

# Evaluation of nonspatial approaches and equation forms used to predict tree crown recession

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**Abstract:** Two nonspatial approaches for modeling tree crown recession ( $\Delta\text{HCB}$ ) were evaluated by using 5341 observations from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The first approach applies a static height-to-crown-base (HCB) equation at the start and end of the growth period and uses the difference in these predictions as an estimate of  $\Delta\text{HCB}$ . This allometric method can be applied to species lacking  $\Delta\text{HCB}$  data from permanent plots. The incremental method directly predicts  $\Delta\text{HCB}$  from an equation developed from adequate permanent plot data. Two allometric and six incremental equation forms were examined. Also examined were three approaches for determining the end-of-growth-period tree and plot attributes used by the allometric method. Although the allometric method can produce unbiased estimates of  $\Delta\text{HCB}$ , the best allometric equation forms explained about one-half of the variation explained by the best incremental equation form. The two best incremental equation forms were modifications of a nonlinear logistic equation form previously developed for Douglas-fir. The modifications included using measured stand age (BHA) or predicted tree growth effective age (GEA) instead of measured tree age. The best equation form used BHA, which limits its application to modeling data collected from just even-aged stands. The equation form using GEA could be applied to modeling data sets from both even- and uneven-aged stands.

**Résumé :** Deux approches non spatiales utilisées pour modéliser l'élagage du houppier ( $\Delta\text{HBH}$ ) ont été évaluées à l'aide de 5341 observations faites sur le douglas (*Pseudotsuga menziesii* (Mirb.) Franco). La première approche utilise une équation statique de hauteur à la base du houppier ( $\Delta\text{HBH}$ ) au début et à la fin d'une période de croissance et utilise la différence entre ces prédictions comme estimation de  $\Delta\text{HBH}$ . Cette méthode allométrique peut être appliquée aux espèces pour lesquelles il n'y a pas de mesures de  $\Delta\text{HBH}$  provenant de placettes permanentes. La méthode différentielle prédit directement  $\Delta\text{HBH}$  à l'aide d'une équation développée à partir de données adéquates provenant de placettes permanentes. Deux formes d'équations allométriques et six formes d'équations différentielles ont été examinées. Trois approches ont également été étudiées pour déterminer les attributs à la fin de la période de croissance aux échelles de l'arbre et de la placette qui sont utilisés par la méthode allométrique. Même si la méthode allométrique fournit des estimations non biaisées de  $\Delta\text{HBH}$ , les meilleures formes d'équations allométriques expliquent à peu près la moitié de la variation expliquée par la meilleure forme d'équation différentielle. Les deux meilleures formes d'équations différentielles sont des variantes d'une équation logistique non linéaire développée précédemment pour le douglas. Les modifications incluent la mesure de l'âge du peuplement (AHP) ou la prédiction de l'âge apparent relativement à la croissance des arbres (AAC) au lieu de la mesure de l'âge des arbres. La meilleure forme d'équation utilise l'AHP, ce qui restreint son application uniquement à la modélisation de données récoltées dans des peuplements équiennes. La forme d'équation qui utilise l'AAC pourrait être utile pour modéliser des ensembles de données provenant à la fois de peuplements équiennes et inéquiennes.

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## Introduction

The dimensions of a tree crown, such as crown length (CL) and largest crown width (LCW), are strongly correlated with the total leaf area of a tree (Maguire and Hann 1989), a measure of the tree's potential for producing photosynthate. Given that LCW can be predicted from CL, diameter at

breast height ( $D$ ), and total height ( $H$ ) of the tree (e.g., Hann 1997), it is unsurprising that relative CL, or crown ratio (CR,  $\text{CL}/H$ ), has been found to be useful for predicting the height growth rate ( $\Delta H$ ), diameter growth rate ( $\Delta D$ ), and change in per-unit-area expansion factor due to mortality ( $\Delta\text{EF}$ ) in several nonspatial tree-list models (Vanclay 1994, 1995) of stand development that are being broadly used in making forest management decision: FVS/PROGNOSIS (Wykoff et al. 1982), CACTOS (Wensel and Daugherty 1985), ORGANON (Hester et al. 1989; Hann 2003), MELA (Hynynen 1995), and PROGNAUS (Monserud et al. 1997), for example.

The inclusion of CR in these dynamic models and equations requires a way to update the attribute during simulation. Given the relationship of CR to CL and  $H$  and the fact that CL is the difference between  $H$  and height to crown base (HCB), a change in CR ( $\Delta\text{CR}$ ) is the net result of an increase in CL and  $H$  due to  $\Delta H$  and a decrease in CL due

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to crown recession ( $\Delta\text{HCB}$ ). Therefore, the addition of CR to nonspatial tree-list models requires the addition of a fourth dynamic equation for predicting either  $\Delta\text{HCB}$  or  $\Delta\text{CR}$ .

Two approaches have been taken in modeling  $\Delta\text{HCB}$  or  $\Delta\text{CR}$ : the allometric method and the incremental method (Liu et al. 1995). The allometric method has been the most commonly used approach to predict  $\Delta\text{HCB}$  or  $\Delta\text{CR}$ . The method applies a static HCB or CR equation at the start and end of the growth period, and the difference in these predictions provide an estimate of either  $\Delta\text{HCB}$  (e.g., CACTOS (Wensel and Daugherty 1985), ORGANON (Hester et al. 1989; Hann 2003)) or  $\Delta\text{CR}$  (e.g., FVS/PROGNOSIS (Wykoff et al. 1982), MELA (Hynynen 1995), PROGNAUS (Monserud et al. 1997)). Therefore, the parameters in the allometric method have been estimated to minimize the squared residuals about HCB or CR instead of  $\Delta\text{HCB}$ . The allometric method has been appealing because of the scarcity of data to model  $\Delta\text{HCB}$  or  $\Delta\text{CR}$  directly for the many species often found in these nonspatial tree-list models of stand development.

A few studies have used the incremental method to model  $\Delta\text{HCB}$  directly, so that the parameters of the equations have been estimated to minimize the squared residuals about  $\Delta\text{HCB}$ . Krumland and Wensel (1981) developed nonspatial  $\Delta\text{HCB}$  equations from 357 measurements of coastal redwood (*Sequoia sempervirens* (D. Don) Endl.) and 108 measurements of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) taken on permanent plots in northern California. Maguire and Hann (1990b) constructed and evaluated eight alternative, nonspatial  $\Delta\text{HCB}$  equations for Douglas-fir by aging the time of death of branches below HCB to estimate  $\Delta\text{HCB}$  (Maguire and Hann 1987, 1990a) for 357 trees located on temporary plots in southwest Oregon. Short and Burkhart (1992) used an extensive data set of loblolly pine (*Pinus taeda* L.) from 186 permanent installations to develop both spatial and nonspatial equations of  $\Delta\text{HCB}$  for both unthinned and thinned stands. Finally, Liu et al. (1995) expanded the analysis of Short and Burkhart (1992) to improve the  $\Delta\text{HCB}$  response to thinning for their spatial equation.

Although Maguire and Hann (1990b) and Short and Burkhart (1992) did evaluate several alternative, nonspatial equation forms for the incremental method of predicting  $\Delta\text{HCB}$ , we could find no study that has compared the ability of the two methods to predict  $\Delta\text{HCB}$  using nonspatial equation forms. Liu et al. (1995) did develop both a spatial incremental equation and an allometric equation and then compared their abilities to predict future values of HCB. However, conducting an evaluation using a yield value, such as future HCB, instead of an increment value can inflate the resulting measures of fit used in the evaluation, which can mask true differences between the methods. This is particularly true if  $\Delta\text{HCB}$  is relatively small in relation to HCB at the initial measurement.

Evaluating the accuracy and precision of the application of the allometric method to nonspatial equations is particularly important given the sensitivity of nonspatial tree-list models such as FVS/PROGNOSIS, CACTOS, ORGANON, MELA, and PROGNAUS to crown size and the value of the

economic decisions being made with models such as these (Davis et al. 2001). The recent emphasis on the collection of crown-dimension data on permanent sample plots has now provided an adequate database for modeling  $\Delta\text{CR}$  or  $\Delta\text{HCB}$  for Douglas-fir in the Pacific Northwest (e.g., Chappell and Osawa 1991). The objectives of the present study were to use the data for Douglas-fir (*i*) to compare the predictive ability of the allometric method to that of the nonspatial incremental method; (*ii*) to compare the predictive ability of the nonspatial incremental equation forms that have been developed by Krumland and Wensel (1981), Maguire and Hann (1990b), and Short and Burkhart (1992); and (*iii*) to suggest improvements in the alternative approaches if warranted.

Variables are defined and their abbreviations given at first mention in the text. For easy reference, they are also summarized in Table 1, including units of measure for each variable.

## Alternative equation forms

### Allometric method

The allometric method predicts either  $\Delta\text{HCB}$  or  $\Delta\text{CR}$  by taking the difference between predicted values from a static equation at the end and the start of the growth period:

$$[1] \quad \Delta\text{HCB} = \text{PHCB}_E - \text{PHCB}_S$$

$$[2] \quad \Delta\text{CR} = \text{PCR}_E - \text{PCR}_S$$

where  $\text{PHCB}_E$  is the predicted HCB at the end of the growth period,  $\text{PHCB}_S$  is the predicted HCB at the start of the growth period,  $\text{PCR}_E$  is the predicted CR at the end of the growth period, and  $\text{PCR}_S$  is the predicted CR at the start of the growth period.

Equation 2 can be reformulated as a predictor of  $\Delta\text{HCB}$  (see Appendix A for the derivation):

$$[3] \quad \Delta\text{HCB} = \text{PHCB}_E - \text{PHCB}_S + (\Delta H)(\text{BR}_S - \text{PBR}_S)$$

where  $\text{BR}_S$  is the measured bole ratio at the start of the growth period and equals  $\text{HCB}_S/\text{H}_S$ ,  $\text{HCB}_S$  is the measured HCB at the start of the growth period, and  $\text{PBR}_S$  is the predicted BR at the start of the growth period and equals  $\text{PHCB}_S/\text{H}_S$ . Therefore, the use of eq. 3 produces an estimate of  $\Delta\text{HCB}$  that is similar to that from eq. 1, but with an "adjustment" when  $\text{BR}_S$  differs from  $\text{PBR}_S$ . The predicted  $\Delta\text{HCB}$  ( $\text{P}\Delta\text{HCB}$ ) will be reduced if  $\text{PBR}_S$  is greater than  $\text{BR}_S$  and increased if the opposite is true. Because  $(\text{BR}_S - \text{PBR}_S)$  has a range of  $\pm 1$ , the largest "adjustment" possible is  $\pm\Delta H$ .

The resulting predicted values of  $\Delta\text{HCB}$  from either eq. 1 or 3 are often restricted to being nonnegative. This is done to prevent "unreasonable" reductions in HCB due to factors such as density management. Under this restriction, it is assumed that epicormic branching is unlikely or insignificant for the species.

A static estimator of HCB for Douglas-fir was needed to predict  $\Delta\text{HCB}$  in eqs. 1 and 3. The following equation form was selected because it has been previously used for many of the tree species in the Pacific Northwest (Ritchie and Hann 1987; Zumrawi and Hann 1989; Hanus et al. 2000; Hann et al. 2003):

**Table 1.** Variable abbreviations and their definitions, including units of measurement.

Abbreviation	Units	Definition
BA	m <sup>2</sup> /ha	Basal area of the plot
BHA	Years	Breast height age of the plot
BR		Bole ratio of the subject tree (1 – CR)
CA	m <sup>2</sup>	Crown area of the subject tree
CCCB	%	Crown closure at crown base of the subject tree
CCF	%	Crown competition factor of the plot
CCFL	%	Crown competition factor of trees with <i>D</i> greater than that of the subject tree
CL	m	Crown length of the subject tree
CR		Crown ratio of the subject tree
CW	m	Crown width of the subject tree
<i>D</i>	cm	Diameter at breast height of the subject tree
ΔCR		Change in crown ratio of the subject tree
Δ <i>D</i>	cm/5 years	Diameter growth rate of the subject tree
ΔEF	Trees·ha <sup>-1</sup> ·5 years <sup>-1</sup>	Mortality rate of the subject tree
Δ <i>H</i>	m/5 years	Height growth rate of the subject tree
ΔHCB	m/5 years	Crown recession of the subject tree
EF	Trees/ha	Expansion factor of the subject tree
GEA	Years	Growth effective age of the subject tree
<i>H</i>	m	Total height of the subject tree
HCB	m	Height to crown base of the subject tree
LCW	m	Largest crown width of the subject tree
PBR		Predicted bole ratio of the subject tree
PCR		Predicted crown ratio of the subject tree
PΔ <i>D</i>	cm/5 years	Predicted diameter growth rate of the subject tree
PΔEF	Trees·ha <sup>-1</sup> ·5 years <sup>-1</sup>	Predicted mortality rate of the subject tree
PΔ <i>H</i>	m/5 years	Predicted height growth rate of the subject tree
PΔHCB	m/5 years	Predicted crown recession of the subject tree
PHCB	m	Predicted height to crown base of the subject tree
QMD	cm	Quadratic mean diameter of the plot
SI	m	Douglas-fir site index for the installation
SPΔ <i>D</i>	cm/5 years	Scaled predicted diameter growth rate of the subject tree
SPΔ <i>H</i>	m/5 years	Scaled predicted height growth rate of the subject tree

**Note:** A subscript of E or S on variable abbreviations in the text indicates that the variable is for the end or start of the growth period, respectively.

$$[4] \quad HCB = \frac{H}{1.0 + \exp\left[a_0 + a_1H + a_2CCFL + a_3 \ln(BA) + a_4\left(\frac{D}{H}\right)\right]}$$

where CCFL is the crown competition factor (Krajicek et al. 1961) of trees with *D* larger than that of the subject tree, BA is the basal area per hectare of the plot, and *a<sub>i</sub>* are the parameter estimates. The expected behavior from eq. 4 is for HCB to increase with increasing values of *H*, CCFL, and BA and to decrease with increasing values of *D*/*H* (Ritchie and Hann 1987; Zumrawi and Hann 1989; Hanus et al. 2000; Hann et al. 2003).

**Incremental method**

Krumland and Wensel (1981) used the following variation of a logistic equation (Sit and Poulin-Costello 1994) to predict crown recession directly using the incremental method (i.e., ΔHCB):

$$[5] \quad \Delta HCB = \frac{b_{1,1}CL_S + b_{1,2}\Delta H}{1.0 + \exp(b_{1,3} + b_{1,4}CCCB_S)}$$

where CCCB<sub>S</sub> is crown closure at crown base of the subject tree at the start of the growth period, CL<sub>S</sub> is CL at the start of the growth period, and *b<sub>1,i</sub>* are parameter estimates for ΔHCB in eq. 5.

The numerator of a logistic equation such as eq. 5 expresses the maximum value for ΔHCB, and the denominator determines how much of the maximum will be realized in the subject tree. For eq. 5, ΔHCB is predicted to increase as CCCB<sub>S</sub> increases.

Short and Burkhart (1992) examined several equation forms before settling on the following combined exponential and power function (Sit and Poulin-Costello 1994):

$$[6] \quad \Delta\text{HCB} = \exp \left[ b_{2,1} + b_{2,2} \ln(H_S) + b_{2,3} \sqrt{\text{CR}_S} + b_{2,4} \left( \frac{\text{QMD}_S}{D_S} \right) + b_{2,5} \text{BHA}_S \right]$$

where  $\text{CR}_S$  is the CR at the start of the growth period,  $\text{QMD}_S$  is the quadratic mean diameter at the start of the growth period,  $\text{BHA}_S$  is the breast height age of the stand at the start of the growth period, and  $b_{2,i}$  are the parameter estimates for  $\Delta\text{HCB}$  in eq. 6. The expected behavior from eq. 6 is for  $\Delta\text{HCB}$  to increase with increasing values of  $H_S$ ,  $\text{CR}_S$ , and  $\text{QMD}_S/D_S$  and to decrease with an increasing value of  $\text{BHA}_S$  (Short and Burkhart 1992).

The  $\Delta\text{HCB}$  models of Maguire and Hann (1990b) used tree age, which was not available for all trees in this analysis. Like Short and Burkhart (1992) did in their comparisons, we substituted  $\text{BHA}_S$  for tree age in the logistic equation form found by Maguire and Hann (1990b) to best characterize their data set. However, the use of  $\text{BHA}_S$  does restrict the application of the equation form to data sets from even-aged stands. To explore a formulation that would be applicable to data from a broader range of stand structures, we also substituted the growth effective age of the subject tree at the start of the growth period ( $\text{GEA}_S$ ) in the same equation form, where  $\text{GEA}$  is the age of a dominant tree with the same  $H$  and site index (SI) as the tree of interest.  $\text{GEA}$  has been successfully used to model  $\Delta H$  of trees growing in both even- and uneven-aged stand structures (Ek and Monserud 1974; Krumland and Wensel 1981; Wensel et al. 1987; Hann and Ritchie 1988; Hann et al. 2003). These substitutions resulted in the following logistic equations:

$$[7] \quad \Delta\text{HCB} = \frac{\text{CL}_S + \Delta H}{1.0 + \exp[b_{3,0} + b_{3,1} \ln(\text{CR}_S) + b_{3,2} \text{CR}_S + b_{3,3} \text{BHA}_S + b_{3,4} \ln(\text{CCF}_S)]}$$

$$[8] \quad \Delta\text{HCB} = \frac{\text{CL}_S + \Delta H}{1.0 + \exp[b_{4,0} + b_{4,1} \ln(\text{CR}_S) + b_{4,2} \text{CR}_S + b_{4,3} \text{GEA}_S + b_{4,4} \ln(\text{CCF}_S)]}$$

where  $\text{CCF}_S$  is the crown competition factor of the stand at the start of the growth period,  $b_{3,i}$  are parameter estimates for  $\Delta\text{HCB}$  in eq. 7, and  $b_{4,i}$  are parameter estimates for  $\Delta\text{HCB}$  in eq. 8.

Again, the numerator of these logistic equations expresses the maximum value for  $\Delta\text{HCB}$ . For both equations,  $\Delta\text{HCB}$  is predicted to increase as  $\text{CCF}_S$  increases, to decrease as either  $\text{BHA}_S$  or  $\text{GEA}_S$  increases, and to first increase, peak, and then decrease as  $\text{CR}_S$  increases.

### Estimation and evaluation data

This analysis utilized the data from three sources of untreated, permanent plots in even-aged Douglas-fir stands in southwestern British Columbia, western Washington, and northwestern Oregon. The first source of data consisted of 10 research installations established on one private and four public ownerships to explore a variety of silvicultural objectives. Six of the installations were in plantations and the remainder in naturally regenerated stands. Plot sizes ranged from 0.020 to 0.081 ha, with the 0.081-ha plot being most common.  $\text{BHA}$  at establishment ranged from 6 to 18 years, with an average of 13.3 years. The intervals between remeasurements ranged from 1 to 19 years, with most of the intervals in the 2- to 5-year range. The total length of remeasurements ranged from 8 to 37 years, with an average of 28.3 years. There were relatively few measurements of  $H$  and  $\text{HCB}$  on these installations (approximately 6% of the sample trees), and the measurements of  $\text{HCB}$  were concentrated in the later years of remeasurement. As a result, this data source provided only 507 observations with measured  $\Delta\text{HCB}$  to the modeling data set.

The other two sources were the Type I and II installations of the Stand Management Cooperative (Chappell and Osawa 1991). The Type I installations available for the present study were from 13 Douglas-fir plantations, with  $\text{BHA}$  at establishment ranging from 2 to 9 years. The Type II installations were from 10 Douglas-fir plantations, with  $\text{BHA}$  at establishment ranging from 12 to 34 years. The plots were 0.202 ha, the remeasurement intervals were either 2 or 4 years, and the total length of measurements ranged from 8 to 12 years for both types of Stand Management Cooperative installations.  $H$  and  $\text{HCB}$  were measured on more than 25% of the sample trees from the Type I installations and more than 31% of the sample trees from the Type II installations, providing a total of 3208 and 1626 observations with measured  $\Delta\text{HCB}$ , respectively, to the modeling data set.

All of the incremental equation forms evaluated in the present study were developed for fixed-length growth periods. We chose to use a 5-year growth period, because (i) it is used in the CACTOS, ORGANON, and PROGNAUS stand-development models and (ii) the use of growth periods 5 years or longer minimizes the effect of possible serial correlation (Gertner 1985). The interpolation and extrapolation procedures described by Hann et al. (2003) were used on the data from those installations not having remeasurements at exact 5-year intervals. In the application of these procedures, the resulting 5-year growth values always started with an actual measurement.

The allometric method is usually applied only when single measurements of  $\text{HCB}$  on each sample tree are available. We chose to use measurements of both  $\text{HCB}_S$  and  $\text{HCB}$  at the end of the growth period ( $\text{HCB}_E$ ) to fit eq. 4, to expand the data set to a broader range of tree and stand conditions. In-

**Table 2.** The mean, standard deviation (SD), and range of the variables in the  $\Delta\text{HCB}$  data set for Douglas-fir trees.

Variable	Units	Mean (SD)	Range
<b>Individual tree (<math>n = 5341</math>)</b>			
$D_S$	cm	20.5 (7.5015)	4.1–59.9
$D_E$	cm	25.0 (7.7807)	4.6–64.8
$H_S$	m	15.59 (6.2903)	4.30–42.37
$H_E$	m	19.68 (6.0509)	4.97–45.96
$\Delta H$	m	4.09 (1.2780)	0.00–8.29
$\text{HCB}_S$	m	5.14 (5.1784)	0.09–29.02
$\text{HCB}_E$	m	8.12 (5.7014)	0.09–31.15
$\Delta\text{HCB}$	m	2.98 (1.9988)	0.00–9.69
$\text{GEA}_S$	Years	17.4 (7.2969)	4.1–58.8
$\text{CCFL}_S$	%	85.4 (72.3260)	0.0–464.9
$\text{CCFL}_E$	%	110.3 (83.2848)	0.0–452.1
$\text{CCCB}_S$	%	131.3 (50.3552)	24.0–332.0
$\text{CL}_S$	m	10.45 (2.7264)	1.52–22.49
$\text{CR}_S$		0.72 (0.1828)	0.12–0.99
$\text{CR}_E$		0.62 (0.1923)	0.05–0.99
<b>Individual plot (<math>n = 174</math>)</b>			
$\text{BA}_S$	$\text{m}^2/\text{ha}$	29.60 (19.6133)	3.00–76.00
$\text{BA}_E$	$\text{m}^2/\text{ha}$	36.90 (17.4835)	5.70–81.40
$\text{CCF}_S$	%	221.80 (129.6386)	26.50–523.10
$\text{QMD}_S$	cm	19.70 (5.5178)	9.20–35.30
$\text{BHA}_S$	Years	20.80 (10.3863)	10.00–49.80
<b>Installation-wide (<math>n = 32</math>)</b>			
SI	m	36.53 (6.8545)	23.65–49.41

**Note:** The means were computed from the number of observations reported for each variable.

cluding both  $\text{HCB}_S$  and  $\text{HCB}_E$  in the modeling data set could improve the performance of the allometric method over what might occur in usual applications.

$\text{CCF}_S$  and  $\text{CCFL}_S$  were calculated by using the maximum-crown-width equations of Paine and Hann (1982).  $\text{CCCB}_S$  was determined by (i) computing the crown width (CW) of each sample tree at the height of the subject tree's crown base using the LCW equations of Hann (1997) and the crown-profile equations of Hann (1999) and Hann and Hanus (2001), (ii) converting CW to crown area (CA) by assuming the crowns are circular at a given height, (iii) multiplying each sample tree's CA by the tree's expansion factor (EF) and summing across all sample trees, and (iv) expressing the sum as a percentage of the plot's area.

The calculation of  $\text{CCCB}_S$  requires values of  $H_S$  and  $\text{HCB}_S$  for all trees on each plot. Therefore,  $H_S$  and  $\text{HCB}_S$  had to be estimated for those trees with missing values. While these trees were used to calculate  $\text{CCCB}_S$ , they were otherwise excluded from the  $\Delta\text{HCB}$  tree data set used in conducting this analysis.

Missing values of  $H_S$  were estimated using the height-diameter equations of Hanus et al. (1999a) for Douglas-fir and the equations of Wang and Hann (1988) and Hanus et al. (1999a, 1999b) for minor species. Missing values of  $\text{HCB}_S$  were estimated using eq. 4 for Douglas-fir or the equations of Zumrawi and Hann (1989) and Hanus et al. (2000) for minor species. Both the  $H_S$  and  $\text{HCB}_S$  equations were scaled

to the actual measurements of  $H_S$  and  $\text{HCB}_S$ , respectively, for each plot and growth period combination by application of weighted, simple linear regression through the origin. A weight of  $D^{-1}$  (Hanus et al. 1999a, 1999b; Wang and Hann 1988) was used for the  $H_S$  equations and a weight of  $H^{-2}$  (Ritchie and Hann 1987; Zumrawi and Hann 1989; Hanus et al. 2000; Hann et al. 2003) was used for the  $\text{HCB}_S$  equations. Hanus et al. (1999b, 2000) found that scaling reduced variation caused by between-plot or between-growth-period differences not explained by the "regional" equations.

GEA was determined by solving an existing dominant height growth equation to express GEA as a function of  $H$  and SI. The Douglas-fir dominant height growth equation of Bruce (1981), which incorporates King's (1966) SI for Douglas-fir, was used to calculate GEA in the present study.

The tree, plot, and installation-wide explanatory variables, along with their units of measure, are summarized in Table 2.

## Parameter estimation and fit analysis

### Allometric method

Weighted, nonlinear regression was used to estimate the parameters and their approximate standard errors for eq. 4. A weight of  $H^{-2}$  was required to homogenize the variance of the residuals (Ritchie and Hann 1987; Zumrawi and Hann 1989; Hanus et al. 2000; Hann et al. 2003). A  $t$  test was employed to test whether the parameters were significantly different from zero ( $p = 0.05$ ).

Equation 4 was then used to determine  $\text{PHCB}_S$  and  $\text{PHCB}_E$  in eqs. 1 and 3. It was assumed that the user would know the attributes used in eqs. 3 and 4 for the start of the growth period (i.e.,  $H_S$ ,  $\text{CCFL}_S$ ,  $\text{BA}_S$ ,  $D_S$ ,  $\text{BR}_S$ , and  $\text{PBR}_S$ ). We examined three methods for determining the attributes at the end of the growth period (i.e.,  $H_E$ ,  $\text{CCFL}_E$ ,  $\text{BA}_E$ ,  $D_E$ , and  $\Delta H$ ) in eqs. 3 and 4: (i) using the measured attributes, (ii) predicting the attributes from previously developed  $\Delta D$ ,  $\Delta H$ , and  $\Delta\text{EF}$  equations for the species, and (iii) predicting the attributes from the previously developed  $\Delta D$ ,  $\Delta H$ , and  $\Delta\text{EF}$  equations that have been scaled to the data sets used in the present study. The first method defines the maximum predictive ability possible from eqs. 1 and 3, given the equation form selected to predict HCB. The second method should be a more realistic estimate of the predictive ability of eqs. 1 and 3 as they will be applied. Because the existing  $\Delta D$ ,  $\Delta H$ , and  $\Delta\text{EF}$  equations were developed from different data sets than were used in the present study, the third method should provide an approximation of the predictive ability of the indirect approaches if all of the static and dynamic equations for a nonspatial tree-list model of stand development were developed from a common data set. This approximation will probably be less accurate and (or) precise than developing all equations with a common data set and more accurate and (or) precise than using equations developed from an independent data set.

The  $\Delta D$ ,  $\Delta H$ , and  $\Delta\text{EF}$  equations of Hann et al. (2003) were used for Douglas-fir, and the equations of Hann and Ritchie (1988), Ritchie and Hann (1990), Hann and Wang (1990), Hann and Larsen (1991), Zumrawi and Hann (1993), and Hann et al. (2003) were used for minor species on the plots. These equations were developed for different variants

**Table 3.** Parameter estimates and standard errors (SE) for eq. 4 fit to combined starting and ending HCB values for Douglas-fir.

Parameter	Estimate (SE)
$a_0$	4.42332 (0.05810)
$a_1$	-0.01078 (0.00113)
$a_2$	-0.00137 (0.00009)
$a_3$	-1.19702 (0.01600)
$a_4$	0.38043 (0.02590)

**Table 4.** Index of fit, the mean residual (predicted - actual), and the mean square error (MSE) from the application of the allometric method using predicted ending values from  $P\Delta H$ ,  $P\Delta D$ , and  $P\Delta EF$ ; predicted ending values from  $SP\Delta H$ ,  $SP\Delta D$ , and  $SP\Delta EF$ ; and actual measured ending values from  $\Delta H$ ,  $\Delta D$ , and  $\Delta EF$  to Douglas-fir  $\Delta HCB$  data.

Equation	$P\Delta H$ , $P\Delta D$ , and $P\Delta EF$	$SP\Delta H$ , $SP\Delta D$ , and $SP\Delta EF$	$\Delta H$ , $\Delta D$ , and $\Delta EF$
<b>Index of fit</b>			
1	0.2402	0.2600	0.3465
3	0.1951	0.2139	0.3090
<b>Mean residual (m)</b>			
1	0.2514	0.1153	-0.0536
3	0.2471	0.1110	-0.0579
<b>MSE (m<sup>2</sup>)</b>			
1	3.0356	2.9564	2.6109
3	3.2157	3.1406	2.7607

of ORGANON, and they are all for a 5-year growth period. For each of the three sources of data, predicted  $\Delta D$  ( $P\Delta D$ ) and predicted  $\Delta H$  ( $P\Delta H$ ) from the equations were scaled (producing  $SP\Delta D$  and  $SP\Delta H$ ) to the measured  $\Delta D$  and  $\Delta H$  values by applying weighted simple linear regressions through the origin. The weights used by Ritchie and Hann (1990), Hann and Larsen (1991), Zumrawi and Hann (1993), and Hann et al. (2003) in the development of their  $\Delta D$  and  $\Delta H$  equations were also used in this scaling process. Because the size of the mortality data was judged to be inadequate, we did not attempt to calibrate the predicted  $\Delta EF$  ( $P\Delta EF$ ) equations, which could lower the accuracy and (or) precision of the scaling approach for estimating attributes at the end of the growth period.

For those observations with direct measurements of  $\Delta HCB$ , residuals of predicted  $\Delta HCB$  ( $P\Delta HCB$ ) minus  $\Delta HCB$  were determined and used to calculate a mean residual (a measure of bias) and the sum of squared residuals for eqs. 1 and 3 and each of the three methods for determining end-of-growth-period values. A mean square error for the residuals (MSE) was formed by dividing the sum of squared residuals by the difference between the number of observations and the number of parameters estimated for eq. 4.

#### Incremental method

Equations 5, 7, and 8 include the dynamic attribute of  $\Delta H$ . As with the allometric method, we examined three approaches

for determining  $\Delta H$ : (i) using the measured values of  $\Delta H$ , (ii) using  $P\Delta H$ , and (iii) using  $SP\Delta H$ . For each of these three approaches, the parameter estimates, their standard errors, and the MSE for eqs. 5 through 8 were estimated by applying nonlinear regression to the Douglas-fir data with direct measurements of  $\Delta HCB$ . Following Short and Burkhart (1992) and Liu et al. (1995), we chose to ignore any possible effects that might arise due to lack of independence between observations caused by the cross-sectional and longitudinal nature of our data set, because (i) the data set has a large number of observations that are dominated by cross-sectional measurements and (ii) the use of a 5-year growth period should minimize any possible effect of serial correlation in the longitudinal data (Gertner 1985).

A  $t$  test was used to test whether the parameters were significantly different from zero ( $p = 0.05$ ). The variance of the residuals was examined for homogeneity using both residual plots and the Levene's test using medians on approximate repeats (as suggested by Draper and Smith (1998), pp. 54-59). The normality of the residuals was examined through the application of the Bowman and Shenton (1975) bivariate test for large samples (as suggested by Kmenta (1997), p. 267) to our sample estimators of the skewness and kurtosis statistics (i.e.,  $\sqrt{\beta_1}$  and  $\beta_2$ , respectively). Finally, a mean residual ( $P\Delta HCB - \Delta HCB$ ) was calculated for each equation.

#### Evaluation of alternative methods

The mean residual, the MSE, and an index of fit were used to compare the two allometric equation forms, the four incremental equation forms, and the three methods of determining the ending values for each of the allometric equation forms and  $\Delta H$  for each of the incremental equation forms. The index of fit represents the proportion of variation in the dependent variable explained by the equation (Short and Burkhart 1992). It was calculated by dividing the MSE for each equation by the variance of  $\Delta HCB$  and subtracting the result from one. Therefore, the index of fit used in the present study is analogous to the adjusted coefficient of determination used for linear equations. By employing data reported in Krumland and Wensel (1981), Maguire and Hann (1990b), and Short and Burkhart (1992), we were also able to determine the index of fit for each of their incremental equation forms chosen for evaluation in this analysis.

#### Results and reanalysis

The parameter estimates and their standard errors for the fit of eq. 4 to the Douglas-fir HCB data are found in Table 3. The signs and magnitudes of the parameters are in agreement with the previous work of Ritchie and Hann (1987), Zumrawi and Hann (1989), Hanus et al. (2000), and Hann et al. (2003). This fit yielded a weighted MSE of 0.00772 and a weighted index of fit of 0.7265.

Of the two allometric equation forms examined, eq. 1 provided higher index of fit values but about the same mean residual (i.e., bias) as eq. 3 (Table 4). The predictive ability of both allometric equation forms improved as the estimators of  $\Delta D$ ,  $\Delta H$ , and  $\Delta EF$  improved (Table 4). For example, eq. 1 explained 26% of the variation in  $\Delta HCB$  with scaled predictions of  $\Delta D$ ,  $\Delta H$ , and  $\Delta EF$  and nearly 35% with measured values.

**Table 5.** Index of fit, the mean residual (predicted – actual), and the mean square error (MSE) for the incremental equation forms fit to the Douglas-fir ΔHCB data using PΔH, SPΔH, or ΔH.

Equation	PΔH	SPΔH	ΔH
<b>Index of fit</b>			
5	0.3765	0.3985	0.3954
6*	0.2543	0.2543	0.2543
7	0.4920	0.4937	0.4986
8	0.4376	0.4449	0.4557
9	0.5087	0.5096	0.5137
10	0.4554	0.4618	0.4740
<b>Mean residual (m)</b>			
5	0.0026	-0.0072	0.0036
6*	-0.0166	-0.0166	-0.0166
7	-0.0182	-0.0203	-0.0215
8	-0.0202	-0.0244	-0.0329
9	0.0047	0.0023	0.0015
10	0.0034	-0.0009	-0.0085
<b>MSE (m<sup>2</sup>)</b>			
5	2.4910	2.4031	2.4155
6*	2.9792	2.9792	2.9792
7	2.0296	2.0228	2.0032
8	2.2469	2.2177	2.1746
9	1.9628	1.9592	1.9429
10	2.1758	2.1502	2.1015

\*Equation 6 does not include ΔH and therefore is invariant across its three measures.

Both allometric equation forms underpredicted ΔHCB when actual measurements of ΔD, ΔH, and ΔEF were used and overpredicted ΔHCB when estimators of ΔD, ΔH, and ΔEF were used (Table 4). The scaled estimators provided a smaller overprediction bias than did the unscaled estimators. When compared with an average ΔHCB of 2.98 m (Table 2), the overprediction bias ranged from 8% for eq. 1 with unscaled estimators of ΔD, ΔH, and ΔEF to less than 4% for eq. 3

with scaled estimators. The underprediction bias was approximately 2% for both equations when using actual measurements of ΔD, H, and ΔEF.

The parameters of direct eqs. 5, 7, and 8 were all significantly different from zero ( $p = 0.05$ ), and they were of the same sign as reported by Krumland and Wensel (1981) and Maguire and Hann (1990b). For eq. 6, the  $b_{2,3}$  parameter on  $CR^{1/2}$  was not significantly different from zero, and it was of the opposite sign from that reported in Short and Burkhart (1992).

In general, the incremental method provided better estimates of ΔHCB (Table 5) than the allometric method (Table 4), and the mean residuals in Table 5 indicate that the incremental method produced estimators that are, for all practical purposes, unbiased. In the equations employing scaled estimators, for example, the incremental method produced indices of fit ranging from 0.2543 for eq. 6 to 0.4937 for eq. 7, whereas the indices of fit ranged from 0.2139 to 0.2600 with the allometric method. The index of fit values for the four incremental equation forms (Table 5) show that eq. 7 provided the best fit to the ΔHCB data, followed by eq. 8, eq. 5, and finally eq. 6. However, the poor predictive performance of eq. 5 may have been negatively affected by an unknown amount, because of the need to predict H and HCB for a number of sample trees on each plot. Finally, these results also show that the substitution of BHA<sub>S</sub> in the Maguire and Hann (1990b) equation (i.e., eq. 7) proved to be more effective at predicting ΔHCB than did the substitution of GEA<sub>S</sub> (i.e., eq. 8).

Equations 7 and 8 predict a peak in ΔHCB at a CR of approximately 0.64 for eq. 7 and approximately 0.62 for eq. 8, and then a decline in ΔHCB as CR increases to 1.0. However, graphs of PΔHCB from these equations indicated that, for long-crowned, young trees on plots with low density (i.e., trees with CR = 1.0, a small GEA, on plots with small values of CCF), PΔHCB was larger than that observed in the data. After examining several modifications to eqs. 7 and 8, the following formulations were found to produce more reasonable predictions at the extremes of CR and to explain slightly more variation (Table 5):

$$[9] \quad \Delta HCB = \frac{CL_S + \Delta H}{1.0 + \exp \left[ b_{5,0} + b_{5,1} \ln(CR_S) + b_{5,2} CR_S + b_{5,3} BHA_S + b_{5,4} \ln(CCF_S) + b_{5,5} \left( \frac{CR_S}{CCF_S} \right) \right]}$$

$$[10] \quad \Delta HCB = \frac{CL_S + \Delta H}{1.0 + \exp \left[ b_{6,0} + b_{6,1} \ln(CR_S) + b_{6,2} CR_S + b_{6,3} GEA_S + b_{6,4} \ln(CCF_S) + b_{6,5} \left( \frac{CR_S}{CCF_S} \right) \right]}$$

where  $b_{5,i}$  are parameter estimates for ΔHCB in eq. 9 and  $b_{6,i}$  are parameter estimates for ΔHCB in eq. 10.

Parameter estimates and their standard errors for eqs. 9 and 10 were estimated by nonlinear regression (Table 6). The variance for the residuals of these final two equations was found to be homogeneous across PΔHCB, but the resid-

uals were not normally distributed ( $p < 0.0001$ ) (Table 7). For normally distributed residuals, the expected value of the skewness statistic,  $\sqrt{\beta_1}$ , is 0, and the expected value of the kurtosis statistic,  $\beta_2$ , is 3.0. Therefore, our residuals were slightly skewed and leptokurtic in comparison to the normal distribution (Table 7).

**Table 6.** Parameter estimates and standard errors (in parentheses) for eqs. 9 and 10 fit to the Douglas-fir  $\Delta HCB$  data using  $\Delta H$ ,  $P\Delta H$ , or  $SP\Delta H$ .

(A) Equation 9.						
Variable used	Estimate (SE) of parameter					
	$b_{5,0}$	$b_{5,1}$	$b_{5,2}$	$b_{5,3}$	$b_{5,4}$	$b_{5,5}$
$\Delta H$	-4.1754 (0.4653)	-3.7715 (0.3002)	5.6858 (0.4967)	0.0520 (0.0014)	-0.3000 (0.0654)	120.8845 (10.7936)
$P\Delta H$	-5.4068 (0.4765)	-4.1626 (0.3068)	6.4714 (0.5076)	0.0566 (0.0014)	-0.2320 (0.0666)	128.0030 (10.9501)
$SP\Delta H$	-5.0701 (0.4696)	-4.1609 (0.3030)	6.4405 (0.5005)	0.0529 (0.0014)	-0.2648 (0.0659)	123.7958 (10.8238)
(B) Equation 10.						
Variable used	Estimate (SE) of parameter					
	$b_{6,0}$	$b_{6,1}$	$b_{6,2}$	$b_{6,3}$	$b_{6,4}$	$b_{6,5}$
$\Delta H$	-5.0028 (0.4714)	-4.3067 (0.3078)	6.3075 (0.5135)	0.0537 (0.0017)	-0.2717 (0.0667)	123.7249 (11.1484)
$P\Delta H$	-6.0932 (0.4866)	-4.6515 (0.3171)	6.9861 (0.5296)	0.0565 (0.0017)	-0.2044 (0.0687)	130.4725 (11.4593)
$SP\Delta H$	-5.7654 (0.4780)	-4.6514 (0.3122)	6.9717 (0.5206)	0.0527 (0.0017)	-0.2383 (0.0677)	126.3699 (11.2885)

**Table 7.** The  $p$  value from a Levene's test for homogeneity of variance and the skewness and kurtosis statistics for the residuals from fits of direct eqs. 9 and 10 to the Douglas-fir  $\Delta HCB$  data using  $\Delta H$ ,  $P\Delta H$ , or  $SP\Delta H$ .

Variable	$p$	Skewness	Kurtosis
<b>Eq. 9</b>			
$\Delta H$	0.5837	0.0943	3.6356
$P\Delta H$	0.3834	0.1058	3.6753
$SP\Delta H$	0.5350	0.1136	3.6551
<b>Eq. 10</b>			
$\Delta H$	0.3481	-0.0666	3.4434
$P\Delta H$	0.7459	-0.0598	3.3972
$SP\Delta H$	0.9014	-0.0448	3.3861

## Discussion

The allometric method in nonspatial tree-list models of stand development can provide unbiased estimates of  $\Delta HCB$ . Liu et al. (1995) reported a similar result from their analysis using a spatial incremental equation. This finding is fortunate because of the difficulty in obtaining adequate data to model  $\Delta HCB$  directly for the large number of species in some of these models. Unlike Liu et al. (1995), the results of the present study make it clear that the allometric method explains substantially less of the variation in  $\Delta HCB$  than can the incremental method. Of the two allometric equation forms examined, eq. 1 was superior to eq. 3.

Scaling the  $P\Delta D$  and  $P\Delta H$  equations improved both the accuracy and the precision of the allometric method (Table 4), and we suspect that scaling  $\Delta EF$  would have further improved the outcome. These results indicate to us that the accuracy and precision of the allometric method are optimal when all equations are developed from a common data set that has been collected from the population of interest.

Incremental eqs. 9 and 10 fit the  $\Delta HCB$  better than the other four incremental equations tested (Table 5). The use of  $BHA_S$  in eq. 9 provided a better fit to the data than the use of  $GEA_S$  in eq. 10.  $GEA$ , however, can be applied to trees from both even- and uneven-aged stands (e.g., Hann and Ritchie 1988). Thus, all six of the incremental equation forms examined can be applied to data collected from even-aged stands, but only the forms of eqs. 5 (which does not include an age), 8, and 10 can be applied to modeling data collected in uneven-aged stands. However, it would be an extrapolation to apply eq. 10 and the parameters from Table 6 to an uneven-aged stand, because all of the modeling data in the present study were collected in even-aged stands.

Krumland and Wensel's (1981) application of eq. 5 to their data sets resulted in the largest indices of fit found in the literature: 0.30 for redwood and 0.50 for Douglas-fir. Our application of eq. 5 resulted in indices of fit that are better than that of redwood but worse than that of Douglas-fir. The appeal of eq. 5 is its simplicity (i.e., the amount of  $\Delta HCB$  is related to just the amount of crowding at the base of the crown) and its applicability to trees from both even- and uneven-aged stands. It is possible that eq. 5 would have

performed better in this evaluation if  $H$  and HCB had been measured on all of the sample trees in our modeling data sets.

Incremental eq. 6 (Short and Burkhart 1992) provided the worst fit to the data. The index of fit for eq. 6 was larger than the value of 0.16 reported by Short and Burkhart (1992) for their unthinned and thinned loblolly pine data. Unlike Maguire and Hann (1990b) and the present study, Short and Burkhart (1992) found no peak in  $\Delta\text{HCB}$  over CR when they developed eq. 6. The different behavior in  $\Delta\text{HCB}$  over CR is further reinforced by our discovery that the parameter estimate on the CR term in eq. 6 was not significantly different from zero ( $p = 0.05$ ). This variation in findings may be due to differences in how the two species respond to their environment or to differences in the modeling data. Unfortunately, Short and Burkhart (1992) did not provide a detailed description of their data, but our data do exhibit larger averages, with more variation for CR,  $D$ ,  $H$ , and  $\Delta\text{HCB}$  than reported by Liu et al. (1995) for untreated trees from the same plots used by Short and Burkhart (1992). The data used by Liu et al. (1995) did include data from another remeasurement of the plots.

The equation forms and parameter estimates for the statistically best performing equations (i.e., eqs. 7, 8, 9, and 10) predict a crown-recession behavior that is consistent with our general knowledge of the process. Crown recession occurs when branches at the base of the crown die as a result of prolonged side shading (Oliver and Larson 1996). Equations 7, 8, 9, and 10 use the density variable  $\text{CCF}_S$  as an indicator of the level of side shading at the base of the crown. This density effect is reduced as stand age (either  $\text{BHA}_S$  or  $\text{GEA}_S$ ) increases, because a fixed level of density corresponds to a decreasing level of side shading as a stand matures (e.g., a BA of 10 m<sup>2</sup> represents a higher level of competition in a very young stand than it would in a very old stand).

$\text{CR}_S$  in eqs. 7, 8, 9, and 10 both characterizes the tree's crown position within the stand and acts as a surrogate for the degree of heterogeneity in local stand density (Maguire and Hann 1990b). In uniformly spaced plantations, average CR decreases as density increases and, as the plantation matures and the trees begin to differentiate themselves, the CR of individuals within the stand is largest for dominant trees and becomes progressively smaller as crown position is lost (e.g., Curtis and Reukema 1970). Curtis and Reukema (1970) also found that HCB at a given stand age was greatest for dominant trees and declined with loss of crown position, indicating that  $\Delta\text{HCB}$  is higher in dominant trees with larger CR than that in trees in lower crown positions with smaller CR. Finally, trees growing in a more open portion of an irregularly spaced stand would have a larger CR and a smaller  $\Delta\text{HCB}$  than would be expected for the dominant trees in a uniformly spaced stand with the same density and stand age.

The modification to eqs. 7 and 8 that produced eqs. 9 and 10 causes the location of the peak in  $\Delta\text{HCB}$  over CR to shift from a CR value of approximately 0.6 to a value near 1 as  $\text{CCF}$  decreases towards 0. We believe that the modification developed in the present study indicates that heterogeneity in local density becomes less influential on  $\Delta\text{HCB}$  in stands with low density that, as a result, contain more long-crowned trees.

Equation 5 uses  $\text{CCCB}_S$  as its indicator of the amount of side shading at the base of the crown.  $\text{CCCB}_S$  integrates

both overall plot density and the vertical position of each tree's crown base within the plot. Equation 5, however, does not include a variable to characterize the degree of heterogeneity in local stand density.

The poorest performing equation (i.e., eq. 6) uses both  $\text{CR}_S$  and  $\text{QMD}_S/D_S$  to quantify tree position within the plot. As noted earlier,  $\text{CR}_S$  (which was not significantly different from zero in this study) can also indicate irregularity in tree spacing within the plot. Equation 6 does not include a direct measure of density for indexing the amount of shading at the base of the crown. However, eq. 6 does contain  $\text{BHA}_S$ , which could be providing an indirect measure of the level of competition in the stand (e.g., Mäkinen 1999). Finally, the inclusion of both  $H_S$  and  $\text{BHA}_S$  in eq. 6 could provide an indirect measure of site quality (Maguire and Hann 1990), and site quality has been found to be significant in some of the allometric equations used to predict HCB (e.g., Ritchie and Hann 1987; Hanus et al. 2000; Hann et al. 2003).

The use of  $\text{P}\Delta H$  or  $\text{SP}\Delta H$  in place of  $\Delta H$  in the incremental method reduced the fit of the equations to the data (Table 5). Despite this reduction in equation fit, it is more realistic to expect their use in practical applications of the  $\Delta\text{HCB}$  equations. The fits with  $\text{SP}\Delta H$  probably best mimic the usual situation where all dynamic equations are estimated from a common data set.

Both the Maguire and Hann (1990b) study and the present study analyzed very similar equation forms using 5-year  $\Delta\text{HCB}$  data from the same species and region. The ranges in the size of the tree and stand attributes were also similar between the two studies. Despite these similarities, our findings differ from those of Maguire and Hann (1990b) in four ways. Our indices of fit are larger than the value of 0.284 from their study. Our equations peaked at a larger CR than the value of 0.38 that they reported. The skewness and kurtosis statistics in the present study (Table 7) are much closer to the values expected under normality than the values of 1.73 for skewness and 8.29 for kurtosis reported by Maguire and Hann (1990b). Our finding that the residuals exhibited homogeneous variance agrees with the results from Short and Burkhart (1992) but differs from those of Maguire and Hann (1990b).

We can identify three differences between the studies that might be related to these disparities:

(i) Instead of the 0.020- to 0.202-ha research plots used in the present study, the Maguire and Hann (1990b) data were collected from operational stands using a grid of sampling points spread over a minimum of 1.2 ha.

(ii) The Maguire and Hann (1990b) data set included trees from uneven-aged stands.

(iii) The  $\Delta\text{HCB}$  data used by Maguire and Hann (1990b) came from the techniques developed by Maguire and Hann (1987, 1990a) to determine  $\Delta\text{HCB}$  through the post dating of branch mortality on trees from temporary plots.

We have found that both operational stands and uneven-aged stands exhibit a greater amount of within-stand variation in density than do carefully selected research installations or even-aged stands. This could explain the smaller index of fit and the shift of the peak of  $\Delta\text{HCB}$  to smaller values of CR reported by Maguire and Hann (1990b). Finally, we suspect the third difference may be related to the dissimilar error structures found in the two studies.

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## Appendix A

Change in CR can be expressed as

$$[A1] \quad \Delta CR = \frac{CL_S + \Delta H - \Delta HCB}{H_S + \Delta H} - \frac{CL_S}{H_S}$$

Equation A1 can be solved algebraically for  $\Delta HCB$ :

$$[A1] \quad \Delta HCB = \Delta H (BR_S) - \Delta CR (H_S) - (\Delta H)(\Delta CR)$$

Because BR is defined as  $1 - CR$ , eq. 2 can be reexpressed as:

$$[A2] \quad \Delta CR = PBR_S - PBR_E$$

where  $PBR_E$  is the predicted BR at the end of the growth period.

Substituting eq. A2 for  $\Delta CR$  in eq. A1 and collecting terms provides

$$[A3] \quad \Delta HCB = (H_S + \Delta H)(PBR_E) - (H_S)(PBR_S) + (\Delta H)(BR_S - PBR_S)$$

Finally, recognizing that  $(H_S + \Delta H)(PBR_E)$  and  $(H_S)(PBR_S)$  are ways of calculating a value for  $PHCB_E$  and  $PHCB_S$  respectively, eq. A3 can be reexpressed as

$$[3] \quad \Delta HCB = PHCB_E - PHCB_S + (\Delta H)(BR_S - PBR_S)$$