

**Interactive effects of Swiss needle cast and commercial thinning on
Douglas-fir growth and development on state forests:
Retrospective report**

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Problem

Many Douglas-fir stands in western Oregon are being damaged by Swiss needle cast (SNC), a disease caused by the fungus *Phaeocryptopus gaeumannii* (Hansen et al. 2000). Observations and limited data suggest that thinning stands with severe Swiss needle cast may increase symptom development and exacerbate thinning shock. The interaction of pre-commercial thinning and Swiss needle cast in stands 10 to 30 years old is currently being investigated by the Swiss Needle Cast Coop (SNCC). However, the growth and development following thinning of older stands (30-60 yrs old) with varying degrees of Swiss needle cast damage are largely unknown.

Although Swiss needle cast occurs throughout the range of Douglas-fir, it is most severe in the forests on the west slope of the Coast Range. Based on aerial surveys (Kanaskie et al. 2001), the current zone with noticeable damage extends on average up to about 24 miles inland from the coast. However, not all stands within this zone are severely damaged, and the most severe damage tends to be within about 18 miles of the coast. In northwestern Oregon, about 257,000 acres of Douglas-fir forest occur within about 24 miles of the coast (Kanaskie et al. 2001), and all are experiencing some impact from Swiss needle cast. Of this total area, about 160,000 acres (more than 60 percent) are 30-60 years old and are growing at densities that mark them as potential candidates for thinning, or for partial cutting with retention to older ages.

Thinning is a key component of the Oregon Department of Forestry's (ODF) structure-based management (Oregon Dept. of Forestry 2001). Foresters currently must make complex stand management decisions in regard to the feasibility of thinning under treatment of SNC intensification, but have few data to support their decisions. Monitoring the response of stands to partial cutting across a range of initial Swiss needle cast intensity is essential to the overall ODF monitoring program and to the successful implementation of ODF's Northwest Forest Plan.

Objective

This report addresses the retrospective phase of a larger project whose objectives are to assess the effect of commercial thinning on disease symptoms and tree growth in stands with different initial levels of Swiss needle cast. The retrospective study targeted 30-60 years old stands thinned between 5 and 10 years ago, with the intention of testing for a connection between post-thinning growth and the current level of SNC infection. Specific objectives were to test the following hypotheses: 1) volume and basal area growth declined increasing current intensity of SNC; and 2) response to thinning declined with increasing current intensity of SNC. This retrospective phase cannot answer the question as to whether thinning itself exacerbates SNC or whether growth response to thinning depends on initial SNC intensity. However, an ongoing permanent plot phase of the study will eventually be able to address these questions.

Methods

Twenty-four fixed area plots were established in northwestern Oregon during the winter of 2001-2002 (Table 1). These plots were measured during the dormant season to reconstruct annual basal area growth over a growth period twice as long as the time since thinning.

Plot locations were selected across a range of disease severity classes and residual densities, and were distributed across different topographical aspects and ODF districts (Tillamook, Forest Grove, Astoria, West Oregon, Coos, Clackamas-Marion). Target stands were 30 to 60 years of age, with at least 75% of the basal area in Douglas-fir, and had undergone commercial thinning at least five, and no more than ten years ago. Four of the stands had actually undergone thinning only four years previous. Plot locations were chosen from among candidate timber sales provided by ODF districts in the northwestern quarter of the state.

In a representative part of each stand, a square, 0.2 hectare plot (0.5 acre), was established. On each plot, all trees >5 cm were tagged and measured for DBH (nearest 0.1 cm), and a subsample of 40 Douglas-fir were measured for total height, and height to lowest live branch (nearest 0.01 m). This subsample included the 10 largest Douglas-fir by dbh and the 4 smallest by dbh, with the remaining 26 distributed evenly across the diameter range of the plot. All Douglas-fir were cored for sapwood width and radial growth over a growth period twice as long as the time since thinning. Sapwood area at crown base was estimated using a previously constructed sapwood taper equation for Douglas-fir (Maguire and Batista 1996). In addition, ages were obtained for the 10 largest Douglas-fir. The 10 largest trees were given foliage retention ratings as an estimate of Swiss Needle Cast infection severity. The SNC standard rating is the number of years that foliage is retained, averaged across the upper, middle and lower third of the crown. Due to the height of crowns and associated visibility problems in these older, larger trees, a single rating was given for the whole tree, based on average retention over the whole crown.

Table 1. Plot Information

<i>Plot</i>	<i>Dist</i>	<i>Miles from coast</i>	<i>SI (ft/50y)</i>	<i>RD (at thin)</i>	<i>Qmd-DF (inches)</i>	<i>Folret (yrs)</i>	<i>CL:SA (cm/cm²)</i>	<i>DFBA (ft²/acre)</i>	<i>BA in other sp. (ft²/acre)</i>	<i>AGE (yrs)</i>	<i>yst</i>
BC	FG	28	99.4	28.3	14.7	3.475	7.23	43.91	0	49.3	9
BR	Coos	10	120.4	30.5	16.6	2.375	6.22	47.31	2.79	45.4	5
BS20	Till	21	130.6	17.4	15.6	2.861	7.20	27.88	0	39.8	6
BS35	Till	21	139.9	36.8	14.3	3.125	12.39	56.37	0	41.7	6
C20	Till	15	132.8	19.1	15.4	3.523	5.72	25.18	4.36	35.1	7
C35	Till	17	140.4	28.2	12.9	2.375	10.95	40.16	0.74	34.6	6
Cbf	WO	19	143.6	31.1	13	3.125	10.78	45.39	0	37.6	5
Cbs	WO	21	123.7	33.2	12.7	2.85	9.87	47.39	0.26	54.5	5
Cedr	Till	16	136.1	29.1	13.5	2.1	9.54	41.99	1.18	62.5	5
Coch	FG	26	137.2	41.6	19.8	3.6	5.97	70.65	2.61	34	6
Cole	Ast	12	107.5	45.3	18.5	2.11	13.55	78.36	0.05	37.7	4
Fox	Till	16	124.7	33.7	16.3	2.75	7.51	54.97	0	45.1	6
Gbsn	CM	82	105	33.4	12	3.1	10.97	46.35	0.09	40.1	4
Guts	Till	14	119.6	15.9	20.3	1.96	7.20	29.01	0	47.9	5
KF	Till	14	132.0	25.9	13.3	2.34	8.99	38.16	0	35	5
KiLo	Till	15	131.9	36.4	12.4	2.0	11.27	52.01	0	34.2	7
Moot	Till	8	115.8	28.7	18.1	2.19	11.12	44.78	3.88	54.5	5

Mrph	Till	21	126.4	31.7	15.7	2.78	6.64	49.14	1.52	39.8	7
Sleep	FG	28	140.8	34.9	18.6	4.375	6.37	59.33	0.61	52.5	8
Smill	CM	71	104.3	48.4	14.7	2.55	11.97	74.31	0.35	56.3	6
Stbrn	FG	28	96.3	31.7	13.9	3.65	6.18	35.63	12.46	42.3	8
Stm	Till	19	137.1	29.6	15.6	2.6	7.44	47.31	0	53.8	5
TB	Coos	12	126.6	33.2	13.4	2	7.02	49.22	0	33.1	4
Wpt	Ast	5	118.9	45.3	13.3	1.8	11.40	61.25	6.49	36.8	4
Totals											
Max		82	143.6	48.4	20.3	4.375	13.55	78.36	12.46	62.5	9
Min		5	96.3	15.9	12.0	1.8	5.72	25.18	0.0	33.1	4
Mean											5.7
		22.5	124.6	32.1	15.2	2.73	8.9	48.57	1.57	43.5	5

*All values are plot means

Analysis

Periodic annual volume and basal area increment, annual percentage volume growth, and post-thin/pre-thin basal area growth ratio were all used as dependent variables in regression equations. Although basal area increment was measured directly, volume increment required estimating past height growth of the site trees from site index equations (Bruce 1981). Letting t be the time since thinning, the estimated heights in years 2001- t and 2001-2 t were combined with the tree basal area backdated to 2001- t and 2001-2 t to calculate an average volume to basal area ratio (VBAR) for each year (2001-2 t , 2001- t , and 2001) and each plot; Plot volumes were calculated by multiplying each VBAR by the plot basal area for each period.

Various stand attributes were computed from the plot data for 2001-2 t and 2001- t . Basal area and volume growth in their various forms were then regressed against traditional covariates influencing stand growth, including Douglas-fir basal area, basal area of other species, site index, relative density, quadratic mean diameter, crown attributes (foliage retention, crown sparseness, crown ratio, and crown length), and indicator variables introduced for location and site effects.

Results and Discussion

Periodic basal area increment

As would be expected, plot initial conditions varied with respect to Douglas-fir basal area, relative density, as well as current foliage retention and CL:SA, site index and basal area in other species (Table 1), underscoring the need to consider covariates in the analysis. Approximately 73% of the variation in the logarithm of periodic annual basal area increment was explained by the following model (MSE of 0.0195):

$$[1] \quad \ln(\text{PBAI}) = b_0 + b_1 \ln(\text{FOLRET}) + b_2 \text{CLSA} + b_3 \text{SI} + b_4 \ln(\text{RD}) + b_5 \ln(\text{CL})$$

where PBAI = Periodic basal area increment since thin ($\text{m}^2/\text{ha}/\text{yr}$)

FOLRET	=	Current average foliage retention for the plot (yrs)
CL:SA	=	Current crown length to sapwood area ratio (cm/cm ²)
SI	=	50 yr site index (feet)
RD	=	Relative density immediately after thinning (Curtis 1982)
CL	=	Current crown length (m)

Parameter estimates (Table 2) indicate that stand-level periodic annual basal area increment increased with increasing foliage retention, site index, and relative density and decreased with increasing crown sparseness and crown length. Although a decline in growth with increasing crown length is counter intuitive, longer crowns at a given RD would suggest greater average tree size (mean diameter) and fewer trees per hectare.

Although this final model did not include a specific term for non-Douglas-fir basal area, only two of the 24 plots contained more than 10% non-DF basal area. The average percentage of DF basal area in the other 12 plots which contained other species was 97.3%.

Table 2. Parameter estimates for model [1].

Variable	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > T
b ₀	0.25520	0.85169	0.30	0.7679
b ₁	0.37700	0.14073	2.68	0.0153
b ₂	-0.07350	0.02082	-3.53	0.0024
b ₃	0.00944	0.00258	3.66	0.0018
b ₄	0.56839	0.12597	4.51	0.0003
b ₅	-1.28339	0.28824	-4.45	0.0003

Foliage retention is an effective index of disease severity, and has been previously shown to be strongly correlated with stand growth (Maguire et al. 2002). Along with crown sparseness, another indicator of foliage density (Maguire and Kanaskie 2002), the two measures together reflect a crown's capacity for production. The effect of foliage retention and greater crown density (lower CL:SA) on annual basal area increment is illustrated graphically in figure 1, assuming a relative density of 35, and with all other variables set at their mean levels.

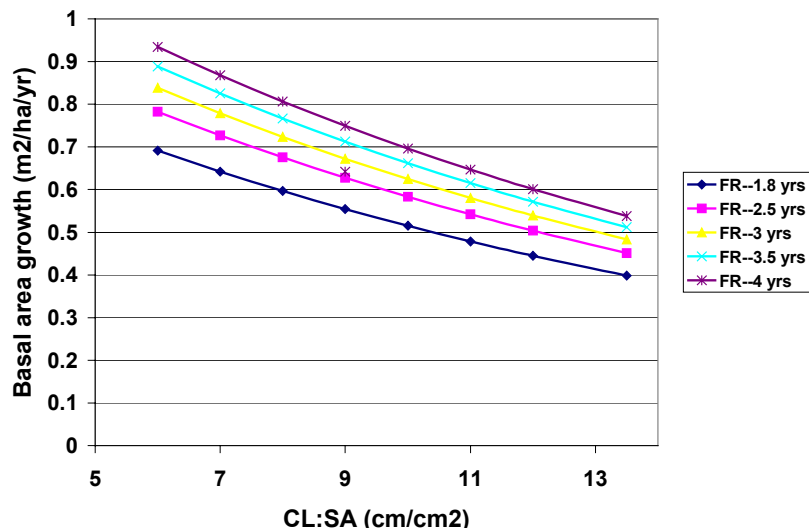


Figure 1 Periodic annual basal area increment implied by model [1], assuming a site index of 124.6 (ft, 50 yrs.), a crown length of 16.68 m, (the average of all 24 plots), and an RD of 35.

If the healthiest stand is represented by the highest value of foliage retention and the lowest value of CL:SA (represented by the Forest Grove district averages: 3.775 yrs foliage retention, 6.44 cm/cm^2 CL:SA), growth losses associated with poorer levels of these two variables can reach as high as 50% (Fig. 2; minimum retention = 1.8 years and maximum CLSA = 13.54 cm/cm^2).

At a given foliage retention, model [1] suggests that relative growth loss increases with decreasing residual RD (Fig. 3). Assuming a healthy stand is represented by the average foliage retention on the Forest Grove district and an RD of 35, the basal area growth of a stand with a foliage retention of 1.8 years would reflect a 25% loss relative to a stand with a foliage retention of 3.8 years (Fig. 3).

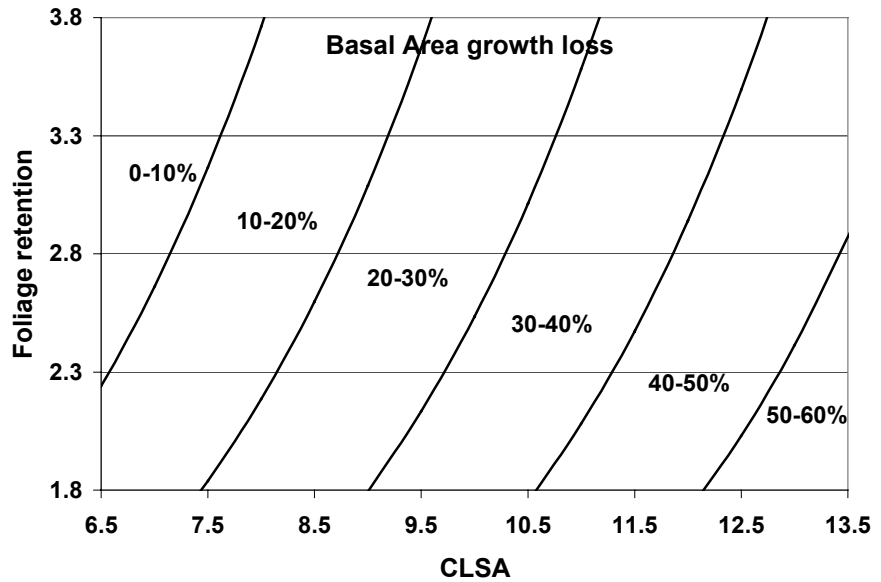


Figure 2 Basal area growth loss implied by model [1], assuming a maximum foliage retention of 3.78 years, a maximum crown sparseness of 6.4 cm/cm^2 , a site index of 124.6 (ft, 50 yrs.), a crown length of 16.68 m, (average of all 24 plots), and an RD of 35.

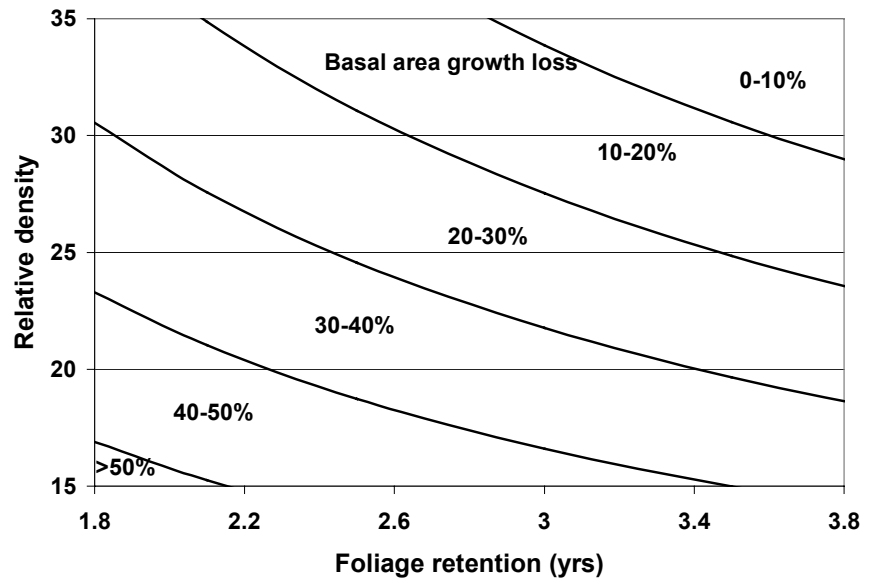


Figure 3 Basal area growth loss implied by model [1], assuming a maximum foliage retention of 3.78 years, a relative density of 35, a CL:SA of 8.9 cm/cm^2 , a site index of 124.6 (ft, 50 yrs.), and a crown length of 16.68 m (average of all 24 plots).

Periodic annual volume increment

Approximately 90% of the variation in the logarithm of periodic annual volume increment was explained by the following model (MSE of 0.00716):

$$[2] \quad \ln(\text{VOLPAI}) = b_0 + b_1 \ln(\text{FOLRET}) + b_2 \text{CLSA} + b_3 \text{SI} + b_4 \ln(\text{RD}) + b_5 \ln(\text{CL})$$

- where VOLPAI = Periodic annual volume increment since thin (m³/ha/yr)
- FOLRET = Current average foliage retention for the plot (yrs)
- CL:SA = Current crown length to sapwood area ratio (cm/cm²)
- SI = 50 yr site index (feet)
- RD = Relative density immediately after thinning (Curtis 1982)
- CL = Current crown length (m)

Table 3. Parameter estimates for model [2].

Variable	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > T
b ₀	0.84946	0.51593	1.65	0.1170
b ₁	0.20720	0.08525	2.43	0.0258
b ₂	-0.04608	0.01261	-3.65	0.0018
b ₃	0.01359	0.00156	8.69	< 0.0001
b ₄	0.73089	0.01256	9.58	< 0.0001
b ₅	-0.79742	0.17461	-4.57	0.0002

Parameter estimates (Table 3) indicate the same relationships as in basal area growth: stand-level periodic annual volume increment increased with increasing foliage retention, site index, and relative density and decreased with increasing crown sparseness and crown length.

Volume growth varies dramatically across the range in foliage retention and CL:SA (Fig. 4). Expected volume growth losses experienced by stands having lower levels of foliage retention and higher levels of crown sparseness than a “healthy” stand: that is, relative to

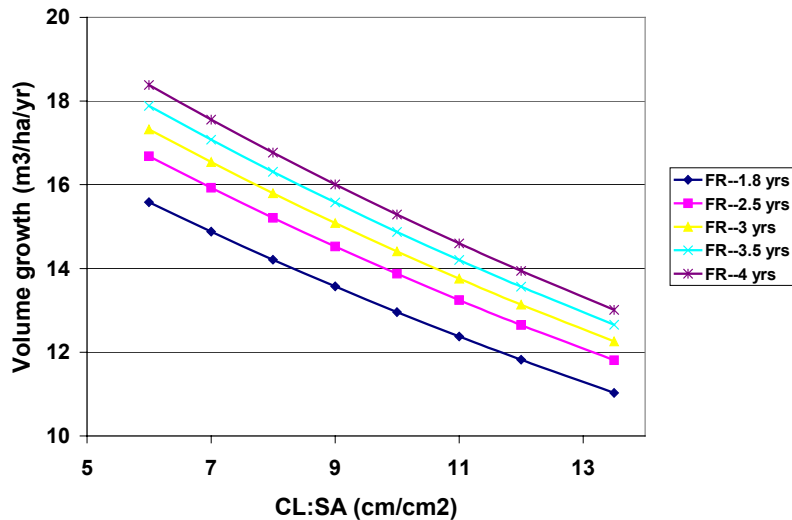


Figure 4 Periodic annual volume increment implied by model [2], assuming a site index of 124.6 (ft, 50 yrs.), a crown length of 16.68 m. (average of all 24 plots), and an RD of 35.

Forest Grove district averages: 3.78 years for foliage retention and 6.44 cm/cm² for CL:SA, range up to 40% (Fig 5).

In reality, volume growth losses at the lowest foliage retention levels may be greater, given the assumptions made in calculating volumes.

In particular, reconstructing height growth from site index or height growth equations is problematic for plots that have been experiencing high levels of SNC. Because heavily infected trees usually exhibit decreased height growth, actual height growth within these stands would be less than the height growth calculated using a site index equation, particularly if height growth

slowed only recently due to SNC (see Maguire et al. 2002). In this case, height growth prior to SNC would reflect a higher site index than after SNC; hence, site index based on the cumulative height growth over both periods would lead to overestimates of recent post-SNC height growth. In addition, because diminished height growth usually appears only in the most heavily infected stands (Maguire et al. 2002), volume growth losses in figure 5 would be underestimated primarily for lower needle retention and high CL:SA.

For a given relative density, a stand with a foliage retention of

1.8 years would be experiencing about a 14% loss in volume growth versus a stand with a foliage retention of almost 3.8 years, all else being equal (Fig 6). However, the loss would likely be larger since CL:SA also increases with foliage loss (Maguire and Kanaskie 2002).

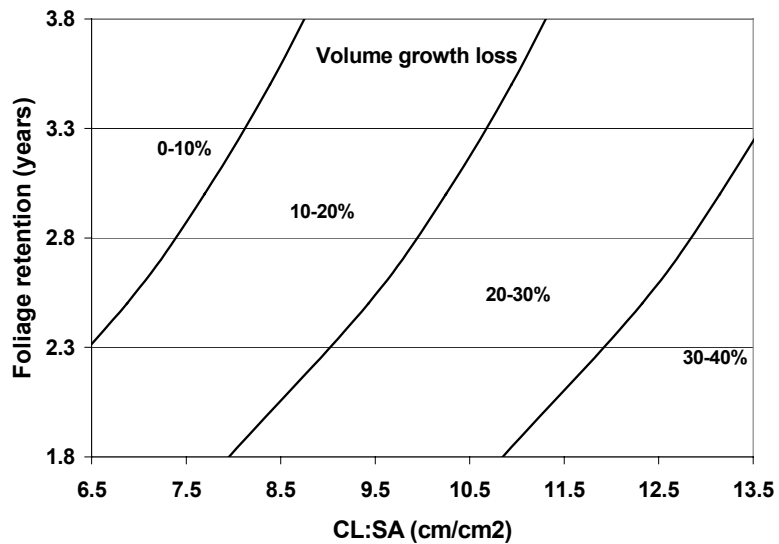


Figure 5 Volume growth loss implied by model [2], assuming a maximum foliage retention of 3.78 years, a maximum crown sparseness of 6.4 cm/cm², and assuming a site index of 124.6 (ft, 50 yrs.), a crown length of 16.68 m, (average of all 24 plots), and an RD of 35.

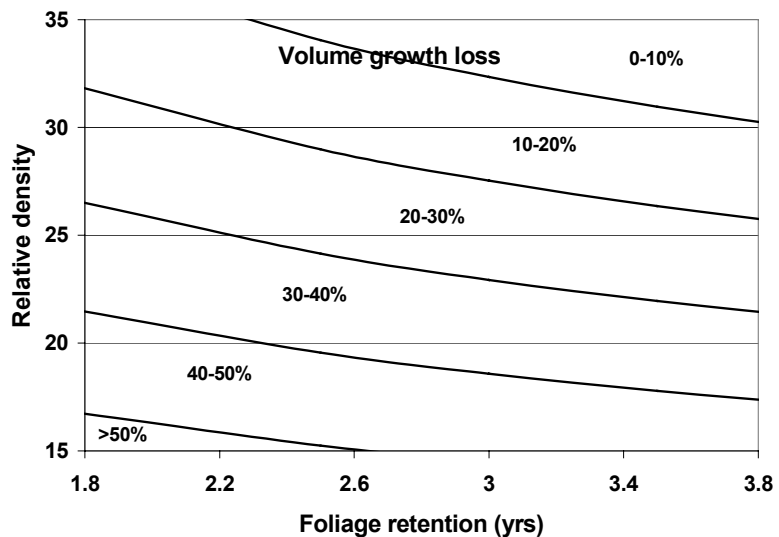


Figure 6 Volume growth loss implied by model [2], assuming a maximum foliage retention of 3.78 years, a relative density of 35, and assuming a CL:SA of 8.9 cm/cm², a site index of 124.6 (ft, 50 yrs.), and a crown length of 16.68 m (average of all 24 plots).

In short, the growth losses associated with SNC in these thinned stands, are similar to those reported in unthinned stands (Maguire et al. 2002). Stands with the most severe SNC are growing only about 50% of the basal area and volume that stands with the least severe SNC are growing.

Annual percentage volume growth

The decision whether or not to cut timber, if based on economics alone, often depends on the current annual growth rate, and how it compares to a desirable rate of return. The model describing the logarithm of average annual percentage volume growth over the period since thinning explained approximately 93% of the variation in this response (MSE=0.00645):

$$[3] \quad \ln(AVOL) = b_0 + b_1 \ln(FOLRET) + b_2 \ln(CL:SA) + b_3 \ln(RD) + b_4 \ln(SI) + b_5 \ln(CL) + b_6 \ln(CR)$$

- where AVOL = % annual volume growth (since thin)
- = $[(\text{volume in 2001})/(\text{volume in 2001-t})]^{1/t} - 1$
- FOLRET = average foliage retention for the plot (yrs)
- CL:SA = crown length to sapwood area ratio (cm/cm²)
- RD = Relative density immediately after thinning (Curtis 1982)
- SI = 50-yr site index (feet)
- CL = Crown length (m)
- CR = Crown ratio (expressed as a decimal)

Table 4. Parameter estimates for model [3].

Variable	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > T
b ₀	-2.22549	0.82941	-2.68	0.0157
b ₁	0.31666	0.08820	3.59	0.0023
b ₂	-0.41936	0.13912	-3.01	0.0078
b ₃	-0.23466	0.07169	-3.27	0.0045
b ₄	1.72049	0.18232	9.44	< 0.0001
b ₅	-2.42567	0.18561	-13.07	< 0.0001
b ₆	1.68501	0.29792	5.66	< 0.0001

Parameter estimates (Table 4) indicate that average annual percentage volume growth increased with increasing foliage retention, site index, and crown ratio, and decreased with increasing crown sparseness, relative density, and crown length.

Stands with low foliage retention (1.8 years) have an average of a 4% annual average volume growth following thinning (Fig. 7) although a slightly lower value can be expected, considering the negative correlation between foliage retention and CL:SA (Maguire and Kanaskie 2002). Similarly, expected volume growth overestimates for stands with low foliage retention would also suggest that % volume growth would be even lower. Applying average covariate values

from stands with a foliage retention between 1.8 and 2.19 years, the model implied average annual growth rate estimates ranging from 3.2 to 4.1%, depending on the level of CL:SA.

Comparison of these growth rates with growth rates from other thinned plots provides a useful perspective. The Levels-of-Growing-Stock installation near Hoskins, Oregon has helped define relationships between density and growth in repeatedly thinned stands. Stand attributes from the medium thinning at age 35 (Marshall and Curtis 2001), were entered into equation 3 to predict % volume

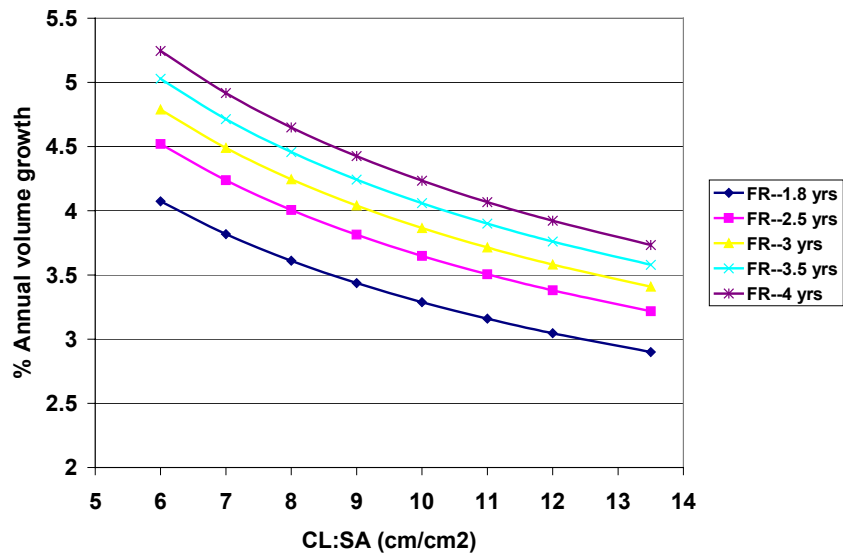


Figure 7 Average annual percentage volume growth implied by model [3], assuming a CL:SA of 8.9 cm/cm², a site index of 124.6 (ft, 50 yrs.), a crown length of 16.68 m, a crown ratio of 0.535 (average of all 24 plots), and an RD of 35.

growth. The calculated covariates, combined with a foliage retention of 3.5 years and a CL:SA of 6.4 cm/cm², gave a percentage volume growth of 8.25%, equal to the value measured at Hoskins. Had this same stand had a foliage retention of only 1.8 years and the study average CL:SA of 8.9 cm/cm², the calculated growth percentage would be 5.8%. While such a heavy SNC presence would probably have an effect on the other crown covariates, these percentages seem realistic given the higher site quality of the Hoskins site.

In summary, stands with severe SNC exhibit a relative volume growth rate as low as 3%, as opposed to 5% for stands with few SNC symptoms.

Ratio of post-thin/pre-thin basal area growth

The use of the post-thin/pre-thin growth ratio makes it possible to assess the response a stand makes to thinning. Because the ratio is based on equal periods of time prior to and after thinning, a value greater than 1 indicates that growth has accelerated in the residual trees over the specified time period. It is important to emphasize that this ratio only reflects the pre-thin growth of the residuals rather than growth of the entire pre-thinned stand.

Approximately 63% of the variation in the ratio of post-thin/pre-thin basal area growth was explained by the following model (MSE = 0.0249):

$$[4] \quad \text{BagRat} = b_0 + b_1 \ln(\text{FOLRET}) + b_2 \ln(\text{RD}) + b_3 \text{WO}$$

where BagRat = Ratio of BAG (PostBAG/PreBAG)
 FOLRET = average foliage retention for the plot (yrs)
 RD = Relative density
 WO = 1 if West Oregon district, 0 otherwise

Table 5. Parameter estimates for model [4].

Variable	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > T
b_0	2.29242	0.43994	5.21	0.0001
b_1	0.32988	0.14127	2.34	0.0301
b_2	-0.44106	0.11994	-3.68	0.0015
b_3	0.40819	0.11799	3.46	0.0025

Parameter estimates (Table 5) indicate that in stands thinned between four and nine years ago, the post-thin/pre-thin basal area growth ratio increased with increasing foliage retention and decreasing relative density. The site indicator variable indicates that the ratio is significantly greater in the West Oregon district than in the others. The limited number of explanatory variables in this model can be attributed to using a ratio as the dependent variable—covariates otherwise necessary in explaining growth are accounted for in both pre-and post-thin growth. Represented graphically (Fig. 8), the model indicates that at an RD of 35, post-thin basal area growth equals or exceeds pre-thin growth (over equal time periods) at foliage retention levels of 2.3 years and above (on all districts except West Oregon). At foliage retention levels below 2.3 years, post-thin basal area growth is less than pre-thin growth, and decreases at an increasing rate as foliage retention decreases. It is also evident that at low foliage retention levels, heavier thinning or lower residual stand density does stimulate a greater basal area growth response.

Twelve plots were thinned a sufficiently long time ago that two 3-yr growth periods were available prior to thinning. For trees in these plots, the basal area growth was computed for these two periods and the ratio was calculated by dividing the three year basal area growth just prior to thinning by the three year basal area growth prior to that period for all residual trees on a plot. The latest season of growth used for this comparison was 1995, and the average current foliage retention of the stands used in this comparison was 3.13 years, suggesting

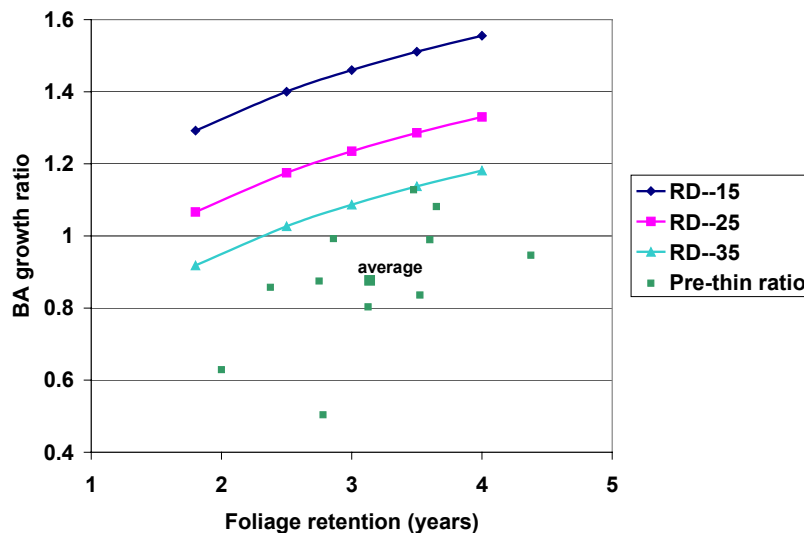


Figure 8 Post-thin/Pre-thin basal area growth ratio implied by model [4], applicable to sites other than those on the West Oregon district. Includes pre-thin ratios from 12 plots thinned at least 6 years previously.

For trees in these plots, the basal area growth was computed for these two periods and the ratio was calculated by dividing the three year basal area growth just prior to thinning by the three year basal area growth prior to that period for all residual trees on a plot. The latest season of growth used for this comparison was 1995, and the average current foliage retention of the stands used in this comparison was 3.13 years, suggesting

limited influence of SNC. The average basal area growth ratio for the twelve plots was 0.88, and ranged from 0.50 to 1.13 (Fig. 8). Given that the model-implied ratio at an RD of 35 and a foliage retention of 1.8 years is 0.92, the growth of the residuals in such a stand is little better than the same trees would be in a higher density stand about to be thinned.

Although this study only allows current SNC levels to be used to estimate growth responses to thinning, these results provide some insight into the utility of a conventional thin in stands where SNC infection is significant. Even at low foliage densities, basal area growth of individual trees after a heavy thinning, may be significantly greater than pre-thin levels. Equation [4] implies that a stand with a foliage retention of 2.4 years and a relative density of 25 would have an individual tree growth response equal ratio to a “healthy” stand (having a foliage retention of 3.775 years) thinned to an RD of 35. For an equivalent response, a stand with the lower foliage retention of 1.8 years would need to have been thinned to an RD of 20. Although the response to thinning does decline with increasing SNC severity at the end of the post-thinning period, individual tree growth can apparently be accelerated by thinning, although this conclusion assumes that SNC severity is not influenced by thinning. The permanent plot phase of this project is needed to confirm this assumption or quantify any change in SNC evoked by thinning.

Conclusions

Results from this retrospective study make it possible to predict how previously thinned stands are currently growing. However, one weakness of this approach is that foliage retention is known only for the end of the post-thin growth period; hence, it can't be used to predict a future response at the time of thinning. Thinning has anecdotally been observed to negatively effect foliage retention. If this is true, then the assumed independent (orthogonal) effects of thinning and foliage retention collapses, and more intense thinning to enhance individual tree growth could actually reduce needle retention sufficiently to offset the expected growth acceleration. The second phase of the study, consisting of paired control and treatment plots, should rectify this problem. In having initial conditions on treatment and control plots, the change in needle retention between measurement periods attributable to thinning can be assessed by comparison to the unthinned control. Having control plots over a range in stand densities will also make it possible to test for treatment effects on plot growth after accounting for effects on initial SNC severity and subsequent foliage dynamics.

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