

Sources of Variation in the Self-Thinning Boundary Line for Three Species with Varying Levels of Shade Tolerance

Aaron Weiskittel, Peter Gould, and Hailemariam Temesgen

Abstract: The species self-thinning boundary line has been widely analyzed with a variety of statistical techniques. Most previous studies in the forestry literature have reported that the relationship does not differ across a range of stand and site factors, but these studies have primarily used statistical techniques that make model fitting subjective or interpretation of covariate significance difficult. There is growing evidence that the use of stochastic frontier analysis is an effective statistical means for objectively fitting the species self-thinning boundary line, offering the opportunity to test the influence of additional covariates. Using extensive even-aged coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla*), and red alder (*Alnus rubra* Bong.) data sets in the Pacific Northwest, we examined the assumption that the intercept and slope of the species self-thinning boundary line are insensitive to stand and site factors. Likelihood ratio tests indicated that site index, stand origin (natural versus planted), and purity (proportion of basal area in the primary species) significantly influenced the species self-thinning boundary line intercept for each of the species examined in this study. In Douglas-fir and western hemlock, the slope of the self-thinning boundary was also dependent on stand origin as well as site index in the case of Douglas-fir. Fertilization did not significantly influence the intercept or slope of the species self-thinning line for Douglas-fir and western hemlock. In addition, the inclusion of site aspect and dryness index marginally improved the red alder model of self-thinning, but neither site soil nor climatic variables improved the models for western hemlock and Douglas-fir. Thus, the species self-thinning boundary line can vary significantly among stands, and its variation is driven by several distinct factors; stochastic frontier analysis is an effective tool for identifying these factors. FOR. SCI, 55(1):84-93.

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THE MAXIMUM SIZE-DENSITY RELATION is a key stand property that governs both stand dynamics and potential productivity (Jack and Long 1996). The relationship between maximum tree size and density is typically expressed as a line when both density (trees per hectare [TPH]) and mean tree size (quadratic mean diameter [QMD]) are log-transformed:

$$\ln(\text{TPH}) = \beta_0 + \beta_1 \ln(\text{QMD}). \quad (1)$$

The maximum stand density index (SDI_{\max}) is the maximum number of trees at a given reference diameter (commonly 25.4 cm is used) that can exist in a self-thinning population. SDI_{\max} can be expressed as

$$\text{SDI}_{\max} = e^{[\beta_0 + \beta_1 \cdot \ln(25.4)]}, \quad (2)$$

where β_0 and β_1 are the species-specific intercept and slope of the self-thinning line, respectively (Equation 1). Four critical assumptions are inherent to SDI_{\max} : (1) a predictable species-specific relationship between maximum size and density exists; (2) the relationship is linear in log-log space (i.e., Equation 1); (3) the slope of the maximum size-density boundary line (-1.605) is universal; and (4) the intercept

(β_0) is constant for a given species and region (Jack and Long 1996). These assumptions are generally regarded as reasonable approximations but have been difficult to test rigorously.

Permanent plot data have illustrated the fact that stands self-thin at differing levels of SDI_{\max} , and there is still inadequate consensus on the processes actually driving this variation (Reynolds and Ford 2005), which has led some authors to conclude that each stand has its own dynamic self-thinning trajectory (Pittman and Turnbull 2003). Thus, the general acceptance that the maximum size-density boundary line is constant for a given species (i.e., independent of site quality and stand age) may be due to the lack of rigorous testing of such a relationship rather than to overwhelming evidence in support of it (Jack and Long 1996). Several studies have shown that individual stands do not always approach the maximum size-density relationship because of genetics or environmental constraints (Weller 1987, Zeide 1987, Hynynen 1993), but identification of the key factors driving regional variation still remains unclear. For example, Poage et al. (2007) found that a variety of stand or site factors did not explain > 30% of the variability

Aaron R. Weiskittel, School of Forest Resources, 5755 Nutting Hall, The University of Maine, Orono, ME 04469-Phone: (207) 581-2841; Fax: (207) 581-2875; aaron.weiskittel@umit.maine.edu; Peter J. Gould, US Forest Service, PNW Research Station, Olympia, WA 98512-pgould@fs.fed.us; Hailemariam Temesgen, Department of Forest Resources, Oregon State University, Corvallis, OR 97331-hailemariam.temesgen@oregonstate.edu

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in western hemlock (*Tsuga heterophylla* [Raef.] Sarg.) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) SDI_{max} . In the Pacific Northwest, coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) individual stand SDI_{max} has been reported to vary between 680 and 1,669 trees per ha at a mean dbh of 25.4 cm (Hann et al. 2003). In this analysis, the mean value (1,153) was significantly lower than the commonly used value of 1,511 suggested by Reineke (1933), but the values of individual stands plotted over site index, latitude, purity (proportion of basal area in Douglas-fir), and stand origin (natural or plantation) showed no distinct trends (Hann et al. 2003). In addition, Hann et al. (2003) indicated that fertilization had no influence on the SDI_{max} trajectory, and the overall size-density slope did not differ from the value set forth by Reineke (1933). These results are also consistent for red alder (*Alnus rubra* [Bong.]) as Puettmann et al. (1993b) found that initial density and stand origin had no effect on the size-density relationship. Conversely, site index has been identified as a key factor influencing the dynamic and species self-thinning behavior in Douglas-fir (Pittman and Turnblom 2003) and radiata pine (*Pinus radiata* [D. Don.]) (Bi 2001), respectively. In addition, recent studies have highlighted initial stand density (Turnblom and Burk 2000, VanderSchaaf 2004, Reynolds and Ford 2005) and stand composition (Puettmann et al. 1992, Woodall et al. 2005) as important factors influencing the species self-thinning line and, consequently, SDI_{max} . These differing findings can partly be attributed to the size and quality of the available data as well as the variety of statistical techniques that have been used to examine the species self-thinning boundary line.

Most studies on the species self-thinning line have used subjective or significantly limited statistical techniques for fitting the boundary line, which has made testing the influence of other site and stand factors difficult. Several commonly used statistical techniques for examining maximum size-density relations such as ordinary least squares regression and principal components analysis have multiple limitations (Weller 1987). For example, VanderSchaaf and Burkhart (2007) recently showed that ordinary least squares regression gave the least stable parameter estimates for the loblolly pine (*Pinus taeda* L.) maximum size-density species boundary line, whereas mixed-effects models gave the most stable estimates. However, the slope of the mixed-effects model varied widely (range of -1.2 to -2.5) in this analysis, and the factors that contributed to this variation were not identified (VanderSchaaf and Burkhart 2007).

Zhang et al. (2005) recently compared several statistical techniques for estimating the maximum size-density relationship and found that stochastic frontier analysis (SFA) had important advantages over other techniques such as ordinary least squares regression, quantile regression, and principal components analysis (major axis analysis). SFA is an econometric technique that finds the envelope curve bounding a mass of points (Aigner et al. 1977). Also, this approach is quite powerful because it uses all of the available data, and it can incorporate differences in sites, which allows for more objective and precise inferences about the

line (Bi et al. 2000). Bi (2004) found that this type of analysis gave a more realistic estimate of the maximum asymptotic stand density by separating the effects of density-dependent and density-independent mortalities during self-thinning in the model specification. Most importantly, this method estimates parameter standard errors directly and, consequently, allows statistical inference on the model coefficients, which is very difficult with other commonly used methods (Zhang et al. 2005).

The goal of this study was to illustrate the use SFA to examine maximum size-density relations in three species with varying levels of shade tolerance, namely, coastal Douglas-fir, red alder, and western hemlock. However, our study differs from previous studies that have used SFA to fit the species self-thinning boundary line (e.g., Bi 2001, Zhang et al. 2005, de Montigny and Nigh 2007) by integrating a variety of other factors beyond site index such as stand origin and purity as inputs into the frontier production function.

Methods

Three regional data sets were combined to achieve our goal (Figure 1). The data sets included Douglas-fir and western hemlock data from the Stand Management Cooperative (SMC) (University of Washington) and red alder data from a variety of sources compiled by the University of Washington. Each data set is described separately below.

Douglas-Fir

For this analysis 319 SMC installations in western Oregon, Washington, and Vancouver Island, British Columbia, were used. The data consisted of 93 plantations and 226 even-aged natural stands. These installations covered a wide range of growing conditions that are typical for the region (Table 1). The overall climate for the region is humid oceanic, with a distinct dry summer and a cool, wet winter. Twenty-year annual mean rainfall for these locations ranged from 100 to 300 cm and January mean minimum and July mean maximum temperatures ranged from -7.5 to 1.31°C and 20.1 to 29.5°C, respectively (Daymet, 2008). Elevation varied from 88 to 737 m above sea level, and all aspects were represented. Soils varied from a moderately deep sandy loam to a very deep silty clay loam. The plantations were established between 1953 and 1993 at varying densities and levels of vegetation control. The initial planting densities for these installations averaged 1,275 stems ha⁻¹ with a range of 247 to 3,048 stems ha⁻¹. The natural stands were regenerated between 1906 and 1993.

In the natural stands, various plot sizes (ranging from 0.04 to 0.2 ha), plot shapes, and remeasurement lengths were used. In the plantations, several square 0.2-ha permanent plots were established by the SMC at each installation between 1986 and 1998. Since establishment, the plots have received a variety of silvicultural treatments with three primary regimens. Type 1 installations were established in young plantations (i.e., 10-15 years) and have received differing silvicultural treatments since plot establishment. The treatments in the type 1 installation used in this analysis included control plots ($n = 29$) and plots

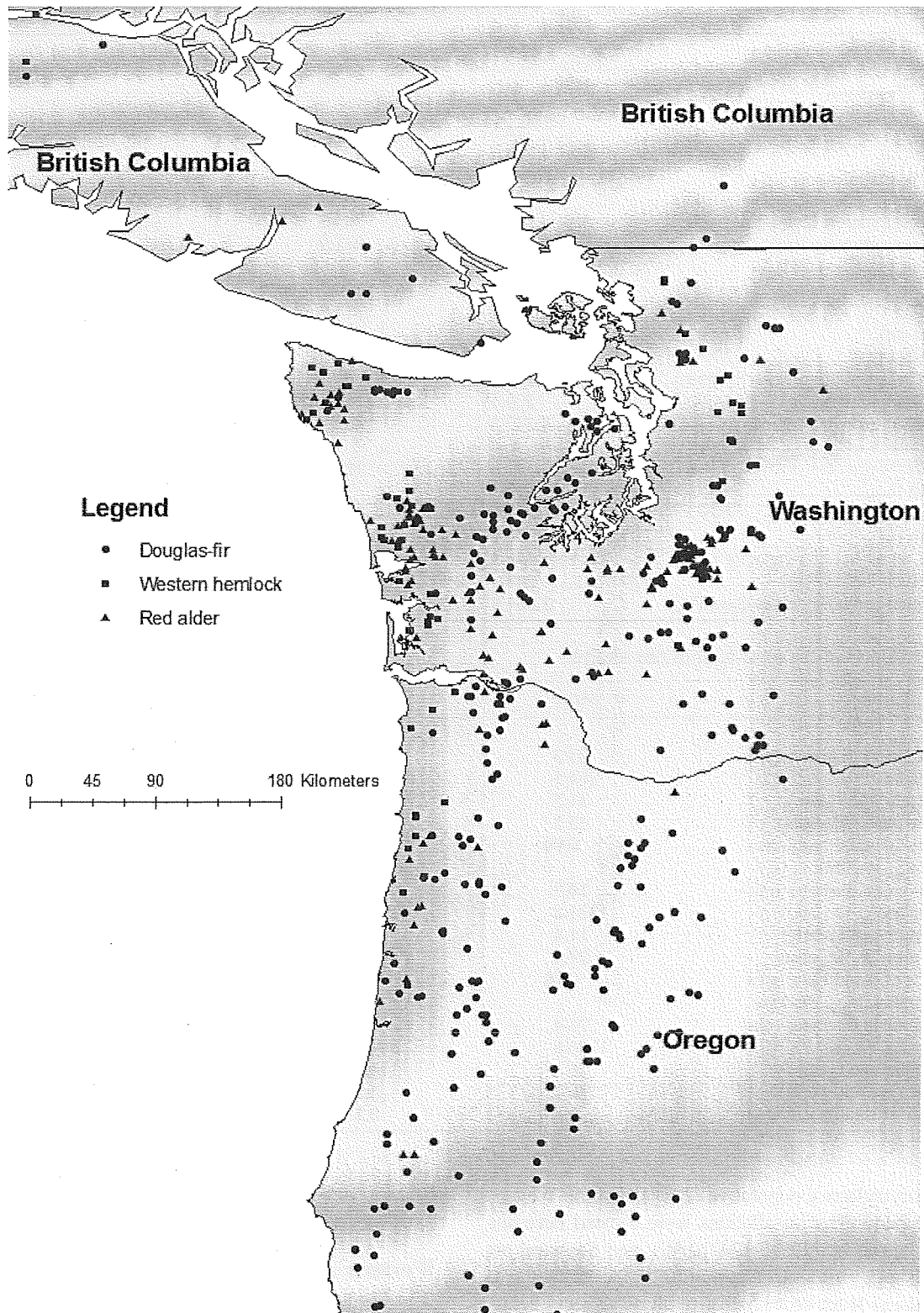


Figure 1. Location of the Douglas-fir (●), western hemlock (■), and red alder (▲) permanent research installations used in this analysis.

receiving fertilization with 448 kg ha^{-1} of urea every 4 years ($n = 17$). Finally, the SMC has established 30 initial spacing trials (type 3) that have at least five square 0.2-ha plots with planting densities of 247, 494, 741, 1,680, and $3,048 \text{ trees ha}^{-1}$. All of these plots are remeasured every 4 years for growth (Table 2). A total of 3,804 observations were available for this analysis.

Red Alder

For this analysis 121 installations in western Oregon, Washington, and Vancouver Island, British Columbia, were used. The data consisted of 62 plantations and 59 even-aged natural stands and were obtained from a variety of sources including the British Columbia Ministry of Forests, the

Table 1. Attributes of the Douglas-fir, red alder, and western hemlock permanent research installations used in this analysis

Variable	Mean	SD	Minimum	Maximum
Douglas-fir ($n_{\text{installation}} = 217$)				
Aspect (°)	193.0	101.9	0.0	360.0
Slope (%)	26.5	21.2	0.0	90.0
Elevation (m)	236.8	221.3	4.6	1,158.2
Soil depth (m)	0.80	0.25	0.22	1.65
Soil total water holding capacity (mm)	144.3	58.2	36.7	366.9
Annual precipitation (cm)	184.1	44.7	98.7	299.2
Mean annual growing degree-days (°C)	2,653.7	341.9	1,649.5	3,283.6
Red alder ($n_{\text{installation}} = 273$)				
Aspect (°)	154.5	104.2	0.0	360.0
Slope (%)	15.4	17.7	0.0	98.0
Elevation (m)	213.4	163.0	1.0	912.0
Soil depth (m)	0.82	0.31	0.15	1.65
Soil total water holding capacity (mm)	169.88	63.88	36.26	374.69
Annual precipitation (cm)	209.69	51.96	109.62	354.12
Mean annual growing degree-days (°C)	4,233.3	435.9	2,622.4	4,864.7
Western hemlock ($n_{\text{installation}} = 57$)				
Aspect (°)	141.8	124.8	0.0	358.0
Slope (%)	18.1	13.8	0.0	54.0
Elevation (m)	291.1	249.1	24.0	906.0
Soil depth (m)	0.69	0.27	0.23	1.52
Soil total water holding capacity (mm)	136.5	61.7	33.8	297.8
Annual precipitation (cm)	248.5	36.7	155.4	467.3
Mean annual growing degree-days (°C)	3,991.3	453.1	2,731.3	4,741.8

Table 2. Attributes of the plots used in this analysis

Variable	Mean	SD	Minimum	Maximum
Douglas-fir ($n_{\text{plot}} = 1,372$)				
Quadratic mean diameter (cm)	25.3	8.1	4.6	73.6
Stems per ha	864.5	628.8	98.8	4694.9
Breast-height age (years)	31.5	15.8	4.4	69.2
Site index (m at 50 years)	35.5	6.3	18.2	58.1
Proportion of stand basal area	0.94	0.12	0.23	1.00
Red alder ($n_{\text{plot}} = 599$)				
Quadratic mean diameter (cm)	10.7	8.3	0.7	48.8
Stems per ha	1321.8	1126.8	37.1	3660.5
Breast-height age (years)	11.4	13.9	1.0	86.0
Site index (m at 50 years)	27.4	5.8	11.4	49.6
Proportion of stand basal area	0.98	0.07	0.11	1.00
Western hemlock ($n_{\text{plot}} = 303$)				
Quadratic mean diameter (cm)	23.4	6.6	7.7	43.7
Stems per ha	1136.6	889.5	98.8	5782.1
Breast-height age (years)	26.3	14.6	1.5	53.0
Site index (m at 50 years)	36.1	3.5	22.7	43.9
Proportion of stand basal area	0.89	0.15	0.08	1.00

Hardwood Silviculture Cooperative (2008), and the Weyerhaeuser Company. The installations were located between Coos Bay, Oregon (43°12'N, 124°12'W), and Sayward on Vancouver Island, British Columbia (50°22'N, 125°58'W). Elevation ranged from 46 to 549 m with all aspects being represented. Slopes were generally mild (< 15°), but steep installations were also included. The soils were generally deep silty loams formed in colluvium. The stands were established between 1881 and 1996.

The Hardwood Silviculture Cooperative data set included the type 2 plots (0.13 ha in size), which were established between 1989 and 1997. Each type 2 installation included at least five different initial densities ranging from 254 to 3,048 trees per ha. Since canopy closure, the plots have received a variety of thinning regimens. The mean site index was 27.7 ± 5.8 m (base age of 25 years) (Nigh and

Courtin 1998) with a range of 27.0 to 46.6 m. A total of 2,026 observations were available for this analysis.

Western Hemlock

For this analysis 72 SMC installations in western Oregon, Washington, and Vancouver Island, British Columbia, were used. The data consisted of 12 plantations and 60 even-aged natural stands. The installations covered a range of growing conditions similar to that for the Douglas-fir installations. Elevation ranged from 19 to 1,098 m with all aspects being represented. The plantations were established between 1977 and 1991 with varying densities and levels of vegetation control. The natural stands were regenerated between 1968 and 1988. The initial planting densities of the plantations averaged 1,445 stems ha⁻¹ with a range of 777 to 2,286 stems ha⁻¹.

Various plot sizes (ranging from 0.04 to 0.2 ha), plot shapes, and remeasurement lengths were also used in the western hemlock natural stands. In the plantations, several square 0.2-ha permanent plots were established by the SMC at each installation between 1986 and 2001. Similar to the Douglas-fir plantations, type 1 (various silvicultural regimes) and type 2 (varying levels of initial planting densities) plots were available. A total of 2,009 observations were available for this analysis.

Data Analysis

Maximum size-density was modeled using a stochastic frontier function (Aigner et al. 1977). The model can be expressed in the form,

$$Y_{it} = x_{it}\beta + (V_{it} - U_{it}), \quad (3)$$

where Y_{it} is the logarithm of the production of the it th plot in the t th time period, x_{it} is the $k \times 1$ vector of input quantities of the it th plot in the t th time period, β is a vector of unknown parameters, V_{it} are random variables assumed to be $N(0, \sigma_v^2)$ and independent of the U_{it} which are non-negative random variables that are assumed to account for the technical inefficiency in production and truncations at zero of the $N(m_{it}, \sigma_u^2)$ distribution. Preliminary analysis showed no significant different log-likelihood values between the half-normal and truncated-normal models so, consequently, the half-normal model was used. In this study, Y_{it} was $\ln(\text{TPH})$, V_{it} was equivalent to the random error component in a standard linear regression, and x_{it} included $\ln(\text{QMD})$ as well as several other stand-level and environmental covariates that were used to explain differences in the species self-thinning boundary line. As in Bi et al. (2000), U_{it} was assumed to represent the level of site occupancy. The β coefficients were estimated along with the variance parameters σ^2 and γ :

$$\sigma^2 = \sigma_v^2 + \sigma_u^2, \quad (4)$$

$$\gamma = \sigma_u^2 / \sigma_v^2 + \sigma_u^2, \quad (5)$$

where the subscript v refers to the two-sided error term and the subscript u references the one-sided error term. The σ^2 and γ coefficients are the diagnostic statistics that indicate the relevance of the use of the stochastic frontier function and the correctness of the assumptions made on the distribution form of the error term. Goodness of fit and correctness of the distributional form assumed for the composite error term are indicated by σ^2 . The systematic influences that are unexplained by the production function and are the dominant sources of random errors are indicated by γ . The statistical significance of γ shows that in the specified model, there is the presence of a one-sided error component. This implies that a traditional response function estimated by ordinary least squares cannot adequately represent the data, and the use of a stochastic frontier function estimated by the maximum likelihood estimation is warranted. In addition, SFA can yield an upper limiting boundary line only when σ_v^2 is small and close to zero (Zhang et al. 2005). Parameters were estimated using a maximum likelihood

estimator, which was achieved with FRONTIER v4.1 (Coelli 1996).

The influence of other covariates on the self-thinning boundary line intercept and slope was examined in two stages. First, several stand factors were examined for significance, including stand origin (natural versus planted), site index, fertilization, stand purity (proportion of basal area in the primary species), slope, aspect, and elevation. The combined effect of plot slope and aspect was modeled using the cosine and sine transformations suggested by Stage (1976). Site indices for Douglas-fir, red alder, and western hemlock were obtained using the equations of Bruce (1981), Nigh and Courtin (1998), and Bonner et al. (1995), respectively. In addition, the skewness of the diameter distribution was also used as a potential covariate as suggested by Sterba and Monserud (1993) for uneven-aged mixed species stands. The general model form used in this analysis was

$$\begin{aligned} \ln(\text{TPH}) = & \beta_0 + \beta_1 \ln(\text{QMD}) + \beta_2 \ln(\text{SI}) \\ & + \beta_3 \text{Planted} + \beta_4 \ln(\text{PBA}) + \beta_5 \text{SK}_{1.5}, \end{aligned} \quad (6)$$

where SI is species site index (m), PBA is the proportion of basal area in the primary species, Planted is an indicator variable for stand origin (1 if planted, 0 otherwise), and $\text{SK}_{1.5}$ is the skewness of the dbh^{1.5} distribution. In addition, all interactions were tested. Preliminary analysis indicated that this selected model form was more parsimonious than an alternative model form that included the proportion of basal area in other conifers as well as other hardwood species.

In the second stage of the analysis, mean climate information from Daymet (2008) and USDA National Resource Conservation Service soil attributes were obtained for each research installation located in the United States and with global positioning systems coordinates. Variables such as mean annual precipitation, growing degree-days, and soil water holding capacity were combined with the stand-level information to assess the influence of climate and soils information on a subset of the data for each species. Significance of the covariates was tested using likelihood ratio tests because autocorrelation may influence estimated parameter standard errors in these types of models (e.g., Bi 2001).

Results

The value of γ was highly significant for all species, indicating that a traditional response function estimated by ordinary least squares regression would not adequately represent the data and the use of a stochastic production frontier function was warranted. In addition, σ_v^2 was small and near zero, indicating that SFA can yield an upper limiting boundary line. The intercept and slope of the self-thinning boundary line for each of the species are given in Table 3. Both the intercept and slope estimated using ordinary least squares regression were significantly lower than those given by SFA for each of the species. Western hemlock had the largest intercept and the steepest slope of the three species examined (Figure 2), whereas red alder had the smallest intercept and slope. The Douglas-fir self-thinning boundary

Table 3. Summary of parameter and variance estimates with standard errors (SE) of Equation 1 by species and fitting technique

Species	SFA								Akaike information criterion
	Ordinary least squares		Intercept	Slope	σ^2	σ_v^2	σ_e^2	γ	
	Intercept	Slope							
Douglas-fir	10.7509 (0.0489)	-1.2618 (0.0153)	11.2087 (0.1815)	-1.5473 (0.0548)	0.7823 (0/0408)	0.0491	0.7132	0.9356 (0.0129)	2,353.6
Red alder	9.7315 (0.1919)	-1.1133 (0.0641)	10.8665 (0.2699)	-1.2208 (0.1053)	1.1819 (0.0845)	0.0287	1.1532	0.9757 (0.0082)	946.6
Western hemlock	12.1299 (0.2813)	-1.6545 (0.0876)	13.0391 (0.0887)	-1.7336 (0.0301)	0.5992 (0.0486)	0.0030	0.5962	0.9950 (0.0027)	4,216.7

SE are shown in parentheses.

line showed the highest goodness of fit and western hemlock had the lowest. The implied SDI_{max} values (predicted TPH when $QMD = 25.4$ cm) for Douglas-fir, red alder, and western hemlock were 1,451, 1,003, and 1,688, respectively.

Likelihood ratio tests and considerable reductions in AIC indicated that other stand-level covariates significantly influenced the intercept of the self-thinning boundary line for all species ($P < 0.0001$) (Table 4). In all species, the intercept of the self-thinning boundary line was significantly

influenced by site index, stand origin (planted versus natural), and stand purity. Although not all plots had initiated self-thinning yet, the intercept of the self-thinning boundary line increased with site index and stand purity, whereas it was significantly lower in plantations in all species (Figure 3). The slope of the self-thinning boundary line was significantly influenced by stand origin in Douglas-fir and western hemlock. In Douglas-fir, the slope of the self-thinning boundary line was also significantly influenced by

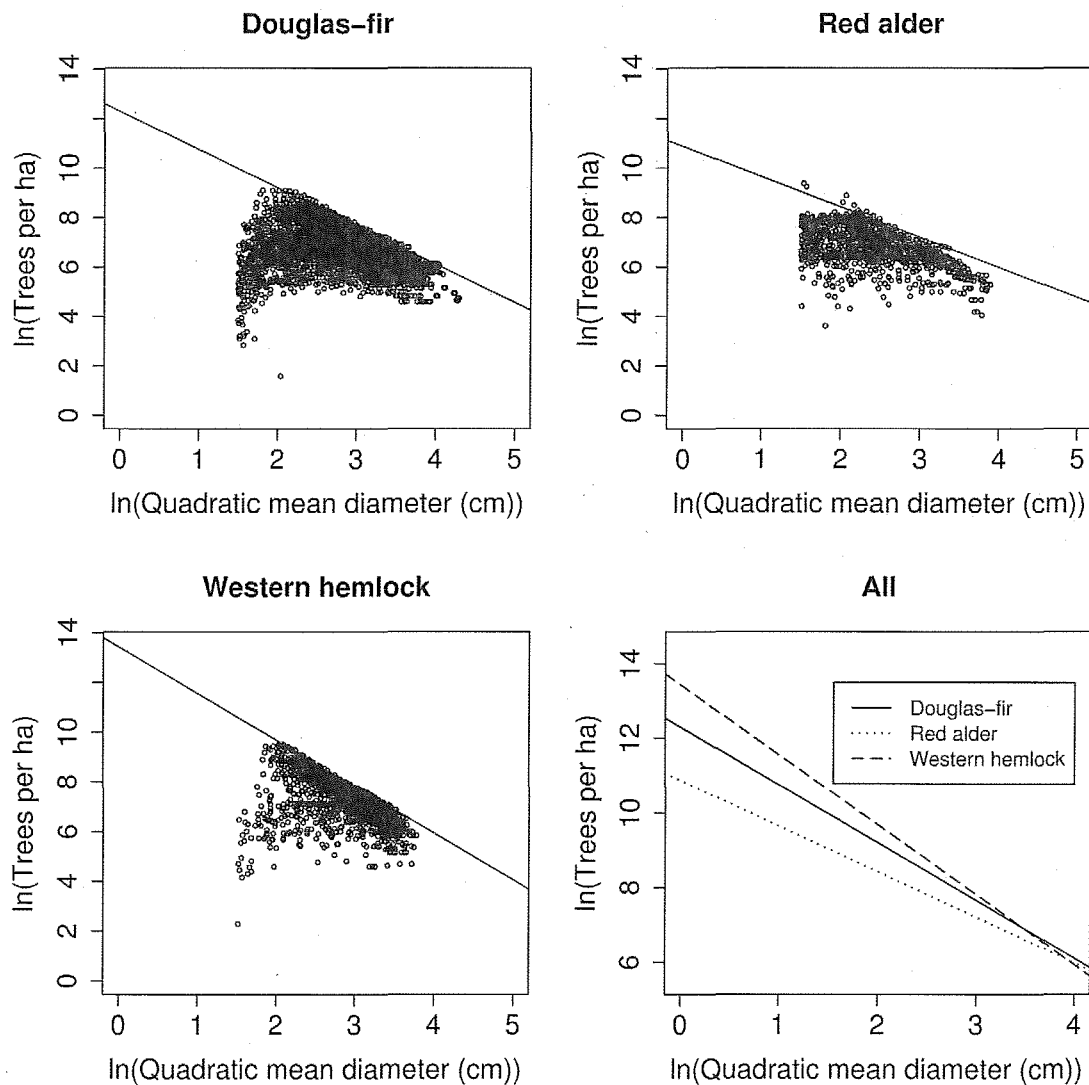


Figure 2. Plots of natural logarithm of trees per ha (cm) over the natural logarithm of quadratic mean diameter with stochastic frontier analysis-estimated self-thinning boundary line by species.

Table 4. Final maximum size density models using only stand-level covariates with SEs and Akaike information criterion (AIC) values by species

Species	Model	AIC
Douglas-fir	$\ln(\text{TPH}) = 8.8965 - 0.1989 \cdot \ln(\text{QMD}) + 0.8556 \cdot \ln(\text{SI}) - 4.0927 \cdot \text{Planted} + 0.6488 \cdot \ln(\text{PBA}_{\text{DF}})$ (0.0816) (0.0132) (0.0241) (0.0629) (0.0264) $+ 1.1494 \cdot (\ln(\text{QMD}) \cdot \text{Planted}) - 0.3522 \cdot (\ln(\text{QMD}) \cdot \ln(\text{SI}))$ (0.0219)	720.2
Red alder	$\ln(\text{TPH}) = 5.2419 - 0.4121 \cdot \ln(\text{QMD}) + 0.9736 \cdot \ln(\text{SI}) - 0.1391 \cdot \text{Planted} + 1.66765 \cdot \ln(\text{PBA}_{\text{RA}})$ (0.3496) (0.0309) (0.0935) (0.0557) (0.1317)	893.2
Western hemlock	$\ln(\text{TPH}) = 12.6428 - 1.8863 \cdot \ln(\text{QMD}) + 0.2387 \cdot \ln(\text{SI}) - 5.3373 \cdot \text{Planted} + 0.9976 \cdot \ln(\text{PBA}_{\text{WH}})$ (0.1793) (0.0212) (0.0590) (0.1542) (0.0292) $+ 1.5531 \cdot (\ln(\text{QMD}) \cdot \text{Planted})$ (0.0219)	1,725.3

SEs are shown in parentheses. Variables include QMD (cm), site index (SI) (m), indicator variable for plantations (Planted: 1 if planted, 0 otherwise), and proportion of basal area in the primary species (PBA).

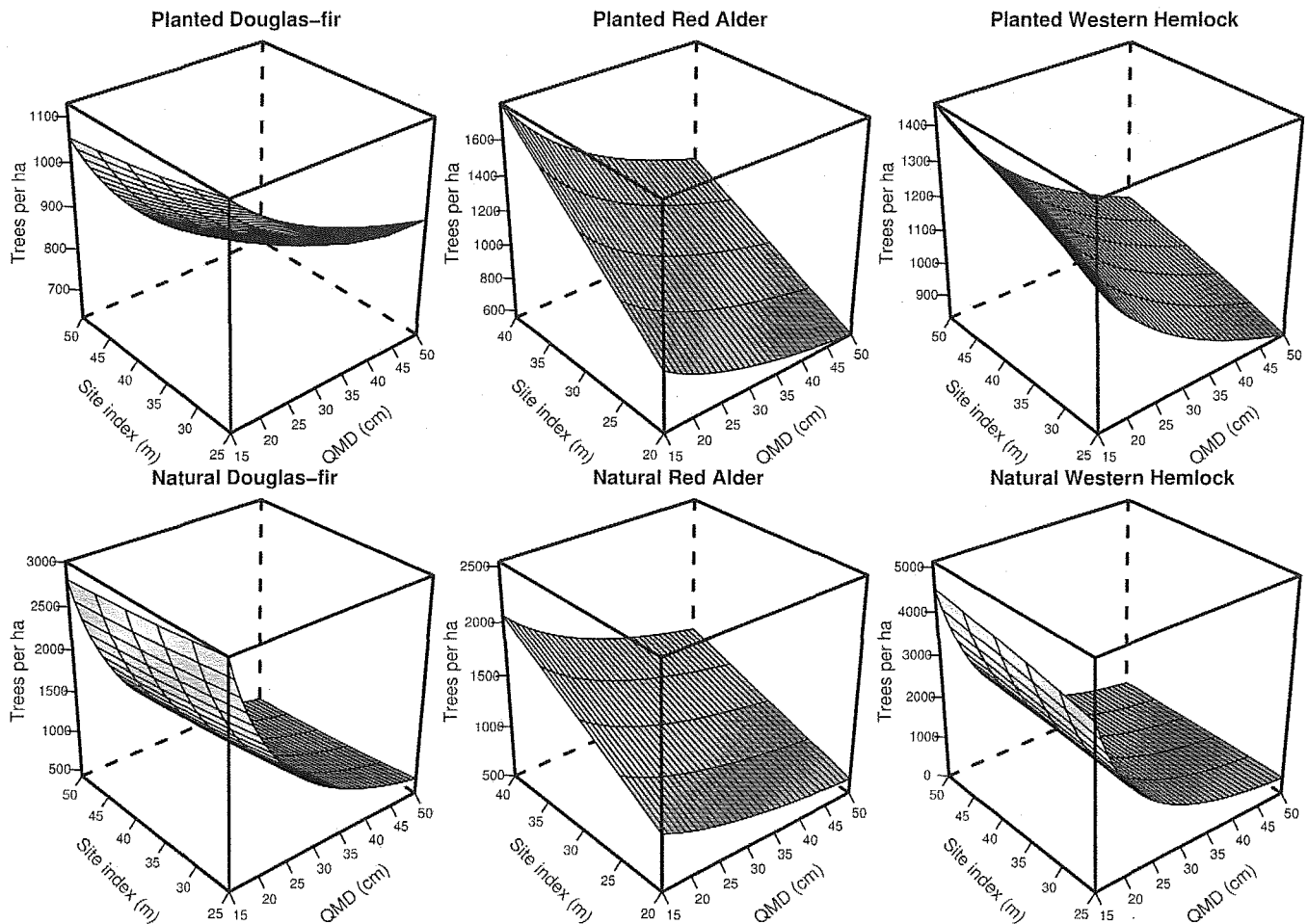


Figure 3. Three-dimensional graphs of trees per ha over QMD (cm) and site index (m) by species and stand origin for a given level of stand purity (0.95).

site index. Fertilization did not have a significant influence on the species self-thinning boundary intercept or slope in Douglas-fir and western hemlock. In addition, the skewness of the diameter distribution did not significantly influence the self-thinning boundary line for any of the species examined.

On the basis of a subsample of the data, climate and soils information significantly influenced the self-thinning boundary line only in red alder (Table 5). The self-thinning

boundary line in red alder was influenced by stand-level covariates as well as the cosine transformation of aspect and mean 25-year annual dryness index (ratio of growing degree-days >5°C to annual precipitation [cm]). The intercept of the self-thinning boundary line was significantly lower on north-facing slopes than on south-facing ones and increased with the dryness index in this species. The slope of the self-thinning boundary line was not significantly influenced by any of the soil or climatic covariates.

Table 5. Maximum size density model for red alder using stand-level climate and soils covariates.

Species	Observations	Model	AIC ¹	AIC ²
Red alder	1,244	$\ln(\text{TPH}) = 7.7001 - 0.5869 \cdot \ln(\text{QMD}) + 0.6062 \cdot \ln(\text{SI}) - 0.2761 \cdot \text{Planted}$ <p style="text-align: center;">(0.6063) (0.0477) (0.0637) (0.2969)</p> $+ 2.1407 \cdot \ln(\text{PBA}_{\text{RA}}) - 0.1083 \cdot \text{COSA} + 0.3098 \cdot \ln(\text{DI})$ <p style="text-align: center;">(0.0579) (0.0855) (0.0359)</p>	2,754.6	720.2

SEs are shown in parentheses. The Akaike information criterion (AIC) values are given for models including just stand-level covariates as well as those that contained stand level with climate and soils covariates. Likelihood ratio tests indicated that all parameter estimates were significant at $\alpha = 0.05$. Variables included QMD (em) site index (SI) (m), indicator variable for plantations (Planted: 1 if planted, 0 otherwise), proportion of basal area in the primary species (PEA), cosine transformation of aspect (COSA) [$\cos(2 \cdot \text{aspect}/360)$], and mean dryness index (DI).

¹ Model with stand-level covariates only.

² Model with stand-level information with climatic and soils covariate.

Discussion

Previous analyses on the species self-thinning boundary line generally considered it to be a one-dimensional or, at most, a two-dimensional surface (e.g., Bi 2001). In this analysis we used SFA to indicate that it is a multidimensional surface as site index, stand origin, and stand purity all significantly influenced both the self-thinning boundary line intercept in three ecologically distinct species. The slope of the self-thinning boundary line was also sensitive to stand origin in Douglas-fir and western hemlock. Consequently, this study supports the idea that the species self-thinning line can vary significantly within a region, which studies on the dynamic self-thinning line have also suggested (e.g., Turnblom and Burk 2000, Pittman and Turnblom 2003). The conclusions from this study differ from those of others who have concluded that the species self-thinning boundary was insensitive to site index (e.g., Tang et al. 1995) or stand origin (e.g., Puettmann et al. 1993b). The study also supports previous studies suggesting that mixed species stands have different SDI_{max} values than pure ones (e.g., Puettmann et al. 1992; Woodall et al. 2005). Our conclusions probably differ from the conclusions of these other studies for at least two reasons, namely, the power of our tests owing to our large data sets and the fitting approach used. Relatively large data sets across a range of site qualities were available for the present study, particularly for Douglas-fir. This availability makes it more likely that we were able to detect differences in the boundary line compared with studies that used smaller data sets or those with a limited range of site qualities.

Although the slope of the self-thinning boundary line has been regarded as constant, the intercept of the boundary line varies among species and is dependent on species shade tolerance (Jack and Long 1996). In this study we used extensive data sets for a shade-intolerant hardwood (red alder), a conifer with intermediate shade tolerance (Douglas-fir), and an extremely shade-tolerant conifer (western hemlock) (Burns and Honkala 1990). The slopes of the self-thinning boundary line were significantly different among species, which suggests that this value is also not constant and can vary among species. Pretzsch and Biber (2005) reached a similar conclusion for three species in Germany. Similar to previous studies, the steepness of the slope did follow shade tolerance rankings as western hemlock had the steepest slope and red alder had the smallest slope. However, the slope of the self-thinning boundary

line and the implied species SDI_{max} were different from those of previous studies with the same species. Previously SDI_{max} values for Douglas-fir, red alder, and western hemlock were estimated to be 1,484 (Long 1985), 1,116 (Puettmann et al. 1993a), and 2,108 (Scott et al. 1998), respectively. Except for Douglas-fir, the estimates given in this analysis are considerably lower than these previous values. The differences may be attributed to increased long-term data, the greater availability of plantation data, and differing statistical techniques. Most of these previous studies were based on data from natural stands, which have higher SDI_{max} values, as indicated by this study.

In all of the species examined in this study, stand origin had the most significant impact on the self-thinning boundary line and the intercept of the line was statistically lower in plantations. Stand origin also influenced the slope of the self-thinning boundary line in Douglas-fir and western hemlock. This finding supports the idea proposed by Reynolds and Ford (2005) that differences in initial stand conditions affect self-thinning behavior. The influence of initial stand conditions has also been reported in other studies on the dynamic self-thinning line as Turnblom and Burk (2000) concluded that plantation stands of red pine established at high and low densities self-thin in different ways. On the other hand, previous studies have also found that initial planting density had no significant influence (e.g., Tang et al. 1995). Naturally established stands tend to have higher aggregation of individuals and significantly different developmental patterns than plantations (e.g., Dowling 2003). The finding that plantations self-thin at a lower density supports the observation that highly clumped plants may experience less overall competitive effect than regularly spaced plants at the same initial density (Reynolds and Ford 2005). By evenly spacing individuals and removing competing vegetation, plantations effectively alter the allometric relationship between tree size and the area occupied by the tree, which intensifies competition and, ultimately, the self-thinning trajectory of these stands. In this analysis, the decrease in SDI_{max} ranged from 15% for red alder to 45% for Douglas-fir at a given level of site index and stand purity. These results illustrate the strong influence that initial stand conditions can have on the maximum size-density relationship. However, the reductions observed for western hemlock and red alder should be taken with caution as the number of plantations relative to the number of natural stands was small, and most of these plantations were still relatively

young. Unfortunately, very few of these plots in this study were stem mapped, and spatial indices of stem clumpiness could not be calculated. The use of a suitable spatial index in future studies would probably be a more effective predictor of the self-thinning boundary line than a simple indicator for stand origin as was used in the present study.

Bi (2001) proposed a generalized form of the maximum size-density relationship that included site productivity and validated the model using radiata pine data. The model also performed well on the data from the classic self-thinning experiment of Yoda et al. (1963) on *Erigeron canadensis* (Bi 2004). Other studies have not shown a significant influence of site productivity on the species self-thinning boundary line (Madgwick et al. 1970, Smith and Hann 1984, Tang et al. 1995, de Montigny and Nigh 2007). The results of this study support the findings of Bi (2001) as site index significantly increased the intercept of the self-thinning boundary line in all of the species that were examined. This present study also showed that the slope of the self-thinning boundary line was significantly influenced by site index in Douglas-fir, suggesting that, similar to stand origin, site index presumably alters the allometric relationship between tree size and biomass. Higher quality sites are able to support greater levels of biomass (Gholz, 1982) and tend to progress through stand development at faster rates than sites of lower quality (Turnblom and Burk 2000). Although statistically significant, the influence of site index on SDI_{max} was relatively small compared with that of stand origin and purity. For example, red alder was the most responsive to changes in site index as SDI_{max} increased by >9% for a 10% increase in site index, whereas Douglas-fir and western hemlock SDI_{max} increased only by 1-3%. However, this result might be partially confounded with red alder site index being sensitive to planting density, particularly at extremely low densities (Weiskittel et al. in review). Consistent with the results of Hann et al. (2003), fertilization had no significant effect on the Douglas-fir or western hemlock self-thinning boundary line intercept or slope.

The productivity and stand dynamics of mixed-species stands have been shown to be significantly different from those of pure ones (e.g., Garber and Maguire 2004, Amoroso and Turnblom 2006). This analysis indicates that stand composition can also influence maximum size-density relationships in three species with varying levels of shade tolerance. Likewise in a recent analysis of eight common species in the United States that included Douglas-fir, the SDI_{max} that any particular species attained was significantly influenced by the species composition of the subject stands (Woodall et al. 2005). The level of the response to stand composition was also found not to be easily explained by species shade tolerance (Woodall et al. 2005), which is similar to the findings of this present study. For example, red alder SDI_{max} increased by 97% when stand purity was changed from 0.6 to 0.9, whereas Douglas-fir and western hemlock SDI_{max} increased by 30 and 50% for a similar change in stand composition, respectively. Woodall et al. (2005) reported a 69% increase in Douglas-fir SDI_{max} when stand purity was changed from 0.5 to 0.9 and a 46% increase was found in this study. Woodall et al. (2005), however, did not account for additional factors such as stand

origin or site index that can significantly influence estimated SDI_{max} as suggested by this study. Mixed-species stand behavior is different from behavior of pure stands because of alterations in the level of inter- and intraspecific competition (e.g., Garber and Maguire 2004, Amoroso and Turnblom 2006). This difference in competition effectively modifies key allometric relationships and limits the ability of a given species to reach its maximum potential size.

Zeide (2001) proposed a self-thinning model that included the effects of tree age and environmental change and found a 16% increase in the number of trees of a given size per unit of area between 1952 and 1987 as a result of changes in climatic conditions. Given this finding and the significance of site index, a high significance of climatic and soil variables was expected in this analysis. In contrast, climate and soil variables were not significant for Douglas-fir or western hemlock and only marginally improved the red alder model. This finding is consistent with results of Hann et al. (2003) and Poage et al. (2007), who were unable to relate variation in the self-thinning boundary line to other environmental factors. In this study we found that the red alder boundary line was sensitive to both site aspect and an index of dryness. A previous analysis on red alder site index also highlighted the species sensitivity to aspect and moisture availability (Harrington 1986). However, the limited predictive power of soil and climatic variables may be the result of using interpolated climate and modal pit soils information.

Conclusions

SFA proved to be an effective means for identifying key sources of variation in the self-thinning boundary line of three different species of the Pacific Northwest. The use of extensive data sets for each of the species and SFA suggested that estimated SDI_{max} was significantly lower than that in previously published values. In addition, the intercept of the species self-thinning boundary was significantly influenced by site index, stand origin, and stand purity for all three species. The slope was also significantly influenced by stand origin in Douglas-fir and western hemlock. The intercept of the self-thinning boundary line increased with stand purity, whereas it decreased with site index and was significantly lower for plantations in comparison with natural stands. These results suggest that the species self-thinning boundary line is highly variable within a region and is driven by several stand-specific factors that influence the relationship between tree size and its area occupied. However, stand-level mean climate and soils information only marginally improved the self-thinning model for red alder in this study. Further examination of the variation in the self-thinning behavior of other species with SFA is warranted by these results. A better understanding of the factors that affect self-thinning could be useful for refining density management diagrams and improving mortality equations in growth models.

Literature Cited

- AIGNER, D., K. LOVELL, AND P. SCHMIDT. 1977. Formulation and estimation of stochastic frontier production function model. *J. Econometrics* 6:21-37.

- AMOROSOM.M., ANDE.C., TURNBLOM2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. *Can. J. For. Res.* 36:1484-1496.
- BI, H. 2001. The self-thinning surface. *For. Sci.* 47:361-370.
- BI, H. 2004. Stochastic frontier analysis of a classic self-thinning experiment. *Aust. Ecol.* 29:408-417.
- BI, H., G. WAN, AND N.D. TURVEY. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. *Ecology* 81:1477-1483.
- BONNER,G.M., R.J. DE JONG,P. BOUDEWYN,AND J.W. FLEWELLING. 1995. *A guide to the STIM growth model.* Canadian Forest Service, Pacific Yukon Region. Information Rep. BC-X-353. 38 p.
- BRUCE,D. 1981. Consistent height-growth and growth-rate estimates for remeasured plots. *For. Sci.* 4:711-725.
- BURNS,RM., ANDB.H. HONKALA.1990. *Silvics of North America. Vol. 1: Conifers.* US Forest Service, Washington, DC. 675 p.
- COELLI,T.J. 1996. *A guide to FRONTIER 4.1: A computer program for stochastic frontier production and cost estimation.* Centre for Efficiency and Production Analysis, University of New England. 33 p.
- DAYMET. *Daily surface weather data and climatological summaries.* Available online at daymet.org; last accessed Sept. 30, 2008.
- DE MONTIGNY, L., AND G. NIGH. 2007. Density frontiers for even-aged Douglas-fir and western hemlock stands in coastal British Columbia. *For. Sci.* 53:675-682.
- DOWLING, C.D. 2003. *Comparing structure and development of Douglas-fir old-growth, plantations, and young natural forests in western Oregon.* Oregon State University, Corvallis, OR 129 p.
- GARBER,S.M., AND D.A. MAGUIRE.2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. *For. Sci.* 50(1):92-105.
- GHOLZ, H.L.. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469-481.
- 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.* College of Forestry Research Laboratory, Oregon State University, Corvallis, OR 85 p.
- HARDWOOD SILVICULTURE COOPERATIVE2008. Available online at www.cof.orst.edu/coops/hsc/geninfo/index.htm; last accessed Jan. 6, 2009.
- HARRINGTON,C.A. 1986. *A method of site quality evaluation for red alder.* US For. Servo Gen. Tech. Rep. PNW-192. 22 p.
- HYNYNEN,J. 1993. Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies*, and *Betula penula*. *Scand. J. For. Res.* 8:326-336.
- JACK, S.B., AND J.N. LONG. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. *For. Ecol. Manag.* 86:205-220.
- LONG, JN. 1985. A practical approach to density management. *For. Chron.* 61:23-27.
- MADGWICK,H.A.J., E.H. WHITE., G.K. XYDIAS,AND A.L. LEAF. 1970. Biomass of *Pinus resinosa* in relation to potassium nutrition. *For. Sci.* 16:154-159.
- NIGH, G.D., AND P.J. COURTIN.1998. Height models for red alder (*Alnus rubra* Bong.) in British Columbia. *New For.* 16:59-70.
- PITTMAN,S.D., ANDE.C., TURNBLOM.2003. A study of self-thinning using coupled allometric equations: Implications for coastal Douglas-fir stand dynamics. *Can. J. For. Res.* 33:1661-1669.
- POAGE, N.J., D.D. MARSHALL, AND M.H. MCCLELLAN. 2007. Maximum stand-density index of 40 western hemlock-Sitka spruce stands in southeast Alaska. *West. J. Appl. For.* 22:99-104.
- PRETZSCH, H., AND P. BIBER. 2005. A re-evaluation of the Reineke's rule and stand density index. *For. Sci.* 51:304-320.
- PUETTMANN, KJ., D.S. DEBELL, AND D.E. HIBBS. 1993a. *Density management guide for red alder.* Forest Research Laboratory, Oregon State University, Corvallis, OR 6 p.
- PUETTMANN K.J., D.W. HANN., AND D.E. HIBBS. 1993b. Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. *For. Sci.* 39:7-27.
- PUETTMANN, KJ., D.E. HIBBS, AND D.W. HANN. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: Extension of size-density analysis to species mixture. *J. Ecol.* 80:449-458.
- REINEKE, L.H. 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46(7):627-638.
- REYNOLDS, J.H., AND E.D. FORD. 2005. Improving competition representation in theoretical models of self-thinning: A critical review. *J. Ecol.* 93:362-372.
- SCOTT,W., R. MEADE,R. LEON,D. HYINK, AND R. MILLER. 1998. Planting density and tree-size relations in coast Douglas-fir. *Can. J. For. Res.* 28:74-78.
- SMITH,N.J., AND D.W. HANN.1984. A new analytical model based on the -3/2 power rule of self-thinning. *Can. J. For. Res.* 14:605-609.
- STAGE, AR. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. *For. Sci.* 22:457-460.
- STERBA, H., AND RA. MONSERUD.1993. The maximum density concept applied to uneven-aged mixed-species stands. *For. Sci.* 39:432-452.
- TANG, S., F.R. MENG, AND C.H. MENG. 1995. The impact of initial stand density and site index on maximum stand density index and self-thinning index in a stand self-thinning model. *For. Ecol. Manag.* 75:61-68.
- TURNBLOME.C., AND T.E. BURK. 2000. Modeling self-thinning of unthinned Lake States red pine stands using nonlinear simultaneous differential equations. *Can. J. For. Res.* 30:1410-1418.
- VANDERSCHAAF, CL. 2004. Can planting density have an effect on the maximum size-density line of loblolly and slash pine? P. 115-126 in *Northeastern and Southern Mensurationists joint conference*, Doruska, P.P., and P.J. Radtke (eds.). Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA
- VANDERSCHAAF, CL., AND H.E. BURKHART 2007. Comparison of methods to estimate Reineke's maximum size-density relationship boundary slope. *For. Sci.* 53:435-442.
- WEISKITTEL, AR, D.W. HANN, AA. BLUHM AND D.E. HIBBS. Modeling plantation red alder dominant height growth and development of a dynamic base-age invariant site index equation. Submitted to *For. Ecol. Manag.* In review.
- WELLER, D.E.. 1987. A reevaluation of the -3/2 power rule of self-thinning. *Ecol. Monogr.* 57:23-43.
- WOODALL,C.W., P.D. MILES., AND J.S. VISSAGE.2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. *For. Ecol. Manag.* 216:367-377.
- YODA, K, T. KIRA, H. OGAWA, AND K. HOZUMI. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol. Osaka City Univ.* 14:107-129.
- ZEIDE, B. 1987. Analysis of the 3/2 power law of self-thinning. *For. Sci.* 33:517-537.
- ZEIDE, B. 2001. Natural thinning and environmental change: An ecological process model. *For. Ecol. Manag.* 154:165-177.
- ZHANG, L, H. BI, J.H. GOVE, AND L.S. HEATH. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. *Can. J. For. Res.* 35:1507-1514.