Response of branch growth and mortality to silvicultural treatments in coastal Douglas-fir plantations: Implications for predicting tree growth

Aaron R. Weiskittel [a,*], Douglas A. Maguire [a], Robert A. Monserud [b]

[a] *Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA*
[b] *PNW Research Station, USDA Forest Service, 620 SW Main, Suite 400, Portland, OR 97205, USA*

Abstract

Static models of individual tree crown attributes such as height to crown base and maximum branch diameter profile have been developed for several commercially important species. Dynamic models of individual branch growth and mortality have received less attention, but have generally been developed retrospectively by dissecting felled trees; however, this approach is limited by the lack of historic stand data and the difficulty in determining the exact timing of branch death. This study monitored the development of individual branches on 103 stems located on a variety of silvicultural trials in the Pacific Northwest, USA. The results indicated that branch growth and mortality were significantly influenced by precommercial thinning (PCT), commercial thinning, fertilization, vegetation management, and a foliar disease known as Swiss needle cast [caused by *Phaeocryptopus gaeumannii* (T. Rohde) Petr.]. Models developed across these datasets accounted for treatment effects through variables such as tree basal area growth and the size of the crown. Insertion of the branch growth and mortality equations into an individual-tree modeling framework, significantly improved short-term predictions of crown recession on an independent series of silvicultural trials, which increased mean accuracy of diameter growth prediction (reduction in mean bias). However, the static height to crown base equation resulted in a lower mean square error for the tree diameter and height growth predictions. Overall, individual branches were found to be highly responsive to changes in stand conditions imposed by silvicultural treatments, and therefore represent an important mechanism explaining tree and stand growth responses.
© 2007 Elsevier B.V. All rights reserved.

Keywords: Douglas-fir; Intensive management; Crown dynamics; Branch modeling; Fertilization; Thinning; Swiss needle cast; Vegetation management; Branch mortality; Branch radial growth; Growth and yield modeling

1. Introduction

Growth occurs at multiple scales in forests, but is typically only simulated at the whole-stand or individual-tree levels. Individual branches have a significant influence on tree growth as they control the amount and display of leaf area (Vose et al., 1994). In addition, the number and size of branches on a stem control lumber recovery potential (e.g. Maguire et al., 1991b), contribute critical features of habitat for some wildlife species (Hayes et al., 1997; Sullivan et al., 2000), and influence interception of both incoming radiation (Whitehead et al., 1990; Kucharik et al., 1998) and precipitation (Keim, 2004). Although several models have been developed for predicting crown dynamics (Mitchell, 1975; Ford et al., 1990; Ford and Ford, 1990; Gavrikov and Karlin, 1992; Sorrensen-Cothern et al., 1993; Grace, 2003), relatively few predict dynamics of individual branches and these have generally not been fully incorporated into typically used forest growth models.

Studies of branch growth and development have most often been based on either age chronosequences (e.g. Ishii and McDowell, 2002) or retrospective growth analysis on a limited sample of harvested branches (e.g. Kershaw et al., 1990). The former approach is limited by the difficulty of removing the effects of factors other than age, because the chronosequence is assembled with stands or trees from many sites to create an artificial time series. Retrospective growth analysis is restricted by the extremely narrow growth rings, or lack of growth rings, in the lower branches of a crown (e.g. Reukema, 1959) and the difficulty of identifying the exact year of death. A branch can fail to form a perceivable increment for half or more of its total life span in at least some and probably many conifer species (Andrews and Gill, 1939; Kershaw et al., 1990; Mäkinen and Colin, 1999). Remeasurement of individual branches on standing trees provides the most accurate estimates of branch

growth and mortality, but the cost and safety risks of repeatedly climbing trees to measure branches has prevented wide application of this approach.

Static models of branch size and number exist for several species including silver birch [*Betula pendula* Roth. (Mäkinen et al., 2003)], Scots pine [*Pinus sylvestris* L. (Mäkinen and Colin, 1999)], Norway spruce [*Picea abies* (L.) Karst. (Mäkinen et al., 2004)], radiata pine [*Pinus radiata* D. Don. (Grace et al., 1999)], and Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco (Maguire et al., 1994)]. These models have generally been based on data from managed stands, but not typically across a wide variety of intensive silvicultural regimes. Conflicting responses to some silvicultural treatments have also been reported. Mäkinen et al. (2001), for example, found that branch diameter growth of both newly initiated and older branches in Norway spruce were significantly enhanced with fertilization, while Mäkinen et al. (2004) concluded that variables describing site fertility and fertilization regime did not significantly influence branch radial growth in the same species. Potential reasons for this discrepancy are differing levels of applied fertilizer, varying lengths of time since fertilization, and range in responsiveness of the trees.

Weiskittel et al. (2007) recently examined the impacts of intensive management on Douglas-fir branch characteristics and found maximum branch diameter to be significantly influenced by vegetation management, precommercial thinning (PCT), fertilization, and commercial thinning. Because a wider array of stand conditions was represented, predictive equations developed from this dataset with only bole and crown variables performed significantly better than branch equations previously developed by Maguire et al. (1994, 1999). This result also suggested that branch radial growth patterns are highly correlated with tree growth, even across a wide range of silvicultural treatments, and that the basic allometric relationships between branch, crown, and stem dimensions are not altered even by fertilization. Both fertilization (e.g. Brix, 1981) and thinning (e.g. Short and Burkhart, 1992) have been shown to significantly influence crown recession rates, but validation of this process at the individual branch-level has been minimal. However, Albaugh et al. (2006) recently did find that fertilization reduced individual branch longevity.

Forest growth models represent crown dynamics at varying levels of detail. Some models predict the growth of individual branches and others represent the development of different crown segments. Mitchell (1975) represents the growth of individual Douglas-fir branches by empirical growth equations, while Ford and Ford (1990) base their branch growth equations on theoretical relationships between foliage development, biomass production, phenology, and branch morphology. In contrast, Grote and Pretzsch (2002) and Sorrensen-Cothern et al. (1993) divide the crown into segments of equal length, simulate physiological processes in each segment, and sum the estimates to predict tree-level production. Traditional empirical growth and yield models generally represent crown dynamics by statically estimating height to crown base from initial tree, stand, and site conditions and again from predicted tree, stand, and site conditions, with crown recession represented by the difference

(Hann and Hanus, 2004). Both initial crown size and the rate of crown response to silvicultural treatments control stem growth response to intensive forest management. Improved modeling of crown dynamics by predicting individual branch growth and mortality, therefore, may lead to better predictions of tree growth across a wide range of stand conditions.

Our overall goal was to examine growth and mortality responses of individual Douglas-fir branches to intensive management regimes in the Pacific Northwest, USA. Specific objectives were to: (1) test the effects of vegetation management, PCT, fertilization, and commercial thinning, as well as Swiss needle cast (SNC; foliar disease caused by [*Phaeocryptopus gaeumannii* (T. Rohde) Petr.]) on Douglas-fir individual branch growth and mortality; (2) develop equations for predicting branch responses to silvicultural treatments based on initial tree and stand conditions; and (3) compare the individual-tree growth predicted under the dynamic equations developed in this study to growth predicted under application of static equations developed previously for Douglas-fir.

2. Methods

2.1. Study sites

Study sites were located over four installations in the Oregon Coast Range, two installations in the Oregon Cascade foothills, one installation in the southern Washington Cascade foothills, and one installation on the fringe of Willamette Valley in the foothills of Oregon Coast Ranges (Fig. 1). The climate in this
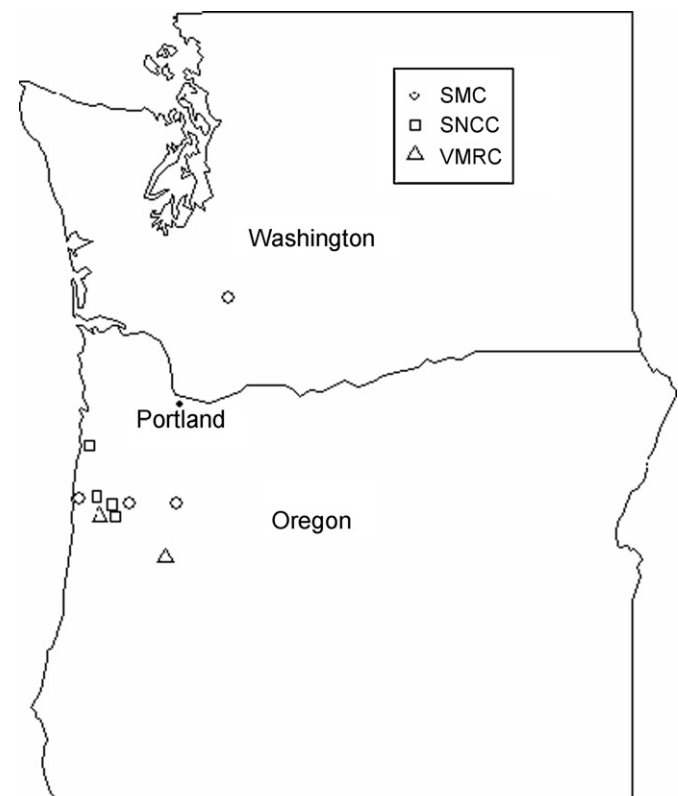

Fig. 1. Location of the study sites.

Table 1
Attributes of the installations sampled for branch growth and mortality

Installation	Latitude	Longitude	Elevation (m)	Slope (%)	Aspect (°)	# of trees sampled
SMC						
708	46.4583	−122.0688	275	5	300	12
718	44.6530	−122.7043	335	10	280	12
726	44.6917	−123.9429	90	10	225	16
914	44.6408	−123.2954	230	18	90	12
SNCC						
Devitt Ridge	44.7138	−123.7205	305	6	220	6
Jensen	44.6413	−123.5181	260	15	220	7
Simpson	44.5362	−123.4743	245	25	266	6
16	45.709	−123.9144	60	180	40	3
VMRC						
Marcola	44.6380	−123.5780	260	10	135	15
Summit	44.1730	−122.8590	234	190	10	15

The different datasets were from the Swiss Needle Cast Cooperative (SNCC), Stand Management Cooperative (SMC), and Vegetation Management Research Cooperative (VMRC).

study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 100–300 cm year^{-1} and January mean minimum and July mean maximum temperatures range from −2 to 2 °C and from 20 to 28 °C, respectively (Franklin and Dyrness, 1973). Variation in precipitation and temperature for this area is strongly correlated with elevation and proximity to the coast. Elevation ranged from sea level to 825 m. Aspects facing all cardinal directions were represented in the data.

The sampled plantations were 8- to 22-years-old at breast height and contained ≥75% Douglas-fir by basal area, with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and other conifer and hardwood species. A more complete description of the stands was outlined by Weiskittel et al. (2006b).

2.2. Data collection

Several datasets were combined to address the above objectives (Tables 1–4). The first was based on 19 sample trees in three PCT installations and 3 sample trees from one growth impact study plot that form part of the SNC cooperative permanent plot network (SNCC, Oregon State University) (Maguire et al., 2004). The second dataset comprised 52 trees in four Stand Management Cooperative installations (SMC; University of Washington) (Maguire et al., 1991a). The third dataset represented 30 trees in two Vegetation Management Research Cooperative installations (VMRC; Oregon State University) (Rose and Rosner, 2005; Rose et al., 2006). All sample trees were measured for diameter at breast height (DBH), total height (HT), and height to crown base (HCB; lowest live branch).

At each research installation, three trees per plot were measured in at least two different plots. Plots sampled from the PCT installations included a control (630–989 trees ha^{-1}), one thinned in 1998 to 494 trees ha^{-1}, and one thinned in 1998 to 247 trees ha^{-1}. Plots sampled from each SMC installation included a control (CONT), fertilized (FERT), thinned (THIN),

and fertilized + thinned (THIN + FERT). Plots were fertilized 1–4 years prior to sampling with 224 kg N ha^{-1} as urea, and were fertilized at the same rate 4 years prior to the most recent fertilization; therefore, the plots received a total of 448 kg N ha^{-1} as urea over a period of 5–8 years prior to branch measurement. Thinning prescriptions were defined by

Table 2
Initial attributes of the plots sampled for branch diameter growth and mortality by dataset in 2004

Variable	Mean	Standard deviation	Minimum	Maximum
SNCC (n_{plot} = 7)				
Trees ha^{-1}	663.4	196.5	456.9	988.0
Basal area (m^2 ha^{-1})	20.2	5.6	9.7	25.3
Relative density	4.5	0.9	2.5	5.4
Mean BH age (years)	12.8	2.1	9.6	15.6
Site index (m at 50 years)	49.5	5.9	36.7	53.5
SMC (n_{plot} = 14)				
Trees ha^{-1}	743.3	592.8	245.0	2800.5
Basal area (m^2 ha^{-1})	26.6	7.9	6.5	38.5
Relative density	5.6	1.9	1.5	9.1
Mean BH age (years)	19.9	1.9	16.0	21.5
Site index (m at 50 years)	39.3	1.5	37.5	41.2
VMRC (n_{plot} = 10)				
Trees ha^{-1}	1014.2	94.1	719.0	1101.3
Basal area (m^2 ha^{-1})	14.9	5.1	2.7	24.8
Relative density	4.0	1.1	1.1	5.9
Mean BH age (years)	7.9	0.2	7.8	8.2
Site index (m at 50 years)	38.8	2.0	37.0	41.0
ALL (n_{plot} = 31)				
Trees ha^{-1}	860.7	396.3	245.0	2800.5
Basal area (m^2 ha^{-1})	20.1	8.2	2.7	38.5
Relative density	4.7	1.6	1.1	9.1
Mean BH age (years)	13.1	5.7	7.8	21.5
Site index (m at 50 years)	40.6	4.7	36.7	53.5

The different datasets were from the Swiss Needle Cast Cooperative (SNCC), Stand Management Cooperative (SMC), and Vegetation Management Research Cooperative (VMRC). Relative density and site index are estimated based on the equations of Curtis (1982) and Bruce (1981), respectively.

Table 3
Tree-level attributes for the sample trees used in this analysis by study

Variable	Mean	Standard deviation	Minimum	Maximum
SNCC (n_{tree} = 22)				
DBH (cm)	24.0	6.1	11.6	32.6
HT (m)	14.89	2.97	9.19	19.93
HCB (m)	1.96	1.73	0.14	6.35
DGR (cm year^{-1})	1.12	0.48	0.29	1.85
HGR (m year^{-1})	1.09	0.48	0.39	2.18
SMC (n_{tree} = 52)				
DBH (cm)	27.9	6.5	12.2	42.7
HT (m)	18.28	3.01	10.15	23.97
HCB (m)	4.49	3.15	0.05	11.75
DGR (cm year^{-1})	1.19	0.60	0.20	2.91
HGR (m year^{-1})	0.76	0.41	0.10	2.51
VMRC (n_{tree} = 30)				
DBH (cm)	14.5	3.2	9.8	21.2
HT (m)	10.35	1.75	7.46	14.67
HCB (m)	0.37	0.48	0.01	1.77
DGR (cm year^{-1})	1.31	0.55	0.49	2.04
HGR (m year^{-1})	0.94	0.41	0.20	1.92
ALL (n_{tree} = 103)				
DBH (cm)	24.7	7.8	9.8	42.7
HT (m)	15.99	4.15	7.46	23.97
HCB (m)	3.12	3.05	0.01	11.75
DGR (cm year^{-1})	1.17	0.57	0.20	2.91
HGR (m year^{-1})	0.87	0.45	0.10	2.51

Diameter at breast height (DBH; cm), total tree height (HT; m), height to crown base (HCB; m; lowest live branch), diameter growth rate (DGR; cm year^{-1}), and height growth rate (HGR; m year^{-1}).

Table 4
Attributes of the individual branches remeasured for growth by study

Variable	Mean	Standard deviation	Minimum	Maximum
SNCC (n_{branch} = 264)				
BD (mm)	24.03	7.91	2.80	43.25
BHT (m)	8.44	4.42	0.35	17.00
RHACB	0.60	0.27	0.10	1.01
BDG (mm year^{-1})	1.67	1.68	0.01	13.01
SMC (n_{branch} = 669)				
BD (mm)	26.24	9.17	3.40	56.40
BHT (m)	11.26	4.41	0.63	18.90
RHACB	0.58	0.26	0.10	0.97
BDG (mm year^{-1})	1.73	1.59	0.01	10.80
VMRC (n_{branch} = 223)				
BD (mm)	18.13	6.62	3.00	37.65
BHT (m)	4.36	2.62	0.30	10.18
RHACB	0.50	0.24	0.11	0.84
BDG (mm year^{-1})	1.19	1.24	0.01	7.53
ALL (n_{branch} = 1156)				
BD (mm)	24.17	8.99	2.80	56.40
BHT (m)	9.28	4.91	0.30	18.90
RHACB	0.57	0.26	0.10	1.01
BDG (mm year^{-1})	1.61	1.56	0.01	13.01

Branch diameter (BD; mm), branch height above ground (BHT; m), tree total height (HT; m), relative height above crown base (1.1 − ((HT − BHT)/crown length); RHACB), and branch diameter growth rate (mm year^{-1}).

relative stand density (stand basal area/$\sqrt{}$quadratic mean diameter) (Curtis, 1982) and called for thinning to either 35 or 40 relative density after reaching 55 and 60, respectively. The sampled VMRC plots included: the control, 3.34 m^2 of total vegetation control (TVC) per tree, 9.29 m^2 of TVC per tree, complete removal of woody only vegetation (WDY), and complete removal of herbaceous only vegetation (HRB).

Within each plot, three trees were randomly selected at the 25th, 63rd, and 93rd diameter percentile, which were used to ensure an intermediate, co-dominant, and dominant tree in each plot. Each tree was then climbed in the late summer of 2004 and every branch (living + dead) between the stem base and the 3-year-old whorl was measured for height at insertion and diameter. Branch diameter was measured both horizontally and vertically approximately 5 cm from the bole to avoid the basal swell. All measured branches were also coded as either true north (<90° or >270°) or south (>90° or <270°). The 3-year-old whorl, every third whorl after the 3-year-old whorl, and the bottom three whorls with at least one live branch were selected for sampling. At each of these sampling locations, a subsample of branches (3 whorl, 2 interwhorl) was measured for aspect (azimuth to nearest degree), angle of insertion, total length, and non-foliated length. All live branches at these locations were then tagged for future reference. In the late summer of 2006 (August to September), each tree was reclimbed and all tagged branches were remeasured for diameter growth (to the nearest 0.1 mm) and condition (live versus dead).

2.3. Data analysis

2.3.1. Treatment effects

Treatment effects on branch mortality and growth were tested by analysis of covariance with initial branch size, branch location, and tree size as the covariates. Treatments were tested using indicators variables. The sampling scheme has a distinct hierarchical structure (multiple measurements within whorls, within trees, within plots, and within installations), so violated the assumption that error terms were independent and uncorrelated. A multilevel, mixed-model analysis allowed for four random effects on branch growth and mortality: installation effects, plot effects, tree effects, and whorl effects. When heteroscedasticity was detected in the residual plots, the final equation was weighted by a power variance function of the primary independent variable. A continuous first-order auto-regressive term (φ) on distance from the tree tip to reduce any remaining significant autocorrelation was tested and a like-lihood ratio test indicated that it did significantly improve the performance of the branch diameter growth model, but not the branch mortality model. Nested model forms were compared with likelihood ratio tests. Models were fitted with the NLME and glmmPQL package of S-PLUS v6.2 (Mathsoft, Seattle, WA).

2.3.2. Predictive equations

Initial model forms for branch dynamics were based on nonlinear diameter growth equations and logistic mortality equations developed for individual trees (Hann et al., 2003).

Influential variables were identified by all subsets regression from an initial set that included bole and crown size, tree social position in the stand, observed tree growth, and stand density. Several variables describing branch location within the tree were tested including depth into crown (DINC, m), branch height above ground (BHT, m), and relative height above crown base (RHACB; $1.1 - $ (DINC/crown length)). RHACB was calculated with 1.1 rather than 1.0 so that it would be nonzero for the lowest live branch (i.e. DINC = crown length) thereby avoiding computational problems in log-transformed and nonlinear regressions. Severity indices for Swiss needle cast (SNC) included mean plot-level foliage retention (years; FOLRET), tree-level crown sparseness (CLSA, ratio of crown length to sapwood area at crown base), and mean plot-level crown sparseness (Maguire and Batista, 1996; Maguire and Kanaskie, 2002). FOLRET is visually assessed with the aid of binoculars in each crown third of 10 dominant and co-dominant trees and averaged for each stand. Healthy stands have a FOLRET of 3–4, while stands with severe SNC have values between 1 and 2 (Maguire et al., 2002). Final models were selected on the basis of residual analysis, Akaike's information criterion (AIC) and biological interpretability. Because the data were collected on a 2-year remeasurement cycle, the growth parameters were annualized using the technique of Cao (2000).

2.3.3. Simulation

The relative performance of branch growth and mortality equations over the more conventional approach of modeling change in height to crown base at the crown level was assessed by simulating 4-year growth responses to various silvicultural treatments. Tree growth data for verification and testing were collected from 56 plots from nine SMC installations in Oregon and Washington, USA. The plantations were established between 1971 and 1982 at varying densities and levels of vegetation control, and covered a wide range of growing conditions. Initial planting densities ranged from 905 to 1575 trees ha^{-1}, and some plots have received subsequent silvicultural treatments involving both thinning and nitrogen fertilization.

The branch-based simulations were performed by combining the branch growth and mortality equations with annualized diameter and height growth equations developed for individual trees (Weiskittel et al., 2007a). In the conventional approach, growth was simulated by forecasting crown size with a static height to crown base equation (Hann et al., 2003). Preliminary analysis indicated that the fertilization and thinning modifiers for diameter growth, height growth, and height to crown base (Hann et al., 2003) did not significantly improve the projections, so they were left out. Height to crown base in the SMC verification dataset was defined as the lowest whorl with at least three live branches (compacted crown ratio). Because the tree growth equations defined height to crown base as lowest live branch (uncompacted crown ratio) (Weiskittel et al., 2007a), each SMC height to crown based was converted to height of lowest live branch (Monleon et al., 2004). Mean bias (observed − predicted), mean square error (MSE), and mean percent bias were calculated for diameter growth, height

growth, and change in height to crown base of each individual-tree in the verification dataset, then these statistics were compared between the two simulation approaches. Validation statistics for diameter growth were computed from all Douglas-fir trees on the 56 plots, and validation statistics for height and height to crown based were computed from only the Douglas-fir height subsample from the same 56 plots.

3. Results

3.1. Branch diameter growth

3.1.1. Treatment effects

Control of competing vegetation on the VMRC plots had no significant effect on branch diameter growth. However, branch growth increased significantly after precommercial thinning on the SNCC PCT plots ($p = 0.0345$), and declined with increasing SNC severity ($p = 0.05$; Fig. 2). Branch growth was more closely related to tree-level crown sparseness than either foliage retention or stand-level crown sparseness. On average, severe SNC (FOLRET = 1.5 years) reduced branch growth by 36% when compared to a healthy stand (FOLRET = 3.5 years), while precommercial thinning increased growth by 49% on average.

In the SMC dataset, both thinning ($p = 0.0021$) and fertilization ($p = 0.0003$) had a significant influence on branch diameter growth. The effects of these treatments, however, depended on time since treatment ($p = 0.0060$; Fig. 3). Fertilization initially led to a faster growth rate, while thinning temporarily reduced growth. Several years after treatment, branches on thinned plots were growing similar to the control, while those on fertilized trees were growing more slowly. In contrast, the combination of thinning and fertilization initially elevated branch diameter growth to a rate faster than that of the control but slower than that of the fertilized trees; however, by the fourth growing season after last treatment the branches on
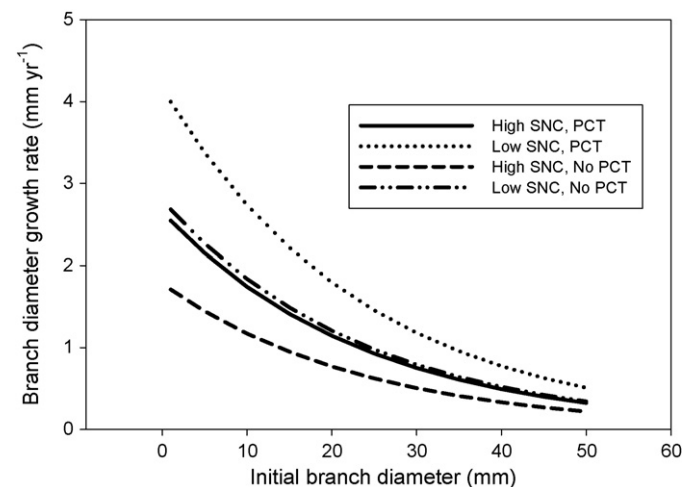

Fig. 2. Predicted branch diameter growth (mm year^{-1}) for a mid-crown whorl branch over initial branch diameter (mm) at varying levels of Swiss needle cast (SNC) disease with and without precommercial thinning (PCT). The difference levels of SNC are high (foliage retention = 1.5 years) and low (foliage retention = 3.5 years).
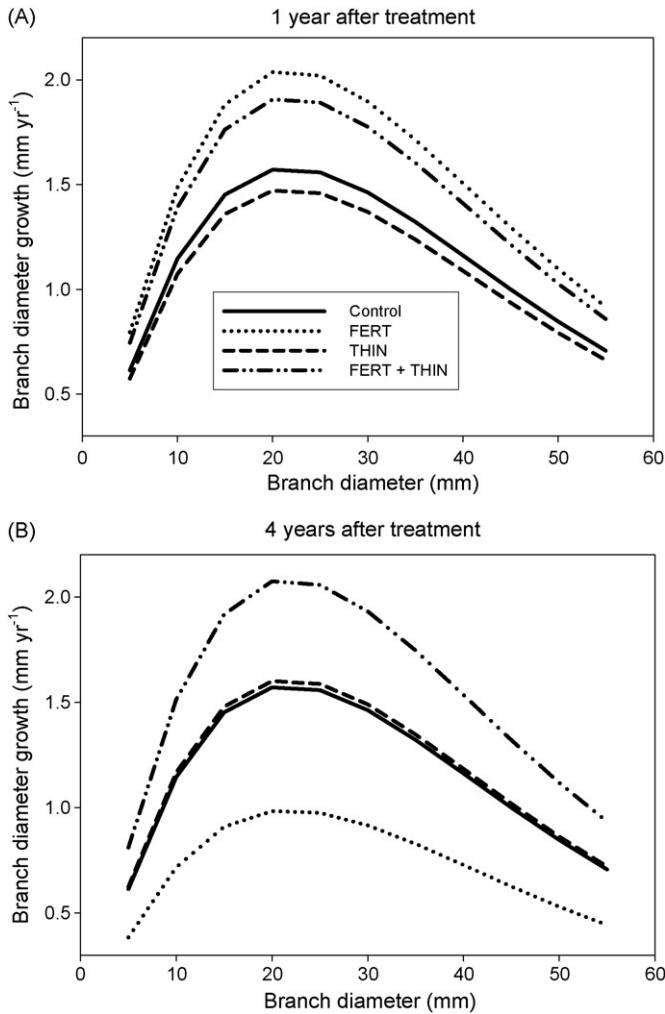
(A) 1 year after treatment

(B) 4 years after treatment

Fig. 3. Predicted branch diameter growth (mm year^{-1}) for a mid-crown whorl branch over initial branch diameter (mm) one (graph A) and four (graph B) years following treatment.

thinned and fertilized plots were growing up to 0.5 mm year^{-1} faster than all other treatments.

3.1.2. Predictive equation

Individual branch diameter growth in the comprehensive dataset was significantly correlated with tree DBH growth and volume growth, but was not correlated with tree HT growth.

Table 5
Parameter estimates and standard errors for branch diameter growth (Eq. (1)) determined using nonlinear multilevel mixed effects regression

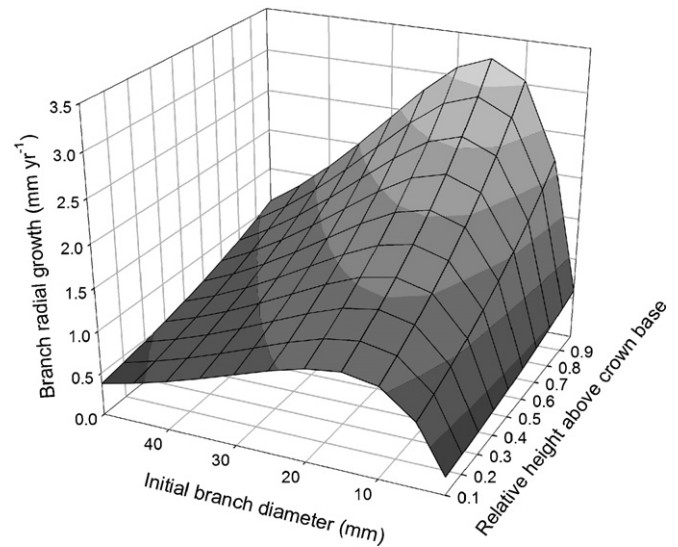| Parameter	Estimate	Standard error
β_{10}	−0.8201	0.3809
β_{11}	−0.0646	0.0119
β_{12}	0.9564	0.2885
β_{13}	0.3232	0.0811
β_{14}	1.1801	0.1178
β_{15}	−0.3202	0.1148
β_{16}	0.1776	0.0540
β_{17}	0.0365	0.0109
φ	0.4507	–

Fig. 4. Predicted branch radial growth using equation (1) over initial branch diameter (mm) and relative height above crown base. The other covariates were set at their mean levels, which were 5 cm cm^{-2}, 50 cm^2, and 10 m for crown sparseness, tree basal area growth, and height to crown midpoint, respectively.

The final model form was:

$$BDG = \exp(\beta_{10} + \beta_{11} * BD + \beta_{12} * \ln(BD) + \beta_{13} * W + \beta_{14} * RHACB + \beta_{15} * CLSA + \beta_{16} * BAGR + \beta_{17} * HCM) + \varepsilon_1 \tag{1}$$

where BDG is annualized branch diameter growth rate (mm year^{-1}), BD is initial branch diameter (mm), W is an indicator variable for branch type (1 if whorl branch, 0 otherwise), RHACB is relative height above crown base, HCM is height to crown midpoint (m), BAGR is annualized tree basal area growth rate measured over the same growth period (m^2 year^{-1}), CLSA is tree crown sparseness index (Maguire and Kanaskie, 2002) with sapwood area at crown base predicted using the equation of Maguire and Batista (1996), the β_i's are parameters estimated from the data, and $\varepsilon_1^{iid} \sim N(0, \sigma_1^2)$ (Table 5; Fig. 4). The fixed effects explained 23% of the original variation in branch diameter growth and had a root mean square error (RMSE) of 0.38 mm. No significant treatment effects were detected after accounting for these covariates. The marginal residuals showed no trends with explanatory variables.

3.2. Branch mortality

3.2.1. Treatment effects

Annual probability of branch mortality was significantly influenced by respective treatments in the PCT/SNC, VMRC, and SMC datasets. Although precommercial thinning had no significant effect, the probability of branch mortality increased with increasing SNC severity as measured by mean stand crown sparseness ($p < 0.0001$; Fig. 5).

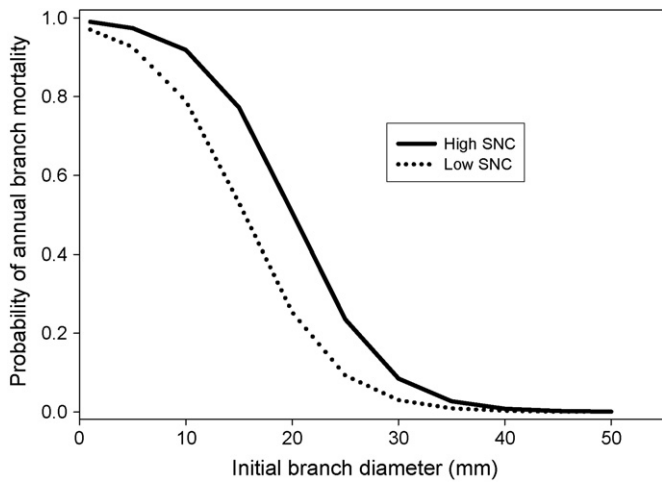All vegetation control treatments on the VMRC plots had a significant effect on branch mortality rate, with the

Fig. 5. Predicted probability of annual branch mortality over initial branch diameter in a stand with high (CLSA$_{mean}$ = 6) and low (CLSA$_{mean}$ = 4) Swiss needle cast (SNC).

exception of 3.34 m^2 of total vegetation control (TVC). The probability of branch mortality was significantly higher in the herbaceous only treatment ($p = 0.0015$) than in the control, but significantly lower in both the woody only ($p = 0.0014$) and 9.29 m^2 of TVC treatments ($p = 0.0181$; Fig. 6).

Branch mortality was particularly sensitive to silvicultural treatments in the SMC dataset. Thinning ($p < 0.0001$), fertilization ($p < 0.0001$), and the interaction of these treatments ($p = 0.0008$) significantly influenced the probability of branch mortality after accounting for several other covariates (i.e. branch size and location, tree size). In the first growing season following treatment, the probability of branch mortality was significantly higher in fertilized plots and significantly lower in thinned plots when compared to
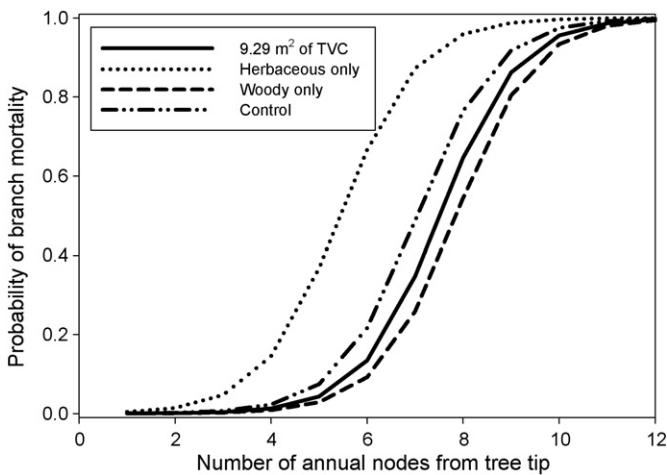

Fig. 6. Predicted probability of individual branch mortality 14 years after application of several different vegetation management treatments over the number of annual nodes from tree tip at a mean branch and tree diameter at breast height of 15 mm and cm, respectively. The vegetation management treatments included 9.29 m^2 of total vegetation control (TVC), herbaceous only removal, and woody only removal.
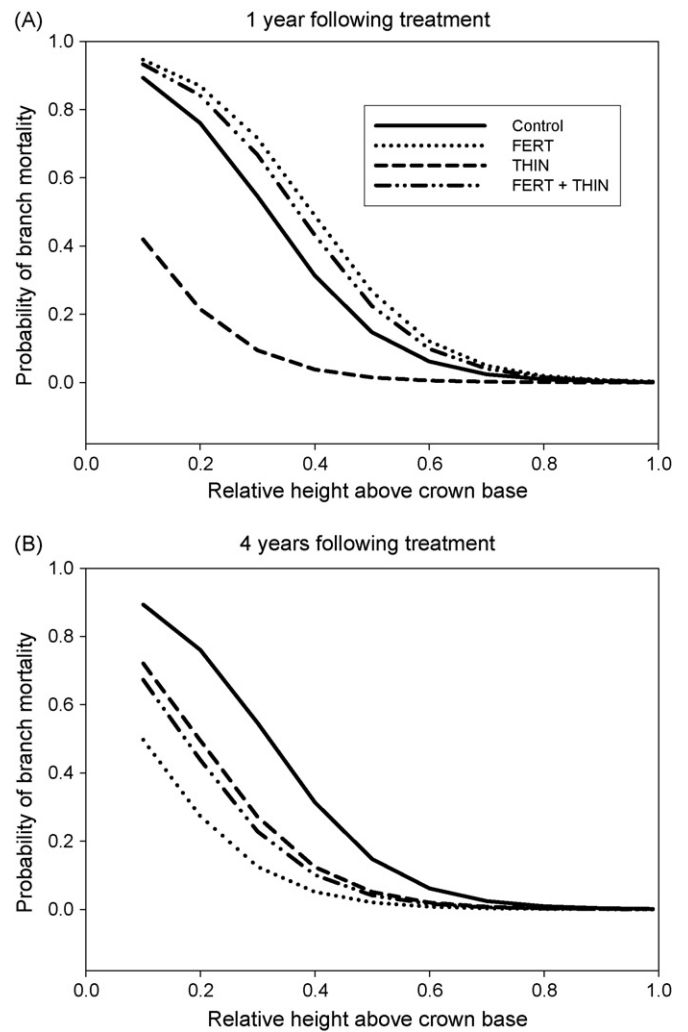

Fig. 7. Predicted annual probability of individual branch mortality at a mean branch diameter, summation of branch diameters above subject branch, and height to crown midpoint over relative height above crown base one (graph A) and four (graph B) years following treatment.

the control (Fig. 7). However, in the fourth growing season after treatment, the probability of branch mortality was significantly lower under all three treatments relative to the control.

3.2.2. Predictive equation

Variables representing branch size, branch height, tree size, stand density, and plot-level SNC severity were significant predictors of annual branch mortality. The final form of the equation was:

$$\text{logit}(P_{\text{MORT}})$$
$$= \beta_{20} + \beta_{21} * \text{BD} + \beta_{22} * \text{RHACB} + \beta_{23} * \ln(\text{BDA}) + \beta_{24} * \text{HCM} + \beta_{25} * \text{RD}_{\text{DF}} + \beta_{26} * \text{CLSA}_{\text{mean}} + \varepsilon_2 \qquad (2)$$

where $\text{logit}(P_{\text{MORT}})$ is $\ln[P_{\text{MORT}}/(1 - P_{\text{MORT}})]$, P_{MORT} is an indicator for mortality (1 if dead, 0 otherwise), BDA is the initial diameter sum of all live branches above the subject branch (mm), RD_{DF} is initial Douglas-fir relative density

Table 6
Parameter estimates and standard errors for branch mortality (Eq. (2)) determined using nonlinear multilevel mixed effects regression

Parameter	Estimate	Standard error
β_{20}	−11.8914	1.8335
β_{21}	−0.1394	0.0095
β_{22}	−7.2184	0.6241
β_{23}	2.0107	0.2292
β_{24}	−0.0649	0.0271
β_{25}	0.4070	0.0537
β_{26}	0.1299	0.0331

($m^2 \, ha^{-1} \, \sqrt{cm^{-1}}$) (Curtis, 1982), $CLSA_{mean}$ is initial mean stand-level crown sparseness index (Maguire and Kanaskie, 2002), the β_i's are parameters estimated from the data, and $\varepsilon_1^{iid} \sim N(0, \sigma_1^2)$ (Table 6; Fig. 8). The fixed effects explained 46% of the original variation in branch mortality. No significant treatment effects were observed after accounting for these variables. The equation correctly classified 85.3% of the observations.

3.3. Simulation

Simulation of crown dynamics with branch growth and mortality equations ((1) and (2)) reduced mean square error (MSE) of crown recession by 15% on the fertilized and thinned SMC plots, when compared to simulation with a static height to crown base equation (Table 7). Bias was quite high (−68%) with the static HCB approach, but precision was better. Branch-level crown dynamics improved mean accuracy in both diameter and height growth (reduction in mean bias), but the static HCB resulted in a lower MSE for the growth predictions. At the stand-level, the simulation of crown dynamics led to very slight improvements of volume growth for each of the treatments when compared the static HCB equation (Table 8).
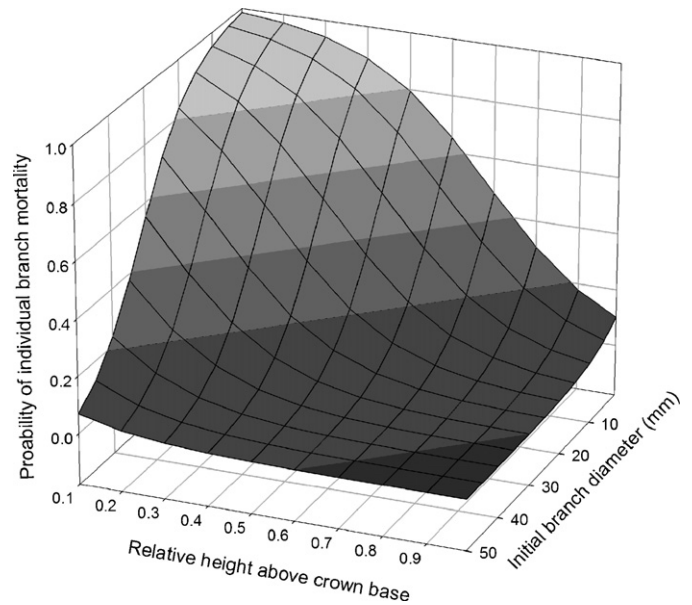

Fig. 8. Predicted individual branch probability of mortality using equation (2) over initial branch diameter (mm) and relative height above crown base. The other covariates were set at their mean levels, which were 180 cm, 12 m, 5, and 5 cm cm^{-2} for summation of branch diameter above the subject branch, height to crown midpoint, relative stand density, and mean crown sparseness, respectively.

4. Discussion

Repeated measurement of tagged branches provided unique insight into the response of branch growth and mortality to silvicultural treatment. On permanent plots, the change in height to crown base or change in crown ratio is the more common attribute to monitor (e.g. Curtis and Marshall, 2005), but change in both of these crown measures is the net outcome of individual branch responses to any increase in the availability of light, water, nutrients, and growing space imposed by treatments. Stem dissection can provide reasonable estimates of past branch growth and mortality (Andrews and

Table 7
Mean bias (observed − predicted), mean square error (MSE), and percent bias (%) for diameter at breast height (DBH, cm), height (HT, m), and height to crown base (HCB, m) using the Weiskittel et al. (2007a) growth model with static HCB and dynamic crown equations on 56 Stand Management Cooperative plots with varying levels of intensive management in Oregon and Washington, USA

Model	DBH (cm; $n = 9162$)			HT (m; $n = 2608$)			HCB (m; $n = 2608$)		
	Mean bias	MSE	%Bias	Mean bias	MSE	%Bias	Mean bias	MSE	%Bias
Static HCB equation	−0.19	1.11	−1.57	−0.56	0.96	−3.76	−0.84	0.99	−68.08
Dynamic crown equations	−0.01	1.22	−0.66	−0.63	1.00	−4.09	−0.08	0.92	−22.34

Table 8
Mean square error (MSE) and its standard deviation for predicted stand-level volume growth (m^3 ha^{-1}) on the verification dataset representing 56 Stand Management Cooperative plots receiving various silvicultural treatments

Model	Control ($n = 11$)	Thinned ($n = 9$)	Fertilized ($n = 17$)	Fertilized + thinned ($n = 19$)
Static HCB equation	3.33 ± 2.62	2.20 ± 1.69	2.45 ± 1.31	1.14 ± 1.27
Dynamic crown equations	3.29 ± 2.65	2.17 ± 1.70	2.39 ± 1.31	1.12 ± 1.29

Gill, 1939; Maguire and Hann, 1987), but some estimation error is inevitable, and the technique does not allow accurate reconstruction of initial stand conditions.

4.1. Branch growth

The profile of Douglas-fir maximum branch diameter over height within the live crown has previously been found sensitive to several intensive management practices (Weiskittel et al., 2006b). Maximum branch diameters, for example, were larger in the upper crown of fertilized trees and smaller in the lower crown relative to untreated trees of similar size. Because the profile of maximum branch size can typically be estimated from tree diameter, height, and crown length, this result suggested that fertilization altered to some degree the allometric relationships between tree and branch dimensions, presumably by altering branch growth and/or mortality for a given set of initial conditions. Maximum branch diameter profiles are important components of individual-tree growth and yield models that simulate silvicultural influences on knot size as one determinant of wood quality (Colin and Houllier, 1991; Maguire et al., 1991b). However, because these static models accommodate the decline in maximum branch diameter near crown base (Colin and Houllier, 1991; Maguire et al., 1999; Mäkinen et al., 2004), their repeated application to simulated or real trees over time can imply negative diameter growth in the lowest branches. Direct modeling of branch growth is therefore more appealing because growth can easily be constrained to a minimum of zero.

In this study of intensively managed Douglas-fir stands, the radial growth of a branch depended on both branch- and tree-level variables. The former included initial branch diameter, position within the crown, and branch type (interwhorl vs. whorl), and the latter included crown size and diameter growth rate. In general, branch diameter growth accelerated rapidly, peaked when the branch was around 6 mm in size and then decreased markedly as a negative exponential function of branch age. This growth pattern has been observed in other studies and other coniferous species (Kershaw et al., 1990; Mäkinen, 1999a,b). However, Mäkinen (2002) observed a different pattern in a broadleaved tree, *Betula pendula*. In this species branch radial increment was higher in the second year than in the first, and was more variable during the first 5–6 years of branch development than in conifer species (Mäkinen, 2002).

Half or more of the life of a branch can be spent without perceivable increment (Kershaw et al., 1990) due both to self-shading within a tree crown (Sampson and Smith, 1993) and to competition from other trees (Mäkinen, 1996). Although incompletely understood, branch diameter growth is most likely influenced by a combination of light interception, plant growth regulators, water potentials, and respiratory load (Kozlowski and Pallardy, 1997). In addition, wind may be a particularly important factor in certain areas as indicated by Watt et al. (2005). Light availability; however, appears to be the primary driving factor for branch diameter growth (Mäkinen, 2002). In our study of Douglas-fir, relative height of the branch

within the crown can be interpreted as a surrogate for light availability, although it may also be related to one or more of the other factors listed above. In fact, relative height of the branch was the strongest predictor variable probably because it integrated the effects of branch age, light environment, and competition for water and nutrients.

If silvicultural treatments have little or no effect on allometric relationships within the tree, and if treatment effects on tree diameter, height, and crown length are known or are predictable, then treatment effects on branch growth are implied by changes in these standard tree dimensions. Several studies have found annual variation in radial increment to be similar in the stem and branches (Cannell, 1974; St. Clair, 1994; Mäkinen, 1999b), and this relationship likewise does not change noticeably after a change in stand conditions (Mäkinen, 1999b). Consistent with this result, the intensity of inter-tree competition was shown to have little influence on radial growth trends in branches (Mäkinen, 1996; Wichmann, 2002). Branch radial growth in our study of Douglas-fir was likewise related to tree basal area growth, with little additional effect of change in stand conditions imposed by silvicultural treatment. However, other tree-level variables such as height to the crown midpoint and crown sparseness probably represented past and present inter-tree competition and site conditions, respectively, and therefore also accounted for some of the variation in branch radial growth. Tree basal area growth was not sufficient to account for all the variation in branch radial growth across a wide range of stand conditions, so information on local inter-tree competition is desirable for increasing the accuracy and precision of predictions. Some previous research has shown that branch radial growth also varies by aspect in the crown, with growth being greatest in the south-facing half of trees (Wichmann, 2002). Only moderate evidence for differential growth by aspect was observed in this study, however, and its high variability was consistent with results for other species (Grace et al., 1999).

In general, branch diameter growth in the upper, free-growing part of the crown is influenced by physical site conditions and genetic potential, whereas growth in the lower portion of the crown is largely controlled by the local competitive environment (Mäkinen, 1996). Stand structure, particularly stand density, has been shown to influence branch radial growth (Colin and Houllier, 1991; Mäkinen, 1999a), but as indicated above, past and current competition effects often are sufficiently represented by the combination of tree-level variables, particularly those incorporating relative crown size. The branch diameter growth patterns that we observed in Douglas-fir were significantly influenced by thinning, fertilization, and Swiss needle cast severity. SNC significantly reduces the leaf area held by individual branches throughout the crown (Weiskittel et al., 2006a), leaving the branch with a lower photosynthetic capacity and reduced growth potential. However, even at severe levels of SNC, branch radial growth responded positively to precommercial thinning and could achieve rates similar to those observed in healthy, unthinned stands.

Fertilization has been shown to significantly increase diameter growth of *Picea abies* branches initiated both before

and after treatment (Mäkinen et al., 2001). Although the corresponding increase in stem diameter suggested that allometric relationships between the stem and branches were maintained, the greater increase in branch growth in the top half of the tree was similar to the response of upper branches of fertilized Douglas-fir observed in this study. Response to fertilization in Douglas-fir, however, depended on time since application. Initially, branch diameter growth was uniformly enhanced by fertilization for a given set of initial branch and tree conditions; however, 4 years after treatment and for a given set of initial conditions, branch diameter growth was actually slower in the fertilized plots. Because tree diameter growth rate for the same growth period is a predictor variable, a given tree diameter increment represents a greater basal area increment by the fourth year after treatment, particularly if the trees have responded to the fertilizer. Fertilization effects therefore accumulate in the tree basal area growth variable with each year, as well as in variables such as height to crown midpoint and mean CLSA. These cumulative treatment effects on predictor variables change the expectation for branch growth, and interpretation of branch growth is therefore similar to distinguishing between direct and indirect effects on stem growth responses in successive years after fertilization. Part of the change in stem to branch allometry, particularly that related to the faster branch growth in the upper part of the crown and slower growth in the lower part, is probably attributable to the rapid buildup of leaf area after fertilization (e.g. Gough et al., 2004) and the consequent increased levels of self-shading (e.g. Balster and Marshall, 2000). This short term direct effect likely diminishes with increasing time since treatment, leading to the common conclusion that site fertility and fertilization regime do not influence branch radial growth patterns relative to overall tree growth rate (Mäkinen et al., 2004).

The primary effect of thinning on branch radial growth is exerted through the increase in branch longevity and, hence, duration of radial growth before suppression (Brix, 1981; Mäkinen, 1999a). Branch radial growth was significantly greater even 8 years after precommercial thinning in Douglas-fir than in unthinned stands, for a given set of initial conditions. Although commercial thinning also had a significant positive effect on branch radial growth, the increase for a given branch and tree size was quite small. The change in branch radial growth with time since thinning was similar to thinning 'shock' sometimes observed at the tree level; that is, branch growth was initially reduced by the thinning relative to the control, but climbed to a level slightly greater than those on trees from unthinned plots. The combination of thinning and fertilization, however, maintained branch radial growth that was significantly higher than the control and the thinned or fertilized treatments.

4.2. Branch mortality

Crown recession has been modeled for a number of different forest types (Krumland and Wensel, 1981; Maguire and Hann, 1987; Short and Burkhart, 1992; Hann and Hanus, 2004). Although branch growth and mortality has been of interest to

tree physiologists (Ford and Ford, 1990; Sprugel, 1991), few crown recession models have been driven by simulating suppression mortality of individual branches. This approach has been limited by the lack of long-term monitoring of tagged branches on permanent plots and by several difficulties associated with reconstructing branch mortality by stem dissection. With regard to the latter, branch mortality can be difficult to date exactly because branches can remain alive after annual ring formation has ceased (Mäkinen, 2002). Some hardwood branches can stay alive an average of 2–4 years without producing annual rings (Mäkinen, 2002), while values between 0 and 10 years are common for many conifers (Reukema, 1959; Kershaw et al., 1990; Fujimori, 1993). In addition, xylem in the stem can still be connected directly to the xylem of the branch for several years after the branch has lost all its green needles (Shigo, 1985). From a physiological perspective, branch mortality is generally thought to occur when its net carbon balance becomes negative (Witowski, 1996); however, the concept of negative branches (Larson, 1963) continues to be debated (e.g. Lacointe et al., 2004). The carbon balance of a branch is usually regarded as driven by light availability. However, Portz et al. (2000) found that branch mortality in *Pinus contorta* var. *latifolia* occurred not only from low light, but also from reduced stomatal conductance and lowered photosynthesis, both of which were imposed by shade-initiated reductions in earlywood, tracheid diameter and branch hydraulic conductivity.

Previous studies have suggested that the timing of branch mortality is largely governed by its distance from the tree tip, relative branch diameter in the whorl, and tree age and social position (Kershaw et al., 1990; Mäkinen and Colin, 1999). In our Douglas-fir trees, branch mortality was likewise a function of its diameter and location in the crown, as well as several tree- and stand-level factors. Whorl and tree age were avoided as a covariates because their proximate effects were assumed to represent other ultimate factors more closely related to the driving mechanisms. The summation of branch diameters above the subject branch simultaneously accounted for factors associated with whorl age, tree age, relative position of the tree in the stand, and relative diameter of the branch within the whorl. The probability of branch mortality was also positively related to two stand-level variables, relative density and mean crown sparseness, representing the degree of canopy crowding and crown deterioration, respectively. Umeki and Kikuzawa (2000) similarly found that branch mortality was related to inter-tree competition, even after accounting for the size of both the branch and the tree.

Stand density and age have been shown to be strong determinants of branch mortality rate. Branches tend to stay alive for a longer time in older and less dense stands than in young and highly dense stands (Kershaw et al., 1990; Fujimori, 1993; Mäkinen and Colin, 1999). The age effect can be largely attributed to the deceleration in height growth and corresponding rate of canopy rise as the trees age. Genetics apparently plays a relatively minor role in determining branch mortality rates, as suggested by lack of significant differences in height to live crown and number of live whorls among families and low

estimates of heritability (St. Clair, 1994). Maguire and Kanaskie (2002) suggested that one mechanism leading to greater CLSA in stands with severe SNC could be deeper penetration of light into the lower canopy and slower crown recession. However, the greater probability of branch mortality that paralleled increasing SNC severity in this study was consistent with Weiskittel's (2003) observation that height to crown base was also greater in trees with severe SNC, all other conditions being equal. Although SNC infection levels tend to be highest in the upper crown (Manter et al., 2003), the disease also drastically reduces branch leaf area in the lower crown (Weiskittel et al., 2006a).

Despite the lack of a significant effect of competing vegetation control on branch radial growth, these treatments did alter branch mortality patterns. Compared to control plots with no treatment of competing vegetation, complete removal of herbaceous species accelerated branch mortality rate, but, both complete removal of woody species and total vegetation removal slowed the branch mortality rate. Hardwood basal area was much higher in the treatments not receiving any woody vegetation control (i.e. control and complete removal of herbaceous species), particularly at the hardwood conversion site in the central Oregon Coast Range (Rose and Rosner, 2005; Rose et al., 2006). The lack of hardwood competition allowed trees receiving complete removal of woody species and total removal of both woody and herbaceous species to maintain their crowns, particularly in the total vegetation control treatment. Although trees in the herbaceous only treatment had to compete with more woody species, so they had higher branch mortality rates than the control. However, volume growth was significantly greater in the herbaceous only treatment (Rose and Rosner, 2005).

Thinning in the intensively managed Douglas-fir stands reduced branch mortality rates immediately after thinning and up to 4 years later. Fertilization, however, initially accelerated branch mortality relative to the controls, but this effect reversed by year four to a lower rate of mortality. The response to combined thinning and fertilization tracked the response to fertilization only, but with slightly less dramatic departure from control responses. In general, these results agree with those of other studies. Thinning has been found to significantly slow branch mortality rate (e.g. Brix, 1981), and fertilization can significantly accelerate mortality and reduce branch longevity (e.g. Albaugh et al., 2006). The only apparent point of disagreement is lower probability of mortality after 4 years. The early increase in mortality rate is likely due to the rapid buildup of leaf area, the greater degree of self-shading, and the more rapid rise of the whole canopy caused be accelerated height growth. The later decline in branch mortality rate may be attributable to the greater amount of leaf area on a given branch (Kershaw and Maguire, 1995) and the possibility that this additional leaf area allows the branch to maintain a positive carbon balance for a longer period of time. Fertilization can also significantly increase branch sapwood permeability and hence elevate leaf specific conductivities, even in lower crown branches (Amponsah et al., 2004). The improved water relations may also help to prolong branch longevity following

fertilization, but may also reduce the amount of water available to upper branches. The latter response would also help to explain the observed decline in branch radial growth rates compared to the control several years after fertilization.

4.3. Simulation

Equations that describe branch size and location and that are capable of predicting their growth and mortality have been integrated into several growth and yield simulators (Mäkelä et al., 1997; Siefert, 2003). The applicability of these models for simulating the effects of silvicultural activities on stem wood quality has been demonstrated (e.g. Mäkelä and Makinen, 2003), but their relative performance for predicting growth has not been tested. In this study of intensively managed Douglas-fir stands, simulating the behavior of individual branches significantly improved short-term predictions of individual-tree crown recession across a wide range of silvicultural treatments. However, the improved crown dynamics did not result in a corresponding significant improvement in diameter and height growth predictions. Improved modeling of crown size dynamics apparently did not fully capture the response mechanisms that explain tree growth responses to silvicultural treatments such as the tree leaf area. Additional work may be necessary to characterize branch- or crown-level leaf area differences, to introduce treatment effects on crown or needle growth efficiencies, or to develop empirical diameter and height growth modifiers for various silvicultural treatments. Better growth predictions also feedback into the simulated crown dynamics because branch growth and mortality are closely linked to tree and stand conditions.

5. Conclusion

Tree crowns are the key link between silvicultural treatments and various types of tree growth responses; however, detailed studies of long-term crown and branch responses to silvicultural treatments are lacking, particularly across a range of site and stand conditions. A total of 2828 branches on 103 trees were monitored in this study, representing a variety of silvicultural trials throughout the Pacific Northwest, USA. Individual branch radial growth and/or mortality were sensitive to competing vegetation control, thinning, fertilization, and Swiss needle cast intensity, but their effects were accounted for by inclusion of variables such as tree basal area growth, size and location of the crown, and branch size and relative height in the crown. Patterns in branch growth and mortality were highly dependent on time since silvicultural treatment in this study. Simulations run with the equations developed in this study combined with previously constructed individual-tree growth equations performed better for short-term predictions of crown recession than simulations run with the same growth equations but static models of height to crown base. However, this improvement in simulated crown recession did not translate into significantly better predictions of diameter and height growth. The physiological processes driving both crown dynamics and tree growth responses to silvicultural treatments

are poorly understood, but better representation of branch and crown dynamics may help to improve predictions of growth under a wide range of silvicultural treatments and regimes.

Acknowledgments

References

Albaugh, T.J., Allen, H.L., Fox, T.R., 2006. Individual tree crown and stand development in *Pinus taeda* under different fertilization and irrigation regimes. For. Ecol. Manage. 221, 155–169.

Amponsah, I.G., Lieffers, V.J., Comeau, P.G., Brockley, R.P., 2004. Growth response and sapwood hydraulic properties of young lodgepole pine following repeated fertilization. Tree Physiol. 24, 1099–1108.

Andrews, S.R., Gill, L.S., 1939. Determining the time branches on living trees have been dead. J. Forestry 37, 930–935.

Balster, N.J., Marshall, J.D., 2000. Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. Tree Physiol. 20, 1191–1197.

Brix, H., 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. For. Res. 11, 502–511.

Bruce, D., 1981. Consistent height-growth and growth-rate estimates for remeasured plots. For. Sci. 4, 711–725.

Cannell, M.G.R., 1974. Production of branches and foliage by young trees of *Pinus contorta* and *Picea sitchensis*: provenance differences and their simulation. J. Appl. Ecol. 11, 1091–1115.

Cao, Q.V., 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. For. Sci. 46, 127–131.

Colin, F., Houllier, F., 1991. Branchiness of Norway spruce in north-eastern France: modeling vertical trends in maximum nodal branch size. Ann. For. Sci. 48, 679–693.

Curtis, R.O., 1982. A simple index of stand density for Douglas-fir. For. Sci. 28, 92–94.

Curtis, R.O., Marshall, D.D., 2005. Permanent-plot procedures for silvicultural and yield research. In: General Technical Report PNW-GTR-637. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, p. 86.

Ford, E.D., Avery, A., Ford, R., 1990. Simulation of branch growth in the *Pinaceae*: interactions of morphology, phenology, foliage production, and the requirement for structural support, on the export of carbon. J. Theor. Biol. 146, 15–36.

Ford, E.D., Ford, R., 1990. Structure and basic equations of a simulator of for branch growth in the *Pinaceae*. J. Theor. Biol. 146, 1–13.

Franklin, J.F., Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. In: USDA Forest Service General Technical Report GTR-PNW-8. Portland, OR.

Fujimori, T., 1993. Dynamics of crown structure and stem growth based on knot analysis of a hinoki cypress. For. Ecol. Manage. 56, 57–68.

Gavrikov, V.L., Karlin, I.V., 1992. A dynamic model of tree terminal growth. Can. J. For. Res. 23, 326–329.

Gough, C.M., Seiler, J.R., Maier, C.A., 2004. Short-term effects of fertilization on loblloly pine (*Pinus taeda* L.) physiology. Plant Cell Environ. 27, 876–886.

Grace, J.C., 2003. Links between science and forest management: as illustrated by a model of branch development. In: Mencuccini, M., Moncrieff, J., McNaughton, K., Grace, J. (Eds.), Forests at the Land–Atmosphere Interface. University of Edinburgh, Edinburgh, Scotland, pp. 255–267.

Grace, J.C., Pont, D., Goulding, C.J., Rawley, B., 1999. Modelling branch development for forest management. N. Z. J. Forestry Sci. 29, 391–408.

Grote, R., Pretzsch, H., 2002. A model for individual tree development based on physiological processes. Plant Biol. 4, 167–180.

Hann, D.W., Hanus, M.L., 2004. Evaluation of nonspatial approaches and equation forms used to predict tree crown recession. Can. J. For. Res. 34, 1993–2003.

Hann, D.W., Marshall, D.D., Hanus, M.L., 2003. Equations for predicting height to crown base, 5-year diameter growth rate, 5-year height growth rate, 5-year mortality rate, and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest. In: Research Contribution 40. Oregon State University, College of Forestry Research Laboratory, Corvallis, OR, p. 85.

Hayes, J.P., Chan, S.S., Emmingham, W.H., Tappeiner, J.C., Kellogg, L., Bailey, J.D., 1997. Wildlife response to thinning young forests in the Pacific Northwest. J. Forestry 95, 28–33.

Ishii, H., McDowell, N., 2002. Age-related development of crown structure in coastal Douglas-fir trees. For. Ecol. Manage. 169, 257–270.

Keim, R.F., 2004. Attenuation of rainfall by forest canopies. Ph.D. dissertation, College of Forestry, Oregon State University, Corvallis, OR, p. 150.

Kershaw, J.A., Maguire, D.A., 1995. Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: trends in branch-level mass and leaf area. Can. J. For. Res. 25, 1897–1912.

Kershaw, J.A., Maguire, D.A., Hann, D.W., 1990. Longevity and duration of radial growth in Douglas-fir branches. Can. J. For. Res. 20, 1690–1695.

Kozlowski, T.T., Pallardy, S.G., 1997. Physiology of Woody Plants, 2nd ed. Academic Press, San Diego, CA.

Krumland, B., Wensel, L.C., 1981. A tree increment model system for north coastal California: design and implementation. In: Research Note 15. California Cooperative Redwood Yield Research Project, Department of Forest Conservation, University of California, Berkeley, CA, USA.

Kucharik, C.J., Norman, J.M., Gower, S.T., 1998. Measurements of branch area and adjusting leaf area index indirect measurements. Agric. For. Meteorol. 91, 69–88.

Lacointe, A., Deleens, E., Ameglio, T., Saint-Joanis, B., Lelarge, C., Vandame, M., Song, G.C., Daudet, F.A., 2004. Testing the branch autonomy theory: a ^{13}C/^{14}C double-labelling experiment on differentially shaded branches. Plant Cell Environ. 27, 1159–1168.

Larson, B.C., 1963. Stem form development of forest trees. For. Sci. Monogr. 5, 1–42.

Maguire, D., Kanaskie, A., Mainwaring, D., 2004. Growth responses to pre-commercial thinning under differing levels of initial Swiss needle cast severity in north coastal Oregon. In: Mainwaring, D. (Ed.), Swiss Needle Cast Cooperative 2004 Annual Report. Oregon State University College of Forestry, Corvallis, OR, pp. 28–30.

Maguire, D.A., Batista, J.L.F., 1996. Sapwood taper models and implied sapwood volume and foliage profiles for Coastal Douglas-fir. Can. J. For. Res. 26, 849–863.

Maguire, D.A., Bennett, W.S., Kershaw, J.A., Gonyea, R., Chappell, H.N., 1991a. Establishment report: Stand Management Cooperative silviculture project field installations. College of Forestry, University of Washington, Seattle, WA, p. 42.

Maguire, D.A., Hann, D.W., 1987. A stem dissection technique for dating branch mortality and reconstructing past crown recession. For. Sci. 33, 858–871.

Maguire, D.A., Johnston, S.R., Cahill, J., 1999. Predicting branch diameters on second-growth Douglas-fir from tree-level descriptors. Can. J. For. Res. 29, 1829–1840.

Maguire, D.A., Kanaskie, A., 2002. The ratio of live crown length to sapwood area as a measure of crown sparseness. For. Sci. 48, 93–100.

Maguire, D.A., Kanaskie, A., Voelker, W., Johnson, R., Johnson, G., 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. Western J. Appl. Forestry 17, 86–95.

Maguire, D.A., Kershaw, J.A., Hann, D.W., 1991b. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-fir. For. Sci. 37, 1409–1428.

Maguire, D.A., Moeur, M., Bennett, W.S., 1994. Models for describing basal diameter and vertical distribution of primary branches in young Douglas-fir. For. Ecol. Manage. 63, 23–55.

Mäkelä, A., Makinen, H., 2003. Generating 3D sawlogs with a process-based growth model. For. Ecol. Manage. 184, 337–354.

Mäkelä, A., Vanninen, P., Ikonen, V.-P., 1997. An application of process-based modelling to the development of branchiness in Scots Pine. Silva Fennica 31, 369–380.

Mäkinen, H., 1996. Effect of intertree competition on branch characteristics of *Pinus sylvestris* families. Scand. J. For. Res. 11, 129–136.

Mäkinen, H., 1999a. Effect of stand density on radial growth of branches of Scots pine in southern and central Finland. Can. J. For. Res. 29, 1216–1224.

Mäkinen, H., 1999b. Growth, suppression, death, and self-pruning of branches of Scots pine in southern and central Finland. Can. J. For. Res. 29, 585–594.

Mäkinen, H., 2002. Effect of stand density on the branch development of silver birch (*Betula pendula* Roth.) in central Finland. Trees Struct. Funct. 16, 346–353.

Mäkinen, H., Colin, F., 1999. Predicting the number, death, and self-pruning of branches in Scots pine. Can. J. For. Res. 29, 1225–1236.

Mäkinen, H., Ojansuu, R., Niemistö, 2003. Predicting external branch characteristics of planted silver birch (*Betula pendula* Roth.) on the basis of routine stand and tree measurements. For. Sci. 49, 301–317.

Mäkinen, H., Ojansuu, R., Sairanen, P., Yli-Kojola, H., 2004. Predicting branch characteristics of Norway spruce (*Picea abies* (L.) Karst.) from simple stand and tree measurements. Forestry 76, 525–546.

Mäkinen, H., Saranpää, P., Linder, S., 2001. Effect of nutrient optimization on branch characteristics in *Picea abies*. Scand. J. For. Res. 16, 354–362.

Manter, D.K., Winton, L.M., Filip, G.M., Stone, J.K., 2003. Assessment of Swiss needle cast disease: temporal and spatial investigations of fungal colonization and symptom severity. J. Phytopathol. 151, 344–351.

Mitchell, K.J., 1975. Dynamics and simulated yield of Douglas-fir. For. Sci. Monogr. 17, 1–39.

Monleon, V.J., Azuma, D., Gedney, D., 2004. Equations for predicting uncompacted crown ratio based on compacted crown ratio and tree attributes. Western J. Appl. Forestry 9, 260–267.

Portz, C.G., Silins, U., Lieffers, V.J., 2000. Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. Can. J. For. Res. 30, 1088–1095.

Reukema, D.L., 1959. Missing annual rings in branches of young-growth Douglas-fir. Ecology 40, 480–482.

Rose, R., Rosner, L., 2005. Eighth-year response of Douglas-fir seedlings to area of weed control and herbaceous versus woody weed control. Ann. For. Sci. 62, 481–492.

Rose, R., Rosner, L.S., Ketchum, J.S., 2006. Twelfth-year response of Douglas-fir to area of weed control and herbaceous versus woody weed control treatments. Can. J. For. Res. 36, 2464–2473.

Sampson, D.A., Smith, F.W., 1993. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* var. *latifolia*) forets. Agric. For. Meteorol. 64, 63–79.

Shigo, A.L., 1985. How tree branches are attached to trunks. Can. J. Bot. 63, 1391–1401.

Short, E.A., Burkhart, H.E., 1992. Predicting crown-height increment for thinned and unthinned loblolly pine plantations. Forest Sci. 38, 594–610.

Siefert, T., 2003. Integration of wood quality, grading, and bucking in forest growth models sensitive to silvicultural treatment. Ph.D. dissertation, University of Munich, Munich, Germany, p. 314.

Sorrensen-Cothern, K.A., Ford, E.D., Sprugel, D.G., 1993. A model of competition incorporating plasticity through modular foliage and crown development. Ecol. Monogr. 63, 277–304.

Sprugel, D.G., 1991. The theory and practice of branch autonomy. Annu. Rev. Ecol. Syst. 22, 309–334.

St. Clair, J.B., 1994. Genetic variation in tree structure and its relation to size in Douglas-fir. II. Crown form, branch characters, and foliage characters. Can. J. For. Res. 24, 1236–1247.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2000. Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. Ecol. Applic. 11, 1151–1173.

Umeki, K., Kikuzawa, K., 2000. Patterns in individual growth, branch population dynamics and growth and mortality of branches *Betula platphylla* in northern Japan. Ann. For. Sci. 57, 587–598.

Vose, J.M., Dougherty, P.M., Long, J.N., Smith, F.W., Gholz, H.L., Curran, P.J., 1994. Factors influencing the amount and distribution of leaf area of pine stands. Ecol. Bull. 43, 102–114.

Watt, M.S., Moore, J.R., McKinlay, B., 2005. The influence of wind on branch characteristics of *Pinus radiata*. Trees 19, 58–65.

Weiskittel, A.R., 2003. Alterations in Douglas-fir crown structure, morphology, and dynamics imposed by the Swiss needle cast disease in the Oregon Coast Range. M.S. thesis, Oregon State University, Corvallis, OR, p. 389.

Weiskittel, A.R., Garber, S.M., Johnson, G.P., Maguire, D.A., Monserud, R.A., 2007a. Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder. For. Ecol. Manage. 250, 266–278.

Weiskittel, A.R., Maguire, D.A., Garber, S.M., Kanaskie, A., 2006a. Influence of Swiss needle cast on foliage age class structure and vertical distribution in Douglas-fir plantations of north coastal Oregon. Can. J. For. Res. 36, 1497–1508.

Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Rose, R., Turnblom, E.C., 2006b. Intensive management influence on Douglas-fir stem form, branch characteristics, and simulated product recovery. N. Z. J. Forestry Sci. 36, 293–312.

Weiskittel, A.R., Maguire, D.A., Monserud, R.A., 2007. Modeling crown structural responses to competing vegetation control, thinning, fertilization, and Swiss needle cast in coastal Douglasfir of the Pacific Northwest, USA. For. Ecol. Manage. 245, 96–109.

Whitehead, D., Grace, J.C., Godfrey, M.J.S., 1990. Architectural distribution of foliage in individual *Pinus radiata* D. Don. crowns and the effects of clumping on radiation interception. Tree Physiol. 7, 135–155.

Wichmann, L., 2002. Modelling the effects of competition between individual trees in forest stands. Ph.D. dissertation, Unit of Forestry, Department of Economics and Natural Resources, The Royal Veterinary and Agricultural University, Copenhagen, Denmark, p. 112.

Witowski, J., 1996. Gas exchange of the lowest branches of young Scots pine; a cost–benefit analysis of seasonal branch carbon budget. Tree Physiol. 17, 757–765.