Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 245 (2007) 96–109
Forest Ecology and Management
www.elsevier.com/locate/foreco

Modeling crown structural responses to competing vegetation control, thinning, fertilization, and Swiss needle cast in coastal Douglas-fir of the Pacific Northwest, USA

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Received 21 September 2006; received in revised form 9 March 2007; accepted 4 April 2007

Abstract

Crown structure is a key variable influencing stand productivity, but its reported response to various stand factors has varied. This can be partially attributed to lack of a unified study on crown response to intensive management or stand health. In this analysis of several coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) branch datasets, a significant treatment effect of fertilization, thinning, pre-commercial thinning, varying levels of vegetation control, and intensity of a foliar disease (Swiss needle cast, caused by *Phaeocryptopus gaeumannii* (T. Rohde) Petr.) were all found to influence several key crown structural attributes. Maximum branch size and total and non-foliated crown radii were found to be the most dynamic and sensitive crown variables to the various stand factors as no treatment effects were found for the number of branches within an annual segment or branch angle. When the data sets were combined and used to develop a single predictive equation, treatment effects were largely accounted for by changes in bole and crown size as mean bias was relatively low despite the large range in tree ages examined (4–450 years at breast height). While crown structure is highly variable and sensitive to a variety of stand factors, general empirical equations perform quite well and should be better integrated into models of forest growth and yield.

Keywords: Crown structure; Maximum branch diameter profile; Crown profile; Intensive management; Douglas-fir; Plantation management; Fertilization; Thinning; Vegetation management

1. Introduction

Conifer plantation growth and yield can be manipulated through intensive silvicultural practices such as vegetation control, thinning, and fertilization (e.g. Talbert and Marshall, 2005). Growth responses to silvicultural treatment are largely mediated by changes in crown structure, including total leaf area (Gough et al., 2004; Vose, 1988), foliar nutrient concentration or amount (Brix, 1981a), and crown length, crown width, and corresponding spatial distribution of foliage (Gillespie et al., 1994). Fertilization also promotes greater photosynthetic rates per unit leaf area, at least temporarily (Brix, 1981a; Gough et al., 2004). Accurate quantification of these and other crown responses to specific treatments should enhance our ability to predict stand and tree performance under a wide variety of silvicultural regimes. In addition, it has become increasingly important in commercial species such as Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) to understand the effect of silvicultural treatments and regimes on wood quality, some attributes of which are controlled in part by crown structure and its dynamic responses over time (Brix, 1981a; Maguire et al., 1991b). In particular, branch size, vigor, and location have direct implications for several components of wood quality (Zobel and van Buijtenen, 1989).

Branch response to intensive silvicultural treatments has varied. Fertilization generally induces its strongest effect on the top half of the crown, whereas thinning affects the bottom half (Brix, 1981b). Both thinning and fertilization have been shown to increase the number of branches on a tree (Brix, 1981b; Mäkinen et al., 2001); however, other studies have concluded that the number of branches per whorl is independent of tree size, site index, and stand density (Briggs and Turnblom, 1999; Grotta et al., 2004; Woollons et al., 2002).

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2007.04.002

Response of branch diameter and branch length to fertilization and thinning has also been inconsistent. For example, Mäkinen et al. (2001) found that diameter growth of both newly initiated and older branches in *Picea abies* were significantly enhanced by fertilization, but more recently Mäkinen et al. (2004) concluded that site fertility and fertilization did not significantly influence branch radial growth. In Douglas-fir, Brix (1981b) found that thinning did not influence branch size, although this treatment did allow branches in the lower part of the crown to grow for a longer period of time before suppression. In contrast, Gary (1978) found that the largest 20-year-old branches on *Pinus contorta* were nearly 1.6 times greater in thinned versus unthinned stands 30 years after treatment. Branch elongation has received less attention, but in Douglas-fir was shown to increase throughout the crown with fertilization while remaining insensitive to thinning (Brix, 1981a,b). However, this result contrasts directly with the more general increase in crown length and width with lower stand density (e.g. Curtis and Reukema, 1970). Madgwick et al. (1986) found that fertilized *Picea abies* had a more rapid decrease in branch extension with increasing depth in crown, resulting in a narrower relative crown profile.

The variability in results to date can be attributed to site and species differences, as well as to the lack of comparable sampling designs in these few studies. The most notable differences among these studies are: (a) thinning intensity; (b) time since treatment; (c) number and location of sample branches; (d) the statistical model (particularly with respect to use of covariates). In addition, interactions with other factors such as early competing vegetation control and disease or insect defoliation have not been examined in any detail. Defoliation imposes a relatively rapid change in foliage amount and distribution, so branches and stems are expected to respond accordingly. One example in Douglas-fir is Swiss needle cast [*Phaeocryptopus gaeumannii* (T. Rohde) Petr.] (SNC, Table 1), a disease that has become increasingly important in north coastal Oregon by drastically altering both foliage age class structure (Weiskittel et al., 2006a) and stand productivity (Maguire et al., 2002).

The goal of this study was to test for and quantify the effect of silvicultural treatments (competing vegetation control, thinning, fertilization) and Swiss needle cast on crown structural attributes directly relevant to growth, yield, and wood quality in Douglas-fir. Specific responses included: (a) the number of whorl branches within an annual segment; (b) number of interwhorl branches within an annual segment; (c) maximum branch diameter within a whorl; (d) angle of branch insertion; (e) crown profile (trend in crown radius over height within the crown); (f) profile of non-foliated crown core. The following three hypotheses were tested for each of these six crown structural attributes: (1) the crown attribute is not influenced by silvicultural treatment or SNC; (2) any significant response of the crown attribute to treatment or SNC can be accounted for indirectly by its effect on tree diameter, height, and/or crown length; (3) existing models developed for estimating these attributes in Douglas-fir are adequate for a wider variety of silvicultural regimes and more variable disease conditions than were sampled previously (Maguire et al., 1994, 1999; Roeh and Maguire, 1997), particularly in regard to competing vegetation control, thinning, fertilization, and SNC severity. In short, the allometric relationships that determine crown morphology are tested for their sensitivity to changes imposed by any of these silvicultural treatments or by SNC severity. The results will help guide the design of silvicultural regimes that yield the desired quantity and quality of wood from Douglas-fir stands. The models developed in this study differ from the previous studies in Douglas-fir (e.g. Maguire et al., 1994, 1999; Roeh and Maguire, 1997; Ishii and McDowell, 2002) because new data across a wider range of stand conditions were combined with the data from these previous studies. Further, non-foliated crown core profile models do not currently exist for this species and are important for light interception models (Brunner, 1998).

Table 1
Definitions and units of symbols used in this paper

Symbol	Definition	Units
BA	Branch angle from vertical	°
BD	Branch diameter	mm
BD_{max}	Maximum branch diameter in an annual segment	mm
BHT	Branch height above ground	m
BHT_{rel}	Relative branch height above ground	–
BL	Branch length	m
CL	Crown length	m
CR	Crown ratio	–
DBH	Tree diameter at breast height	cm
DINC	Depth into crown (tree height − branch height)	m
CRD_{NFOL}	Non-foliated crown radius	m
CRD_{TOT}	Total crown radius	m
FERT	Indicator variables for fertilization (1 if fertilized, 0 otherwise)	–
FOLRET	Foliage retention (visual assessment of SNC severity, inverse relationship with disease)	–
HCB	Tree height to crown base (lowest live branch)	m
HCM	tree height to crown midpoint	m
HRB	Complete control of herbaceous vegetation	–
HT	Tree total height	m
NB_I	Total number of interwhorl branches per annual segment	–
NB_T	Total number of branches (live + dead) per annual segment	–
NB_L	Total number of live branches per annual segment	–
NB_W	Total number of whorl branches per annual segment	–
NFBL	Non-foliated branch length	m
PCT	Precommercial thinning	–
SEGAGE	Annual segment age	years
SEGDINC	Annual segment depth into crown	m
SEGHT	Annual segment height above ground	m
$SEGHT_{rel}$	Annual segment relative height	–
SEGLEN	Annual segment length	m
SI	Site index	m
SNC	Swiss needle cast	–
THIN	Indicator for commercial thinning	–
TST	Time since treatment	–
TVC	Total vegetation control	–
WDY	Complete control of woody vegetation	–

2. Methods

2.1. Study sites

The majority of the sites utilized in this study were located in the northern half of the Oregon Coast Range. Other study site

locations included two installations in the Oregon Cascade foothills, one installation in the southern Washington Cascade foothills, and one installation in the Willamette Valley (between the Oregon Coast Range and Cascades). The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 100 to 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. 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 and all topographical aspects were represented.

The sampled plantations ranged in age from 8 to 60-years-old at breast height and contained ≥75% Douglas-fir by basal area, so included varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and other conifer and hardwood species (Table 2).

2.2. Data collection

Several data sets were combined to test the above hypotheses. The first was collected from 122 sample trees in 33 Douglas-fir plantations with varying levels of SNC in 2002 and 2003 (Weiskittel et al., 2006a). The second was based on 18 sample trees in three pre-commercial thinning (PCT) installations established to test the effect of thinning on SNC symptom development and Douglas-fir growth loss (Maguire et al., 2004). The third dataset was collected from 48 trees on 16 plots designed to test the effects of thinning and fertilization on growth, yield, and wood quality (Stand Management Cooperative, SMC, University of Washington) (Maguire et al., 1991a). The fourth dataset was built from 30 trees on 10 plots designed to test the effects of competing vegetation control on early tree growth (Vegetation Management Research Cooperative, VMRC, Oregon State University) (Rose et al., 2006). The SNC dataset was collected in 2002 and 2003, while the remaining data were collected in 2004. A more complete description of these four data sets is given in Weiskittel et al. (2006b).

At each plot, one sample tree was randomly selected from each of the diameter classes containing the 25th, 63rd, and 93rd percentiles of the diameter distribution. All sample trees were measured for diameter at breast height (DBH), total height (HT), and height to crown base (HCB; lowest live branch; Table 3). The sample trees were either felled or climbed and every living branch (at least one green needle and ≥1 mm in diameter) was measured for insertion height (nearest 0.01 m) and diameter (nearest 0.1 mm). All measured branches were also coded by north versus south side of the tree. A subsample of branches was also measured for azimuth of insertion, angle

Table 2
Attributes of the installations and plots sampled in 2002–2003 (SNC), and 2004 (PCT, SMC, VMRC)

Attribute	Mean	Standard deviation	Minimum	Maximum
PCT ($n_{install}$ = 3, n_{plot} = 6)				
Total basal area (m^2 ha^{-1})	20.77	6.69	9.71	28.63
Douglas-fir quadratic mean diameter (cm)	20.42	4.67	14.45	26.37
Trees per hectare	691.61	262.56	456.95	1111.50
Average breast-height age (years)	12.31	1.83	9.60	14.42
Site index (Bruce, 1981; height at 50 years breast height, in m)	51.71	1.74	48.59	53.51
SMC ($n_{install}$ = 4, n_{plot} = 16)				
Total basal area (m^2 ha^{-1})	26.59	7.87	6.48	38.52
Douglas-fir quadratic mean diameter (cm)	23.54	5.52	11.94	33.72
Trees per hectare	743.29	592.82	245.00	2800.53
Average breast-height age (years)	19.88	1.95	16.00	21.55
Site index (Bruce, 1981)	39.29	1.51	37.51	41.16
SNC ($n_{install}$ = 33)				
Total basal area (m^2 ha^{-1})	37.89	15.39	10.45	76.83
Douglas-fir quadratic mean diameter (cm)	29.95	10.66	11.41	53.49
Trees per hectare	524.43	307.92	150.00	1222.65
Average breast-height age (years)	28.82	14.48	11.00	62.43
Site index (Bruce, 1981)	39.37	3.91	26.63	46.20
VMRC ($n_{install}$ = 2, n_{plot} = 10)				
Total basal area (m^2 ha^{-1})	14.96	5.01	2.71	24.84
Douglas-fir quadratic mean diameter (cm)	13.46	2.41	5.91	17.49
Trees per hectare	1014.21	94.13	719.04	1101.03
Average breast-height age (years)	7.97	0.18	7.81	8.17
Site index (Bruce, 1981)	38.81	2.03	37.00	41.11
ALL				
Total basal area (m^2 ha^{-1})	21.00	15.22	0.67	76.83
Douglas-fir quadratic mean diameter (cm)	19.46	10.01	5.18	53.49
Trees per hectare	763.53	500.05	150.00	2800.53
Average breast-height age (years)	15.09	11.92	7.81	62.43
Site index (Bruce, 1981)	38.82	4.43	26.63	53.51

Table 3
Attributes of 218 Douglas-fir trees sampled in 2002–2004 by dataset

Attribute	Mean	Standard deviation	Minimum	Maximum
PCT (n_{tree} = 18)				
DBH (cm)	23.3	6.3	11.6	32.6
HT (m)	14.75	3.19	9.19	19.93
HCB (m)	2.14	2.15	0.30	6.80
SMC (n_{tree} = 48)				
DBH (cm)	27.1	6.9	12.2	42.7
HT (m)	18.34	3.12	10.15	23.97
HCB (m)	6.01	3.47	0.20	12.58
SNC (n_{tree} = 122)				
DBH (cm)	30.4	10.2	12.5	66.6
HT (m)	23.95	7.89	11.90	45.80
HCB (m)	10.02	5.83	0.50	28.33
VMRC (n_{tree} = 30)				
DBH (cm)	14.8	2.9	9.8	21.2
HT (m)	10.55	1.62	7.46	14.67
HCB (m)	0.85	0.62	0.10	2.34
ALL				
DBH (cm)	26.9	9.9	9.8	66.6
HT (m)	20.06	7.81	7.46	45.80
HCB (m)	7.18	5.83	0.10	28.33

of insertation (° from vertical), total length (nearest 0.01 m), and non-foliated length (nearest 0.01 m).

2.2.1. SNC/PCT

The SNC dataset included measurements from 86 trees in 24 young plantations (15–35 years at breast height) and 36 trees in 9 older plantations (35–65 years at breast height). The three sampled PCT installations contained a set of three square 0.08-ha plots. Treatments were implemented in 1998 and included a control, moderate thinning (494 residual trees ha^{-1}), and heavy thinning (247 residual trees ha^{-1}). At each installation, the control plot and one randomly selected thinning plot were sampled (heavy thinning at one installation (~254 trees ha^{-1}) and moderate thinning at the other two (~500 trees ha^{-1})). SNC severity was visually assessed in each plot by estimating the amount of foliage retention (FOLRET) in each crown third of 10 dominant and co-dominant trees. Healthy stands have a FOLRET of 3–4, while stands with severe SNC have values between 1 and 2 (Maguire et al., 2002).

2.2.2. SMC

Three SMC installations were selected from a set representing young plantations that were respaced to varying degrees well before crown closure (Type I installations; Maguire et al., 1991a). The installations were located in the northern Oregon Coast Range, southern Washington Cascades, and central Oregon Cascades. One other SMC installation from the Willamette Valley was also selected from a set representing initial spacing trials (Type III installations; Maguire et al., 1991a). The four plots from respacing trials (Type I) included the control (C), fertilized (FERT), thinned (THIN), and fertilized + thinned (F + T) plots. The FERT plots received 448 kg ha^{-1} of nitrogen as urea and time since treatment varied from 1 to 4 years. Residual tree density in the THIN plots was 50% of initial trees ha^{-1}, so ranged from 455 to 865 trees ha^{-1}. The four plots sampled at the initial spacing trial (Type III) included initial densities of 247, 762, 1865, and 3048 trees ha^{-1}.

2.2.3. VMRC

Five plots were sampled from each of two VMRC installations, one in the mid-Oregon Coast Range and the other in the lower Oregon Cascade foothills. Treatments were defined by area around each subject tree receiving competing vegetation control, including: no treatment (control), 3.34 m^2 of total vegetation control (TVC), 9.29 m^2 of TVC, complete removal of woody only vegetation (WDY), and complete removal of herbaceous only vegetation (HRB). Plots at each installation were randomly selected from the three receiving the same treatment.

2.2.4. Additional datasets

The four data sets described above were supplemented with four additional Douglas-fir branch data sets previously analyzed by Maguire et al. (1994, 1999), Roeh and Maguire (1997), and Ishii and McDowell (2002).The Maguire et al. (1994) dataset included 206 trees from 21 SMC plots sampled prior to canopy closure (4–7 years breast height age). The Roeh and Maguire (1997) dataset contained 260 trees from 53 plots that ranged in breast height age from 4 to 74 years. Maguire et al. (1999) measured maximum branch profile on 96 trees that ranged in breast height age from 20 to 74 years. Ishii and McDowell (2002) sampled 5–6 trees from a 20-, 40-, and 450-year-old stand.

2.3. Data analysis

Various linear and nonlinear regression models were fitted to the data to develop a series of equations describing crown structural attributes. The basic modeling unit was either an annual segment of the main tree stem, or primary branches attached to these annual segments. Each dataset was analyzed separately and treatment effects were tested by including indicator variables for discrete treatments. After assessing treatment effects, a global model for each crown structural attribute was developed from the combined data sets. Final models were chosen on the basis of residual analysis, Furnival's index, Akaike's information criterion (AIC) and biological interpretability.

The data had a distinct hierarchical structure (multiple measurements within trees within plots within installations) and as a result, violated the assumption of independence and zero correlation. A multi-level, mixed-effects model (Pinherio and Bates, 2000) was therefore employed to account for random effects of plots within each installation, trees within each plot, and measurements within each tree. When heteroskedasticity was detected in the residual plots, the final equation was weighted by a power variance function of the primary independent variable. If needed, a continuous, first-order, autoregressive function of distance from tree tip was

introduced to correct for any remaining autocorrelation. Nested model forms were compared with likelihood ratio tests, and bias was calculated as observed minus predicted.

2.3.1. Number of branches within annual segment

While the total number of whorl and interwhorl branches on an annual segment has been modeled using the Poisson distribution (e.g. Mäkinen and Colin, 1999), the normal distribution was assumed in this analysis because Douglas-fir typically has at least 15 branches within an annual segment. The initial model had a form similar to the one presented by Maguire et al. (1994):

$$\mathrm{NB}_i = \beta_{10}\mathrm{SEGLEN}^{\beta_{11}} \times \mathrm{SEGAGE}^{\beta_{12}} \times \mathrm{SEGHT}_{\mathrm{REL}}^{\beta_{13}} \times \mathrm{SEGDINC}^{\beta_{14}} \times \exp(\beta_{15} \times \mathrm{SEGDINC}) \times \mathrm{CR}^{\beta_{16}} \quad (1)$$

where NB_i is the total number of branches, SEGLEN the annual segment length (m), SEGAGE the annual segment age (years; age of top segment is equal to tree total age), SEGDINC the annual segment depth into the crown or distance between tree tip and top of the annual segment (m), $\mathrm{SEGHT}_{\mathrm{REL}}$ the relative height of the segment in the stem (SEGHT/HT), SEGHT the absolute height of the segment tip above ground (m), CR the tree crown ratio, and the β_i's are parameters to be estimated from the data. In each dataset, this model was fitted separately to four classes of $\mathrm{NB_i}$, namely the total number of branches (live + dead; $\mathrm{NB_T}$), the number of whorl branches ($\mathrm{NB_W}$), the number of interwhorl branches ($\mathrm{NB_I}$), and the number of live branches ($\mathrm{NB_L}$). For the $\mathrm{NB_L}$ model, the four data sets described above were merged with the data sets previously analyzed by Maguire et al. (1994) and Ishii and McDowell (2002).

2.3.2. Maximum whorl branch size

A modified Kozak (1988) variable-exponent model was fitted to the data representing vertical trends in maximum branch size (Maguire et al., 1999; Garber and Maguire, 2005). A simple power function of DBH performed better than predicted crown width for scaling maximum branch size (cf. Maguire et al., 1999). Both live and dead branches were included during parameter estimation and the form of the equation was:

$$\mathrm{BD}_{\max} = \beta_{21}\mathrm{DBH}^{\beta_{22}} \frac{1-\sqrt{\mathrm{BHT}_{\mathrm{rel}}}}{1-\sqrt{\beta_{23}}\mathrm{CR}^{\beta_{24}}}^{(\beta_{25}\sqrt{\mathrm{BHT}_{\mathrm{rel}}}+\beta_{26}\exp(-\mathrm{DBH}/\mathrm{HT})+\beta_{27}(\mathrm{BHT}_{\mathrm{rel}}\times(\mathrm{DBH}/\mathrm{HT}))+\beta_{28}\mathrm{CL}+\beta_{29}\mathrm{CR})} \quad (2)$$

where $\mathrm{BD}_{\max}$ is maximum branch diameter within a whorl (mm), CL the crown length (m), $\mathrm{BHT}_{\mathrm{rel}}$ the branch relative height (branch height/total tree height), the β_i's are parameters to be estimated from the data, and all other variables have been defined above. The final equation was fitted to a dataset constructed by merging the data collected for this study with the data sets previously analyzed in Maguire et al. (1994, 1999) and Ishii and McDowell (2002).

2.3.3. Branch angle of insertion

Branch angle of insertation (relative to vertical) was predicted using the function suggested by Roeh and Maguire (1997):

$$\mathrm{BA} = (\beta_{31} + \beta_{32}\mathrm{HT}) \times (1 - \exp(\beta_{33}\mathrm{DINC} + \beta_{34}\mathrm{BHT}_{\mathrm{rel}} + \beta_{35}\mathrm{SI})^{(\exp(\beta_{36}\mathrm{BD}))} \quad (3)$$

where BA is branch angle (°), DINC the depth into the crown (total tree height − branch height), SI is Bruce's (1981) site index (m), BD the branch diameter (mm), and the β_i's are parameters to be estimated from the data.

2.3.4. Total and non-foliated crown profile

Crown profile was estimated using the three-stage approach outlined by Roeh and Maguire (1997). First, insertion angle of every live branch was estimated with Eq. (3) fitted separately to each plot by including a random installation and plot effect, similar to the procedure given by Robinson and Wykoff (2004) for imputing missing tree heights. Similarly, total and foliated branch length was predicted for every measured live branch by fitting the following total branch length model (Roeh and Maguire, 1997) and non-foliated branch length model to each plot separately:

$$\mathrm{BL} = (\beta_{41}\mathrm{DINC}^{\beta_{42}}) \times \exp(\beta_{43}\mathrm{DINC} + \beta_{44} \times \mathrm{BHT}_{\mathrm{rel}}) \times \mathrm{BD}^{\beta_{45}} \times \mathrm{CR}^{\beta_{46}} \quad (4)$$

$$\mathrm{NFBL} = \frac{\mathrm{BL}}{1 + \exp(\beta_{51} + \beta_{52}\mathrm{BD} + \beta_{53}\mathrm{BHT} + \beta_{54}\mathrm{BHT}_{\mathrm{rel}} + \beta_{55}\mathrm{CL})} \quad (5)$$

where BL is total branch length (m), NFBL the non-foliated branch length (m), BHT the branch height above ground (m), and β_i's are parameters to be estimated from the data, and all other variables are defined above. Eqs. (3)–(5) were fitted to the data collected for this study combined with those previously analyzed by Roeh and Maguire (1997) and Ishii and McDowell (2002).

From Eqs. (4) and (5), the crown radius at the height of each live whorl was estimated from the following geometric relationship:

$$\mathrm{CRD}_i = \mathrm{BL} \times \left(\pi \times \sin\left(\frac{\mathrm{BA}}{180}\right)\right) \quad (6)$$

where CRD_i is crown radius (m) and all other variables have been defined above. Total and non-foliated crown radii ($\mathrm{CRD_{TOT}}$ and $\mathrm{CRD_{NFOL}}$, respectively) were estimated at each whorl height as the simple mean of all live whorl branches. Crown profile and unfoliated crown core were described with a model similar to Eq. (2). The model was numerically integrated to estimate volumes of the total crown, unfoliated crown core, and the foliated shell of the crown for each sample tree.

3. Results

3.1. Number of branches within annual segment

Annual segments from the main stem of coastal Douglas-fir held on average 3.8 ± 2.1 whorl and 9.9 ± 8.7 interwhorl branches. In general, the number of branches increased with segment age, segment length, segment relative height in crown, segment depth into the crown, and crown length, while it decreased with depth into the crown and crown ratio (Table 4). No treatment effects could be detected on the number of whorl or interwhorl branches. The south-facing side of an annual segment held up to 14% more branches than the north-facing side. Mean bias for Eq. (1) was -0.45 ± 1.34. The model presented by Maguire et al. (1994) tended to overpredict the number of branches within an annual segment by 3.1 ± 8.1 branches.

3.2. Maximum branch size within annual segment

Silvicultural treatments significantly affected maximum diameter of whorl branches in each of the data sets (Fig. 1). In the SMC dataset, fertilization increased maximum branch size in the upper stem third ($p = 0.0662$), while thinning significantly increased maximum branch size in the lower stem third ($p = 0.0164$). The combination of fertilization and thinning caused a mean maximum branch size profile very similar to the control tree, indicating that these treatments negated each other's effects, at least with respect to the behavior of maximum branch size over relative height in the crown. However, thinning significantly increased crown length, so on an absolute scale the effect of the combined treatments was unique. Also, the effect of both treatments diminished with time since treatment (TST), primarily because the longer term responses of tree diameter, height, and crown length eventually account for the change in branch diameter at a given depth into the crown. In the PCT dataset, precommerical thinning significantly increased maximum branch sizes in the lower 50% portion of the stem ($p = 0.0022$) and there was a significant difference between the moderate and heavy thinning treatments ($p = 0.0235$). For a given bole and crown size, there was very little difference, however, between the treatments. In the VMRC dataset, the 9.29 m^2 TVC treatment showed moderate evidence of significantly decreasing maximum branch sizes in the upper relative crown third when compared to the control ($p = 0.0606$). In the SNC dataset, foliage retention had a significant effect ($p < 0.0001$) on maximum branch size, but the effect differed by relative position in the stem ($p < 0.0001$). Greater levels of SNC increased maximum branch sizes in the lower third of the stem and reduced the variability in maximum branch diameter among different heights.

Aspect had no significant effect on maximum diameter of whorl branches, but tree diameter, height, and either crown length or crown ratio were always significant covariates. The overall maximum branch diameter profile equation performed well across these varied stand conditions after the inclusion of

Table 4
Equation form, parameter estimates, R^2, and residual standard error (RSE) for number of branches and maximum branch size

Model	Equation form	R^2	RSE
1a, Total number of live branches	$NB_L = 21.8035 \times SEGAGE^{-0.3123} \times SEGLEN^{0.1679} \times SEGHT_{rel}^{0.4332} \times SEGDINC^{0.2142} \times \exp(-0.1212 \times SEGDINC) \times CL^{0.4728}$	0.58	6.10
1b, Total number of whorl branches	$NB_W = 8.9097 \times SEGAGE^{-0.2199} \times SEGLEN^{0.0402} \times SEGHT_{rel}^{0.4080} \times SEGDINC^{0.3218} \times \exp(-0.0600 \times SEGDINC) \times CR^{0.2377}$	0.36	1.70
1c, Total number of interwhorl branches	$NB_I = 29.7614 \times SEGAGE^{-0.4039} \times SEGLEN^{0.4883} \times SEGHT_{rel}^{0.3692} \times SEGDINC^{0.3091} * \exp(-0.2011 \times SEGDINC) \times CR^{0.2873} \times CL^{0.4465}$	0.61	5.73
1d, Total number of branches	$NB_{TOT} = 12.4144 \times SEGLEN^{0.1693} \times SEGHT_{rel}^{0.0954} \times SEGDINC^{0.0856} \times \exp(-0.0478 \times SEGDINC) \times CR^{0.4021}$	0.55	6.36
2, Maximum branch size	$BD_{max} = 0.6839 \times DBH^{0.9142} \frac{1-\sqrt{BHT_{rel}}}{1-\sqrt{0.8934 \times CR^{-0.0566}}} (0.8872 \times \sqrt{BHT_{rel}} + 0.2244 \times \exp(-DBH/HT) - 0.05895 \times (BHT_{rel} \times (DBH/HT)) - 0.2483 \times \log(HCM) + 0.1988 \times \log(CL))$	0.80	4.45

All parameters are significant at $\alpha = 0.1$.

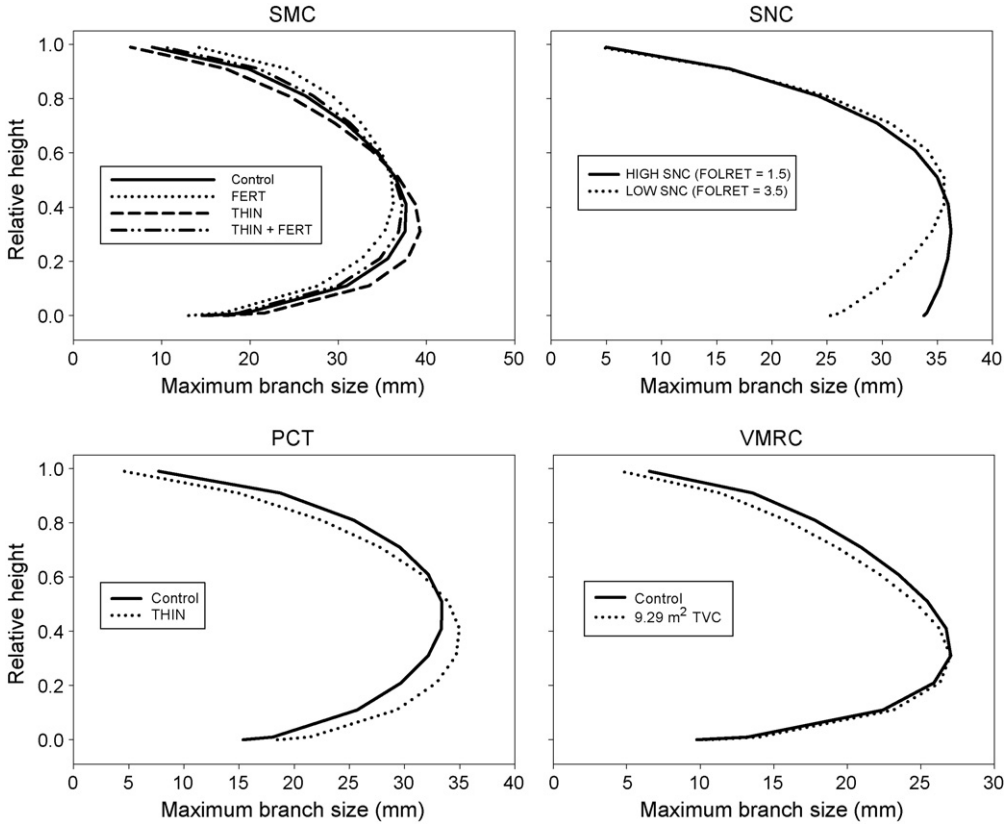

Fig. 1. Trend in maximum branch diameter over relative height in the crown, estimated from Eq. (2) for the mean tree in each individual dataset. For the SMC graph, the time since treatment (TST) was assumed to be 3 years for both fertilization and thinning.

height to crown midpoint (HCM) rather than CR. In general and for a given bole size, decreasing the crown length by 50% is related to a 21.2% mean reduction in maximum branch size in the lower half of the stem. Mean bias for the final model was -2.01 ± 9.53 mm. The equation previously presented by Maguire et al. (1999) equation tended to underpredict maximum branch size by an average of 9.3 ± 11.3 mm.

3.3. Branch angle of insertation

No treatment effects could be detected on the insertion angle of branches. Branch angle increased with greater HT/DBH, BD, SI, and BHT, and decreased with increasing relative height on the tree (Table 5). Mean bias for the final model (Eq. (3)) was $1.7 \pm 14.1^{\circ}$. The model previously developed by Roeh and Maguire (1997) underpredicted branch angle by an average of $10 \pm 25.3^{\circ}$. For this larger dataset, predictors HT/DBH and branch height (BHT) performed better than HT and DINC (cf. Roeh and Maguire, 1997).

3.4. Total and non-foliated crown profile

Silvicultural treatments significantly affected crown profile in all of the data sets (Fig. 2). In the SMC dataset, thinning and its interaction with fertilization had a significant effect on crown profile ($p = 0.0004$ and 0.0002, respectively); however, fertilization had no effect ($p = 0.1694$). For a given bole and crown size, thinning decreased crown radii in the lower relative third of the crown and the combination of thinning and fertilization produce crown radii similar to the control. The profiles did not vary significantly by time since treatment ($p = 0.2256$). In the SNC dataset, foliage retention had a significant effect on crown profile ($p = 0.0023$), but its effect varied by relative position in the crown ($p = 0.0151$). Crown radii in the near the crown midpoint were slightly greater on healthy trees (FOLRET = 3.5 years), while heavily diseased trees (FOLRET = 1.5 years) had relatively greater crown radii in the lower 10% of the crown. In the PCT dataset, precommerical thinning significantly increased crown radius in the lower half of the crown ($p = 0.0279$). There was no significant difference between the heavy and moderate thinning treatments. In the VMRC dataset, complete removal of only herbaceous ($p < 0.0001$) or only woody vegetation caused a significant treatment effect ($p < 0.0001$ and 0.0002, respectively), while the area treated around subject trees had no significant effect on subject tree profile. Both complete removal treatments increased crown radius at all crown heights relative to the control treatment, with herbaceous removal producing slighter greater crown radii woody removal. Complete removal of both herbaceous and woody vegetation, however, had the greatest effect on crown profile. Mean bias for the final equation fitted was 0.09 ± 0.74 m. Mean bias for the regional crown profile model for Douglas-fir (Hann, 1999) underpredicted crown radius on average by 0.81 ± 0.85 m.

Table 5
Equation form, parameter estimates, R^2, and residual standard error (RSE) for branch angle, total and foliated branch length and total and foliated crown radius

Model	Equation form	R^2	RSE
3, Branch angle	$BA = \left(92.2171 - 7.2944 \times \frac{HT}{DBH}\right) \times (1 - \exp(-0.1114 \times BHT + 2.4781 \times BHT_{rel} - 0.0683 \times SI))^{(\exp(0.0146 \times BD))}$	0.30	16.98
4, Total branch length	$BL = (0.1444 \times DINC^{(0.3995)}) \times \exp(-0.0125 \times DINC + 0.2007 \times BHT_{rel}) \times BD^{0.7068} \times HCM^{-0.1229}$	0.66	0.33
5, Non-foliated branch length	$NFBL = \frac{BL}{1 + \exp(-2.1105 + 0.0163 \times BD - 0.1726 \times BHT + 8.6618 \times BHT_{rel} + 0.0622 \times CL)}$	0.52	0.05
6, Total crown radius	$CRD_{TOT} = 0.0703 \times DBH^{0.9749} \frac{1 - \sqrt{BHT_{rel}}}{1 - \sqrt{0.8405 \times CR^{0.1917}}}^{(0.3101 \times \sqrt{BHT_{rel}} + 0.9574 * \exp(-DBH/HT) + 0.1203 \times (BHT_{rel} \times DBH/HT) + 0.2541 \times CR - 0.0078 \times CL)}$	0.73	0.42
6, Non-foliated crown radius	$CRD_{NFOL} = 0.1574 \times DBH^{0.5331} \frac{1 - \sqrt{BHT_{rel}}}{1 - \sqrt{0.3445 \times CR^{1.3567}}}^{(0.8872 * \sqrt{BHT_{rel}} - 0.6250 \times \exp(-DBH/HT) + 0.1283 \times (BHT_{rel} \times DBH/HT) - 0.05132 \times CL + 2.2559 \times CR - 0.0098 \times HCM)}$	0.69	0.15

All parameters are significant at $\alpha = 0.1$.

On average, north-pointing branches were 10% longer than otherwise identical south-pointing branches, although, the effect varied by relative height in the stem. Non-foliated branch length, however, did not differ by branch aspect. The effect of branch aspect, however, was not incorporated into the final models because it was not measured on all branches.

Silvicultural treatments also significantly affected non-foliated crown radius in all data sets (Fig. 3). In the SMC dataset, both fertilization and thinning had a significant negative effect on non-foliated crown radii ($p < 0.038$ and 0.0001, respectively), while the interaction between treatments and the time since treatment were not significant. For a given bole and crown size, fertilization and thinning had little relative influence on non-foliated crown radii in the upper two thirds of the crown when compared to the control, while thinning caused longer non-foliated crown radii in the lower third of the crown. The combination of fertilization and thinning, however, significantly reduced non-foliated crown radius in the upper two thirds of the crown. In the SNC dataset, the disease has resulted in greater non-foliated crown radii in the upper two thirds of the crown ($p = 0.0160$), while the profiles are quite similar in the lower third of the crown. In the PCT dataset, thinning significantly reduced non-foliated crown radii throughout the crown ($p = 0.0017$), but no difference was detected between 247 and 494 residual trees per hectare. In the VMRC dataset, the amount of area treated with vegetation control (ATRT), the herbaceous vegetation only removal, and the woody vegetation only removal each had a significant effect on non-foliated crown radii $p = 0.0086$, 0.0001, and 0.0008, respectively). The complete and herbaceous vegetation only treatments modified the non-foliated crown radii very little when compared to the control. Removal of woody vegetation only, however, significantly increased non-foliated crown radii, particularly in the lower crown third. Mean bias for the overall equation was -0.01 ± 0.34 m and the fitted equation explained 69% of the original variation.

Mean foliar volume was 232 ± 323 m^3, while the mean proportion of total crown volume occupied by foliage was 0.90 ± 0.07. A significant treatment effect was found in the SMC and PCT data sets, while neither SNC nor competing vegetation control had any effect on foliar volume after accounting for DBH, HT, and CR. For a given bole and crown size, pre-commercial and commercial thinning increased foliar volume by 41 and 20%, respectively. Foliar volume was modeled as a simple power function of DBH, HT, and CR:

$$FV = 24.2969 \times \left(\frac{DBH}{HT}\right)^{1.7911} \times CR^{4.4125} \quad (7)$$

where FV is foliar volume (m^3) and the other variables have been defined above. The equation explained 76% of the original variation in FV and had a residual standard error of 0.13 m^3.

4. Discussion

Documented crown responses to silvicultural treatments have varied tremendously. In our study of plantation-grown

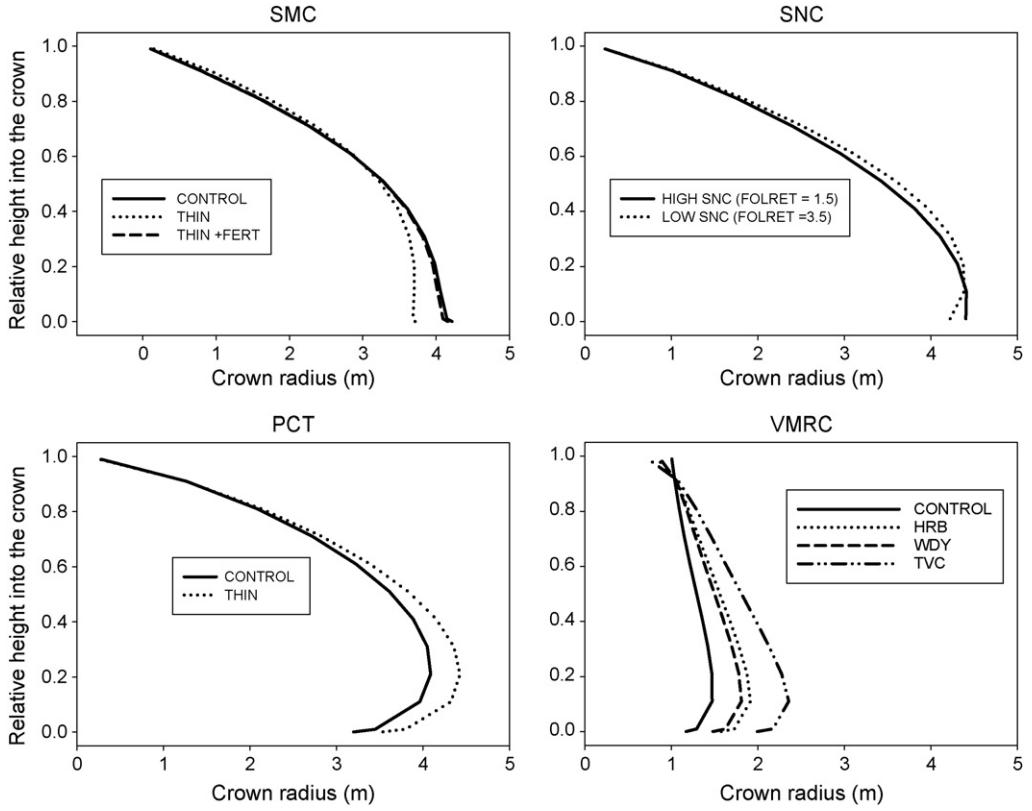

Fig. 2. Trend in crown radius over relative height in the crown (crown profile) estimated from Eq. (6) for the mean tree in each individual dataset. For the SMC graph, the time since treatment was assumed to be 3 years.

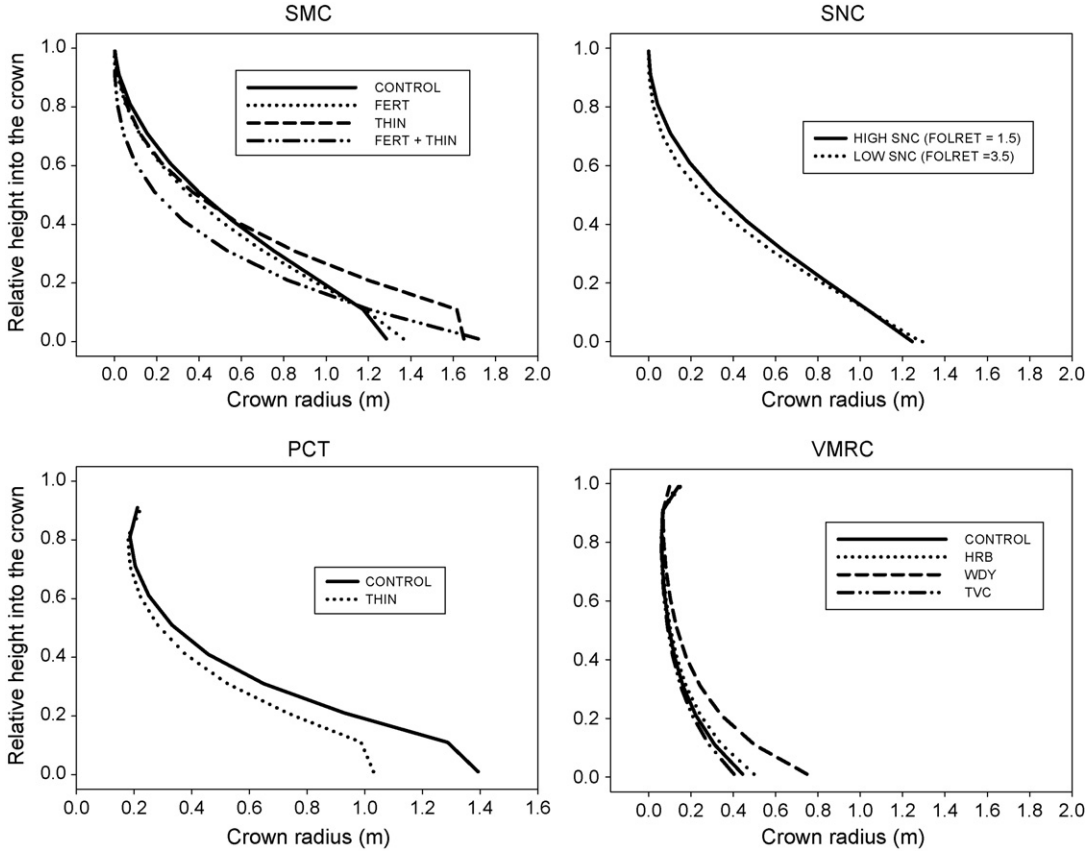

Fig. 3. Non-foliated crown profile (unfoliated core of crown) estimated from Eq. (6) for the mean tree in each individual dataset.

Douglas-fir, crown structure was found to be highly responsive to intensive management, as well as to premature foliage loss under Swiss needle cast. Previously published equations describing Douglas-fir crown structure, however, performed remarkably well under conditions well beyond those under which they were originally parameterized, and little improvement was achieved by introducing alternative model forms. In general, crown structural attributes were readily predicted from DBH, HT, and HCB, because specific combinations of these variables reflect the silvicultural regime under which the tree was grown, and because the allometric relationships between these tree-level variables and the crown structural attributes are not severely altered by the treatments per se. The adequacy of DBH, HT, and HCB was consistent with results from many other studies of branch size and distribution coniferous species (Mäkinen and Colin, 1998; Meredieu et al., 1998).

4.1. Number of branches within annual segment

The number of branches on an annual segment is largely influenced by segment length, or the height increment of the tree for that year (Mäkinen and Colin, 1999). The number of branches can be further modified by the competitive status of the tree—trees at the upper end of the diameter distribution yield a higher density of branches per unit length of segment, most likely due to increased levels of light (Maguire et al., 1994). Total tree size has generally been sufficient to describe past and present competitive interactions at the tree-level in shade-tolerant conifers (Colin and Houllier, 1992; Maguire et al., 1994); hence, in our study, crown length and crown ratio served as useful surrogates for local stand density and competition.

The relationship between branch number and height increment of the stem may change with tree age. Mäkinen and Song (2002) found their model for number of branches was biased when applied to stands averaging 100 years older than the stands used in the construction of the model. Ishii and McDowell (2002) confirmed that branching density declined with age as epicormic branches become more prominent in older trees. Segment age, therefore, was included in the equation to account for this effect. The age of the whorl was also expected to account for the inherent genetic component of the branch number per segment. While there is relatively little genetic variation in the number of branches per whorl in Douglas-fir (e.g. St. Clair, 1994), significant differences among provenances and families within provenances have been found in several other species (Cannell, 1974; Li et al., 1997; Xiao et al., 2003). The significant effect of aspect on branch density per segment length on the analyzed Douglas-fir was contrary to results from Sitka spruce (Cochrane and Ford, 1978) and loblolly pine (Doruska and Burkhart, 1994). Douglas-fir trees in this study held fewer branches on the north side, probably due to the effect of light or temperature on branch initiation or survival. A similar but weak trend was reported for Sitka spruce in a more recent study (Wichmann, 2002).

At the stand-level, the number of branches has been found to increase with greater tree density within the stand (Kellomäki and Tuimala, 1981) and with greater site fertility (Lämmä et al., 1990); however, other studies found that the number of branches per whorl was independent of tree size, site index, and stand density (Briggs and Turnblom, 1999; Mäkinen, 1996; Woollons et al., 2002). Assuming that all these results hold across species, the differences in total number of branches per unit stand area must be attributable to one or both of the following: (1) different density of interwhorl branches; or (2) different summed crown lengths. Stand treatments such as thinning and fertilization have been shown to increase the number of branches on a tree (Brix, 1981b; Mäkinen et al., 2001), the former through increasing crown length and the latter through increasing branch density per unit crown length. Consistent with the positive fertilization effect, Lämmä et al. (1990) found that the number of branches on Scots pine (*Pinus sylvestris* L.) was positively correlated with foliar nitrogen concentration and fine soil fraction, but Mäkinen and Colin (1999) found that site index was not significant in their model for predicting the number of whorl branches in the same species. In our study, no explicit treatment or site effects were observed, which is most likely a result of each of these stand factors being well accounted for by segment length and location. The overall branch number model performed well given the wide range of stand conditions and ages.

4.2. Maximum branch size within annual segment

Branch position within the crown was the best variable for describing variation in maximum branch size because it integrated the effects of branch age, light environment, and local competition. Maximum branch diameter followed a curvilinear relationship over distance from the tree tip, even prior to canopy closure, due to self-shading and shading by adjacent trees (Garber and Maguire, 2005). This general relationship was further modified by tree social position and crown size; that is, a tree receiving more light tended to grow larger branches for a given depth into crown. In contrast to our results, Wichmann (2002) found that maximum branch diameter was greater on the south side of Sitka spruce stems growing in Denmark; however, this relationship has been found highly variable in other species (Grace et al., 1999).

Maximum branch profiles have been found to be readily predictable from DBH and HT, and hence, changes imposed by silvicultural treatments should be captured by tree-level characteristics. In fact, many studies have shown that additional variables describing tree-level competition have had little influence on describing branch size, at least in even-aged stands composed of a single species (Maguire et al., 1994; Mäkinen, 1996; Wichmann, 2002). In mixed-species and/or uneven-aged stands, however, response of branch diameters appears more complicated. In mixed-species spacing trials in central Oregon, Garber and Maguire (2005) have shown that the response of branch diameter was best accounted for by explicit treatment variables representing spacing and species composition, even after accounting for DBH, HT, and HCB. A similar conclusion was reached in our analysis because a significant treatment effect was detected in each of the field trials examined, despite accounting for the effects of treatments on stem diameter, tree

height, and crown size directly by including them as predictor variables.

Fertilization and complete removal of vegetation were the only treatments that significantly influenced branch size in the upper crown, while the other treatments primarily influenced branches in the lower crown. Others have similarly concluded that branch size in the upper crown is influenced more by regional conditions, in contrast to the lower portion of the crown which responds more strongly to local stand conditions created by silvicultural treatments (Mäkinen, 1996). However, the influence of fertilization on coastal Douglas-fir in Oregon differed slightly from responses of Norway spruce in Finland (Mäkinen et al., 2001). Branch diameter growth of both newly initiated and older branches in Norway spruce was significantly increased with fertilization (Mäkinen et al., 2001). In our analysis of coastal Douglas-fir, diameter growth of relatively young branches in the upper crown accelerated in response to fertilization, but diameter growth of older branches in the lower crown decelerated slightly relative to the control trees (Weiskittel et al., in review). This shift in the pattern of branch diameter growth was most likely caused by the greater foliage biomass on branches of fertilized trees (Kershaw and Maguire, 1995), and the correspondingly greater shading of lower branches. Also contrary to our results for coastal Douglas-fir, Mäkinen et al. (2004) concluded that variables describing site fertility and fertilization regime had no significant effect on branch radial growth beyond that accounted for by responses of DBH, HT, and HCB.

Both pre-commercial (Fahlvik et al., 2005; Ruha and Varmola, 1997) and commercial thinning (Gary, 1978; Medhurst and Beadle, 2001) have been shown to increase maximum branch size. Thinning allows branches in the lower parts of residual tree crown to receive more light (and other resources), stimulating growth and facilitating greater longevity (Brix, 1981a,b; Mäkinen, 1999). The mean increase in branch size for the lower half of the crown between thinned and unthinned trees was 2.4 mm after pre-commercial thinning and 1.9 mm after commercial thinning. These increases are much lower than values given in Ruha and Varmola (1997) as well as Gary (1978). This difference in degree of response may be attributable to the way that each investigator corrected for thinning effects on DBH, HT, and HCB, or to differences in thinning intensity, response time, or relative shade tolerance of the species. Most work on response of branch size to thinning has been done with shade-intolerant pine species (*Pinus* spp.), but Douglas-fir is a more shade tolerant species and holds a great amount of leaf area for given tree size (DBH, height, crown length). Thus, Douglas-fir branches in the lower crown may not be able to respond as vigorously to thinning as the pine species because of greater levels of self-shading or the steeper changes in foliage attributes such as specific leaf area.

To our knowledge, the effects of defoliation and competing vegetation control on branch size have not been previously reported. The tendency of SNC to reduce branch size in the middle portion of the crown and increase branch size in the lower portion of the crown was indicative of the disease biology. Manter et al. (2003) indicated that, within individual trees, fungal colonization was consistently higher in the upper portions of the crown where needle retention was reduced nearly 15% compared to a healthy tree. This loss of foliage in the top portion of the crown may have reduced self-shading and increased branch radial growth below this portion, leading to a peak in maximum branch diameter lower in the crown.

The reduction in maximum branch size in the upper crown of the trees with intensive vegetation control was not expected, but was consistent with narrower relative diameter of the upper stem under the same set of treatments (Weiskittel et al., 2006b). This indicates that very intensive vegetation control may significantly alter tree allometry and growth dynamics. However, the results of intensive vegetation the effects of vegetation management agree with the finding of Campbell (1963) who indicated that Douglas fir growing faster in height tend to have smaller diameter branches after stem volume is accounted for.

4.3. Branch angle of insertation

The angle at which branches are attached to the stem has a major influence on crown form as well as wood quality. The initial branch angle of newly formed branches is determined by the angle of the lateral bud on the stem and elongating branches tend to orient according to the light source, gravitational fields, and the effects of growth regulators produced by the dominant leader. Hence, branch angles (from vertical) increase from the apex towards the base of the crown (Roeh and Maguire, 1997), due in part to gradients in growth regulators paralleling distance from the tree apex, in part to the increasing proportion of light received from the side versus top, and in part to the increasing mass of foliage and lateral branches carried by the branch (Kershaw and Maguire, 1995). The deflection of the branch tip due to gravity is largely a function of branch length, however, but also depends on the taper of the branch (Castera and Morlier, 1991). Branch angle, therefore, was concluded to be largely a function of location and size as corroborated by the behavior of coastal Douglas-fir.

Tree social position had a particularly strong influence on branch angle. Balsam fir (*Abies balsamea* (L.) P. Mill.) branches have been shown to become flatter with decreasing relative tree height in the stand (Gilmore and Seymour, 1997). We observed the same response in coastal Douglas-fir, with branch angle declining over increasing height to diameter ratio of the tree (and by inference the relative height of the tree in the stand). Of all the models developed in this study, the branch angle model had the poorest fit, indicating a high degree of variability in this crown structural response. Previous work in Douglas-fir has suggested that little of the variation in branch angle can be attributed to genetics variation, so this trait is not strongly heritable; however, branches in whorls formed at relatively young ages seemed to express family differences more strongly (St. Clair, 1994).

Stand density appeared to exert little control over branch angle in coastal Douglas-fir, consistent with previous work (e.g. Roeh and Maguire, 1997); however, it must be kept in mind that considerable stand density effects are implicit in diameter, height, and crown length of the tree. Field trials that have

explicitly tested silvicultural treatments such as fertilization (Brix, 1981b; Mäkinen et al., 2001) or thinning (Medhurst and Beadle, 2001) have suggested little influence of these treatments on branch angle. Although we observed no treatment effects on branch angle in coastal Douglas-fir, branch angle did increase slightly with increasing site index, as previously observed in this species (Roeh and Maguire, 1997). This pattern may be a result of greater amounts of foliage on a given branch and the corresponding implications for source direction of light, gravitational effects on the greater mass, and gradients in growth regulators as discussed above in the case of increasing depth into the crown.

4.4. Crown profile and non-foliated crown core

Crown profile and non-foliated crown core were the two crown structural attributes most sensitive to silvicultural treatment and SNC disease severity. The sensitivity to direct manipulation of stand density was expected because inter-tree competition typically restricts crown expansion (Deleuze et al., 1996). The rate of branch elongation declines exponentially from the top whorl toward the base of the crown commensurate with reductions in light intensity (Schoettle and Smith, 1991). Branch length also tends to decrease along the stem to tip because of bud ageing, the increased distance for water and nutrient translocation, greater mechanical constraints, and more unfavorable carbon balance (Deleuze et al., 1996).

Branch elongation varies greatly both within individual whorls (Mäkinen, 1999) and among years due to the fluctuations in the climate (Pensa and Jalkanen, 1999). However, in this study, between-year variation in branch length was much greater than the variation within an individual whorl. Schoettle and Smith (1991) found that branches on the south side of lodgepole pine crowns had a significantly greater increment in length than those on the north side. In contrast, the longest branch was most often found on the east and north-east side of Sitka spruce crowns (Wichmann, 2002), and no differences were detected by aspect in first year growth of Scots pine branches (Duursma, 1998). We found the longest branch most commonly on the north or north-west side of the crown in coastal Douglas-fir, leeward to the prevailing winter storms in western Oregon and Washington.

Important variables influencing crown profile were the ratio of DBH to HT and crown size. Generally, trees in lower social position tend to allocate proportionally more to branch elongation rather than height increment (Gilmore and Seymour, 1997), which is mostly capture in the combination of covariates used in this analysis. Similar to maximum branch profile, a treatment effect in each separate dataset was found for crown profile. Several key differences between maximum branch diameter profiles exist, suggesting a change in branch allometry with different treatments. First, fertilization had no significant effect on total crown profile, while thinning led to a reduction of crown radii in the lower crown. This differs slightly from the findings of both Brix (1981a,b) as well as Madgwick et al. (1986). Brix (1981a,b) found that fertilization increased branch elongation at all crown levels in the first growing season following treatment and the effect lasted for 2–4 years, while thinning caused a decrease for 1–3 years and increase thereafter with an end result of no overall effect. Madgwick et al. (1986), on the other hand, found that fertilized trees had a more rapid decrease in branch elongation with increasing depth in the crown, resulting in a narrower relative crown profile. The results of this study were more aligned with the findings of Madgwick et al. (1986). Second, the influence of commercial thinning was different than the effect of pre-commercial thinning as the latter led to the more expected increase in lower crown radii. This difference may be attributable to the size and age of the trees at the time of treatment. Since the pre-commercial thinnings usually occur at an age when the canopy is not completely closed, the lower crowns of the residual trees have not been exposed to extensive shading and are more vigorous, which allows them to utilize the increased growing space more effectively than the commercially thinned residual trees. Third, there is very little relative change in crown profiles for heavily diseased trees when compared to healthy ones of the same size despite a rather significant change in their maximum branch diameter profiles. This may caused by branches at the lower crown levels using their photosynthates to refoliate rather than elongate since light is no longer a limiting factor. Finally, similar to the pre-commercial thinning, all levels of vegetation control caused an increase in crown radii throughout the crown despite little change in maximum branch profiles when compared to the control. This change is expected due to the increases in growing space caused by the vegetation control treatments.

In contrast to crown profile, the non-foliated crown core has rarely been quantified despite important implications for growth efficiency (Jack and Long, 1992; Mitchell, 1975), and its key role in understanding and simulating light interception (Brunner, 1998). Various stand factors significantly modified the profile even after accounting for changes in DBH, HT, and HCB. In contrast to crown profile, the combination of fertilization and commercial thinning had a greater effect on the size of the non-foliated crown core than the individual treatments by themselves. Although fertilization has been reported to decrease needle longevity because of greater rates of self-shading (e.g. Balster and Marshall, 2000), it can significantly increase branch sapwood permeability in lower branches (Amponsah et al., 2004), which may allow a longer foliated branch length to be maintained for a longer period of time, particularly when light conditions are significantly improved by thinning. The overall influence of fertilization on both crown profile and non-foliated crown core, however, resulted in little change in the foliated crown radius throughout the crown, consistent with the results of Balster and Marshall (2000). Second, residual trees in pre-commercially thinned stands were able to maintain longer foliated branch lengths throughout the crown compared to the control, but trees in commercially thinned stands had non-foliated crown cores quite similar to the control trees. This again is likely a function of stand age and the degree of canopy closure prior to the thinning treatment. Although the effects of SNC and vegetation management had a significant effect on the non-foliated crown

core, there was relatively little change for a given tree size. The complete control of woody vegetation, however, significantly increased non-foliated crown core, particularly in the lower portion of the crown when compared to the other treatments.

Pre-commercial and commercial thinning were the only silvicultural treatments that significantly increased foliar volume. The change in crown volume following thinning has largely been attributed to greater light availability lower in the crown and a corresponding increase in branch longevity and crown length (Brix, 1981b). However, the increase we observed in coastal Douglas-fir accounted for the increase associated with thinning responses of diameter, height, and crown length. Hence, other factors such as wider crown profile and smaller non-foliated core were important factors influencing crown structural responses to thinning.

The mean ratio of foliar to total crown volume calculated in coastal Douglas-fir was significantly higher than values reported for older (66–134-year-old) conifers in Utah (Jack and Long, 1992). The latter conifers included both shade tolerant and intolerant species with a mean ratio of foliar volume to total crown volume of 0.3–0.5 (Jack and Long, 1992). Differences in site conditions, species, or stand age probably contribute to these relatively low ratios. The mean breast height age for our coastal Douglas-fir was 15 years, or young enough to have crown volumes composed primarily of fully foliated branches.

5. Conclusion

All the stand factors examined in this study, which included fertilization, pre-commercial thinning, commercial thinning, extended defoliation caused by a foliar disease, and various levels of vegetation management, had a significant effect on key crown structural attributes above and beyond changes in DBH, HT, and HCB. The most sensitive crown structural features were maximum branch size, crown profile, and non-foliated crown core. The number of branches held by annual segments of the main stem and the angle of branch attachment were not influenced by silvicultural treatments or disease severity after accounting for size and location in the stem. Silvicultural treatments affected primarily the lower portion of the crown; however, both fertilization and complete removal of competing vegetation significantly influenced branch sizes in the upper crown. In addition, some of the changes in crown structural attributes induced by silvicultural treatments were highly dependent on the time since treatment, highlighting the variation in response time of crown structural attributes. Overall, models including only tree diameter, height, and crown length performed well across a very wide range in silvicultural regime, stand structure, and disease severity; hence, important crown attributes can be predicted to a degree of accuracy sufficient for most applications from standard tree measurements.

Acknowledgements

We gratefully acknowledge the field assistance from Chet Behling, Jereme Frank, Sean Garber, Rei Hayashi, Doug Mainwaring, Mfon Okon, and Joseph Weiskittel. This study was funded by the Swiss Needle Cast Cooperative, the Oregon Department of Forestry, and the USDA-Forest Service. Special thanks to Green Diamond, Hampton Tree Farms, Longview Fiber, Oregon Department of Forestry, Oregon State University, Port Blakely, Plum Creek Timber Company, Starker Forests, USDA Forest Service, and Weyerhaeuser for granting permission to destructively sample or climb trees. Thanks to the Stand Management Cooperative, Vegetation Management Research Cooperative, Hiroaki Ishii, and Nate McDowell for providing access to their data.

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