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THE ONSET, CESSATION, AND RATE OF GROWTH OF LOBLOLLY PINES IN THE FACE EXPERIMENT.

Susanne Aref, Virginia Tech, David J. Moore and Evan H. DeLucia, UIUC

The Duke Forest FACE experiment was set up to investigate the impact of elevated CO₂ levels on a larger eco system. One of the studies dealt with the impact of elevated CO₂ levels on the onset and cessation of growth of loblolly pine trees (*Pinus taeda L.*). In this study the times of these events were determined for each year, 1996 - 2002. The rate of growth, the growth duration, and actual growth were determined from the models of onset and cessation of growth. Adjusted for initial basal area, the rate of growth, the actual growth, and the current basal area were slightly greater for elevated CO₂ levels. There was no difference between the two CO₂ levels for any of the time variables, onset, cessation, and growth period.

1. INTRODUCTION

In the past 100 years the level of Carbon Dioxide has risen dramatically and may well continue to do so. The Forest-Atmosphere Carbon Transfer and Storage (FACTS-I) is an experiment created to study the effects of elevated carbon dioxide levels on larger ecosystems. The FACTS-I experiment uses Free Air Carbon Dioxide Enrichment (FACE) technology to maintain elevated levels of atmospheric CO₂ in a large area. A FACE experiment was started in 1996 in a plantation in the Duke Forest of 15 year old loblolly pine (*pinus taeda*). One part of the experimental set-up involves six large (30m diameter) rings with pipes that blow air into the rings (Figure 1, face.env.duke.edu/description.cfm). The six rings were organized as three pairs, where one ring in each pair received ambient air, while the other received elevated levels of CO₂. The elevated level of CO₂ was held at 200 μ l/l above the ambient level of about 360 μ l/l.

One of the many teams of scientists working with Duke Forest FACE Experiment studied the onset and cessation of growth of loblolly pines from 1996 through 2002 (Moore et al., 2004). Further data may not be available or be relevant for the data already obtained since there was a severe drought in 2002 and in 2003 an ice storm downed a number of trees which led to changes in the canopy cover. About 30-40 trees in each ring (totaling 209 trees) were selected along walkways in each ring (Figure 2).

2. MATERIALS AND METHODS

The trees were sized into four categories based on diameter at breast height (dbh) quantiles of all loblolly pines in the six rings. The selected trees were outfitted with spring-loaded stainless steel dendrometer bands and diameter changes were recorded every month (Figure 3). The basal area was then calculated from the initial dbh and later diameter changes. The question of interest for this study was whether elevated CO₂ levels changed the onset and/or cessation of growth, and thereby possibly the growth period. Since there were only six observations in a block design with three blocks, the level of significance for the treatment differences between ambient and elevated CO₂ levels was set to be 10%, rather than the usual 5%. The elevated CO₂ level was conjectured to result in faster growth, so that the growth, rate of

growth, actual basal area should be larger at the elevated CO₂ level. The larger growth would be consistent with an earlier onset, a later cessation, and a longer growth period. The alternative hypotheses for the CO₂ treatment should therefore be one-sided and p-values from tests of CO₂ treatments were therefore compared to 20% (if the difference was in the right direction).

The basal area for an individual tree appeared to be fairly constant through winter and then rapidly increased in spring. Often there was a decrease in basal area just before the onset of growth in spring. If the year had a dry period during growing season, there was a decrease in growth for those months though the growing season was not over, see Figure 4. The particular changes in increased or decreased growth were evident across most trees. In a few cases it was difficult to decide if an observation was an outlier since the other trees had the same pattern though not as extreme.

Parametric models consisting of straight lines and quadratic polynomials were used to determine the onset and cessation. For each year the onset of growth was determined from a model of the basal area on a time interval starting late in the previous year and ending late in the current year. The model was a segmented model that consisted of a horizontal line with a time break point, the onset of growth, where growth increased as a quadratic curve.

Most trees were fitted in a general way for each year, while some needed an adjustment in the fitting process without sacrificing the general approach. The onset of growth could not be fitted in 2001 for 37 trees. This was due to a constant basal area for three months in a row in the peak of the growth period for that year (Figure 5). The reason for the constant basal area was a drought during that period. For these trees only the basal area for the middle month of the three months in question was used together with the remaining months. The 2002 season had fairly nonstandard weather during the growing season, so that it was hard to tell whether there was an early time of onset and then some delay or a much later onset than in other years. For the onset of growth variable the 2002 data were not used, while for the starting basal area and rate variables the 2002 data were used.

3. MODELS

The model for time of onset of growth was:

$$\text{Basal area} = \begin{cases} \text{start,} & \text{if date} < \text{onset} \\ \text{start} + \text{rate}(\text{date} - \text{onset}) + \text{curvature} * (\text{date} - \text{onset})^2, & \text{if date} \geq \text{onset} \end{cases}$$

For each year the date in the model was set to begin at 0 which was Oct 25 in the previous year. The data was fitted from that date through Oct 9 in the year in question. Exceptions to this time frame were as follows: In 1999 12 trees were fitted on an interval that went from Oct 25, 1998 through Oct 29, 1999; in 2001 the interval went from Nov 24, 2000 through Nov 28, 2001; in 1997 through 2001 the starting value for onset of growth was set to be between 140 and 160 days corresponding to last half of March, while in 2002 it was set to 210 corresponding to third week of May. The initial value for the parameter start was set to 200 in 1996 increasing to 310 in 2002, while the initial value for the parameter rate was set to 0.25 and the initial value for the parameter curvature was set to -0.0003.

Using SAS proc nlin a typical model statement was:

```
proc nlin data=response outest=par97 noprint;
where day97>0 and day97<350;
parms start=200 rate= 0.25 curvature=-0.0003 onset=140;
x=day97-onset;
if day97<=onset then model basalarea = start;
else if day97>onset then model basalarea = start + rate*x+ curvature*x*x;
by tree ring size;
output out=pred97 p=p r=r;
run;
```

Similarly the time of cessation of growth was modeled from about the time of onset of growth one year into the next year – again as a segmented model, with a quadratic curve ending in a plateau with a differentiable knot between the quadratic and the plateau parts (Figure 6). The cessation time is the differentiable knot. The last part of the growth tapers off rather slowly so the actual cessation is therefore not as precise as the onset. The decision was made to determine the date where a large percentage (90%, 95% or 99%) of the growth had occurred. The cessations at each of these percentage growth points varied more as the percentage increased. The time at which 95% of the growth had taken place was used in the analysis.

The model for cessation of growth was:

$$\text{Basal area} = \begin{cases} \text{start} + \text{rate} * \text{date} + \text{curvature} * \text{date}^2, & \text{if date} < \text{cessation} \\ \text{start} + \text{rate} * \text{cessation} + \text{curvature} * \text{cessation}^2, & \text{if date} \geq \text{cessation} \end{cases}$$

The initial value for the parameter start was set to 150 in 1996 increasing to 290 in 2002, while the initial value for the parameter rate was set to 0.25 and the initial value for the parameter cessation was set to 340. The parameter curvature was obtained from the cessation parameter from the equation

$$\text{curvature} = - \text{rate} / (2\text{cessation}).$$

Using SAS proc nlin a typical model statement was:

```
proc nlin data=response outest=par97 noprint;
where day97>140 and day97<480;
parms start=200 cessation=340 rate=0.25;
x=day97-140;
curvature = -.5*rate / cessation;
ind = (x<cessation);
model basalarea = start + (rate*x+curvature*x*x)*ind +
(rate*cessation+curvature*cessation*cessation)*(1-ind);
by tree ring size;
output out=pred97 p=p r=r;
run;
```

The starting basal area of one year should be the final basal area size of the previous year, indeed the correlation between the two variables was 0.99999. The regression of one variable on

the other variables had an estimated intercept of 0.054 that was not significant at 15% and a slope of 0.9999 in a model with an R^2 of 1. The differences between the two measurements range from -1.55 to 3.83 with a median of -0.078 as compared to the basal areas for 1996 that ranged from 50 to 450 with a median of 200 approximately.

All the analyses of the different dependent variables had the same general structure: The full model fixed and random effects were the same, though the fixed effects left in the models and the structure of the repeated effect year were not the same for the different variables. The full linear model was as follows:

$$y_{ijklm} = \mu + P_i + T_j + (PT)_{ij} + S_k + (TS)_{jk} + (PTS)_{ijk} + \beta b_{ijkl} \\ + tree(PTS)_{(ijk)l} + Y_m + (TY)_{jm} + (SY)_{km} + (TSY)_{jkm} + \varepsilon_{ijklm}$$

where P was the pair; i=1 to 3, T was the treatment; j=1 and 2, S was the size class, k=1 to 4; b was the basal area for year 1996 (initial basal area); tree was the individual tree, l=1 to about 200; Y was year, m=1997 to 2002; ε was the error. The error had an autoregressive structure for starting basal area, yearly growth gain and growth period and had a compound symmetry structure for onset, cessation, and rate. The initial basal area for year 1996 was calculated as a weighted sum of the basal areas for the measurements on hand, which were from April through December. The April basal area received four times the weight of the other months. This variable was included as a covariate in the analyses, since in general larger young trees have faster growing rates than smaller young trees (Figure 7). The covariate was not as significant or not significant at all for the onset, cessation, and growth period variables (Figure 8). The squareroot transformation of the basal area and rate variables were used to obtain homogeneity of variance. The analyses were done with SAS proc mixed, SAS Institute version 8.1.

4. RESULTS

Onset

The analysis of the onset of growth showed that the treatment effect and interactions with treatment were not significant, while the year, size by year effects, and the initial basal area covariate were significant, Table 1 and Figure 9. The slope for the starting basal area covariate was negative for the covariate indicating that onset of growth happened slightly earlier for larger basal areas. The years were (not surprisingly) very different, with differences in sizes changing from year to year. Size was not significant by itself. Size classes do not have consistently different onsets after adjusting for initial basal area, while onsets differ from one year to the next.

Cessation

The initial basal area covariate did not add to the model for the cessation variable and was therefore dropped from the model. Treatments were not significant different for this variable either, while cessation varied with year. Since there was a significant treatment by year interaction the difference in cessation of growth of trees in the elevated and ambient treatments

varied with year. Only in years 1996 and 2001 were there significantly later cessations for the elevated treatment than the ambient treatment. For other years the elevated treatment did not have significantly later cessations than the ambient treatment, indeed for some years the ambient treatment had later cessation estimates than the elevated treatment. Size class was not significant indicating that there were no overall differences between size classes, Table 2. The size class by year interaction was significant, but like the treatment by year interaction differences were not showing any patterns.

Growth period

The growth period was more correlated with the cessation than with the onset, while onset and cessation was the least correlated, see Table 3. The analysis for the growth period variable was similar to the one for cessation, except initial basal area was significant with a positive slope, indicating that trees with larger initial basal area tended to grow for a longer period, Table 4. This agreed with the negative slope for the onset variable, larger trees start growing earlier and therefore for a longer period. Though the interaction of treatment and year was significant, none of the yearly differences between treatments were significant. In 1997, 1999, and 2001 the growth period for trees in the elevated treatment was longer than for trees in the ambient treatment, while in 1998 and 2001 it was the opposite.

Even though some significant differences between levels of CO₂ exist for some years, it appeared that the differences between levels of CO₂ did not add up to an overall treatment difference for any of the onset, cessation, or growth period variables.

Yearly basal area gain

The CO₂ treatment was significant at 18%, while the interaction with year was significant at 2%, see Table 5 and Figure 10. The actual F-value was greater for treatment than the interaction; the two very different levels of significance were driven by the denominator degrees of freedom of 2 and 683, respectively. As seen in Figure 10 the difference between treatment levels was fairly consistent across years.

There was no consistent pattern in the levels of the size classes for each year, while the growth was always larger for the elevated CO₂ level than the ambient level for each year. If it was a randomization trial the fact that the elevated level was greater than the ambient level in all 6 years would occur with a probability of 2^{-6} or $1/64=0.016$. Considering the total growth for the whole period, 1997-2002, the elevated and ambient CO₂ levels differ at 6.5%, while there was neither size effect nor interaction with size, see Table 6.

Rate of growth

The analysis of this variable was much like the analysis for the yearly basal area gain, see Table 7 and Figure 11. Treatment was significant at 19% and the interaction with year was significant at 3% with practically the same F-values. The least squares mean for rates in the elevated treatment was significantly greater than the least squares mean for rates in the ambient treatment at 20% every year except 2002, see Table 8. Like the yearly treatment means for the

basal area gain variable the yearly treatment means for rates also had a fairly parallel pattern for the two treatments over the years, see Figure 11.

Current basal area

Analysis results show that there was no loss of information by treating year as a continuous variable rather than a class variable for the yearly basal area variable, Table 9 and Figure 12. In the analysis with year as a class variable the least squares mean for elevated treatment level was significantly higher than the mean for the ambient treatment level at 15%. From the model with year as a class differences occurred at size levels 2 and 3 from 1999-2002 and from 200-2002 for size level 4, while there were no differences for size level 1. The differences increased with time.

When year was modeled as a continuous variable with 0 being 1996, the treatment intercepts were statistically the same, meaning the covariate was working, while the size intercepts were significantly different. The least squares mean for the elevated treatment was significantly higher than the mean for the ambient treatment level at 17%.

The slopes for year differed for the two levels of CO₂ at 0.0001. The slope for the elevated treatment was significantly greater than the slope for the ambient treatment for each year.

The slopes were also significantly different at 0.0001 for the size classes. Due to the relationship between the covariate and the size class, the estimated start levels were in the opposite order in 1997 size-wise (size 1 has the largest value followed by size 2, then size 3, and finally size 4). There was a change-over in 1999 and 2000, and in 2001 and 2002 the switch-over is complete.

The growth variables were fairly correlated too, especially the growth gain and the rate of growth with a correlation coefficient at 92%, see Table 10.

Correlations between growth and time variables

All correlations were significant at 5%, Table 11. Yearly basal area and rate of growth were correlated with onset, cessation, and growth period in a very similar way. The yearly growth gain had the same pattern of correlation, a negative correlation with onset, and positive correlations with cessation and growth period, but the correlation coefficients were 2.5-3 times larger. The absolute values of the correlation coefficients for the cessation were 1.25-1.5 greater than the corresponding ones for the onset. The correlation coefficients for the growth period were slightly higher than the corresponding ones for the cessation.

5. SUMMARY

For loblolly pines there were evidence that highly elevated CO₂ levels increased the rate and gain of growth. The onset and cessation of growth and therefore the growth period did not appear to be affected of elevated CO₂ levels. The larger growth therefore appeared to depend on the accelerated rate only and not on an extended growth period. Also the higher rates of growth

were not present for the lowest size class and not as pronounced for the largest size class as for the two middle size classes.

REFERENCES

Moore, David, J., Susanne Aref, Adrien Finzi, Jason Hamilton, Ringo M. Ho, Jeffrey S. Phippen, Evan, H DeLucia. Inter-annual variation in the response of tree growth and productivity of a *Pinus taeda* forest exposed to elevated CO₂. Submitted to Global Change Biology, April 2004.

SAS Online Doc version 8. 1999. SAS/STAT User's Guide, Cary, NC:SAS Institute Inc.

face.env.duke.edu/description.cfm

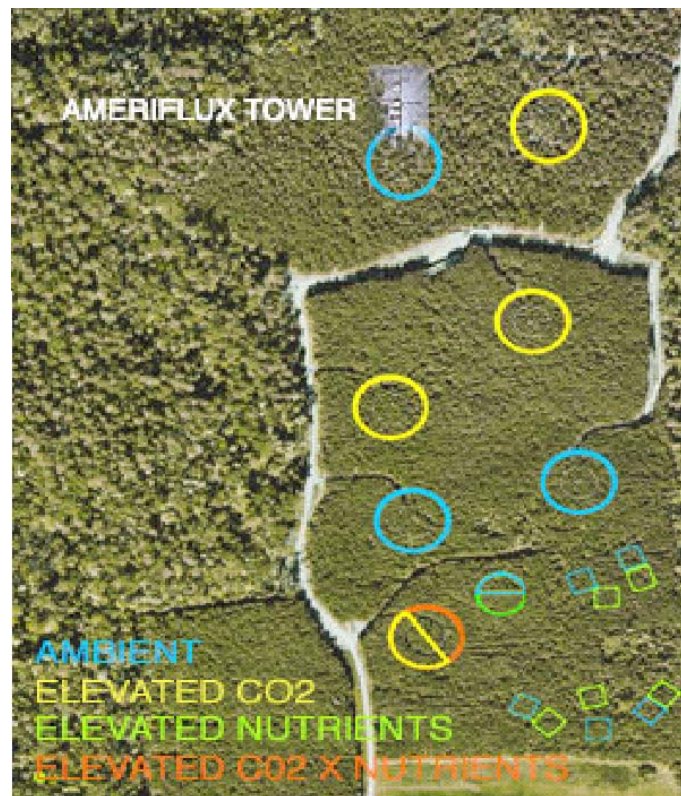


Figure 1. Aerial photo of Duke Forest FACE experiment rings.

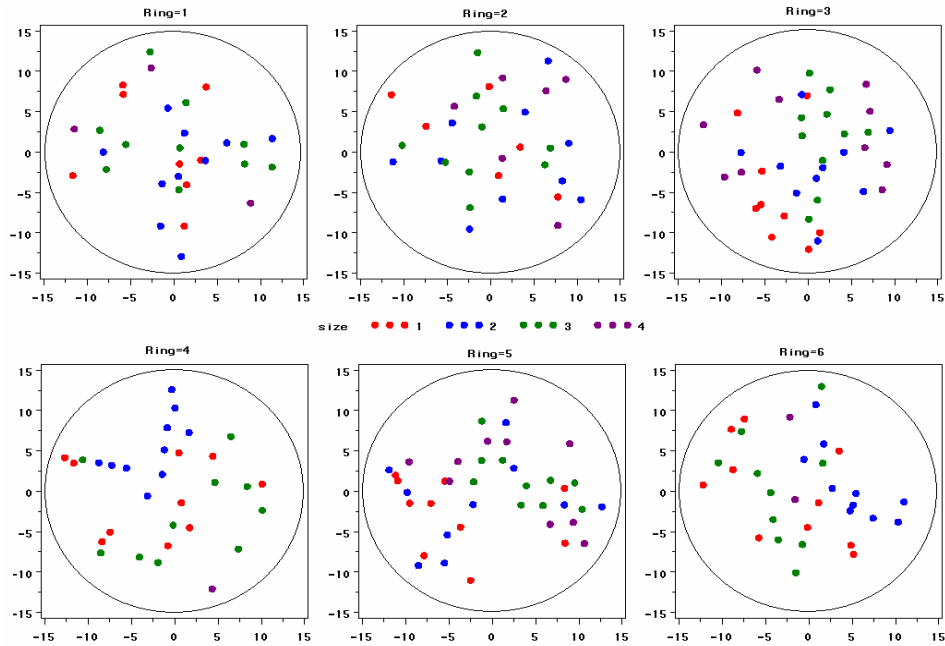


Figure 2. Location of trees used in the study.

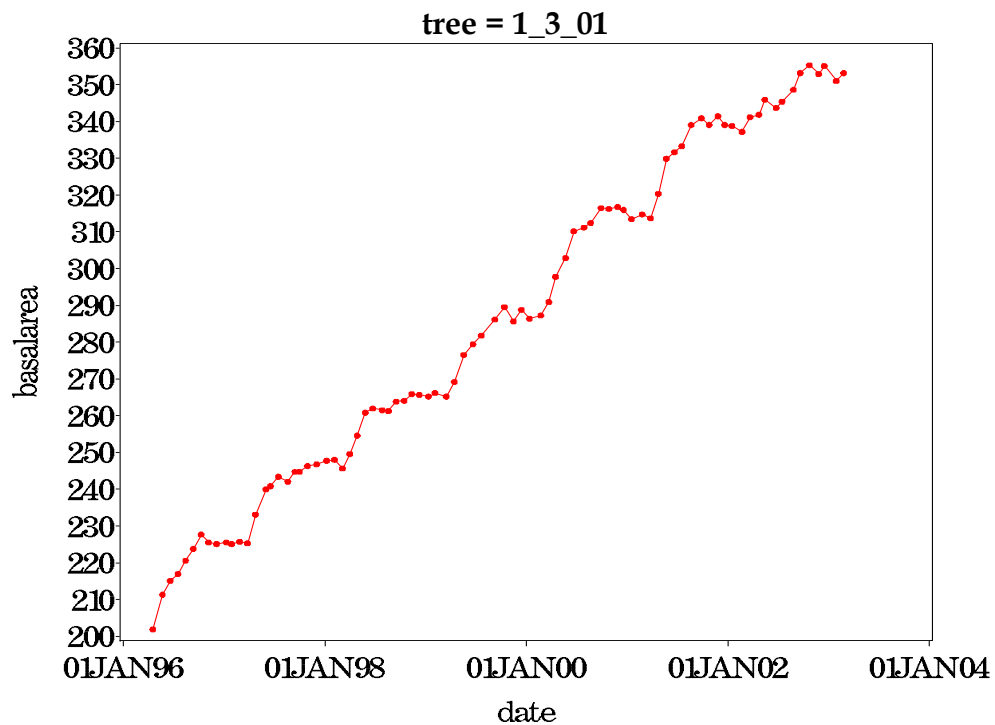


Figure 3. Basal area of tree 1-3-01 from 1996 through 2002.

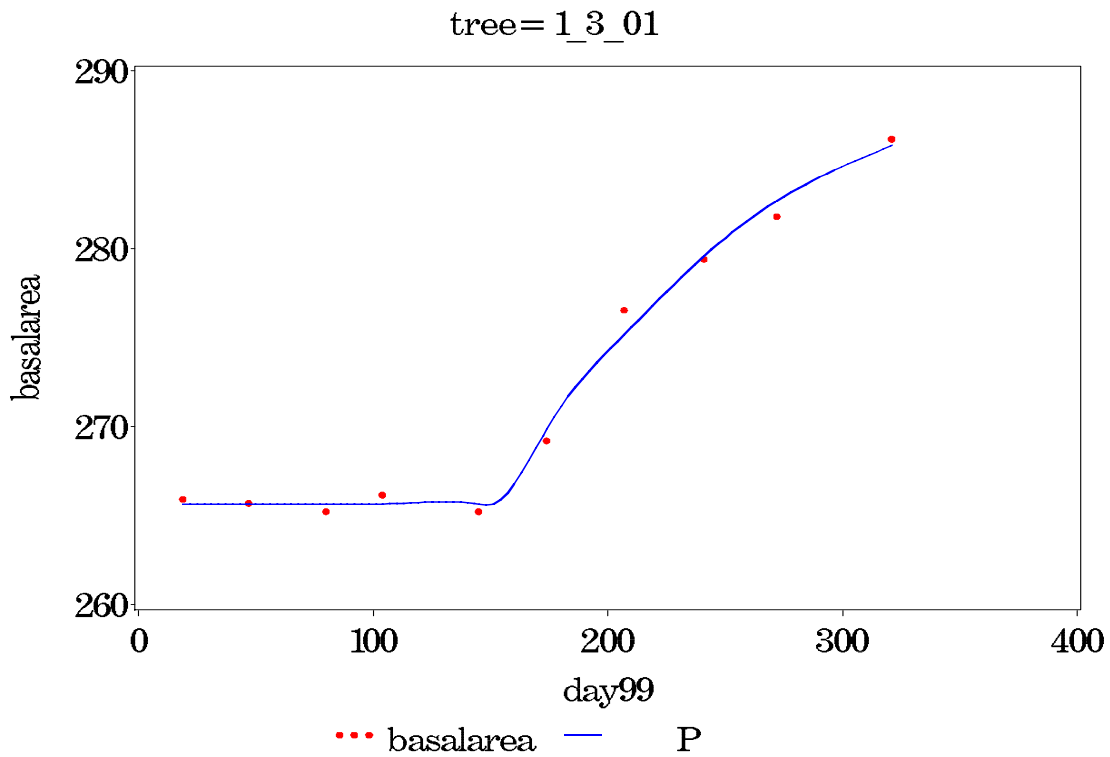


Figure 4. Original data and predicted values from model of onset of growth in 1999.

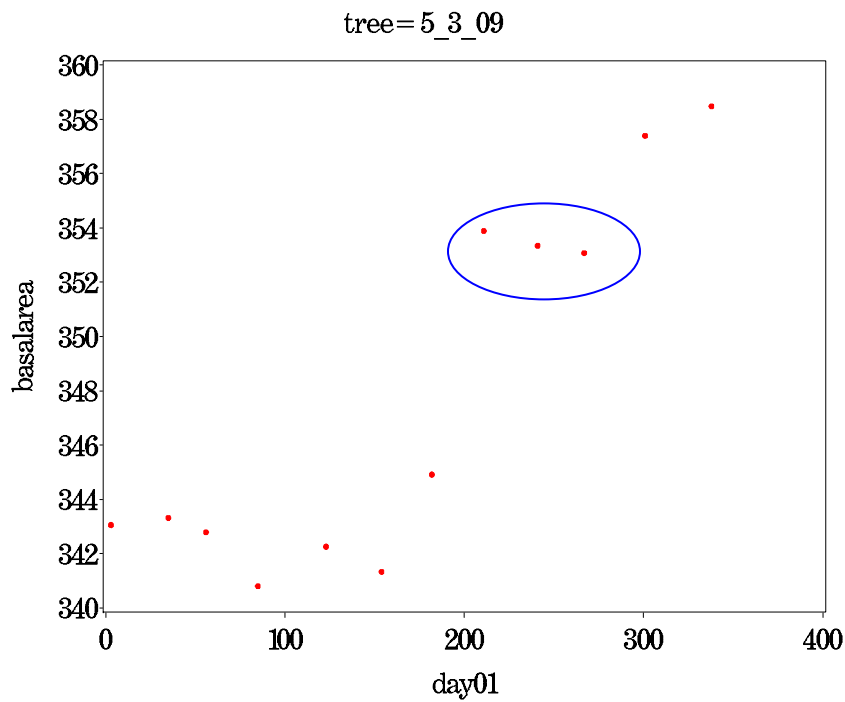


Figure 5. One of the trees with three months of constant data points in 2001.

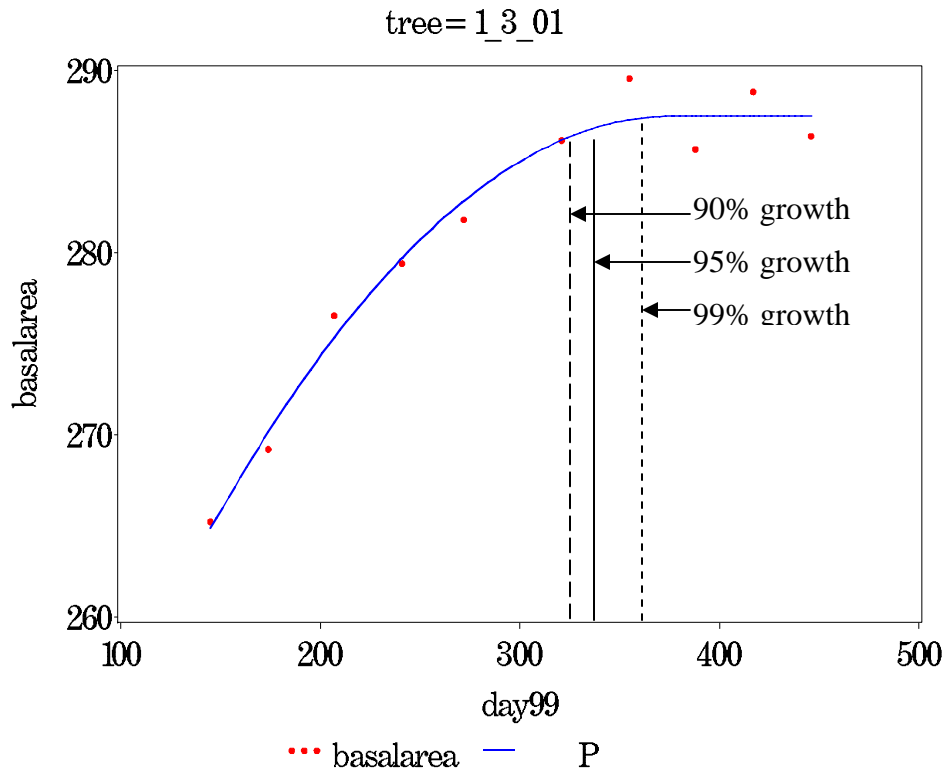


Figure 6. Original data and predicted values from model of cessation of growth in 1999.

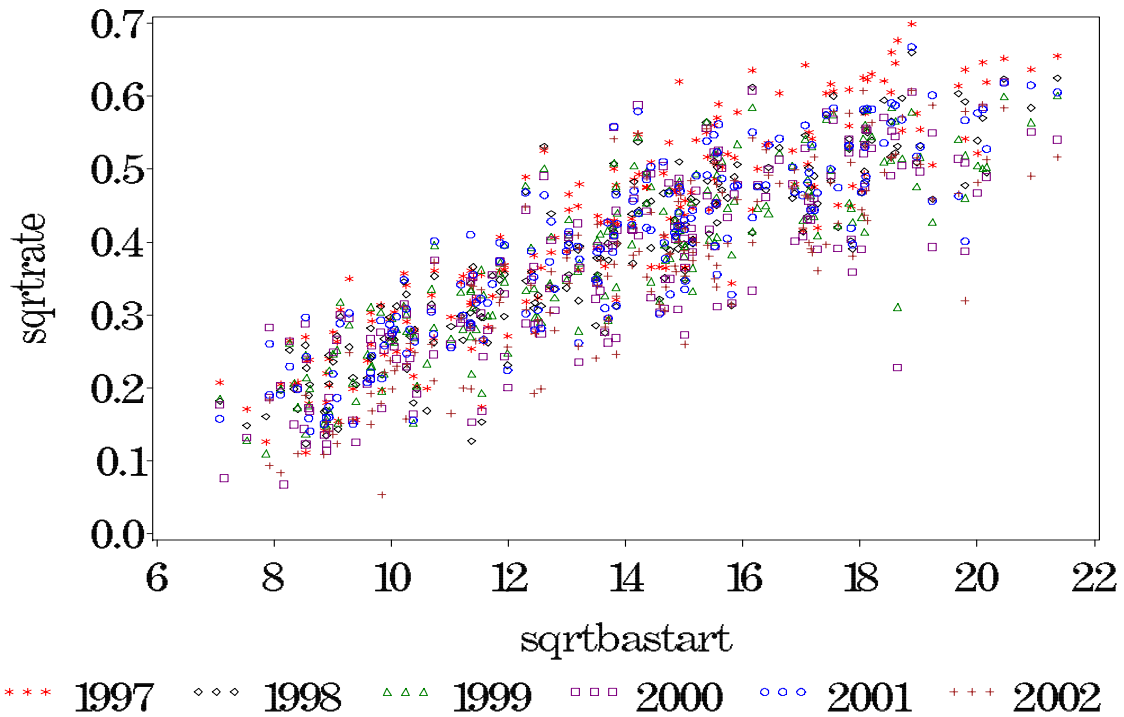


Figure 7. Rates of growth versus the initial basal area (in 1996).

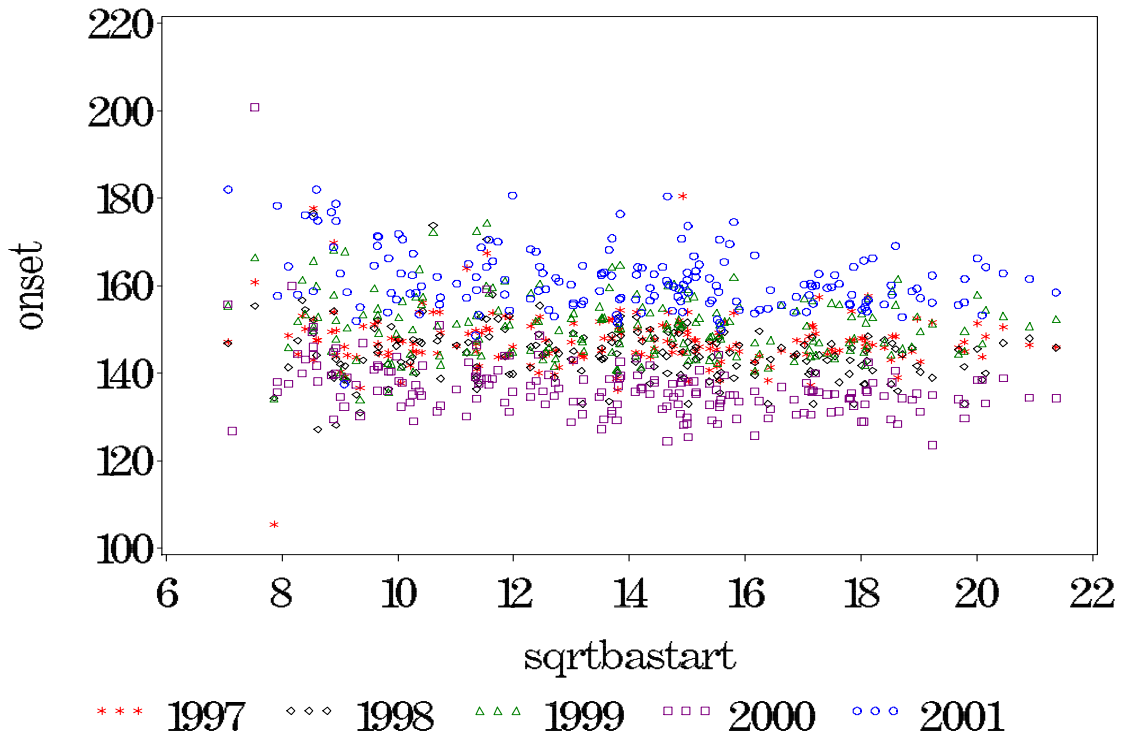


Figure 8. The onset of growth versus the initial basal area (in 1996).

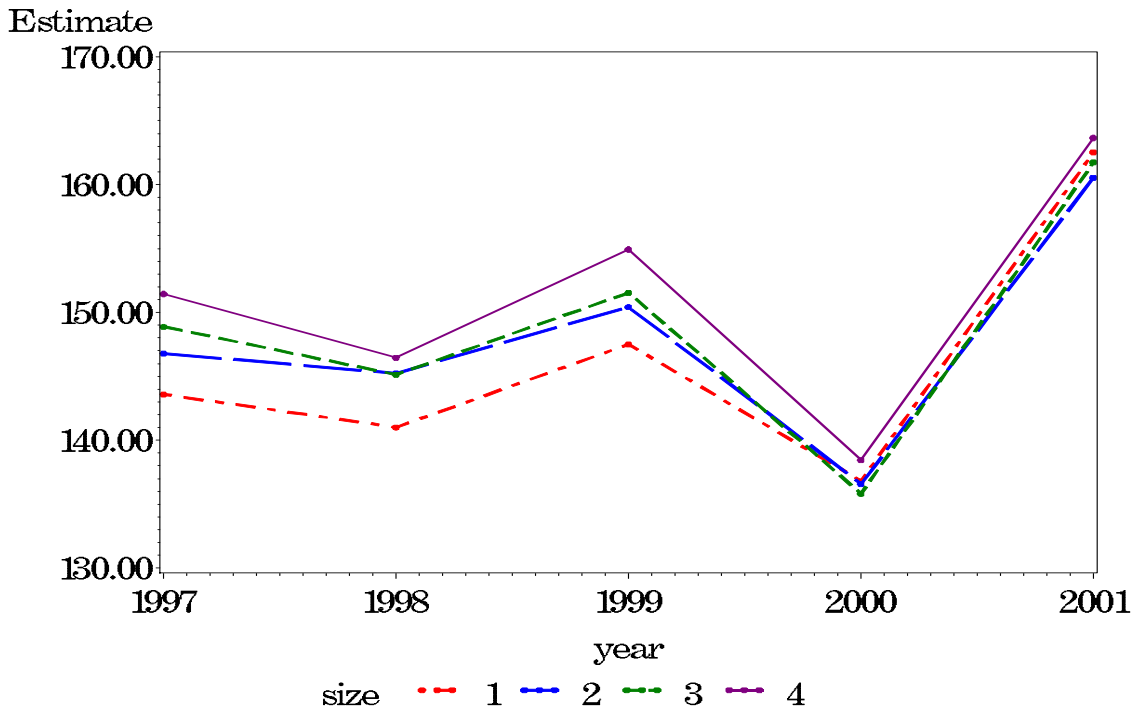


Figure 9. The onset of growth least squares mean versus year for each size class.

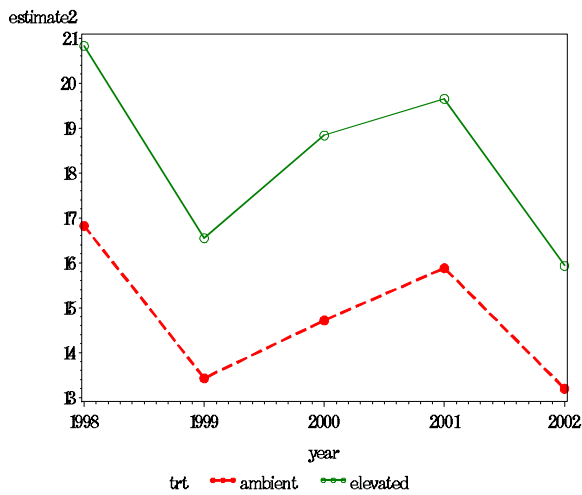


Figure 10. Yearly growth least squares means for each treatment and year.

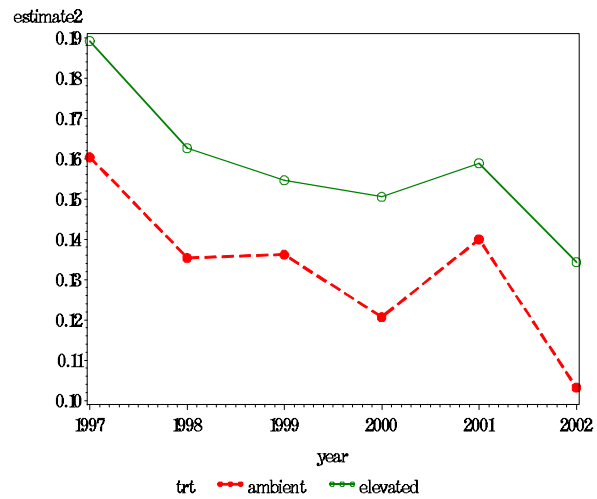


Figure 11. Yearly rate least squares means for each treatment and year.

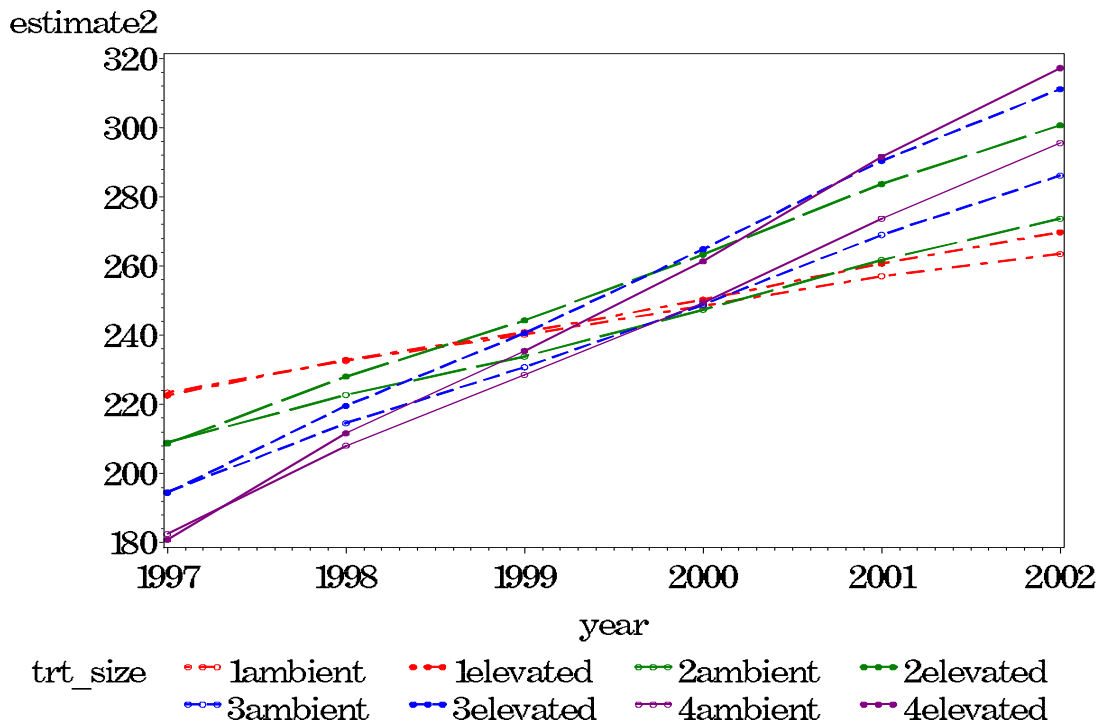


Figure 12. Predicted values from model for actual basal area with year as class.

TABLES

Table 1. Fixed effects for the onset of growth variable.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	2	2.12	0.2829
size	3	14	0.62	0.6153
year	4	722	512.71	<.0001
size*year	12	722	3.64	<.0001
sqrtbastart	1	169	5.23	0.0234

Table 2. Fixed effects for the cessation of growth variable.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	2	2.03	0.2906
size	3	15	1.92	0.1699
year	5	912	87.05	<.0001
trt*year	5	912	5.01	0.0002
size*year	15	912	3.69	<.0001

Table 3. Correlations of growth period variables.

Pearson Correlation Coefficients
Prob > |r| under H0: Rho=0
Number of Observations

	cessation	growthperiod at 95%
onset	0.32465 <.0001 1096	-0.46458 <.0001 1096
cessation		0.68391 <.0001 1096

Table 4. Fixed effects for the 95% growth period variable.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	1.97	0.28	0.6503
size	3	16.5	0.54	0.6606
year	4	612	111.17	<.0001
trt*year	4	611	5.20	0.0004
size*year	12	612	3.37	<.0001
sqrtbastart	1	248	5.50	0.0198

Table 5. Fixed effects for the yearly growth gain variable.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	1.96	4.14	0.1812
size	3	18.8	0.78	0.5219
year	4	684	196.10	<.0001
trt*year	4	683	3.02	0.0173
size*year	12	684	7.53	<.0001
sqrtbastart	1	183	105.47	<.0001

Table 6. Fixed effects for the growth gain from 1997-2002.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	2	13.85	0.0652
size	3	14	0.36	0.7828
sqrtbastart	1	141	74.41	<.0001

Table 7. Fixed effects for the squareroot of the rate variable.

Effect	Num DF	Den DF	F Value	Pr > F
trt	1	2	3.76	0.1920
size	3	17.6	2.47	0.0953
year	5	881	108.79	<.0001
trt*year	5	880	3.75	0.0023
size*year	15	881	6.57	<.0001
sqrtbastart	1	181	115.53	<.0001

Table 8. Difference between elevated and ambient levels means for each year.

year	Den DF	F Value	Pr > F
1998	2.08	4.55	0.1618
1999	2.08	3.46	0.1992
2000	2.08	5.39	0.1412
2001	2.09	4.25	0.1698
2002	2.11	2.71	0.2348

Table 9. Fixed effects for the squareroot of the yearly basal area variable.

Effect	With year as class				With linear year			
	Num DF	Den DF	F Value	Pr > F	Num DF	Den DF	F Value	Pr > F
trt	1	2.06	5.19	0.1468	1	2	1.17	0.3920
size	3	14.3	0.37	0.7772	3	11	9.25	0.0024
trt*size	3	10.7	1.02	0.4221	3	11	0.07	0.9776
year	5	852	1949.95	<.0001	1	1069	8644.58	<.0001
trt*year	5	853	23.21	<.0001	1	1069	100.77	<.0001
size*year	15	853	70.22	<.0001	3	1069	302.24	<.0001
trt*size*year	15	853	1.39	0.1469	3	1069	5.08	0.0017
sqrtbastart	1	174	1108.21	<.0001	1	174	1132.83	<.0001

Table 10. Correlations of growth variables.

Prob > |r| under H0: Rho=0 / Number of Observations

	growth gain	rate
yearly basal area size	0.73393 <.0001 1108	0.80683 <.0001 1096
yearly growth gain		0.92388 <.0001 1096

Table 11. Correlations of growth period variables with growth variables.

	Pearson Correlation Coefficients		
	yearly basal area size	yearly growth	rate
onset	-0.07188 0.0284 930	-0.24201 <.0001 930	-0.09505 0.0034 945
cessation1	0.12234 0.0002 947	0.30005 <.0001 937	0.12923 <.0001 930
growthperiod at 95%	0.13603 <.0001 930	0.33092 <.0001 930	0.14379 <.0001 930