Crown Recession Patterns in Three Conifer Species of the Northern Rocky Mountains

Sean M. Garber, Robert A. Monserud, and Douglas A. Maguire

Abstract: Crown length is a fundamental tree dimension for characterizing growth potential, wildlife habitat, and wood quality. The relative rates of height growth and crown recession determine the progression of crown length over time. We investigated patterns in crown recession of three co-occurring species in the northern Rocky Mountains: western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), and interior Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca*). Past height, diameter, and crown base on 169 forest-grown trees were reconstructed by detailed stem analysis. Crown base was estimated for each year of the tree's life by dating the mortality of all whorl branches. Five-year crown recession was modeled in two parts, the first predicting the probability that a crown recedes and the second estimating recession conditional on its occurrence. The probability of crown recession increased and then decreased with an increasing crown ratio for all three species and similarly peaked over initial tree size. Conditional crown recession increased monotonically with crown ratio for ponderosa pine but peaked at crown ratios between 0.7 and 0.9 in western white pine and Douglas-fir. The resulting models lend insight into factors controlling rates of crown recession and their variation among species and differing initial conditions. FOR. SCI. 54(6):633–646.

Keywords: western white pine, ponderosa pine, interior Douglas-fir, branch reconstruction, crown recession probability, conditional crown recession

LIVE CROWN MEASURES photosynthetic capacity and potential growth and vigor of an individual tree (Assmann 1970, Spurr and Barnes 1980, Valentine et al. 1994). Combined size, structure, geometry, and height of individual crowns also constitute a major feature of wildlife habitat by defining stand canopy structure (Dubrasich et al. 1997, Brokaw and Lent 1999), and these same features control the presence and frequency of fuel ladders and probable fire behavior (Agee 1993, Scott and Reinhardt 2001, Keyes and O'Hara 2002).

From a forest products perspective, crown size and implied branch dynamics also have important implications for wood quality through effects on ring width, length of branch-free bole, maximum branch diameter, stem taper, heartwood/sapwood proportion, and juvenile/mature wood transition (di Lucca 1989, Jozsa and Middleton 1994). These features directly or indirectly influence the commercial value of a tree (Kleine 1986) and have a direct effect on grade distribution of lumber or veneer recovered from trees and logs (Fahey et al. 1991, Western Wood Products Association (WWPA) 1998).

Crown length and width, however, are very dynamic dimensions because of the response of terminal leader growth, branch leader growth, and branch mortality to environmental conditions. Stand structure, site quality, and silvicultural treatments such as stand density manipulation profoundly impact crown development, primarily through influence on height growth and branch longevity (Curtis and Reukema 1970, Cochran and Dahms 2000, Marshall and Curtis 2002). Cumulative effects of past and present inter-tree competition are particularly well represented by current crown size relative to tree diameter and height (Mitchell 1975, Hasenauer and Monserud 1996). Increasing stand density reduces crown length by hastening crown recession (i.e., suppression mortality of branches); conversely, reducing stand density through thinning increases crown length by delaying or slowing crown recession (Assmann 1970, Short and Burkhart 1992).

In short, crown dimensions are an essential feature of any growth model that aspires to predict future growth, assess wood quality, describe habitat structure, estimate fire hazard, and realistically simulate stand dynamics. Thus, growth models must have the capacity to simulate change in crown dimensions as they respond to growing conditions. Change in crown length is a direct consequence of height growth and crown recession, and because height growth has long been a key component of individual-tree growth models, complementary work is needed to reliably predict crown recession or change in crown ratio (i.e., the ratio of live crown length to tree height) (e.g., Wykoff et al. 1982, Maguire and Hann 1990, Hasenauer and Monserud 1996). Despite limited availability of crown size data, crown recession submodels have now become an integral component of many individual-tree forest growth models (Wykoff et al. 1982, Wensel and Daugherty 1985, Hynynen 1995a,

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Hasenauer and Monserud 1996, Dubrasich et al. 1997, Monserud et al. 1997, Hann 2006). Predicted crown length or crown ratio at the end of each growth period in these models becomes a key initial condition for predicting diameter growth (Wykoff 1990), height growth (Ritchie and Hann 1986), and probability of mortality (Monserud and Sterba 1999) over subsequent growth periods.

Mechanics of simulating crown dynamics have differed tremendously, largely due to a variety of objectives motivating a plethora of models. Structural models explore crown growth rules that generate differences in branching architecture (Gavrikov and Sekretenko 1996, Perttunen et al. 1996, Godin 2000, Kurth 2000), and ecophysiological models incorporate aspects of crown structure that have direct bearing on light interception, gas exchange, respiration, and/or overall carbon balance (Oker-Blom and Kellomäki 1983, Ford et al. 1990, Sorrensen-Cothern et al. 1993, Sievänen 1993, Robinson and Ek 2003, Eschenbach 2005). Apart from three-dimensional modeling of crown development (Mitchell 1975), empirical models of individual-tree growth have adopted two general approaches to simulating crown recession: a static approach and a dynamic approach (Maguire and Hann 1990, Liu et al. 1995, Hann and Hanus 2004). The static approach relies on allometric relationships between crown size, stem diameter, and tree height, as well as competitive effects of surrounding trees. In this approach, height to crown base (HCB) or crown ratio (CR) for an individual tree is estimated from stand density, relative position of a tree in a stand, site quality, and bole dimensions (Ek 1974, Daniels et al. 1979, Wykoff et al. 1982, Ritchie and Hann 1986, Hann et al. 2003). During simulation, crown recession is inferred by estimating HCB from both initial and ending stand conditions and tree size (Hann and Hanus 2004).

In the dynamic or incremental approach, crown recession (ΔHCB) is predicted directly as a function of only initial conditions, including stand density, tree size, and relative position in the stand (Krumland and Wensel 1981, Maguire and Hann 1990, Short and Burkhart 1992, Valentine et al. 1994, Hynynen 1995b, Hann and Hanus 2004). This approach is analogous to diameter and height increment models. The advantage of the dynamic approach (ΔHCB) is that the degree of density reduction in managed stands influences projected recession directly (Hasenauer and Monserud 1996). The dynamic approach therefore avoids the need to embed a rule in the growth model to prevent the decline in HCB that would otherwise be predicted after thinning to a lower stand density (e.g., Short and Burkhart 1992). Dynamic models of crown recession have also been shown to explain a higher portion of variability in crown recession than static models of HCB (Hann and Hanus 2004).

Part of the reason that static HCB models are more common than dynamic ΔHCB is the paucity of long-term data with repeated HCB measures. One alternative is to take a retrospective look at crown recession by dating individual branch mortality (Maguire and Hann 1987, Fujimori 1993, Spathelf 2003). The disadvantage of this approach is that essential aspects of past stand structure, particularly stand density, are not known. However, crown ratio can be a powerful surrogate for local stand density and can be reconstructed through the branch mortality dating technique described by Maguire and Hann (1987).

The first objective of this research was to reconstruct patterns in past crown recession for three major conifer species in the Rocky Mountains of northern Idaho: western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), and interior Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca*). The second objective was to test the effect of initial tree diameter, height, and crown ratio on probability of crown recession and amount of crown recession conditional on its occurrence. These three co-occurring species were chosen because they are the most ecologically dominant and economically important species in the region and because of their diverse genetic strategies. Douglas-fir is a genetic specialist, western white pine is a generalist, and ponderosa pine is intermediate (Rehfeldt 1978, 1993, Rehfeldt et al. 1984). Despite the importance of these three species, little attention has been paid to qualitative and quantitative description of their crown dynamics.

Methods

Study Area

The study area is located on the Priest River Experimental Forest in the Panhandle of northern Idaho, USA (48°21′N, 116°50′W). The climate is relatively mild compared with the continental East side of the Rocky Mountain crest and is transitional between a northern Pacific coastal and continental type (Finklin 1983). Species composition in northern Idaho is intermediate between the maritime forests west of the Cascades and the continental forests of the central and eastern Rocky Mountains; stands are most commonly multispecies combinations of conifers, with at least 11 species of conifers occurring naturally on the experimental forest. Sampled stands were found at some of the lowest elevations in the forest, ranging from 800 to 950 m.

Ten stands averaging approximately 80 years in total age were selected to cover a range in growing conditions implied by differences in slope, aspect, and elevation. All sampled stands were naturally regenerated and were classified according to the habitat type system of Daubenmire and Daubenmire (1968) and Pfister et al. (1977). Stands were sampled from the following types, listed in order of increasing moisture availability and shade tolerance of dominant species: (1) *Pseudotsuga menziesii/Physocarpus malvaceous* (Douglas-fir/ninebark), (2) *Abies grandis/Clintonia uniflora* (Grand fir/queencup beadlily), (3) *Thuja plicata/Clintonia uniflora* (western redcedar/queencup beadlily), (4) *Tsuga heterophylla/Clintonia uniflora* (western hemlock/queencup beadlily), and (5) *Tsuga heterophylla/Asarum caudatum* (western hemlock/wild ginger). Generally, the dry Douglas-fir/ninebark habitat types were located on ridges, whereas the moister sites were located midslope. The moistest sites (western hemlock/wild ginger) were located on bottomlands. All stands were a mix of species with basal area ranging from 9.5 to 43.5 m^2 ha^{-1} and tree density ranging from 328 to 1,876 trees ha^{-1}.

Field Measurements

In July of 1988 and 1989, 169 mature dominants and codominants with a normal, healthy crown were felled in the 10 selected stands. Trees selected for destructive sampling had no apparent damage (no obvious disease or pest attack or visibly forked top), a cone crop indicating adequate vigor, and a radial growth pattern that gave no indication of past damage. The 169 sample trees were selected across species and size class in each stand, and trees of a given species were separated by a distance of at least three crown widths. Of the 169 sample trees, 56 were western white pine, 55 were ponderosa pine, and 58 were Douglas-fir.

Sample trees were felled as carefully as possible to avoid breaking branches on felled and adjacent trees. After felling, crown length was measured from tree tip to base of the live crown, defined as the lowest contiguous live whorl, i.e., the lowest live whorl above which all whorls had at least one live branch (Maguire and Hann 1987). Total tree length, stump height, and dbh were then measured, and annual rings were counted on the stump. Annual height increments were measured by whorl locations from tree tip to stump, and the number of live branches was recorded for each whorl. A stem disk was removed just below every tenth whorl, and any discrepancies between ring count and whorl count were reconciled. At the whorl defined as crown base and at every whorl below, a 20–25 cm thick cross-sectional disk containing all whorl branches was cut from the stem, and rings were counted to verify whorl number. Any discrepancy between ring counts and whorl counts was resolved by splitting the stem section down the pith and identifying terminal bud scars. All cross-sectional disks were labeled, air-dried, and removed to the laboratory for further processing. Although branch stubs indicating whorl locations were usually visible even near the base of large trees, ring counts were made to verify whorl count.

Laboratory Measurements

Wedges containing individual branches were sawn out of the cross-sectional disks with a band saw. Extraction of branch wedges exposed the few occluded branches with no external indicators on the surface of the bole. These occluded branches were treated the same as the visible branches. A horizontal cut perpendicular to the axis of the bole was sawn through each branch, ending at bole pith. This horizontal cut avoided the tension and compression wood in rings at the top and bottom of a branch. Each branch section was labeled by whorl and tree number.

In the laboratory, branch diameter inside bark was measured at the point of insertion into the bole, and the number of rings between the outer surface (cambium) of the bole to the ring corresponding to year of branch death was recorded (Maguire and Hann 1987). A ring with dark coloration indicated year of death, as did a change from a concave ring shape at the junction of the bole and a living branch to a convex shape signaling growth of cambium around a dead branch. Year of death was estimated independently on both the right and left side of the branch longitudinal section and on both top and bottom halves of each wedge. Each estimate was rated high or low for the level of confidence in dating branch mortality. The longest and shortest radii from pith to cambium were measured on the breast height cross-sections. Quadratic mean radius was then calculated, and a radius of that length with no growth ring distortions attributable to nearby branches was found on the section and measured for annual increment.

Analysis

Year of branch mortality was estimated as the earliest year in which branch cambium had died back to the bole cambium (maximum estimated time since death for each branch). This approach best accommodated observable differences in the time it takes for branch cambium to die back to the bole around different sides of the branch (Maguire and Hann 1987). After year of mortality for every branch below current crown base was estimated, height to crown base for each year was identified by applying two objective definitions of crown base (see Table 1 for variable definitions): height to first live whorl above the highest dead whorl (HCB_1; same as the lowest contiguous live whorl from Maguire and Hann 1987), and height to first live whorl above the highest two contiguous dead whorls (HCB_2). The first definition maintained consistency with past modeling efforts (Maguire and Hann 1990). The second definition was motivated by dead whorls occasionally observed within the main portion of several western white pine and ponderosa pine crowns, creating artificially short crowns under HCB_1. Because definition of crown base has varied widely in forestry (Monleon et al. 2004), including two alternatives allowed us to assess the sensitivity of recession patterns to selected definition of crown base. Felled sample trees ranged from 17 to 41 m in total height, with crown ratio based on HCB_1 ranging from 0.24 to 0.94 and from 0.34 to 0.95 based on HCB_2 (Table 2).

Table 1. Response and explanatory variables tested during examination of crown recession patterns for *Pinus monticola*, *P. ponderosa*, and *P. menziesii* in northern Idaho

Variable	Definition
AGE	Initial age at stump height
dbh	Initial diameter at breast height (cm)
HT	Initial total tree height (m)
HCB_1	Initial height to the first live whorl above the highest dead whorl (m)
HCB_2	Initial height to the first live whorl above the highest two consecutive dead whorls (m)
CR_1	Initial crown ratio based on HCB_1 ($1 - HCB_1/HT$)
CR_2	Initial crown ratio based on HCB_2 ($1 - HCB_2/HT$)
Δdbh	Periodic annul diameter dbh growth (cm)
ΔHT	Periodic annual height growth (m)
ΔHCB_1	Periodic annual change in HCB_1 (m)
ΔHCB_2	Periodic annual change in HCB_2 (m)
MOIST	Indicator variable for moist habitat types (1 if *Tsuga heterophylla/Asarum caudatum*; 0 otherwise)
MESIC	Indicator variable for mesic habitat types (1 if *Thuja plicata/Clintonia uniflora* or *T. heterophylla/C. uniflora*; 0 otherwise)
HT_{MAX}	Initial height of tallest tree in the stand (m)
HT_{REL}	Initial relative tree height (HT/HT_{MAX})

Table 2. Attributes of *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* sample trees from northern Idaho

Variable	*P. monticola*		*P. ponderosa*		*P. menziesii*	
	Mean	Range	Mean	Range	Mean	Range
n	56		55		58	
Age (years)	57.5	28–85	82.1	44–106	79.1	49–122
dbh (cm)	31.1	21.3–53.1	43.2	26.1–61.8	42.5	26.3–62.4
HT (m)	27.9	17.0–41.3	30.6	20.2–39.1	28.1	20.4–36.7
CR_1	0.71	0.32–0.92	0.51	0.24–0.76	0.58	0.32–0.84
CR_2	0.75	0.38–0.95	0.56	0.34–0.78	0.63	0.40–0.88

The lifespan of each sample tree was divided into 5-year growth periods counting back from the year sample trees were felled (1988 or 1989). Initial HCB_1 for these 5-year periods ranged from 0 to 17.0, 0 to 20.9, and 0 to 16.6 m for western white pine, ponderosa pine, and Douglas-fir, respectively, with corresponding crown ratios (CR_1) of 0.28 to 1, 0.18 to 1, and 0.31 to 1 (Table 3). Initial HCB_2 for the same 5-year periods ranged from 0 to 17.0, 0 to 17.0, and 0 to 15.7 m for western white pine, ponderosa pine, and Douglas-fir, respectively, with corresponding crown ratios (CR_2) of 0.53 to 1, 0.41 to 1, and 0.41 to 1 (Table 4). Initial tree diameter, height, HCB_1, and HCB_2 were determined for each 5-year growth period, allowing computation of 5-year diameter growth (Δdbh), height growth (ΔHT), and crown recession (ΔHCB_1 or ΔHCB_2) (Tables 3 and 4). Crown recession (ΔHCB_2) averaged 1.46, 1.48, and 1.46 m for western white pine, ponderosa pine, and Douglas-fir, respectively. Crown ratio of the subject tree was assumed to represent local stand density, and the relative height (HT_{REL}) of each tree was computed as the initial height of the sample tree in a given 5-year period (HT) relative to the initial height of the tallest sample tree in that stand for the same growth period (HT_{MAX}). Habitat type indicators were also included as potential covariates (see Table 1).

Observed 5-year crown recession was frequently zero for many trees during many growth periods, but a second mode >0 was also apparent in the distribution of both recession and conditional recession (right panel and vertical slices through left panel, respectively, in Figure 1). This pattern suggested that the distributional assumptions of a least-squares regression model would not easily be met, but more importantly, that crown recession should be modeled as two processes or components: probability of 5-year crown recession, $P(\Delta HCB_1 > 0)$ or $P(\Delta HCB_2 > 0)$ and 5-year change in height-to-crown-base conditional on occurrence of crown recession ($\Delta HCB_1 > 0$ or $\Delta HCB_2 > 0$).

Occurrence of crown recession was a binomial response and, hence, was described with a generalized linear model assuming a binomial distribution and logit link function (McCullagh and Nelder 1989):

$$\eta = \ln[\mu/(1-\mu)] = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k, \quad (1)$$

where η is the linear predictor, ln is the natural logarithm, μ is the mean of the conditional binomial distribution, and β_i are parameters to be estimated from the data.

Potential predictor variables included tree descriptors such as total age (AGE), dbh, total height (HT), crown ratio (CR_1 or CR_2 computed from HCB_1 or HCB_2, respectively), diameter and height increment (Δdbh and ΔHT), relative height (HT/HT_{max}), and habitat type indicators (Table 1). Preliminary data exploration indicated that the probability of crown recession peaked over crown ratio, so $\ln(CR_k)$ and $\ln(1.01 - CR_k)$ were included as potential predictors to provide flexibility. Models were fitted using the GENMOD procedure in SAS version 9.1 (SAS Institute, Cary, NC). Nested models were compared by change in deviance tests (McCullagh and Nelder 1989).

Several models forms were tested for describing conditional crown recession. The first was similar to one proposed by Short and Burkhart (1992):

$$\Delta HCB_k = \exp[\gamma_{20} + \gamma_{21}\ln(CR_k) + \gamma_{22}CR_k + \gamma_{23}\ln(HT) + \gamma_{24}(1.01 - CR_k) + \gamma_{25}\ln(1.01 - CR_k)] + \varepsilon_2 \quad (2)$$

where ΔHCB_k is either ΔHCB_1 or ΔHCB_2, CR_k is CR_1 or CR_2, γ_{ij} are parameters to be estimated from the data, ε_2 is

Table 3. Characteristics of *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* sample trees at the beginning of each 5-year period for which crown recession (ΔHCB_1) could be reconstructed

Variable	*P. monticola*		*P. ponderosa*		*P. menziesii*	
	Mean	Range	Mean	Range	Mean	Range
n	227		499		404	
Age (years)	45	15–78	51	6–101	52	15–112
dbh (cm)	22.7	2.6–48.3	28.3	0.2–59.8	29.1	4.4–60.0
HT (m)	20.7	2.5–37.3	18.7	1.6–36.4	19.7	2.7–33.8
HCB_1 (m)	5.3	0.0–17.0	7.4	0.0–20.9	6.4	0.0–16.6
CR_1	0.76	0.28–1.00	0.64	0.18–1.00	0.70	0.31–1.00
Δdbh (cm/yr)	0.6	0.2–1.4	0.5	0.2–1.4	0.6	0.1–1.6
ΔHT (m/yr)	0.5	0.1–1.0	0.4	0.0–1.8	0.4	0.0–0.9
ΔHCB_1 (m)	1.61	0.06–7.31	1.72	0.03–9.91	1.70	0.15–10.39

Table 4. Characteristics of *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* sample trees at the beginning of each 5-year period for which crown recession (ΔHCB_2) could be reconstructed

Variable	*P. monticola*		*P. ponderosa*		*P. menziesii*	
	Mean	Range	Mean	Range	Mean	Range
n	227		499		404	
Age (years)	45	15–78	51	6–101	52	15–112
dbh (cm)	22.9	2.6–48.3	28.3	0.2–59.8	29.1	4.4–60.0
HT (m)	20.9	2.5–37.3	18.7	1.6–36.4	19.3	2.7–33.8
HCB_2 (m)	4.5	0.0–17.0	6.1	0.0–17.0	5.2	0.0–15.7
CR_2	0.81	0.53–1.00	0.71	0.41–1.00	0.76	0.41–1.00
Δdbh (cm/yr)	0.6	0.2–1.4	0.5	0.2–1.4	0.6	0.1–1.6
ΔHT (m/yr)	0.5	0.1–1.0	0.4	0.0–1.8	0.4	0.0–0.9
ΔHCB_2 (m)	1.46	0.09–4.91	1.48	0.03–4.99	1.46	0.15–4.85

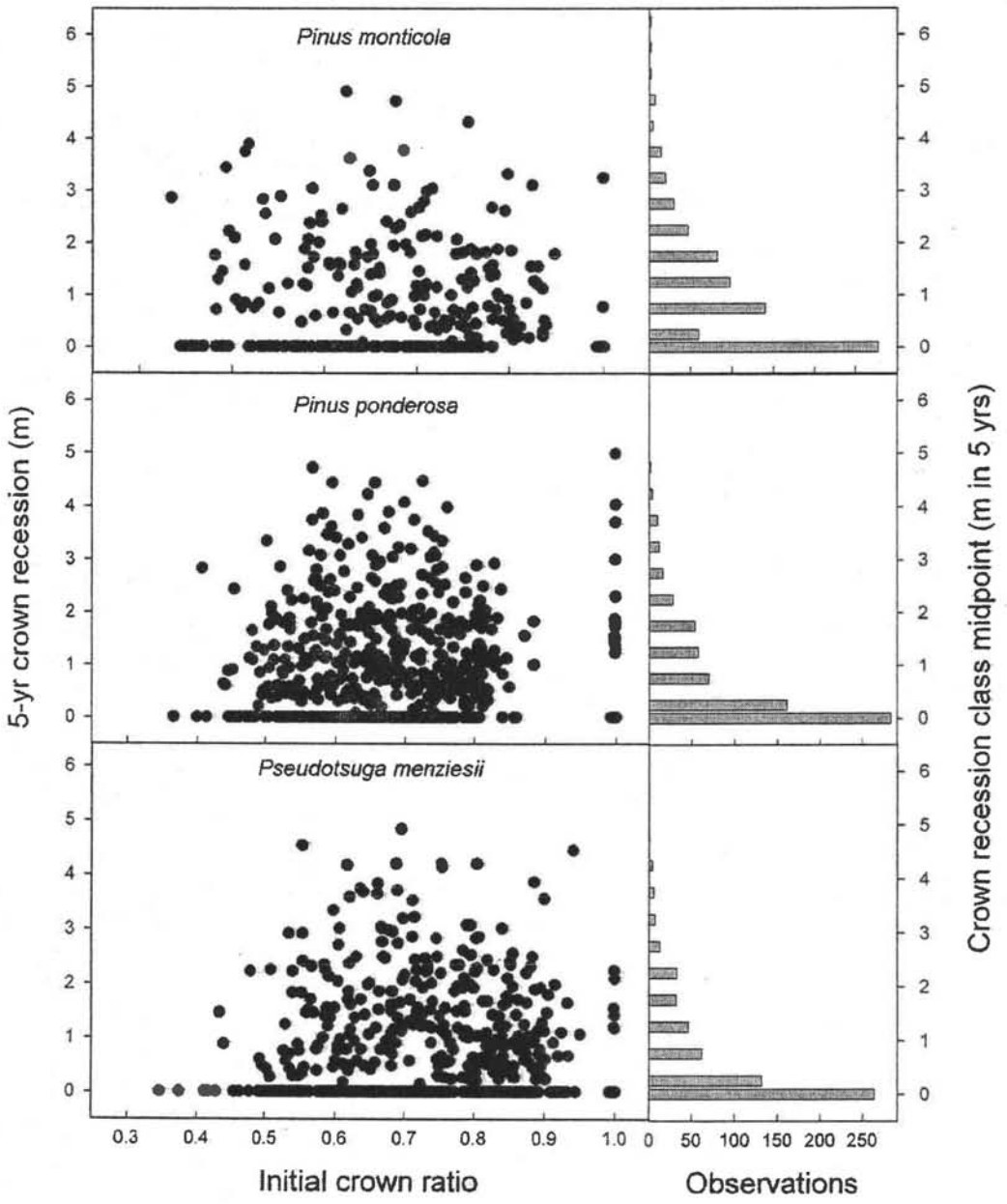

Figure 1. Five-year crown recession for three species in the northern Rocky Mountains as a function of initial crown ratio (left panel) and by frequency across 0.5-m classes (right panel).

a random error with $\varepsilon_2 \sim N(0, \sigma_2^2)$, and all other variables are defined above (see also Table 1).

The two other general model forms tested for conditional crown recession were

$$\Delta HCB_k = \gamma_{31} HT(1 - \exp[(\gamma_{32}/HT)CR_k^{\gamma_{33}/HT}]) + \varepsilon_3 \quad (3)$$

and

$$\Delta HCB_k = CR_k^{\gamma_{41}/HT}/[\gamma_{42} + (\gamma_{43} + \gamma_{44} HT)CR_k + \gamma_{45} CR_k^{\gamma_{46}}] + \varepsilon_4, \quad (4)$$

where γ_{ij} are parameters to be estimated from the data, ε_3 and ε_4 are random errors with $\varepsilon_3 \sim N(0, HT^2\sigma_3^2)$ and $\varepsilon_4 \sim N(0, HT^2\sigma_4^2)$, and all other variables are defined above (see also Table 1). Models were fitted by weighted nonlinear least squares in SAS version 9.1. Significance departure of each parameter estimate from 0 or 1 was tested with extra sums of squares F tests. Where parameter estimates were not significant at $\alpha = 0.05$, the reduced model was preferred. Within-tree temporal autocorrelation was tested by partial autocorrelation functions. Models were evaluated on the basis of residual plots, bias, and mean square error. Parameter estimates were also evaluated with respect to consistency between implied recession patterns and known biological constraints.

Implied 5-year crown recession was computed as the product of recession probability and conditional recession. This average recession rate was evaluated by plotting its behavior over initial crown ratio for trees of varying size.

Results

Reconstructed Crown Recession

The technique for dating branch mortality produced crown recession patterns consistent with established trends in tree and stand development (Figure 2). Change in height

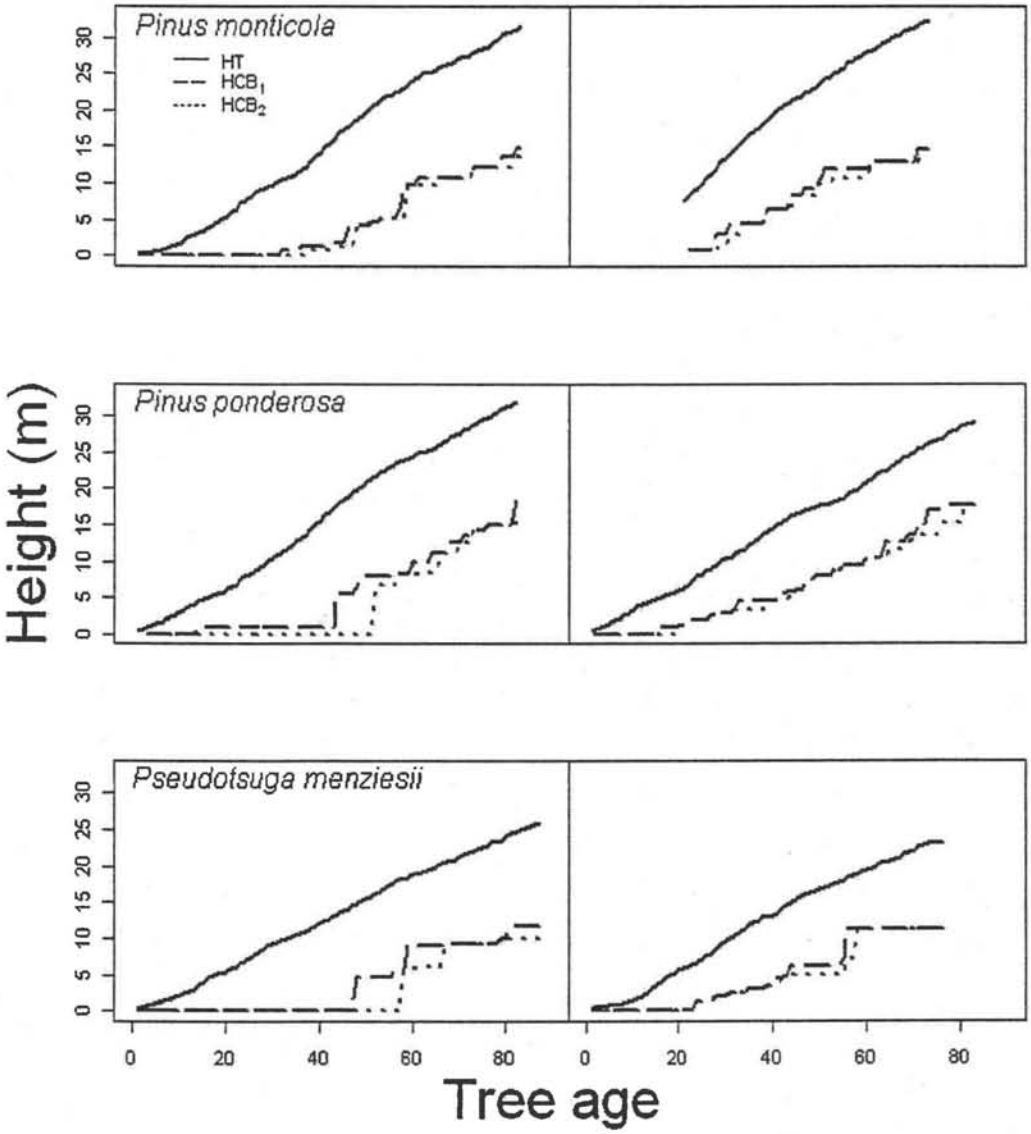

Figure 2. Reconstructed progression of total height (HT; solid line) and HCB_1 (dashed line), and HCB_2 (dotted line) for two *P. monticola*, *P. ponderosa*, and *P. menziesii* sample trees in northern Idaho.

to crown base over time paralleled cumulative height growth of each tree, with crowns lengthening over time as more growing space was made available by self-thinning. One striking feature of the reconstructed crown recession patterns was an occasional surge in branch mortality and a corresponding jump in crown recession. Also, many trees exhibited delays of more than 10 years before onset of branch mortality, but then crown recession was rapid for 1 or 2 years once it started.

Because the data set was constructed by dating branch mortality on only those trees that had survived in the unmanaged sample stands to 1988, a relatively narrow range of initial conditions was covered by the pooled 5-year growth periods (Tables 3 and 4). Lack of any stand density manipulation ensured a strong correlation between crown ratio and age. Very few old or large trees had full crowns, and few young trees with small crowns survived to be sampled in 1988. The crown ratio-age correlation was strongest for ponderosa pine (−0.65) and weakest for Douglas-fir (−0.56), with white pine in between (−0.61). Likewise, age-height correlation was strongest for ponderosa pine (0.89) and somewhat weaker for Douglas-fir (0.84); the correlation for white pine was similar to that for Douglas-fir (0.86).

Probability of Crown Recession

The probability that trees experienced at least some crown recession during a 5-year growth period was controlled primarily by initial crown ratio and initial stem size (diameter and height). Regardless of species or definition of crown base, the probability of crown recession was greatest for trees with initial crown ratios between 70 and 90% (Figure 3). Probability increased as tree diameter increased to approximately 30 cm and then declined again for larger trees (Figure 3; Table 5). The one exception to this general pattern involved the trend in HCB_2 for ponderosa pine; in this case, recession rate was not influenced by initial tree

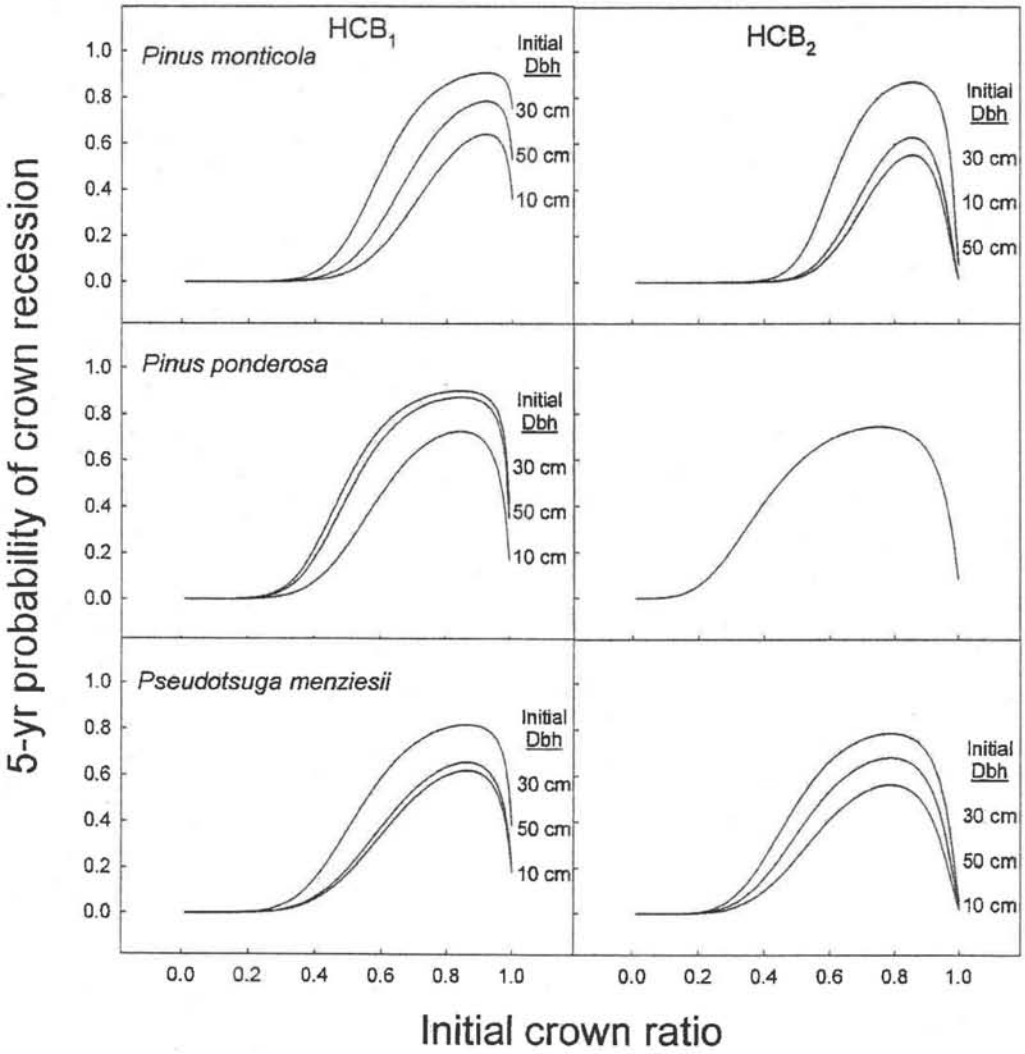

Figure 3. Trends in 5-year probability of crown recession ($\Delta HCB_k > 0$) for a given initial crown ratio and tree diameter. Initial height was assigned from the height-diameter relationship for each species (7.2, 27.0, and 35.7 m for western white pine; 4.1, 20.9, and 30.2 m for ponderosa pine; and 5.8, 21.1, and 28.0 m for Douglas-fir trees with dbh of 10, 30, and 50 cm, respectively).

Table 5. **Parameter estimates, asymptotic standards errors, and fit statistics for models describing the probability of crown recession in *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* from northern Idaho (binomial model 1)**

Predictor variable, X_i	Response					
	P. monticola		*P. ponderosa*		*P. menziesii*	
	ΔHCB_1	ΔHCB_2	ΔHCB_1	ΔHCB_2	ΔHCB_1	ΔHCB_2
Intercept	3.1214 (1.0155)	5.8279 (1.0836)	4.7754 (0.5282)	4.1924 (0.5198)	3.3733 (0.6125)	5.5832 (0.7248)
$\ln(CR_k)$	8.4030 (1.5524)	12.7119 (1.9876)	6.9908 (0.7594)	4.1645 (0.7937)	6.1988 (0.7775)	6.2390 (1.0124)
$\ln(1.01 - CR_k)$	0.84030 (0.3417)	2.3239 (0.3458)	1.3254 (0.1544)	1.4291 (0.1551)	1.0765 (0.1894)	1.7913 (0.2127)
ln(dbh)	−0.1542 (0.0438)	−0.2033 (0.0463)	−0.1059 (0.0219)		−0.1192 (0.0225)	−0.0908 (0.0259)
ln(HT)	0.2412 (0.0539)	0.2743 (0.0585)	0.1991 (0.0369)		0.2217 (0.0432)	0.1862 (0.0502)
AGE						−0.0270 (0.0104)
MOIST		1.0704 (0.2955)				
Residual deviance/ null deviance	1.117/1.288	1.063/1.379	1.122/1.324	1.129/1.362	1.224/1.363	1.124/1.380
Deviance ratio: residual/null	0.87	0.77	0.85	0.83	0.90	0.81

Standard errors are in parentheses.

size. Parameter estimates indicated that at a fixed total height, trees with greater diameter had a lower probability of recession. However, because an increase in diameter was closely matched by an increase in total height in these fully stocked stands, the net result of the combined diameter and height effects was a peak in the probability of recession at median tree size (the average height-diameter relationship specific to each species was maintained when trends were plotted in Figure 3). The only other two variables that were strongly related to probability of crown recession included total age for HCB_2 in Douglas-fir and an indicator for moist habitat types in western white pine (Table 5). Recession probability generally decreased with increasing 5-year diameter growth and increased with increasing height growth. However, these growth variables were not included in the final models so that recession patterns could be described as a function of initial conditions. Relative tree height (HT/HT_{max}) explained very little variability in probability of crown recession.

Residual deviances were fairly high for all models, indicating a large amount of variability around the final model (Table 5). However, there was no evidence of under- or overdispersion. For all three species, slightly better fits were attained with $P(\Delta HCB_2 > 0)$ than with $P(\Delta HCB_1 > 0)$, although the difference between the two ponderosa pine models was negligible (see ratio of residual deviance to null deviance in Table 5). For a given species, $P(\Delta HCB_1 > 0)$ and $P(\Delta HCB_2 > 0)$ were controlled by the same variables.

Conditional 5-Year Crown Recession

Five-year crown recession peaked at intermediate crown ratios for white pine and Douglas-fir trees, generally between 50 and 80% (Figure 4; Tables 6 and 7). In contrast, crown recession increased monotonically with crown ratio in ponderosa pine. There was some evidence of two peaks in the ponderosa pine recession rate over the range of initial crown ratio, one consistent with the peak in white pine and Douglas-fir at medium crown ratios and the other at crown ratios of 100%. However, none of the statistical models could substantiate the peak at medium crown ratios, regardless of model complexity. Large conditional recession rates on full-crowned ponderosa pine trees were consistent with reconstructed jumps in height to crown base after delays in start of crown recession (Figure 2). Initial tree height was the next strongest covariate influencing 5-year crown recession (Table 6). Regardless of species or definition of crown base, recession was faster on taller trees (Figure 4; Tables 6 and 7). Average maximum recession based on HCB_2 ranged from approximately 2.1 m in western white pine and Douglas-fir to approximately 2.5 m in ponderosa pine.

All recession models were weighted by the inverse of tree height to yield constant variance in residuals, except for ΔHCB_1 in Douglas-fir. In this latter case, the model was fitted after transformation by the natural logarithm (Table 7), primarily because the residuals were more normally distributed on this scale. The highly variable nature of crown recession was evident from relatively high mean square errors and low R^2 values, the latter implying that only 9–18% of variation in crown recession was accounted for by the final models (Table 7). Residual variation increased with increasing tree height (or age), but no significant autocorrelation was detected for successive 5-year growth periods within a tree. Slightly better fits were achieved with the response variable ΔHCB_2 than with ΔHCB_1 in all three species.

Average 5-Year Crown Recession

Average 5-year crown recession implied by the product of recession probability and conditional recession peaked over the initial crown ratio, but the crown ratio corresponding to maximum recession varied by species and by initial tree diameter and height (Figure 5). In western white pine and Douglas-fir, maxima occurred near crown ratios of 0.75 and 0.65, respectively, on medium to large trees but at 0.90 on smaller trees. In contrast, the peak for ponderosa pine ranged only from approximately 0.85 to 0.90. Average recession in both Douglas-fir and western white pine was greatest on medium-sized trees, but increased with increasing initial tree size in ponderosa pine. The maximum average 5-year recession rate for all species was approximately 1.5 m.

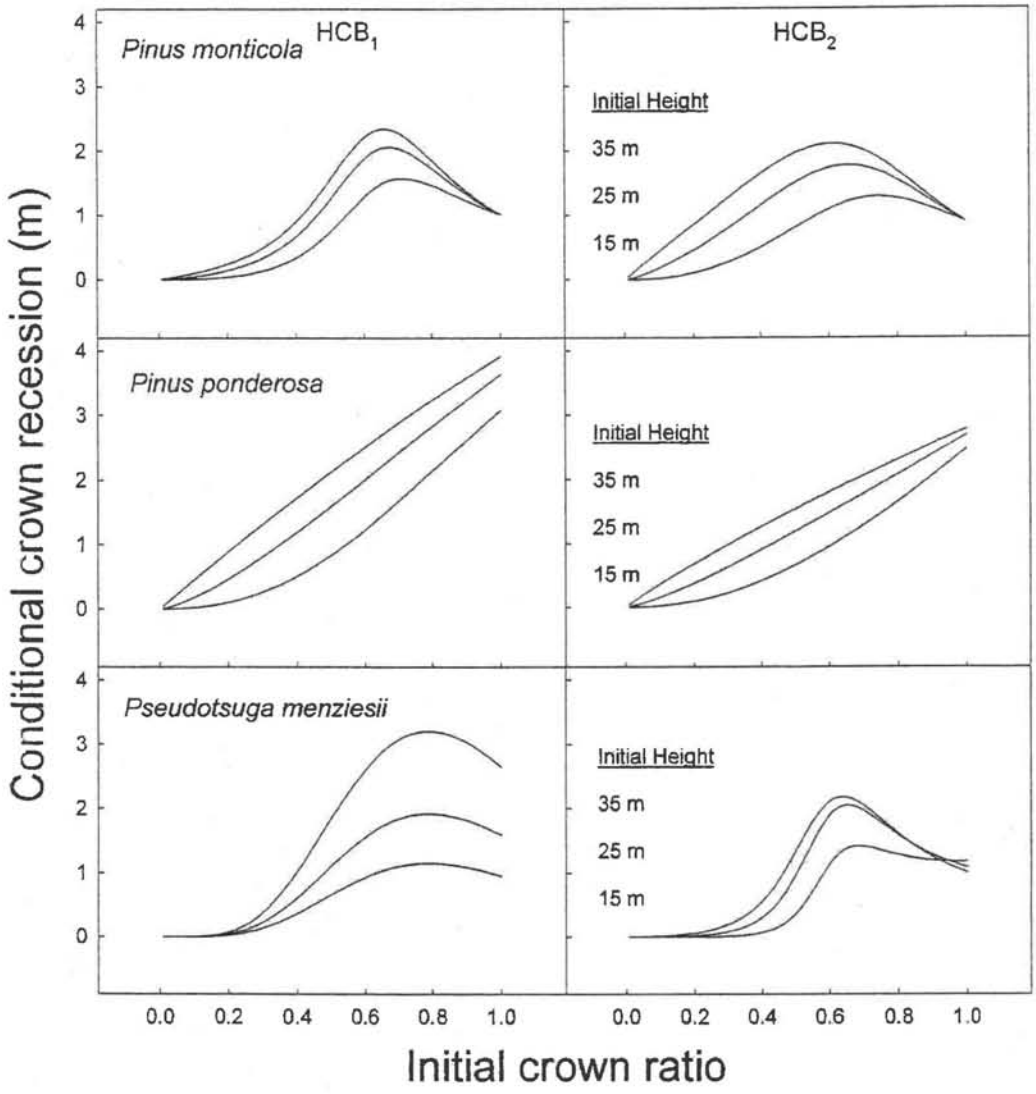

Figure 4. Trends in conditional 5-year crown recession for a given initial crown ratio and initial tree height.

Table 6. Final models for describing conditional 5-yr crown recession in *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* in northern Idaho

Species	Models
P. monticola	$\Delta HCB_1 = \frac{CR_1^{\gamma_{41}/HT}}{\gamma_{42} + \gamma_{43}CR_1 + \gamma_{44}CR_1^2} + \varepsilon_4$
	$\Delta HCB_2 = \frac{CR_2^{\gamma_{41}/HT}}{\gamma_{42} + \gamma_{43}CR_2^{\gamma_{44}}} + \varepsilon_4$
P. ponderosa	$\Delta HCB_1 = (\gamma_{31}HT)(1 - \exp[(\gamma_{32}/HT)CR_1^{\gamma_{33}/HT}]) + \varepsilon_3$
	$\Delta HCB_2 = (\gamma_{31}HT)(1 - \exp[(\gamma_{32}/HT)CR_2^{\gamma_{33}/HT}]) + \varepsilon_3$
P. menziesii	$\Delta HCB_1 = \exp[\gamma_{21} + \gamma_{22}HT + \gamma_{23}\ln(CR_1) + \gamma_{24}(1.01 - CR_1)] + \varepsilon_2$*
	$\Delta HCB_2 = \frac{CR^{\gamma_{41}/HT}}{\gamma_{42} + (\gamma_{43} + \gamma_{44}HT)CR_2 + \gamma_{45}CR_2^2} + \varepsilon_4$

* Model fitted after transformation by natural logarithm, with $\varepsilon_2 \sim \ln(0, \sigma^2)$.

Table 7. **Parameters estimates, asymptotic standards errors, and fit statistics for conditional 5-year crown recession models for *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii* in northern Idaho (models are specified in Table 6)**

Parameter/ response	*P. monticola*		*P. ponderosa*		*P. menziesii*	
	ΔHCB_1	ΔHCB_2	ΔHCB_1	ΔHCB_2	ΔHCB_1	ΔHCB_2
$\gamma_{.1}$	27.9355 (8.9642)	33.9261 (11.1499)	0.3370 (0.0607)	0.4648 (0.1289)	−0.89293 (0.18805)	66.9051 (14.4278)
$\gamma_{.2}$	2.1472 (1.0826)	0.2465 (0.0928)	−14.1134 (4.3658)	−6.5693 (2.4931)	0.05119 (0.00797)	1.6434 (0.3667)
$\gamma_{.3}$	−5.9470 (2.9748)	0.8676 (0.2197)	35.6483 (6.4314)	32.1521 (5.0820)	6.09712 (1.91947)	−5.3877 (1.0174)
$\gamma_{.4}$	4.7837 (2.0343)	5.8850 (2.5915)			7.73549 (2.81153)	0.00739 (0.00237)
$\gamma_{.5}$						4.4797 (0.7398)
Weight	HT^{-1}	HT^{-1}	HT^{-1}	HT^{-1}	1	HT^{-1}
Mean square error*	1.328	0.886	2.054	0.894	1.896	0.829
Root mean standard error*	1.152	0.941	1.433	0.945	1.377	0.911
R^2†	0.13	0.13	0.10	0.10	0.13	0.14

Standard errors are in parentheses.
* From estimates on untransformed and unweighted scale.
† Generalized coefficient of determination, untransformed, and unweighted scale (Kvålseth 1985)

Discussion

Reconstructed Crown Recession

The technique of dating branch mortality by stem dissection has been successfully applied in the past to meet a variety of research objectives (Andrews and Gill 1939, Rapraeger 1939, Reukema 1959, Fujimori and Kiyono 1986, Osawa 1990, Fujimori 1993, Mäkinen 2002). This dating technique, combined with rules for defining crown base by the number and height of live branches, has been shown to accurately track repeated observations of crown base in coastal Douglas-fir (Maguire and Hann 1987). Similar validation has not been done for Rocky Mountain Douglas-fir, ponderosa pine, or western white pine, although the technique has been applied for studying knot formation in western white pine (Rapraeger 1939). Reconstructed crown lift on trees at Priest River tracked approximately proportional to cumulative height growth over time on the same tree and so was consistent with past observations that height growth controls the rate at which the entire canopy rises. As new foliage accumulates at the top of the canopy, branches at the crown base succumb to suppression mortality at a rate proportional to the addition of mass at the top of the crown. Crowns also lengthen over time in undisturbed stands because self-thinning creates more growing space for surviving trees. Crown recession patterns reconstructed at Priest River pertain primarily to the stand component that survived 80 years of stand development. Trees that were relegated to suppressed or intermediate crown classes early in stand development generally would have had a much lower probability of surviving until sampling in 1988; the probability of tree mortality increases with progressively smaller crown ratios characterizing trees in inferior social position (Monserud and Sterba 1999, Hann et al. 2003). The amount of foliage available for fixing carbon in these trees simply becomes inadequate to meet maintenance and construction demands. Suppressed trees or those that eventually die from suppression mortality typically experience a decline in crown ratio and an accompanying decline in available photosynthates per unit of live mass.

Another consequence of sampling trees that survived to 1988 was the strong negative correlation between initial crown ratio and age for the reconstructed 5-year growth periods. Survivors generally would have had relatively large crowns early in stand development, so trees that had small crown ratios at young ages were almost certainly underrepresented among the live trees available for sampling in 1988. This age/crown ratio correlation therefore limited our ability to describe crown recession on young trees of lower crown classes.

Another limitation of studying crown dynamics by dating branch mortality was that stand density could not be accurately reconstructed for the temporary plots from which trees were sampled, primarily because mortality losses were unknown. Stand density and similar conditions representing the competitive effects of adjacent trees have been shown to influence rate of crown recession (Krumland and Wensel 1981, Maguire and Hann 1990, Short and Burkhart 1992, Spathelf 2003, Hann and Hanus 2004). However, Short and Burkhart (1992), found that stand density and competition measures did not account for much additional variation in crown recession of loblolly pine beyond that predictable from initial tree dbh, height, and crown length. Related aspects of crown dynamics have been found to be similarly insensitive to stand density because its cumulative effect is accounted for by each unique combination of tree diameter, height, and crown size. In Scots pine (*Pinus sylvestris* L.), Mäkinen and Colin (1998) found that stand density had a significant influence on branch angle and branch diameter but that it could be excluded without loss of accuracy when relative crown length and stem diameter were included as explanatory variables. Validation of models constructed without stand density as a predictor illustrated that branch characteristics can be accurately predicted from tree-level variables without detailed knowledge of stand history. Similar results have been obtained for models describing branch size variation in Douglas-fir (Maguire et al. 1991, 1999). In many, if not most, species, the combination of initial crown ratio (or crown length), height, and diameter acts as an effective surrogate for local stand density.

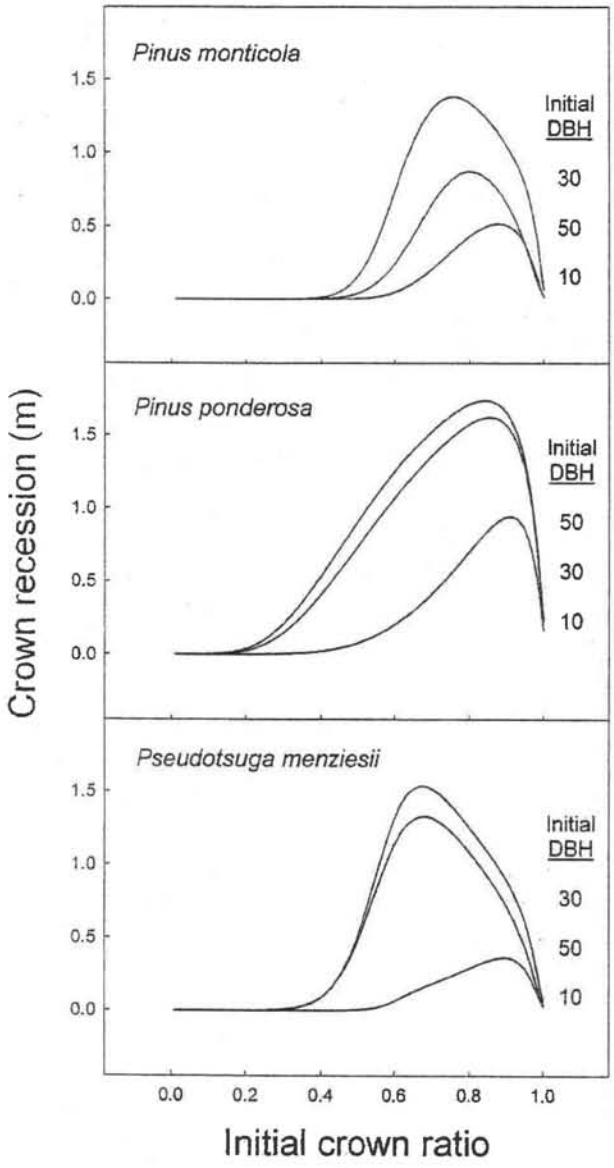

Figure 5. Trends in average 5-year crown recession (ΔHCB_2) for a given initial crown ratio and tree diameter in *P. monticola*, *P. ponderosa*, and *P. menziesii* from northern Idaho. Average recession is the product of recession probability (Figure 2) and conditional crown recession (Figure 3). See Figure 2 legend for corresponding initial heights.

Probability of Crown Recession

Comparison of results from Priest River with those from other crown recession models is difficult because, to our knowledge, no other studies have quantified the probability of crown recession separately from the crown recession rate. The probability of crown recession in all three species peaked at relatively large crown ratios (0.7–0.9). As might be anticipated from delayed crown recession observed on many trees with full crowns (Figure 2), the final descriptive models indicated a low probability of recession on trees with large initial crown ratios. These trees tended to be small, relatively open-grown, younger trees. However, if crown recession had already started on these trees, then it was highly probable that recession continued in subsequent growth periods (60–90% probable, depending on species and initial size). As crown ratios fell below 0.7, the probability of recession gradually declined again, perhaps reflecting the onset of self-thinning and the more erratic nature of crown recession resulting from episodic tree mortality, irregular availability of new growing space, and asymmetry in competition due to random distribution of natural regeneration during the stand establishment stage in this forest type (Moeur 1993).

Crown ratios as low as 0.3–0.4 were generally restricted to larger, older trees, so the lower probability of recession associated with a small initial crown ratio was probably at least partly a consequence of decelerating height growth in older trees. Although height growth trajectories of sampled trees indicated no dramatic deceleration (Figure 2), recession probability did increase with increasing rate of height growth, particularly in ponderosa pine and Douglas-fir. Conversely, recession probability declined with increasing diameter growth rate, reflecting the superior competitive position of trees growing faster in diameter for a given height. Although diameter and height growth were excluded as explanatory variables in the final models, their effects were implied by initial tree dimensions. The probability of crown recession remained highest on medium-size trees (by diameter and height), presumably because crown closure had occurred by the time they reached this size and age, but height growth was still rapid. All else being equal, trees growing faster in height accumulated new crown mass at a more rapid rate and hastened self-shading of lower branches. For trees of a given height and age, however, crowns were less likely to recede on trees of larger diameter because they typically have larger crowns and greater available growing space than thinner trees at the same height.

The probability of recession (HCB_2) declined with increasing age for Douglas-fir trees because older trees of a given height had a slower past height growth rate and, hence, had a lower rate of subsequent crown rise. The greater shade tolerance of Douglas-fir relative to western white and ponderosa pine may have led to weaker correlation between tree height and age and, therefore, greater marginal effect of age on probability of recession.

The higher probability of crown recession in white pine on the moist *Tsuga heterophylla/Asarum caudatum* habitat type could have resulted from greater height growth potential often associated with moist sites in the northern Rocky Mountains. Moister sites may also be associated with a higher density and abundance of shade-tolerant species that are typical of these sites in the northern Rocky Mountains (Cooper et al. 1991). An understory layer of shade-tolerant species can accelerate recession by shading the lower crown of more shade-intolerant and dominant species (Wierman and Oliver 1979).

Conditional 5-Year Crown Recession

Differences in conditional crown recession among the three species were more striking than differences in the probability of recession. Crown recession in western white pine increased with increasing crown ratio up to approximately 0.7 and then gradually declined at higher crown

ratios. This general pattern has been observed previously in coastal Douglas-fir, including even-aged stands in western Oregon and Washington (Hann and Hanus 2004) and both even- and uneven-aged, mixed-species stands in southwestern Oregon (Maguire and Hann 1987). In contrast, ponderosa pine crown recession increased gradually with increasing crown ratio. The rapid recession on trees with large crown ratios probably coincided with crown closure during the period of rapid height growth. Trees with smaller initial crown ratios represented the same trees at later stages of development in the sampled stands, so at these older ages, height growth was slowly decelerating. As would be expected, ΔHCB_1 was more rapid than ΔHCB_2 in Douglas-fir, but only for larger trees. As with the probability of crown recession, the 5-year recession rate increased with increasing tree size. This increase was consistent with results obtained for loblolly pine (*Pinus taeda* L.) in the southeastern United States (Short and Burkhart 1992) and coastal Douglas-fir in the Pacific Northwest (Maguire and Hann 1990, Hann and Hanus 2004). However, lack of old trees with large crown ratios and young trees with small crown ratios cast uncertainty on behavior of crown recession under these conditions. The stands sampled by Short and Burkhart (1992) and Hann and Hanus (2004) were even-aged stands up to 50 years old and represented a wide range of density regimes that minimized correlation between age and crown ratio. The multiaged and mixed-species stands sampled by Maguire and Hann (1990) were generally denser but included tree ages up to 150 years, so some older trees with larger crown ratios in more open stands were included.

Maguire and Hann (1990) reported a peak in crown recession at an initial crown ratio of 0.38 in coastal Douglas-fir, but Hann and Hanus (2004) reported a peak at 0.62–0.64. Conditional crown recession in the Priest River Douglas-fir peaked at initial crown ratios of approximately 0.80 for ΔHCB_1 and 0.65 for ΔHCB_2. As mentioned previously, however, patterns in conditional crown recession at Priest River are not directly comparable to patterns in unconditional recession reported by Maguire and Hann (1990) and Hann and Hanus (2004). Conditional crown recession in western white pine peaked at initial crown ratios between 0.6 and 0.7 for ΔHCB_1 and between 0.6 and 0.8 for ΔHCB_2, depending on initial tree height.

Average 5-Year Crown Recession

Breaking crown recession into two components, recession probability and conditional recession, allowed greater flexibility for modeling reconstructed patterns and accommodating variability imposed by species and differing initial conditions. This approach also retained additional information that would otherwise be lost by pooling zero and nonzero observations. For example, the general pattern in average recession peaked over crown ratio for all species, but conditional recession increased monotonically over crown ratio in ponderosa pine. This behavior may have resulted from ponderosa pine being the dominant species on relatively harsh microsites. In these areas, density of other species may have been low initially, owing to poor germinant and seedling survival, but higher later in stand development under the shelter of an established ponderosa pine overstory. Height growth would remain rapid for many species such as Douglas-fir and western white pine once they established under scattered overstory ponderosa pine. Combined with the shade intolerance of ponderosa pine, this rapid height growth of younger understory trees would have potential for inducing rapid suppression mortality of lower branches on overstory trees after a long period in a relatively open-grown condition.

Natural regeneration is typically dense in the habitat types sampled for this study. The peak in average crown recession for all three species at relatively high crown ratios (0.65–0.90) and at moderate tree sizes would, therefore, correspond to the stage of stand development beyond crown closure (i.e., some recession had occurred) but near the start of intense intertree competition and suppression-induced mortality. Height growth would still be rapid when trees reach this stage in dense, unmanaged stands because they are still relatively young. The variation in crown recession patterns among the three species is probably related to differing morphological and silvical characteristics, including shade tolerance, height growth pattern, crown shape, and crown density as well as to developmental patterns leading to stratification in these mixed-species forests (Cobb et al. 1993).

Applications

Management-oriented growth models are developed with the primary objective of exploring probable effects of alternative silvicultural regimes on growth, yield, stand dynamics, and wood quality (e.g., Wykoff et al. 1982, Hynynen 1995b, Hann 2006). Crown size is a proven indicator of photosynthetic potential and tree vigor (Assmann 1970, Spurr and Barnes 1980), so its efficacy in predicting growth and simulating stand dynamics is attributable to its functional link to interception of solar radiation and its representation of competition for growing space and site resources. In addition to enhancing mechanisms of tree growth and stand dynamics, crown recession models and implied branch growth and longevity help link silvicultural treatment to two key determinants of wood quality, i.e., size of crown wood core (di Lucca 1989) and average or maximum branch diameter (e.g., Colin and Houllier 1991, Maguire et al. 1994, 1999). Quantification of these responses allows estimation of lumber and veneer grade recovery (WWPA 1998, Maguire et al. 1999, Fahey et al. 1991, Todoroki et al. 2005) and facilitates design of optimal silvicultural regimes for desired end products. Better understanding of crown recession also lends insight into the dynamics of wildlife habitat (Dubrasich et al. 1997) and changes in fire hazard (Scott and Reinhardt 2001) through silvicultural influences on horizontal and vertical arrangement of tree crowns.

Literature Cited

AGEE, J.K. 1993. *Fire ecology of Pacific Northwest Forests.* Island Press, Washington, DC. 493 p.

ANDREWS, S.R., AND L.S. GILL. 1939. Determining the time branches on living trees have been dead. *J. For.* 37:930–935.

ASSMANN, E. 1970. *The principles of forest yield studies.* Pergamon Press, Oxford, UK. 506 p.

BROKAW, N., AND R. LENT. 1999. Vertical structure. P. 373–399 in *Maintaining biodiversity in forest ecosystems*, M.L. Hunter (ed.). Cambridge University Press, Cambridge, UK.

COBB, D.F., K.L. O'HARA, AND C.D. OLIVER. 1993. Effects of variations in stand structure on development of mixed-species stands in eastern Washington. *Can. J. For. Res.* 23:545–552.

COCHRAN, P.H., AND W.G. DAHMS. 2000. *Growth of lodgepole pine thinned to various densities on two sites with differing productivities in central Oregon.* US For. Serv. Res. Paper PNW-RP-520. 59 p.

COLIN, F., AND F. HOULLIER. 1991. Branchiness or Norway spruce in north-eastern France: modelling vertical trends in maximum nodal branch size. *Ann. Sci. For.* 48:679–693.

COOPER, S.V., K.E. NEIMAN, AND D.W. ROBERTS. 1991. *Forest habitat types of northern Idaho: A second approximation.* US For. Serv. Gen. Tech. Rep. INT-GTR-236. 135 p.

CURTIS, R.O., AND D.L. REUKEMA. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. *For. Sci.* 16(3):287–301.

DANIELS, R.F., H.E. BURKHART, G.D. SPITTLE, AND G.L. SOMERS. 1979. *Methods for modeling individual tree growth and stand development in seeded loblolly pine stands.* College of Forest and Wildlife Resources. Virginia Polytechnic Institute and State University, Blacksburg, VA. Publ. No. FWS-1-79. 50 p.

DAUBENMIRE, R., AND J. DAUBENMIRE. 1968. *Forest vegetation of eastern Washington and northern Idaho.* Washington Agr. Exp. Sta. Tech. Bull. 60. 140 p.

DI LUCCA, C.M. 1989. Juvenile-mature wood transition. P. 23–38 in *Second growth Douglas-fir: Its management and conversion for value.* Kellogg, R.M. (ed.). Forintek Canada Corp., Vancouver, BC, Canada.

DUBRASICH, M.E., D.W. HANN., AND J.C. TAPPEINER, II. 1997. Methods for evaluating crown area profiles of forest stands. *Can. J. For. Res.* 27:385–392.

EK, A.R. 1974. *Dimensional relationships of forest and open-grown stems in Wisconsin.* Univ. of Wisconsin For. Res. No. 181. 7 p.

ESCHENBACH, C. 2005. Emergent properties modelled with the functional structural tree growth model ALMIS: Computer experiments on resource gain and use. *Ecol. Model.* 186: 470–488.

FAHEY, T.D., J.M. CAHILL, T.A. SNELLGROVE, AND L.S. HEATH. 1991. *Lumber and veneer recovery from intensively managed young-growth Douglas-fir.* US For. Serv. Res. Paper PNW-RP-437. 25 p.

FINKLIN, A.I. 1983. *Climate of Priest River Experimental Forest, northern Idaho.* US For. Serv. Gen. Tech. Rep. INT-GTR-159. 53 p.

FORD, E.D., A. AVERY, AND R. FORD. 1990. Simulation of branch growth in the *Pinaceae*: Interactions of morphology, phenology, foliage productivity, and the requirement for structural support, on the export of carbon. *J. Theor. Biol.* 146:15–36.

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

FUJIMORI, T., AND Y. KIYONO. 1986. Dynamics of crown structure and effects of crown control on tree growth in *Cryptomeria japonica.* P. 172–189 in *Crown and canopy structure in relation to productivity*, Fujimori, T. and D. Whitehead (eds.). Forest and Forest Products Research Institute, Ibaraki, Japan.

GAVRIKOV, V.L., AND O.P. SEKRETENKO. 1996. Shoot-based three-dimensional model of young Scots pine growth. *Ecol. Model.* 88(1–3):183–193.

GODIN, C. 2000. Representing and encoding plant architecture: A review. *Ann. For. Sci.* 57:413–438.

HANN, D.W. 2006. *ORGANON user's manual edition 8.2* (computer manual). Oregon State Univ., Department of Forest Resources, Corvallis, OR. 129 p.

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

HANN, D.W., D.D. MARSHALL, AND M.L. HANUS. 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.* Forest Research Lab., Oregon State University, Corvallis, OR. Res. Contrib. 40. 83 p.

HASENAUER, H., AND R.A. MONSERUD. 1996. A crown ratio model for Austrian forests. *For. Ecol. Manag.* 84:49–60.

HYNYNEN, J. 1995a. *Modelling tree growth for managed stands.* Finnish For. Res. Inst. Res. Paper 576.

HYNYNEN, J. 1995b. Predicting tree crown ratio for unthinned and thinned Scots pine stands. *Can J. For. Res.* 25:57–62.

JOZSA, L.A., AND G.R. MIDDLETON. 1994. *A discussion of wood quality attributes and their practical implications.* Forintek Canada Corp., Western Laboratory, Vancouver, BC. Special Publ. No. SP-34. 42 p.

KEYES, C.R., AND K.L. O'HARA. 2002. Quantifying stand targets for silvicultural prevention of crown fires. *West. J. Appl. For.* 17:101–109.

KLEINE, M. 1986. Sortentafeln für Buche in Österreich. *Centralbl. Ges. Forstw.* 103:15–36.

KRUMLAND, B., AND L.C. WENSEL. 1981. *A tree increment model system for north coastal California: Design and implementation.* Univ. of California, Dept. of Forest Conservation, Berkeley, CA Cooperative Redwood Yield Research Project. Res. Note 15. 56 p.

KURTH, W. 2000. Towards universality of growth grammars: Models of Bell, Pagès, and Takenaka revisited. *Ann. For. Sci.* 57:543–554.

KVÅLSETH, T.O. 1985. Cautionary note about R^2. *Am. Stat.* 39:279–285.

LIU, J., H.E. BURKHART, AND R.L. AMATEIS. 1995. Projecting crown measures for loblolly pine trees using a generalized thinning response function. *For. Sci.* 41(1):43–53.

MAGUIRE, D.A., AND D.W. HANN. 1987. A stem dissection technique for dating branch mortality and reconstructing past crown recession. *For. Sci.* 33(4):858–871.

MAGUIRE, D.A., AND D.W. HANN. 1990. Constructing models for direct prediction of 5-year crown recession in southwestern Oregon Douglas-fir. *Can. J. For. Res.* 20:1044–1052.

MAGUIRE, D.A., S.R. JOHNSTON., AND J. CAHILL. 1999. Predicting branch diameters on second-growth Douglas-fir from tree-level descriptors. *Can. J. For. Res.* 29:1829–1840.

MAGUIRE, D.A., J.A. KERSHAW., AND D.W. HANN. 1991. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-fir. *For. Sci.* 37(5):1409–1428.

MAGUIRE, D.A., M. MOEUR, AND W.S. BENNETT. 1994. Models for describing basal diameter and vertical distribution of primary branches in young Douglas-fir. *For. Ecol. Manag.* 63:23–55.

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

MÄKINEN, H., AND F. COLIN. 1998. Predicting branch angle and branch diameter of Scots pine from usual tree measurements and stand structural information. *Can. J. For. Res.*

28:1686–1696.

MARSHALL, D.D., AND R.O. CURTIS. 2002. *Levels-of-growing-stock cooperative study in Douglas-fir: Report No. 15–Hoskins: 1963–1998.* US For. Serv. Res. Paper PNW-RP-537. 80 p.

MCCULLAGH, P., AND J.A. NELDER. 1989. *Generalized linear models*, 2nd ed. Chapman and Hall, Ltd., London, UK. 511 p.

MITCHELL, K.J. 1975. *Dynamics and simulated yield of Douglas-fir.* Forest Science Monograph 17. Society of American Foresters, Washington, DC.

MOEUR, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* 39(4):756–775.

MONLEON, V.J., D. AZUMA, AND D. GEDNEY. 2004. Equations for predicting uncompacted crown ratio based on compacted crown ratio and tree attributes. *West. J. Appl. For.* 19(4):260–267.

MONSERUD, R.A., AND H. STERBA. 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manag.* 113:109–123.

MONSERUD, R.A., H. STERBA, AND H. HASENAUER. 1997. The single-tree growth simulator PROGNAUS. P. 50–56 in *Proc. of the Forest Vegetation Simulator Conference*, Teck, R., M. Moeur, and J. Adams. US For. Serv. Gen. Tech. Rep. INT-GTR-373.

OKER-BLOM, P., AND S. KELLOMÄKI. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: Comparison of random and grouping canopy models. *Agr. Meteor.* 28:143–155.

OSAWA, A. 1990. Reconstructed development of stem production and foliage mass and its vertical distribution in Japanese larch. *Tree Physiol.* 7:189–200.

PERTTUNEN, J., R. SIEVÄNEN., E. NIKINMAA., H. SALMINEN, H. SAARENMAAS, AND J. VÄKEVÄ. 1996. LIGNUM: A tree model based on simple structural units. *Ann. Bot.* 77:87–98.

PFISTER, R.D., B.L. KOVALCHIK, S.F. ARNO, AND R.C. PRESBY. 1977. *Forest habitat types of Montana.* US For. Serv. Gen. Tech. Rep. INT-RP-34. 174 p.

RAPRAEGER, E.F. 1939. Development of branches and knots in western white pine. *J. For.* 37:239–245.

REHFELDT, G.E. 1978. Genetic differentiation of Douglas-fir populations from the Northern Rocky Mountains. *Ecology* 59(6):1264–1270.

REHFELDT, G.E. 1993. Genetic variation in the Ponderosae of the Southwest. *Am. J. Bot.* 80(3):330–343.

REHFELDT, G.E., R.J. HOFF, AND R.J. STEINHOFF. 1984. Geographic patterns of genetic variation in *Pinus monticola*. *Bot. Gaz.* 145(2):229–239.

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

RITCHIE, M.W., AND D.W. HANN. 1986. Development of a tree height growth model for Douglas-fir. *For. Ecol. Manag.* 15:135–145.

ROBINSON, A.P., AND A.R. EK. 2003. Description and validation of a hybrid model of forest growth and stand dynamics for the Great Lakes region. *Ecol. Model.* 170:73–104.

SCOTT, J.H., AND E.D. REINHARDT. 2001. *Assessing crown fire potential by linking models of surface and crown fire behavior.* US For. Serv. Res. Paper RMRS-RP-29. 59 p.

SHORT, E.A., AND H.E. BURKHART. 1992. Predicting crown-height increment for thinned and unthinned loblolly pine plantations. *For. Sci.* 38(3):594–610.

SIEVÄNEN, R. 1993. A process-based model for the dimensional growth of even-aged stands. *Scand. J. For. Res.* 8:28–48.

SORRENSEN-COTHERN, K.A., E.D. FORD., AND D.G. SPRUGEL. 1993. A model of competition incorporating plasticity through modular foliage and crown development. *Ecol. Monogr.* 63:277–304.

SPATHELF, P. 2003. Reconstruction of crown length of Norway spruce (*Picea abies* (L.) Karst.) and Silver fir (*Abies alba* Mill.)-technique, establishment of sample methods and application in forest growth analysis. *Ann. For. Sci.* 60:833–842.

SPURR, S.H., AND B.V. BARNES. 1980. *Forest ecology*, 3rd ed. John Wiley and Sons, New York, NY. 527 p.

TODOROKI, C.L., R.A. MONSERUD., AND D.L. PARRY. 2005. Predicting internal lumber grade from log surface knots: Actual and simulated results. *For. Prod. J.* 55(6):38–47.

VALENTINE, H.T., A.R. LUDLOW., AND G.M. FURNIVAL. 1994. Modeling crown rise in even-aged stands of Sitka spruce or loblolly pine. *For. Ecol. Manag.* 69:189–197.

WENSEL, L.C., AND P.J. DAUGHERTY. 1985. *CACTOS user's guide: The California Conifer Timber Output Simulator*, version 2.0 (computer manual). California Forest Yield Cooperative, University of California, Department of Forest Resource Management, Berkeley, CA. Res. Note 10. 91 p.

WESTERN WOOD PRODUCTS ASSOCIATION (WWPA). 1998. *Western lumber grading rules 98.* WWPA, Portland, OR. 248 p. + supplements.

WIERMAN, C.A., AND C.D. OLIVER. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir–western hemlock. *Can. J. For. Res.* 9:1–9.

WYKOFF, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.* 36(4):1077–1104.

WYKOFF, W.R., N.L. CROOKSTON, AND A.R. STAGE. 1982. *Users' guide to the stand prognosis model.* US For. Serv. Gen. Tech. Rep. INT-GTR-133. 112 p.