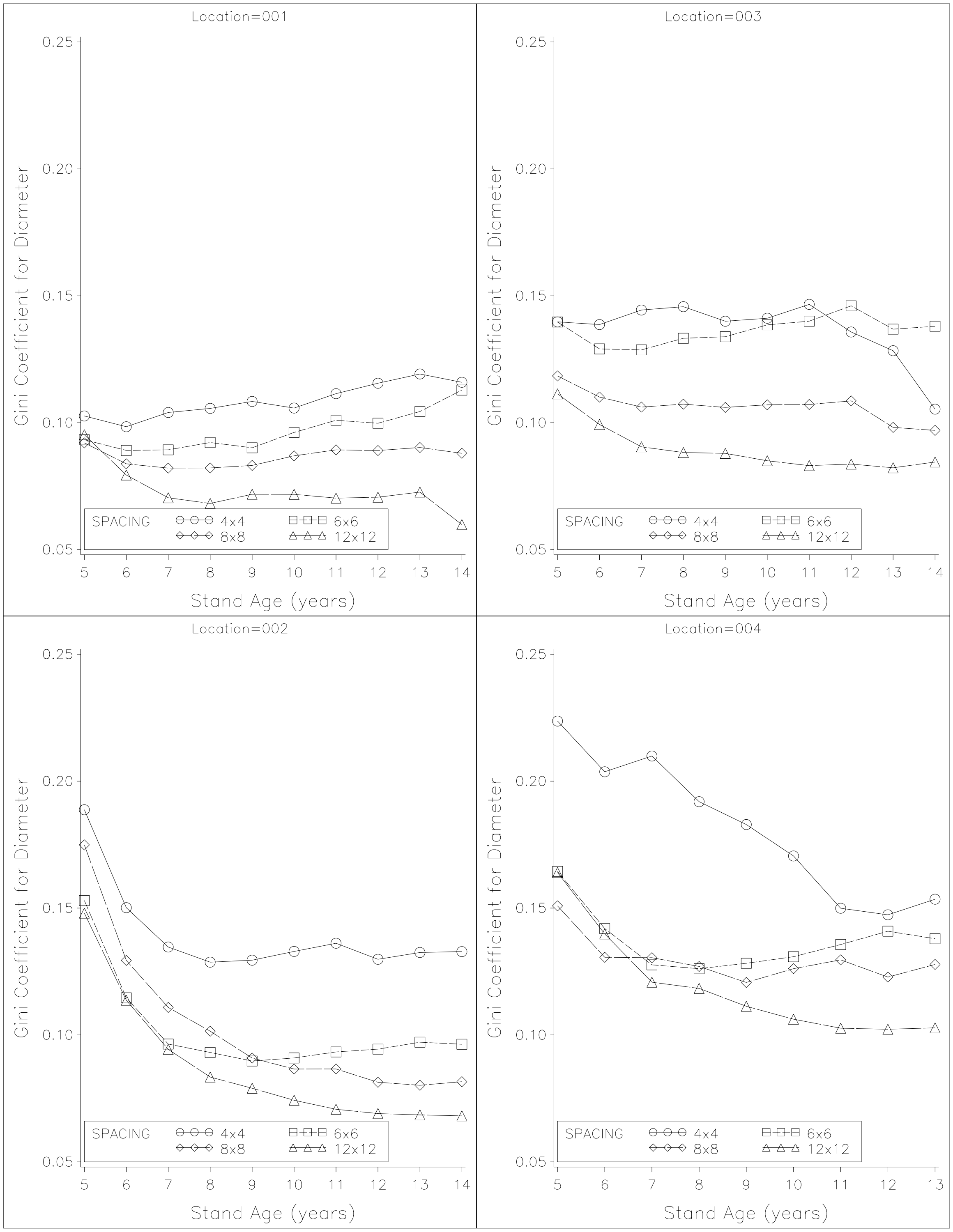

Figure 4.1. Mean inequality trends over time for the Coop spacing study.

Table 4.1. Analysis of time contrasts for Gini coefficients from the Coop spacing data at location 1. Ages 5- through 11-years only.

Source	DF	SS	MS	*F*	Pr > *F*
			Between-plot analysis		
Block	2	0.00095903	0.00095903		
Spacing	3	0.00095903	0.00095903	16.41	0.0027
Error	6	0.00121478	0.00020246		
			Within-plot analysis		
Time.1[a]					
Mean	1	0.00000105	0.00000105	0.01	0.9349
Block	2	0.00024686	0.00012343		
Spacing	3	0.00121975	0.00040658	5.90	0.0319
Error	6	0.00041353	0.00006892		
Time.2					
Mean	1	0.00072703	0.00072703	12.84	0.0698
Block	2	0.00011326	0.00005663		
Spacing	3	0.00025301	0.00008434	4.34	0.0601
Error	6	0.00011670	0.00001945		
Time.3					
Mean	1	0.00010365	0.00010365	5.31	0.1476
Block	2	0.00003902	0.00001951		
Spacing	3	0.00010008	0.00003336	3.26	0.0104
Error	6	0.00006134	0.00001022		
Time.4					
Mean	1	0.00002719	0.00002719	93.76	0.0105
Block	2	0.00000058	0.00000029		
Spacing	3	0.00005089	0.00001696	1.27	0.3673
Error	6	0.00008039	0.00001340		
Time.5					
Mean	1	0.00000155	0.00000155	0.46	0.5686
Block	2	0.00000678	0.00000339		
Spacing	3	0.00001760	0.00000587	0.86	0.5094
Error	6	0.00004077	0.00000680		

[a] Time.*N* denotes the n’th degree polynomial contrast for time.

Table 4.2. Analysis of time contrasts for Gini coefficients from the Coop spacing data at location 2.

Source	DF	SS	MS	*F*	Pr > *F*
		Between-plot analysis			
Block	2	0.01372510	0.00686255		
Spacing	3	0.04532905	0.01510968	7.56	0.0184
Error	6	0.01199685	0.00199948		
		Within-plot analysis			
Time.1[a]					
Mean	1	0.03368425	0.03368425	101.32	0.0097
Block	2	0.00066492	0.00033246		
Spacing	3	0.00409942	0.00136647	1.83	0.2427
Error	6	0.00448878	0.00074813		
Time.2					
Mean	1	0.01733419	0.01733419	397.12	0.0025
Block	2	0.00008731	0.00004365		
Spacing	3	0.00013313	0.00004438	0.33	0.8012
Error	6	0.00079512	0.00013252		
Time.3					
Mean	1	0.00473057	0.00473057	4505.30	0.0002
Block	2	0.00000210	0.00000105		
Spacing	3	0.00014760	0.00004920	0.97	0.4648
Error	6	0.00030326	0.00005054		
Time.4					
Mean	1	0.00086018	0.00086018	174.13	0.0057
Block	2	0.00000987	0.00000494		
Spacing	3	0.00004255	0.00001418	0.66	0.6054
Error	6	0.00012872	0.00002145		
Time.5					
Mean	1	0.00004155	0.00004155	9.05	0.0950
Block	2	0.00000918	0.00000459		
Spacing	3	0.00002558	0.00000853	0.48	0.7083
Error	6	0.00010670	0.00001778		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

Table 4.3. Analysis of time contrasts for Gini coefficients from the Coop spacing data at location 3.

Source	DF	SS	MS	*F*	Pr > *F*
Between-plot analysis					
Block	2	0.02054405	0.01027202		
Spacing	3	0.04855780	0.01618593	5.29	0.0402
Error	6	0.01835763	0.00305960		
Within-plot analysis					
Time.1[a]					
Mean	1	0.00203991	0.00203991	3.53	0.2015
Block	2	0.00115955	0.00057978		
Spacing	3	0.00196571	0.00065524	2.54	0.1525
Error	6	0.00154636	0.00025773		
Time.2					
Mean	1	0.00006480	0.00006480	0.19	0.7043
Block	2	0.00067619	0.00033809		
Spacing	3	0.00225666	0.00075222	12.71	0.0052
Error	6	0.00035497	0.00005916		
Time.3					
Mean	1	0.00099439	0.00099439	70.18	0.0140
Block	2	0.00032609	0.00016305		
Spacing	3	0.00008132	0.00002711	1.03	0.4437
Error	6	0.00015790	0.00002632		
Time.4					
Mean	1	0.00001417	0.00001417	0.37	0.6047
Block	2	0.00007649	0.00003825		
Spacing	3	0.00017170	0.00005723	1.34	0.3464
Error	6	0.00025597	0.00004266		
Time.5					
Mean	1	0.00000010	0.00000010	0.00	0.9702
Block	2	0.00011219	0.00005610		
Spacing	3	0.00001907	0.00000636	0.26	0.8534
Error	6	0.00014798	0.00002466		

[a] Time.*N* denotes the n^{th} degree polynomial contrast for time.

Table 4.4. Analysis of time contrasts for Gini coefficients from the Coop spacing data at location 4.

Source	DF	SS	MS	*F*	Pr > *F*
		Between-plot analysis			
Block	2	0.00371879	0.00185940		
Spacing	3	0.06160668	0.02053556	3.86	0.0750
Error	6	0.03194384	0.00532397		
		Within-plot analysis			
Time.1[a]					
Mean	1	0.01810663	0.01810663	53.14	0.0183
Block	2	0.00068152	0.00034076		
Spacing	3	0.00868996	0.00289665	6.73	0.0240
Error	6	0.00258434	0.00043072		
Time.2					
Mean	1	0.00398563	0.00398563	4.89	0.1576
Block	2	0.00016941	0.00008470		
Spacing	3	0.00084614	0.00028205	6.77	0.0236
Error	6	0.00025001	0.00004167		
Time.3					
Mean	1	0.00029549	0.00029549	6.20	0.1304
Block	2	0.00009528	0.00004764		
Spacing	3	0.00131616	0.00043872	2.48	0.1580
Error	6	0.00105981	0.00017664		
Time.4					
Mean	1	0.00031152	0.00031152	44.25	0.0219
Block	2	0.00001408	0.00000704		
Spacing	3	0.00018522	0.00006174	2.18	0.1909
Error	6	0.00016960	0.00002827		
Time.5					
Mean	1	0.00003353	0.00003353	0.65	0.5050
Block	2	0.00010329	0.00005165		
Spacing	3	0.00002804	0.00000935	0.08	0.9679
Error	6	0.00069170	0.00011528		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

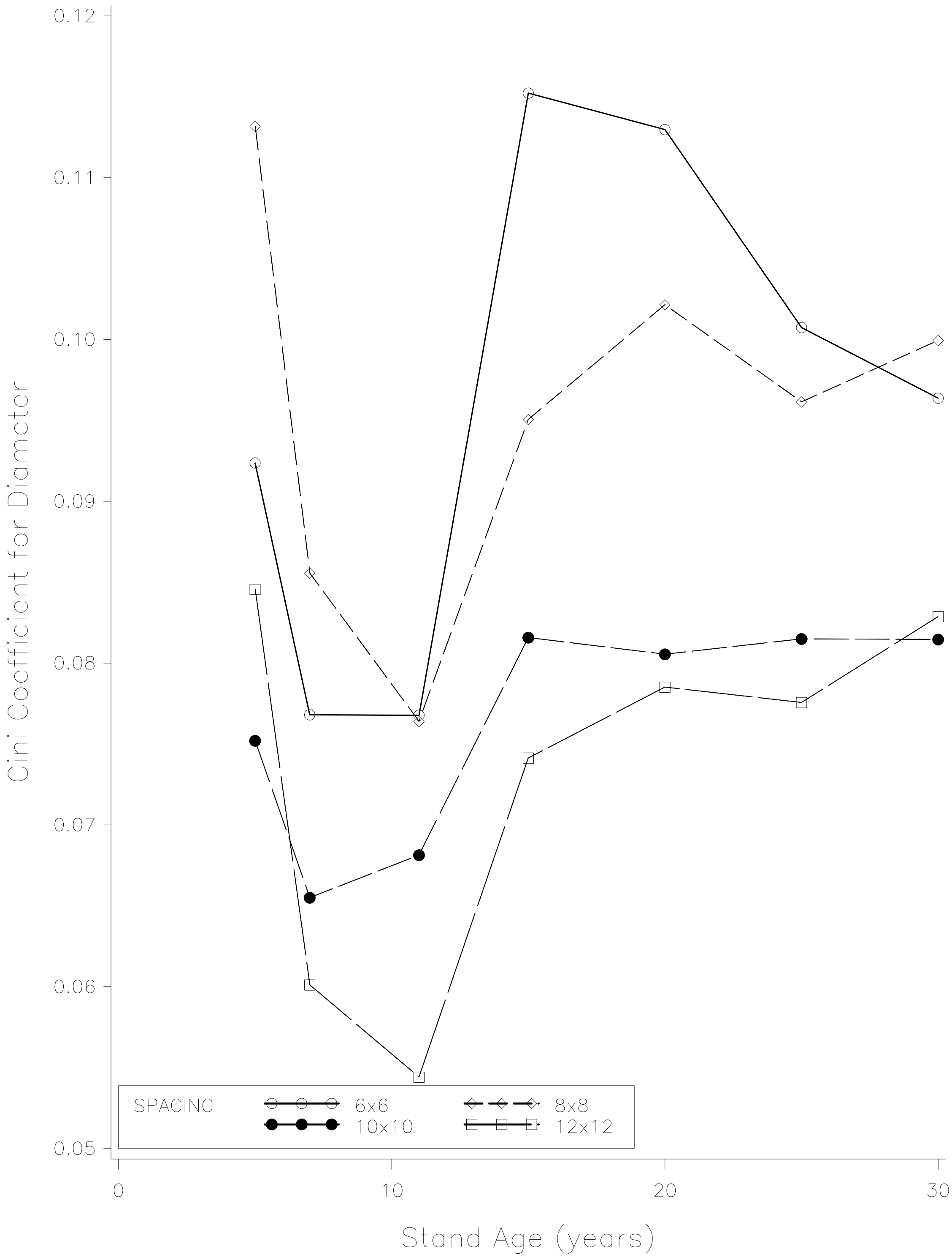

Figure 4.2. Mean inequality trends over time for the Calhoun spacing study.

Table 4.5. Analysis of time contrasts for Gini coefficients from the Calhoun spacing data.

Source	DF	SS	MS	*F*	Pr > *F*
		Between-plot analysis			
Block	3	0.00279106	0.00093035		
Spacing	3	0.01245597	0.00415199	6.65	0.0116
Error	9	0.00562174	0.00062464		
		Within-plot analysis			
Time.1[a]					
Mean	1	0.00175935	0.00175935	3.59	0.1545
Block	3	0.00147132	0.00049044		
Spacing	3	0.00057004	0.00019001	0.51	0.6822
Error	9	0.00332129	0.00036903		
Time.2					
Mean	1	0.00055543	0.00055543	5.76	0.0960
Block	3	0.00028950	0.00009650		
Spacing	3	0.00184353	0.00061451	3.23	0.0749
Error	9	0.00171151	0.00019017		
Time.3					
Mean	1	0.00487350	0.00487350	148.18	0.0012
Block	3	0.00009868	0.00003289		
Spacing	3	0.00044290	0.00014763	1.54	0.2696
Error	9	0.00086125	0.00009569		
Time.4					
Mean	1	0.00172425	0.00172425	150.72	0.0012
Block	3	0.00003432	0.00001144		
Spacing	3	0.00021871	0.00007290	1.39	0.3073
Error	9	0.00047150	0.00005239		
Time.5					
Mean	1	0.00054392	0.00054392	4.04	0.1380
Block	3	0.00040402	0.00013467		
Spacing	3	0.00018360	0.00006120	1.44	0.2949
Error	9	0.00038288	0.00004254		
Time.6					
Mean	1	0.00055358	0.00055358	5.46	0.1016
Block	3	0.00030434	0.00010145		
Spacing	3	0.00014582	0.00004861	0.64	0.6093
Error	9	0.00068566	0.00007618		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

b. Relative Growth Rates

Results and conclusions were similar for all three measures of size (absolute, relative, scaled). Expressing individual-tree size as relative to the median size simplified many of the graphs showing temporal trends in relative growth rates. Consequently, subsequent discussion will be based on the relationship between relative growth rate and relative size.

Individual-tree relative growth rates and the estimated linear relationship with relative size, at selected ages, for all plots of the Coop spacing study are included in Appendix A. On many plots, particularly at young ages, there is considerable variation about the fitted line. However, if one shows mean relative growth rates for size classes, as is commonly presented in the literature, there is much less apparent variation and relationships seem much stronger. Presenting the individual-tree data provides a true picture of the variation in relative growth rates for trees of a given size.

The relationship between individual-tree relative growth rate and size was similar at all locations of the Coop Spacing study (Figure 4.3 and Tables 4.6 to 4.9). There is strong evidence, that averaged over time, density influences the slope of the relative growth rate/size relationship (p-values <0.01 for locations 1, 3, and 4; p-value=0.09 for location 2). The value of the slope coefficient tends to increase with increasing density at a given age.

The data show that the slope tends to increase over time (p-values < 0.01 at locations 1, 2, and 4; p-value=0.03 at location 3). However, the trend is clearly not linear. At all locations there was strong evidence for quadratic and cubic trends (p-values ≤ 0.01 for all but locations 1 and 4 where cubic trend p-value=0.02). Locations 2 and 3 also provide evidence of a significant quartic trend over time.

There is considerably less evidence that density affects the temporal trends. Two of the locations provide evidence that the linear trend is affected by density (location 2 p-value=0.06, location 3 p-value=0.03). The only evidence of a density effect on the curvilinear component is on location 2 (quadratic x density p-value < 0.01).

Through age 14, the patterns evident in the Coop Spacing data occur in the Calhoun Spacing data (Figure 4.4 and Table 4.10). There is strong evidence of an overall linear component to the change in slope over time (p-value < 0.01) with the slope increasing. However, the trend is not linear as indicated by the strong quadratic and cubic effects (p-value < 0.01 and p-value = 0.02). Apparently these trends do not vary with initial spacing.

For comparisons with published reports, we examined the linear correlation between relative growth rate and size. To mitigate against the influence of extreme data points, correlations are estimated via Kendall correlation coefficients (τ) (Tables 4.11 to 4.14). Relative growth rate is initially negatively correlated to size for all spacings. Overtime, relative growth rate becomes positively correlated with size. The switch in linear correlation occurs sooner with higher planting density. The transition from negative to positive correlation is also sharper on tighter spacings.

Since estimates of relative growth rate are based on the derivative of a fitted function to the size/age relationship for individual trees, estimates at the first and last age would tend to be the least reliable. For example, with the Chapman-Richard's function, the relative growth rates computed at the last age may be biased downward if the fitted model approaches an asymptote shortly after the last observation. As a precaution, the above analysis was repeated after dropping the first and last observation from each tree prior to calculating relative growth rates and relative size and recalculating the slope coefficient. Conclusions from the repeated measures analysis and correlation analysis were unchanged when based on the reduced dataset.

For comparison with published reports (Ford 1975, Perry 1985, Larocque and Marshall 1993), relative growth rates for the Coop spacing study where estimated via classical growth analysis. The slope of the linear relationship between mean relative growth rate and relative size exhibits similar patterns (Figure 4.5) as those obtained via functional growth analysis. The increased variation in figure 4.5 reflects the year-to-year variation in absolute growth rates for individual trees.

When working with annual plants or when individual trees cannot be followed across remeasurements, one approach is to base the analysis of relative growth rates on class means (Ford 1975). At each age, the sample is divided into a constant number of classes. The calculation of relative growth rate for each class is based on the change in mean size for that class over time. This approach assumes mortality is confined to the smallest individuals and there is no change in the size ranking of individual plants over time. Both assumptions are not likely to hold in plantations.

The class approach was tested with the Coop spacing data for several number of classes. At each measurement the diameter distribution was divided into 10, 15, or 20 classes of equal width. Due to the relatively small number of trees per plot (initially 49), treatment plots were combined across replications at each site. Analysis of the slope of the linear relationship between relative growth rate and relative size showed no consistent relationship over time or with initial density (Figure 4.6).

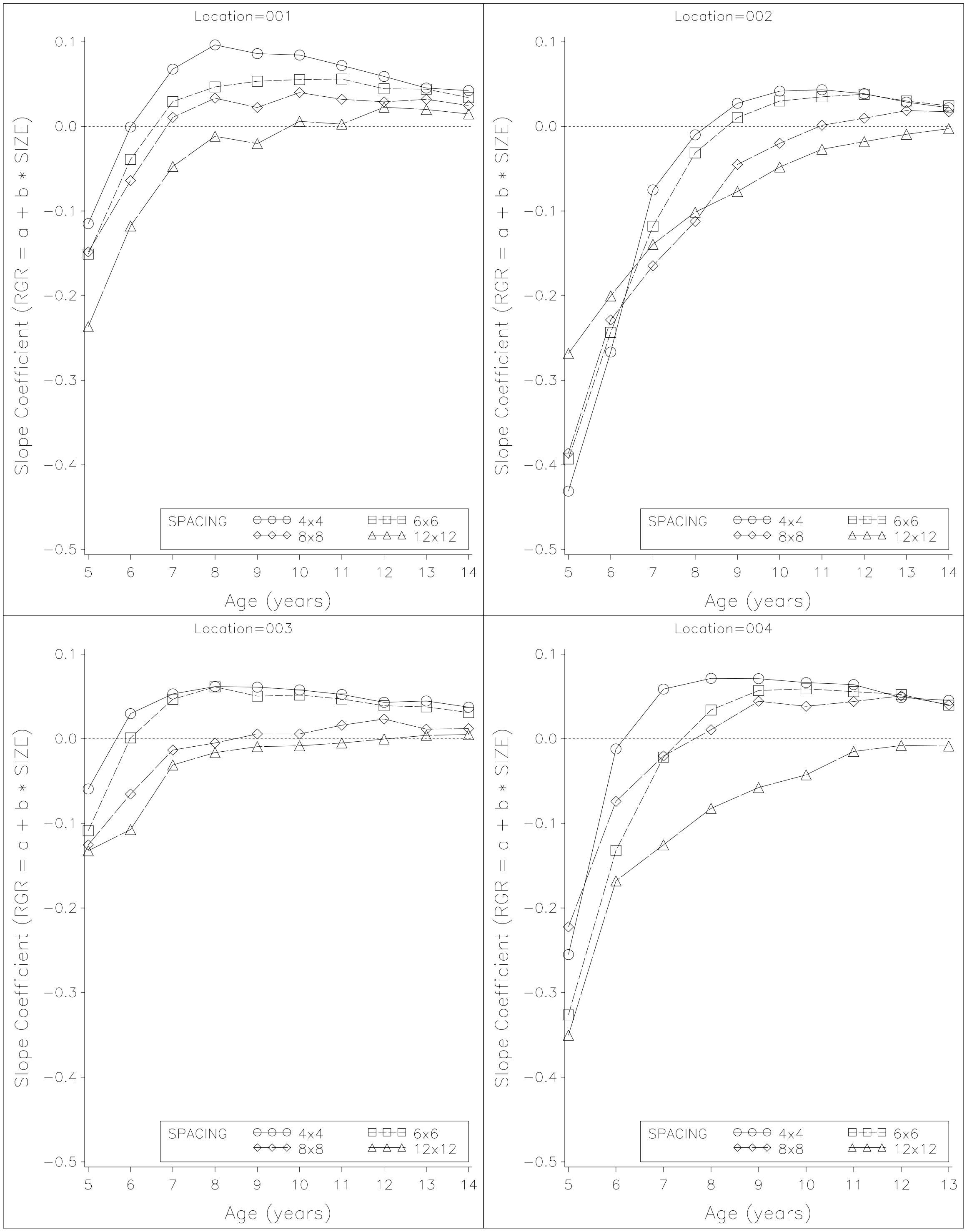

Figure 4.3. Slope of the linear relationship between relative growth and relative size over time for the Coop spacing study.

Table 4.6. Analysis of time contrasts for the slope of relative growth rate over relative size for the Coop spacing data at location 1. Ages 5- through 11-years only.

Source	DF	SS	MS	*F*	Pr > *F*
			Between-plot analysis		
Block	2	0.00076638	0.00038319		
Spacing	3	0.11440308	0.03813436	18.14	0.0021
Error	6	0.01261638	0.00210273		
			Within-plot analysis		
Time.1[a]					
Mean	1	0.29809543	0.29809543	480.51	0.0001
Block	2	0.00124073	0.00062037		
Spacing	3	0.00403026	0.00134342	0.51	0.6884
Error	6	0.01572786	0.00262131		
Time.2					
Mean	1	0.12258478	0.12258478	259.26	0.0038
Block	2	0.00094567	0.00047283		
Spacing	3	0.00111277	0.00037092	0.40	0.7583
Error	6	0.00556316	0.00092719		
Time.3					
Mean	1	0.01325735	0.01325735	54.47	0.0179
Block	2	0.00048678	0.00024339		
Spacing	3	0.00019538	0.00006513	0.09	0.9635
Error	6	0.00439100	0.00073183		
Time.4					
Mean	1	0.00000321	0.00000321	0.01	0.9408
Block	2	0.00091346	0.00045673		
Spacing	3	0.00014682	0.00004894	0.21	0.8890
Error	6	0.00142830	0.00023805		
Time.5					
Mean	1	0.00149602	0.00149602	53.83	0.0181
Block	2	0.00005557	0.00002779		
Spacing	3	0.00036907	0.00012302	0.50	0.6989
Error	6	0.00149105	0.00024851		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

Table 4.7. Analysis of time contrasts for the slope of relative growth rate over relative size for the Coop spacing data at location 2.

Source	DF	SS	MS	*F*	Pr > *F*
			Between-plot analysis		
Block	2	0.00164255	0.00082128		
Spacing	3	0.02743607	0.00914536	3.53	0.0884
Error	6	0.01556178	0.00259363		
			Within-plot analysis		
Time.1[a]					
Mean	1	1.39113770	1.39113770	19090.68	0.0001
Block	2	0.00014574	0.00007287		
Spacing	3	0.03138326	0.01046109	4.33	0.0602
Error	6	0.01448833	0.00241472		
Time.2					
Mean	1	0.44881033	0.44881033	1330.24	0.0008
Block	2	0.00067479	0.00033739		
Spacing	3	0.06720208	0.02240069	10.07	0.0093
Error	6	0.01334385	0.00222398		
Time.3					
Mean	1	0.03557490	0.03557490	158.96	0.0062
Block	2	0.00044760	0.00022380		
Spacing	3	0.01096539	0.00365513	2.52	0.1544
Error	6	0.00869579	0.00144930		
Time.4					
Mean	1	0.00032993	0.00032993	18.70	0.0495
Block	2	0.00003528	0.00001764		
Spacing	3	0.00059720	0.00019907	0.25	0.8607
Error	6	0.00483376	0.00080563		
Time.5					
Mean	1	0.00014203	0.00014203	1.46	0.3503
Block	2	0.00019442	0.00009721		
Spacing	3	0.00287025	0.00095675	2.06	0.2067
Error	6	0.00278305	0.00046384		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

Table 4.8. Analysis of time contrasts for the slope of relative growth rate over relative size for the Coop spacing data at location 3.

Source	DF	SS	MS	F	Pr > F
			Between-plot analysis		
Block	2	0.00655395	0.00327697		
Spacing	3	0.09295050	0.03098350	14.67	0.0036
Error	6	0.01267105	0.00211184		
			Within-plot analysis		
Time.1[a]					
Mean	1	0.09750568	0.09750568	37.49	0.0256
Block	2	0.00520107	0.00260053		
Spacing	3	0.00964475	0.00321492	6.58	0.0252
Error	6	0.00293299	0.00048883		
Time.2					
Mean	1	0.08137033	0.08137033	988.94	0.0010
Block	2	0.00016456	0.00008228		
Spacing	3	0.00217326	0.00072442	2.17	0.1927
Error	6	0.00200342	0.00033390		
Time.3					
Mean	1	0.02269107	0.02269107	101.44	0.0097
Block	2	0.00044738	0.00022369		
Spacing	3	0.00262936	0.00087645	2.04	0.2099
Error	6	0.00257806	0.00042968		
Time.4					
Mean	1	0.00300005	0.00300005	27.85	0.0341
Block	2	0.00021545	0.00010773		
Spacing	3	0.00163904	0.00054635	1.49	0.3100
Error	6	0.00220370	0.00036728		
Time.5					
Mean	1	0.00002173	0.00002173	0.06	0.8260
Block	2	0.00069622	0.00034811		
Spacing	3	0.00156817	0.00052272	1.82	0.2441
Error	6	0.00172464	0.00028744		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

Table 4.9. Analysis of time contrasts for the slope of relative growth rate over relative size for the Coop spacing data at location 4.

Source	DF	SS	MS	*F*	Pr > *F*
			Between-plot analysis		
Block	2	0.00408140	0.00204070		
Spacing	3	0.18891292	0.06297097	20.69	0.0014
Error	6	0.01825688	0.00304281		
			Within-plot analysis		
Time.1[a]					
Mean	1	0.66113388	0.66113388	348.26	0.0029
Block	2	0.00382546	0.00191273		
Spacing	3	0.02337622	0.00779207	1.49	0.3101
Error	6	0.03143307	0.00523884		
Time.2					
Mean	1	0.35056234	0.35056234	340.44	0.0029
Block	2	0.00205946	0.00102973		
Spacing	3	0.01762784	0.00587595	1.45	0.3192
Error	6	0.02433449	0.00405575		
Time.3					
Mean	1	0.07495065	0.07495065	52.99	0.0184
Block	2	0.00282862	0.00141431		
Spacing	3	0.00787921	0.00262640	1.77	0.2520
Error	6	0.00888784	0.00148131		
Time.4					
Mean	1	0.01545643	0.01545643	7.75	0.1085
Block	2	0.00399113	0.00199557		
Spacing	3	0.00274170	0.00091390	1.04	0.4390
Error	6	0.00525815	0.00087636		
Time.5					
Mean	1	0.00183683	0.00183683	2.45	0.2579
Block	2	0.00149837	0.00074919		
Spacing	3	0.00110917	0.00036972	1.22	0.3802
Error	6	0.00181528	0.00030255		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

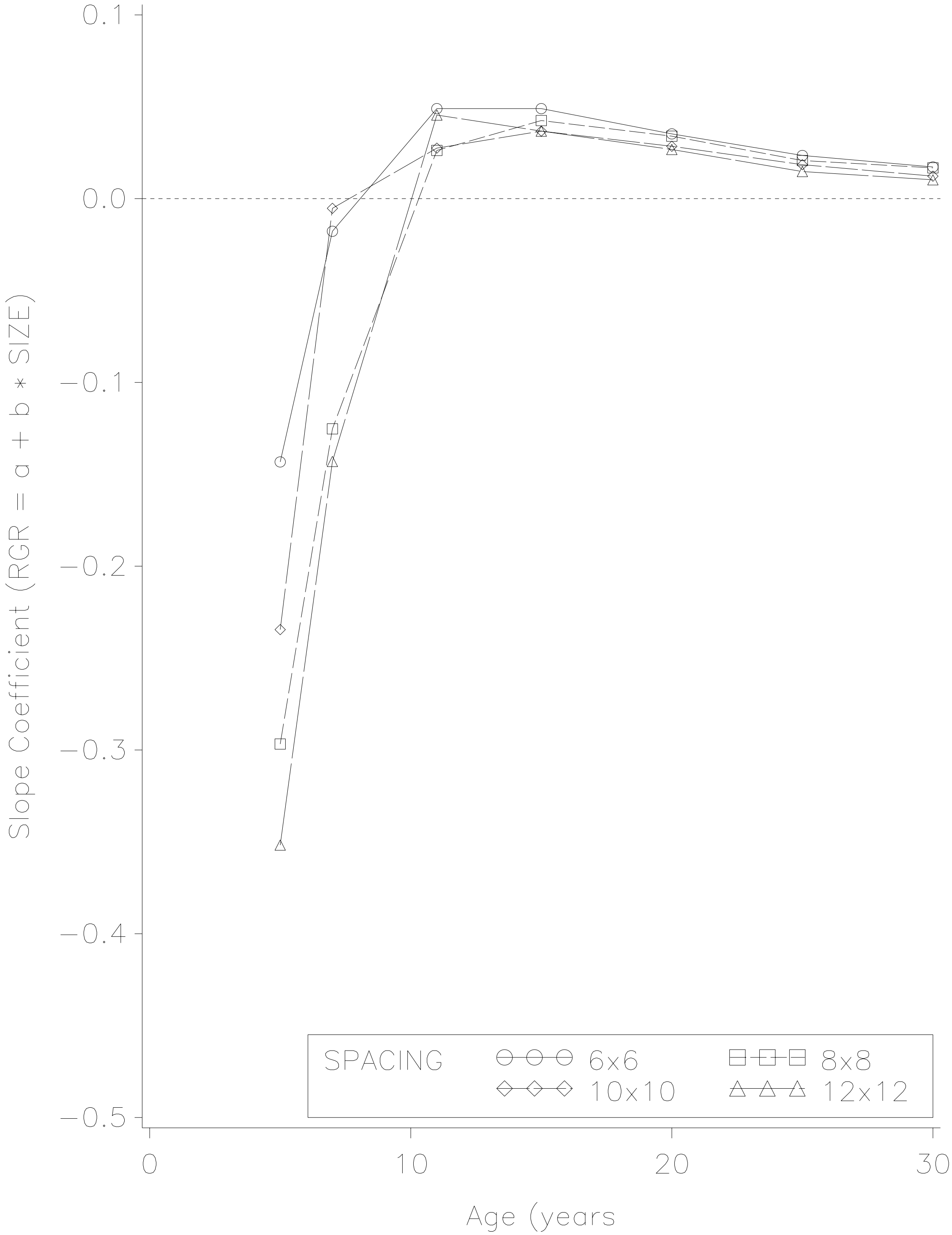

Figure 4.4. Slope of the linear relationship between relative growth rate and relative size over time for the Calhoun spacing study.

Table 4.10. Analysis of time contrasts for the slope of relative growth rate over relative size for the Calhoun spacing data.

Source	DF	SS	MS	*F*	Pr > *F*
			Between-plot analysis		
Block	3	0.00307160	0.00102387		
Spacing	3	0.04809767	0.01603256	2.87	0.0960
Error	9	0.05027587	0.00558621		
			Within-plot analysis		
Time.1[a]					
Mean	1	0.56062300	0.56062300	1122.57	0.0001
Block	3	0.00149823	0.00049941		
Spacing	3	0.06439404	0.02146468	2.44	0.1312
Error	9	0.07916373	0.00879597		
Time.2					
Mean	1	0.47655868	0.47655868	194.63	0.0008
Block	3	0.00734554	0.00244851		
Spacing	3	0.02596955	0.00865652	1.96	0.1904
Error	9	0.03971347	0.00441261		
Time.3					
Mean	1	0.09071251	0.09071251	20.17	0.0206
Block	3	0.01348936	0.00449645		
Spacing	3	0.00410220	0.00136740	0.60	0.6313
Error	9	0.02052776	0.00228086		
Time.4					
Mean	1	0.00014659	0.00014659	0.05	0.8450
Block	3	0.00969670	0.00323223		
Spacing	3	0.00778044	0.00259348	1.30	0.3343
Error	9	0.01801375	0.00200153		
Time.5					
Mean	1	0.00310858	0.00310858	1.71	0.1598
Block	3	0.00545893	0.00181964		
Spacing	3	0.00714055	0.00238018	1.71	0.2345
Error	9	0.01254260	0.00139362		
Time.6					
Mean	1	0.00131906	0.00131906	1.47	0.3120
Block	3	0.00269095	0.00089698		
Spacing	3	0.00222138	0.00074046	1.96	0.1911
Error	9	0.00340526	0.00037836		

[a] Time.*N* denotes the n'th degree polynomial contrast for time.

Table 4.11. Kendall correlation (τ) and p-values for a test of independence between relative growth rate and relative size for location 1 of the Coop spacing study.

	Spacing							
	4 x 4		6 x 6		8 x 8		12 x 12	
Age	τ	p-value	τ	p-value	τ	p-value	τ	p-value
5	-0.33	0.00	-0.28	0.00	-0.28	0.00	-0.40	0.00
6	0.03	0.62	-0.11	0.05	-0.16	0.01	-0.31	0.00
7	0.31	0.00	0.14	0.01	0.00	0.96	-0.19	0.00
8	0.44	0.00	0.30	0.00	0.17	0.00	-0.09	0.10
9	0.50	0.00	0.38	0.00	0.20	0.00	-0.03	0.60
10	0.54	0.00	0.44	0.00	0.24	0.00	0.02	0.68
11	0.58	0.00	0.46	0.00	0.27	0.00	0.06	0.28
12	0.60	0.00	0.52	0.00	0.32	0.00	0.15	0.01
13	0.60	0.00	0.53	0.00	0.35	0.00	0.18	0.00
14	0.59	0.00	0.56	0.00	0.33	0.00	0.13	0.04

Table 4.12. Kendall correlation (τ) and p-values for a test of independence between relative growth rate and relative size for location 2 of the Coop spacing study.

	Spacing							
	4 x 4		6 x 6		8 x 8		12 x 12	
Age	τ	p-value	τ	p-value	τ	p-value	τ	p-value
5	-0.73	0.00	-0.46	0.00	-0.65	0.00	-0.61	0.00
6	-0.61	0.00	-0.40	0.00	-0.62	0.00	-0.55	0.00
7	-0.30	0.00	-0.26	0.00	-0.55	0.00	-0.52	0.00
8	-0.02	0.78	-0.10	0.09	-0.45	0.00	-0.49	0.00
9	0.20	0.00	0.05	0.37	-0.29	0.00	-0.40	0.00
10	0.34	0.00	0.15	0.01	-0.14	0.00	-0.30	0.00
11	0.44	0.00	0.21	0.00	0.00	0.97	-0.17	0.00
12	0.50	0.00	0.31	0.00	0.06	0.26	-0.09	0.11
13	0.52	0.00	0.37	0.00	0.15	0.01	-0.01	0.89
14	0.54	0.00	0.38	0.00	0.22	0.00	0.06	0.27

Table 4.13. Kendall correlation (τ) and p-values for a test of independence between relative growth rate and relative size for location 3 of the Coop spacing study.

	Spacing							
	4 x 4		6 x 6		8 x 8		12 x 12	
Age	τ	p-value	τ	p-value	τ	p-value	τ	p-value
5	-0.12	0.04	-0.26	0.00	-0.34	0.00	-0.33	0.00
6	0.11	0.06	0.03	0.60	-0.26	0.00	-0.28	0.00
7	0.26	0.00	0.17	0.00	-0.06	0.27	-0.17	0.00
8	0.39	0.00	0.27	0.00	0.03	0.63	-0.09	0.12
9	0.41	0.00	0.34	0.00	0.08	0.15	-0.07	0.21
10	0.49	0.00	0.40	0.00	0.17	0.00	-0.02	0.77
11	0.52	0.00	0.43	0.00	0.24	0.00	0.03	0.58
12	0.50	0.00	0.44	0.00	0.27	0.00	0.07	0.22
13	0.52	0.00	0.41	0.00	0.26	0.00	0.10	0.10
14	0.47	0.00	0.41	0.00	0.26	0.00	0.11	0.06

Table 4.14. Kendall correlation (τ) and p-values for a test of independence between relative growth rate and relative size for location 4 of the Coop spacing study.

	Spacing							
	4 x 4		6 x 6		8 x 8		12 x 12	
Age	τ	p-value	τ	p-value	τ	p-value	τ	p-value
5	-0.44	0.00	-0.54	0.00	-0.44	0.00	-0.51	0.00
6	-0.05	0.37	-0.37	0.00	-0.22	0.00	-0.37	0.00
7	0.21	0.00	-0.08	0.15	0.00	0.97	-0.31	0.00
8	0.44	0.00	0.11	0.05	0.11	0.07	-0.29	0.00
9	0.53	0.00	0.28	0.00	0.25	0.00	-0.26	0.00
10	0.57	0.00	0.39	0.00	0.32	0.00	-0.24	0.00
11	0.58	0.00	0.48	0.00	0.39	0.00	-0.16	0.01
12	0.58	0.00	0.52	0.00	0.39	0.00	-0.08	0.15
13	0.59	0.00	0.52	0.00	0.40	0.00	-0.02	0.68

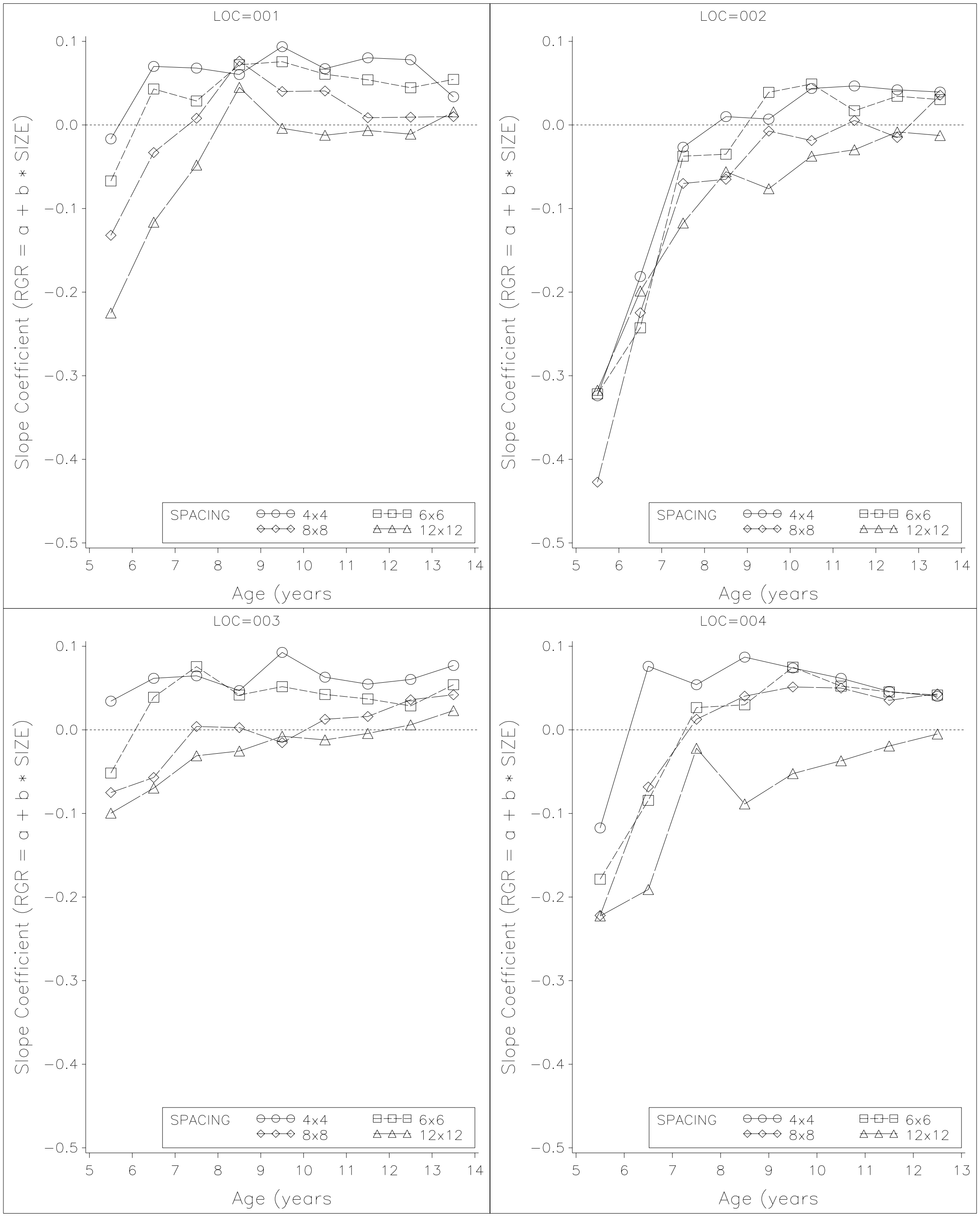

Figure 4.5. Slope of the linear relationship between relative growth rate and relative size over time for the Coop spacing study. Relative growth rate is calculated via classical growth analysis (mean over an observed interval).

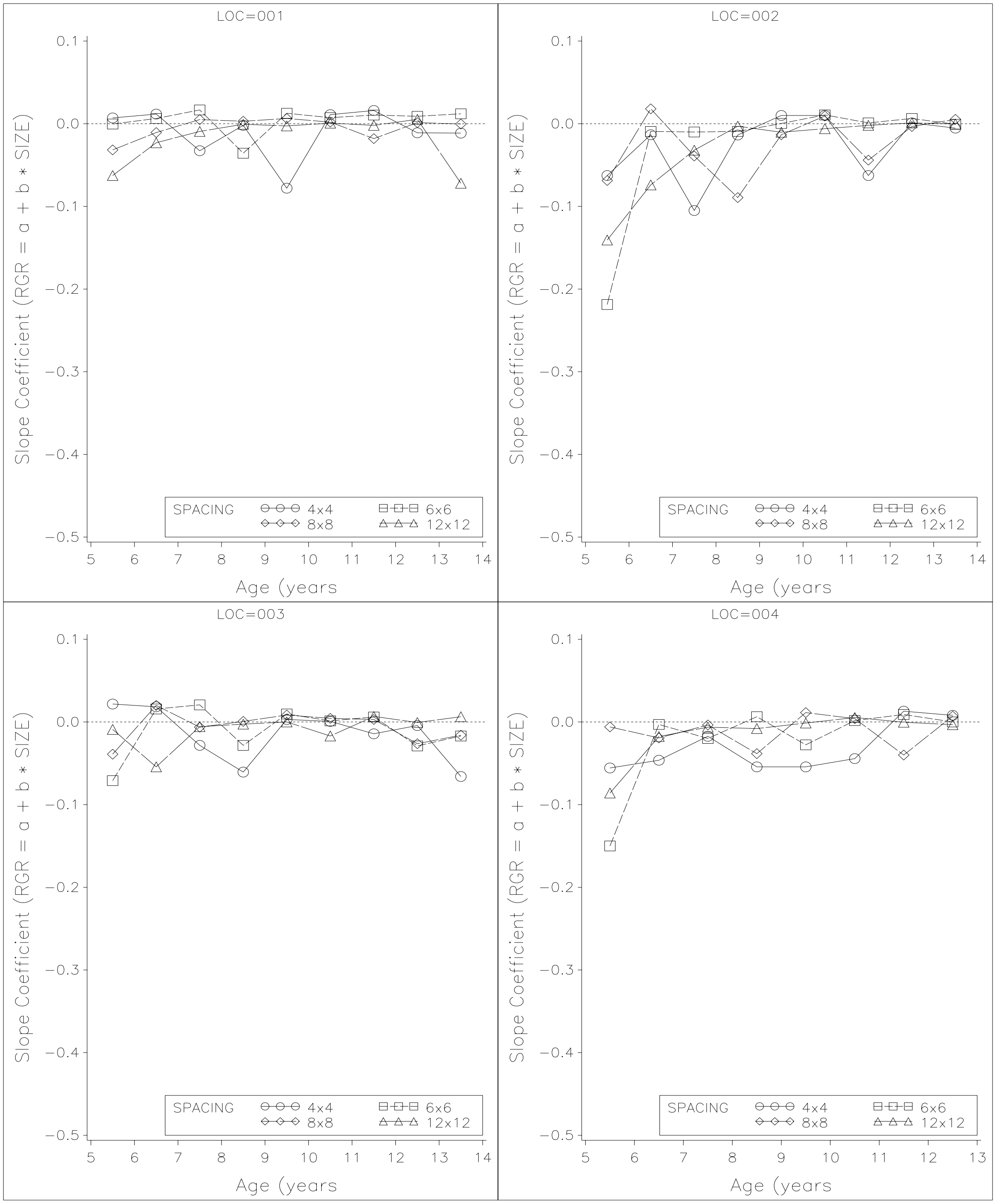

Figure 4.6. Slope of the linear relationship between relative growth rate and relative size over time for the Coop spacing study. Relative growth rate is calculated via classical growth analysis (mean over an observed interval) using diameter class midpoints and 20 classes.

Discussion

a. Size Inequality

From an understanding of general stand dynamics and consideration of the mathematical properties of the Gini coefficient we can describe the pattern of changes in inequality over time expected under the dominance/suppression theory. Initially, inequality would tend to decrease as mean tree size increases proportionately faster than the variation in tree size. With the onset of intra-specific competition, the dominance/suppression view dictates that inequality will increase as size differentiation accelerates. Inequality will continue to increase until sufficient mortality occurs in the smallest size classes to offset increasing size differentiation. At some point, when mortality among the smallest size classes is sufficiently high, inequality would tend to stabilize and eventually decrease. The analysis of the Calhoun spacing study supports this general trend.

On the Coop spacing study, the overall impact of initial density on size inequality is consistent with the dominance/suppression theory of competitive interactions. At a given age, inequality in dbh tends to increase with increasing initial planting density. Density effects tend to become more pronounced overtime for the Coop spacing study.

The temporal trend in inequality is much less consistent across the four locations of the Coop study. In general, size inequality tends to enter a phase of slow increase earlier on the higher initial planting densities. This would be expected under dominance/suppression.

Some of the differences in size inequality trends for the four locations of the Coop study may result from differences in competitive relationships. The decline in size inequality at locations 2 and 4 is consistent with these sites being of poorer quality for loblolly pine relative to locations 1 and 3 (Table 3.3). Slower stand development at these locations would delay the onset of intra-specific competition. Therefore, we would expect size inequality to continue to decrease as mean tree size increases until size variation induced by intra-specific competition begins.

b. Relative Growth Rate

The relationship between relative growth rate and relative size clearly supports the dominance/suppression theory of competitive interactions in loblolly pine plantations. The slope of the linear relationship between individual-tree relative growth rate and size follows a predictable pattern over time. At young ages smaller trees have higher relative growth rates than larger trees. Over time the slope of the relationship increases and the larger trees have a higher relative growth rate than the smaller trees. The trend is highly non-linear. Increases in density accelerate this temporal trend and have a limited effect on the overall shape of the trend.

As shown in the graphs, the age at which the slope switches from negative to positive is related to initial density. The time of the switch is assumed to indicate the point at which a dominance/suppression relationship becomes prominent.

Dominance/Suppression and Stand Dynamics

Analysis and Results

a. Crown Closure

The age at which the relationship between relative growth rate and relative size first achieved a positive slope coefficient was compared to the age at which specified values of the crown projection area index were first achieved. Most of the 12 x 12 spaced plots had not reached CPI values that indicated crown closure. A subset of the Coop spacing study plots which had achieved a positive relationship between relative growth rate and relative size and crown closure were included in this analysis.

A comparison of the age differences indicate the relative growth rate/size relationship becomes positive about the same time the crown projection index approaches a value of 1.15 (Table 4.15). This would be at approximately 15% crown overlap.

Table 4.15. Comparison between the age where the relationship between relative growth rate and relative size first indicates dominance/suppression and the age where specific values of the crown projection area index are first achieved. Based on 12 4x4, 11 6x6, 10 8x8, and 1 12x12 plot from the Coop spacing study.

	Differences in age of D/S and specified CPA			
CPA	Mean	p-value[a]	Median	p-value[b]
0.55	3.0	< 0.01	3	< 0.01
0.65	2.7	< 0.01	3	< 0.01
0.75	2.3	< 0.01	2	< 0.01
0.85	1.9	< 0.01	2	< 0.01
0.95	1.4	< 0.01	1.5	< 0.01
1.05	0.9	< 0.01	1	< 0.01
1.15	0.1	0.86	0	1

[a] Student's t-test for testing if population mean is 0.
[b] Sign test for testing if population median is 0.

b. Crown Ratio

The age at which the relationship between relative growth rate and relative size first achieved a positive slope coefficient was compared to the age at which specified values of the crown ratio were first achieved. Plots on the Coop spacing study which had achieved a positive relationship between relative growth rate and relative size and had reached a crown ratio of 0.55 by the last measurement were included in this analysis.

A comparison of the age differences indicate the relative growth rate/size relationship becomes positive about the same time as the crown ratio falls to 0.65 (Table 4.16).

Table 4.16. Comparison between the age where the relationship between relative growth rate and relative size first indicates dominance/suppression and the age where specific values of the crown ratio are first achieved. Based on 12 4x4, 12 6x6, 12 8x8, and 5 12x12 plots from the Coop spacing study.

	Differences in age of D/S and specified Crown Ratio			
Crown Ratio	Mean	p-value[a]	Median	p-value[b]
0.95	5.0	< 0.01	5	< 0.01
0.85	2.9	< 0.01	2	< 0.01
0.75	1.3	< 0.01	1	< 0.01
0.65	-0.0	0.82	0	1.00
0.55	-1.6	< 0.01	-2	< 0.01

[a] Student's t-test for testing if population mean is 0.
[b] Sign test for testing if population median is 0.

c. Response to Thinning

The effect of thinning was estimated as the difference in the slope of the linear relationship between relative growth rate and relative size. The slope coefficient for each 3-year growth interval was computed for the unthinned and the two thinned plots at each location of the thinning study.

In the first three years following thinning, the average difference in the slope coefficient between the unthinned and heavy thinned plots was 0.0193 (Figure 4.7) with a paired t-test p-value of < 0.01. There is little apparent relationship between the change in slope and other stand attributes. Attempts to model the change explicitly in terms of thinning intensity and other attributes were unsuccessful. However, an analysis of mean values by age and thinning intensity group suggests the degree of change is greater on younger stands for all but the heaviest thinning and tends to increase with thinning intensity (Table 4.17). Graphical analysis of the differences in slope coefficients between unthinned and thinned plots over the four measurement intervals suggest the differences are slowly decreasing (Figures 4.8-4.9).

Table 4.17. Mean change in slope coefficient three years after thinning and p-values for testing differences between the means (μ). n denotes the number of observations in each group.

	Percent Basal Area Thinned					
	< 25		25-45		> 45	
Age Group	μ	n	μ	n	μ	n
≤ 15	0.0144	25	0.0238	107	0.0227	22
> 15	0.0055	27	0.0100	106	0.0184	36

---p-values for test of no difference between means within a basal area thinned class---

	20	40	60
Wilcoxon	< 0.01	< 0.01	0.79
T-test	< 0.02	< 0.01	0.42

Since the thinnings in this study tended to remove smaller trees, the effect of simply removing trees from the diameter distribution and recomputing the slope coefficient from the remaining trees was examined. For each location, a hypothetical plot the same size as the control plot was centered in the thinned plot with its initial tree-list. The dbh distribution was split into 10 equal width intervals and the proportion of trees thinned in each interval tallied. The dbh distribution on the control plot was also divided into 10 intervals and the same proportion of trees as removed on the thinned plot were randomly dropped from each interval. The linear relationship between relative growth rate and relative size was computed for the remaining trees. There was no consistent change in the slope coefficient when trees likely to have been thinned were not included in the calculation of the slope coefficient (Figure 4.10).

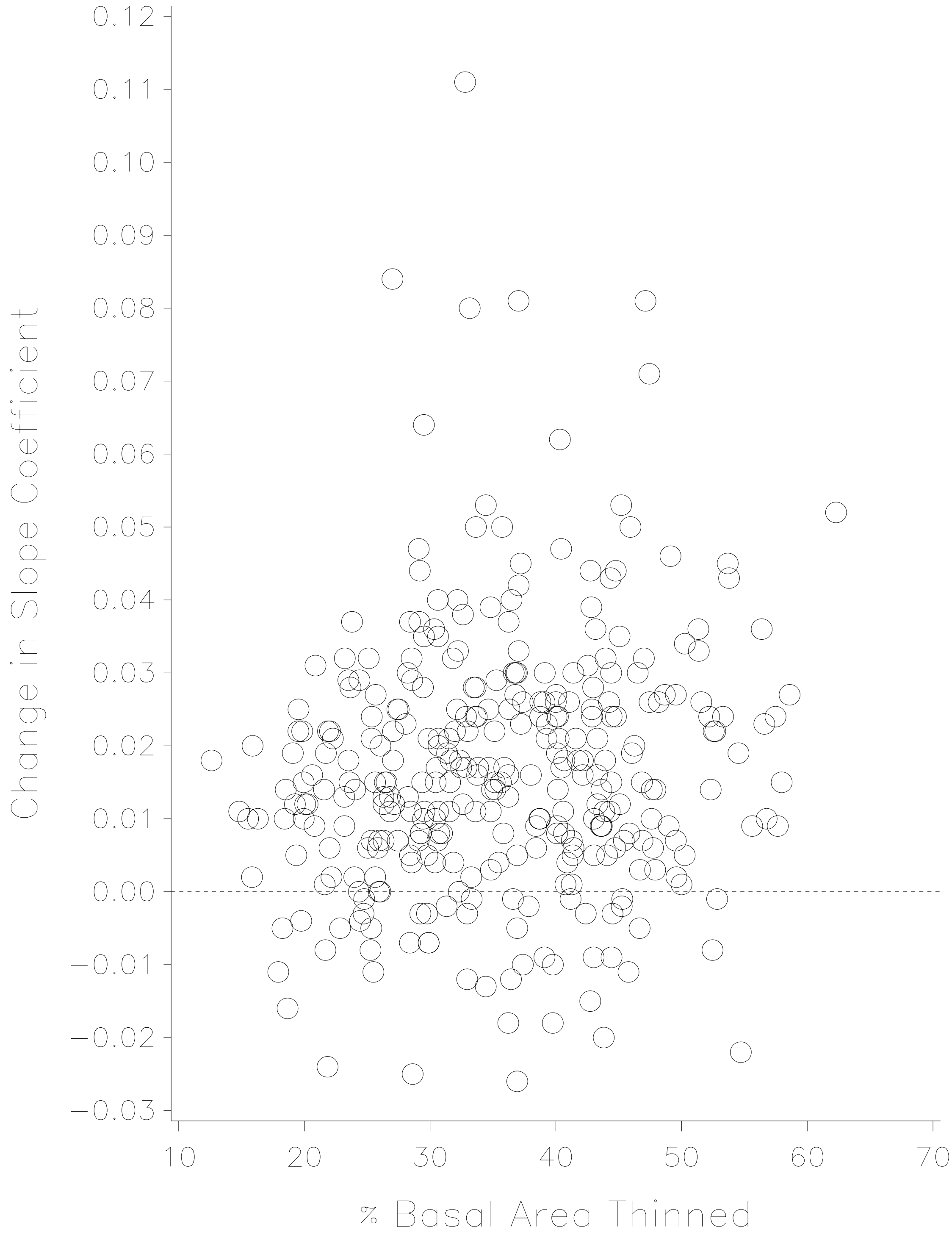

Figure 4.7. Change in the slope of the linear relationship between relative growth rate and relative size for the first 3-year period following thinning.

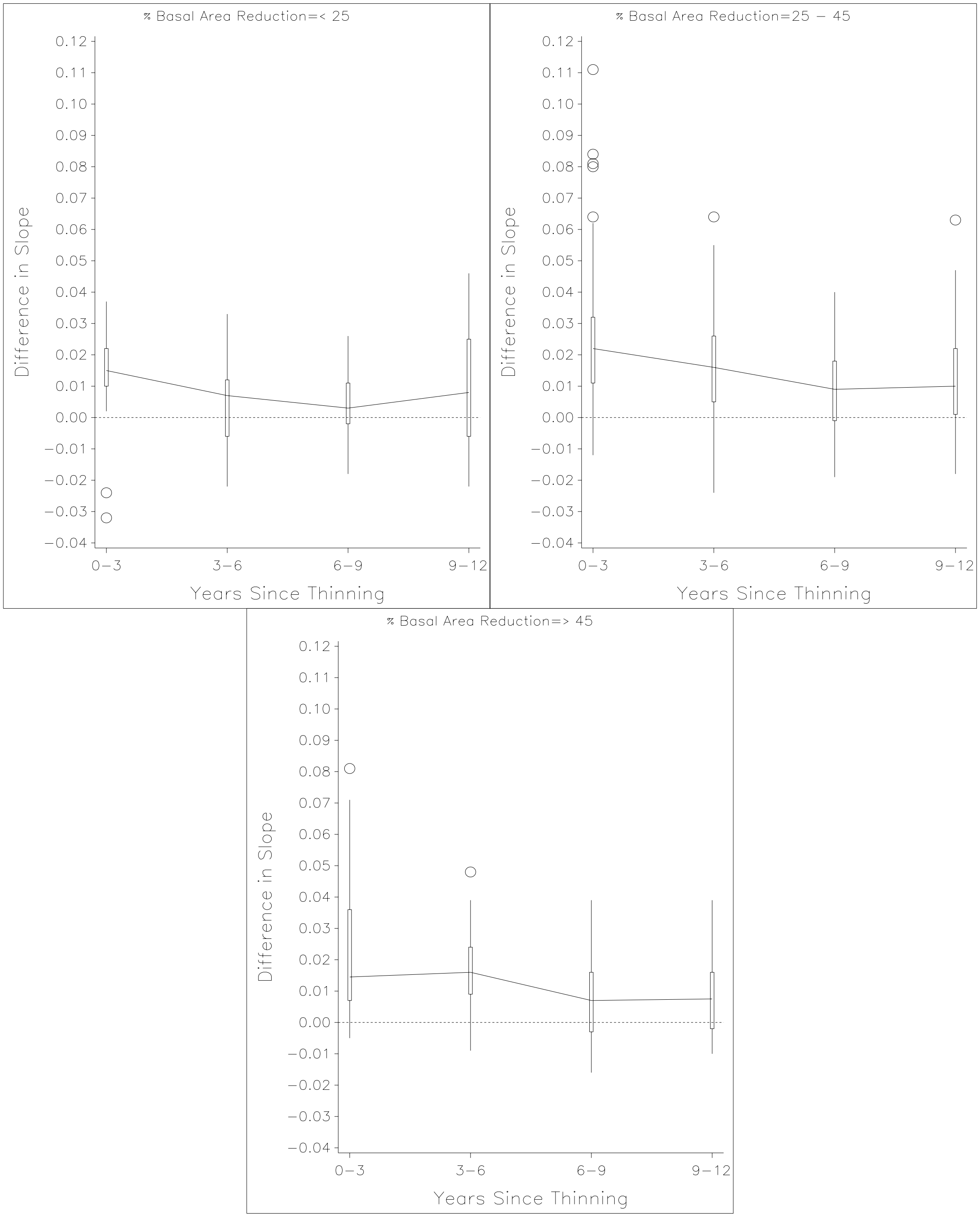

Figure 4.8. Change overtime in the slope of the linear relationship between relative growth rate and relative size for various levels of thinning. For Coop thinning study locations 15-years or younger at time of thinning.

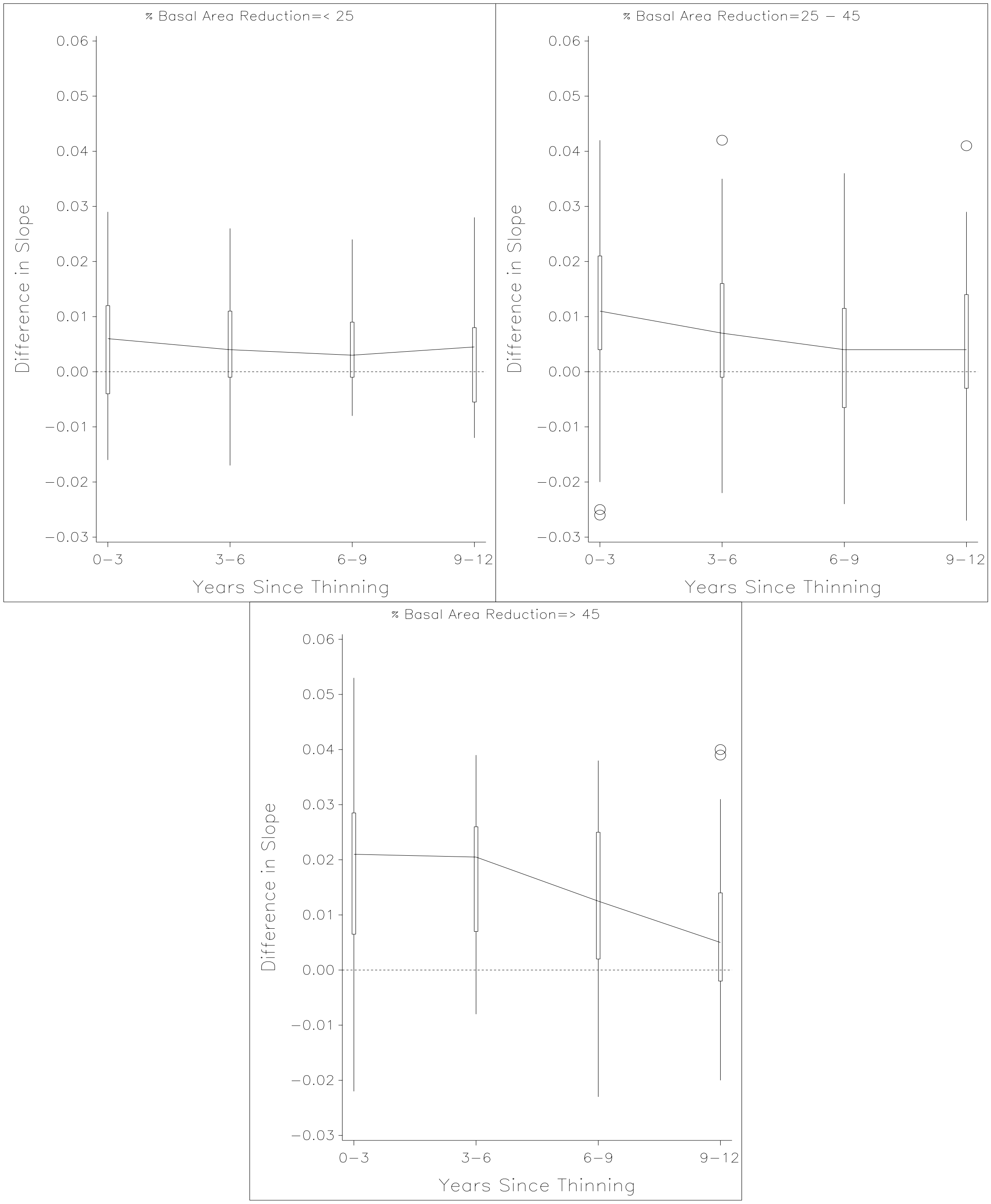

Figure 4.9. Change overtime in the slope of the linear relationship between relative growth rate and relative size for various levels of thinning. For Coop thinning study locations older than 15-years at time of thinning.

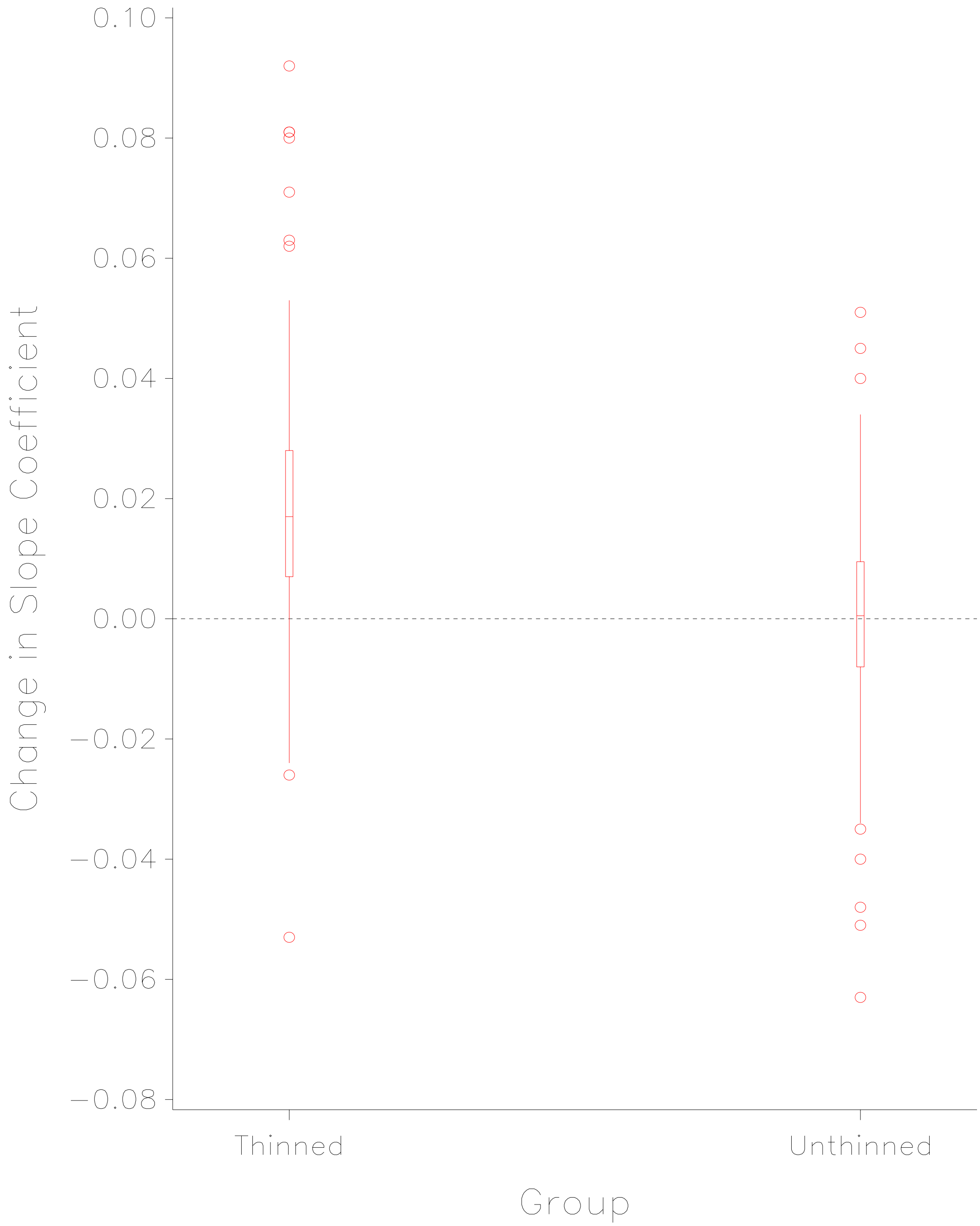

Figure 4.10. Change in the slope of the linear relationship between relative growth rate and relative size following thinning. Compares the change due to growth following thinning to the change resulting from dropping trees on the unthinned plots.

Discussion

The switch in the slope of the linear relationship between relative growth rate and relative size is an indication of a dominance/suppression competitive relationship. Attempts to relate the timing of the change from a negative to positive slope were only marginally successful. Crown projection area and crown ratio have broad threshold values where the change in slope occurs. A positive slope is associated with a crown projection area greater than 1.05 and a crown ratio less than 0.75.

Thinning clearly decreases the slope of the linear relationship between relative growth rate and relative size. The change in the slope is a result of a differential response to thinning and not merely the removal of smaller trees from the distribution used to estimate the relative growth rate / relative size relationship. With the reduction in density, smaller trees are able to acquire proportionately more resources than prior to thinning.

Conclusions

In this study, data from two spacing trials were analyzed to test for the existence of dominance/suppression competitive relationships in loblolly pine plantations. A second objective was to explore the relationship with stand dynamics.

- The results of this analysis strongly support the resource pre-emptive, or dominance/suppression, theory of intra-specific competition in loblolly pine plantations.

- Effects of intra-specific competition are more apparent in the distribution of relative growth rates over relative size as opposed to analysis of size inequality trends.

- The relationship between relative growth rates and relative size follows a consistent trend through time. Growth rates are initially negatively correlated with size. As the population develops and intra-specific competition begins, growth rates gradually become positively correlated with size. On a given site, the higher the initial density the sooner the transition from negative to positive correlation with size.

- Important trends in the slope of the linear relationship between relative growth rate and relative size are not obvious when analysis is based on class means as opposed to individual plants.

- The switch from a negative to positive correlation between relative growth rate and relative size occurs when the crown projection area reaches a value greater than 1.05 and a crown ratio lower than 0.75.

- Thinning reduces the slope of the linear relationship between relative growth rate and relative size. The change is greater on younger stands and with higher thinning levels.