Vertical trends in maximum branch diameter in two mixed-species spacing trials in the central Oregon Cascades

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Abstract: The influence of spacing and competitor species on vertical trends in maximum branch diameter, the thickest branch per whorl, was assessed in two central Oregon spacing studies. One study involved a mix of *Pinus contorta* Dougl. ex Loud. and *Pinus ponderosa* Dougl. ex Laws., the other a mix of *Abies grandis* (Dougl. ex D. Don) Lindl. and *P. ponderosa*. Impacts of autocorrelation became statistically insignificant after introduction of a single random tree effect. Although tree variables such as diameter, height, and crown length were able to account for most stand conditions, models with explicit treatment variables representing spacing and species composition were superior. All profiles of maximum branch diameter were curvilinear and widened with increasing spacing and tree relative height. For trees in mixtures, maximum branch diameter profiles of dominant and subordinate species were wider and thinner, respectively, than the same species in pure stands at the same spacing. However, as spacing increased, profiles of the subordinate species in mixtures had a greater response than those in adjacent pure plots and in the dominant species in the mixture. In contrast, the dominant species had a larger spacing response in the pure plots than in mixed plots.

Résumé : L'influence de l'espacement et des espèces compétitrices sur la variation verticale du diamètre maximum des branches, la plus grosse branche par verticille, a été évaluée dans deux expériences d'espacement dans le centre de l'Oregon. Une expérience comportait un mélange de *Pinus contorta* Dougl. ex Loud. et de *Pinus ponderosa* Dougl. ex Laws. et l'autre un mélange d'*Abies grandis* (Dougl. ex D. Don) Lindl. et de *P. ponderosa*. Les impacts de l'autocorrélation sont devenus statistiquement non significatifs après l'introduction d'un seul effet aléatoire dû aux arbres. Bien que les variables individuelles telles que le diamètre, la hauteur et la longueur de la cime pouvaient expliquer la plupart des caractéristiques du peuplement, les modèles qui comportaient des variables explicites pour les traitements représentant l'espacement et la composition en espèces étaient supérieurs. Tous les profils de diamètre maximum des branches étaient curvilignes et s'élargissaient avec l'augmentation de l'espacement et de la hauteur relative des arbres. Pour les arbres en mélanges, les profils de diamètre maximum des branches étaient plus évasés pour les espèces dominantes et plus minces pour les espèces dominées que pour les mêmes espèces en peuplement pur avec le même espacement. Cependant, les profils de l'espèce dominée réagissaient davantage à l'augmentation de l'espacement en mélange que dans les parcelles adjacentes de peuplement pur et que l'espèce dominante en mélange. Au contraire, l'espèce dominante réagissait plus fortement à l'espacement en peuplement pur qu'en peuplement mélangé.

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Introduction

Crown structure has clear functional links to forest wildlife habitat (Morrison et al. 1987; McComb et al. 1993; Hamer 1995), fire behavior (Agee 1993; Keyes and O'Hara 2002), tree responses to wind stress (Moore 2002), tree shape (Ballard and Long 1988; Dean et al. 2002), and stand occupancy (Krajicek et al. 1961). Crown structure also has a major impact on net primary production (Smith and Long 1989; Long and Smith 1990): branches support foliage necessary for photosynthesis and influence the interception of light by the crown. However, a trade-off exists between the size of branches and physiological processes directly and indirectly related to

production efficiency (Roberts and Long 1992). Larger branches generally support a larger quantity of foliage and therefore have greater photosynthetic potential. However, larger branches can also have increased hydraulic resistance (Waring and Silvester 1994; Protz et al. 2000) and perhaps larger rates of respiration relative to boles (Kinerson 1975; Sprugel 1990), especially at higher crown positions (Ryan et al. 1996). Larger trees with larger crowns typically produce thicker and longer lived branches, resulting in larger knots and more crown wood (Maguire et al. 1991). Hence, a trade-off also exists between individual tree growth and wood quality (Kershaw et al. 1990; Houllier et al. 1995). In short, crown structure has a major impact on growth efficiency, forest productivity, and also on the quality of wood produced in the bole.

Branch diameter is determined by the rate and duration of branch growth. Older branches in whorls near the crown base therefore have the potential for attaining the greatest diameters. However, the largest branches within a tree are often found slightly above crown base, indicating that profiles of the average and maximum branch diameter per whorl are

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curvilinear, increasing with crown depth to a point slightly above the crown base (Colin and Houllier 1991; Gilmore and Seymour 1997; Maguire et al. 1994; Maguire et al. 1999). In even-aged, single-species stands, branch diameters have also been shown to vary among trees growing in different social positions (Colin and Houllier 1991; Gilmore and Seymour 1997), in different stand densities (Magnussen and Yeatman 1987; Ballard and Long 1988; Colin and Houllier 1991; Maguire 1994), under varying thinning regimes (Siemon et al. 1976; Maguire et al. 1991), and of different absolute tree size (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998). Relatively little work has been conducted in stands with more complex structures, such as a mix of species. Since patterns of stand development in species mixtures are more diverse than in single-species, even-aged stands (Oliver and Larson 1996; Garber and Maguire 2004), patterns in crown structure, particularly branch diameter, would be expected to vary with stand density and species composition.

The influence of spacing and species composition on vertical patterns of maximum branch diameter, the thickest branch per whorl, was assessed in two existing mixed-species spacing trials in the central Oregon pumice region. This region is characterized by mixed stands of the shade-intolerant *Pinus ponderosa* Dougl. ex Laws. and the very shade-intolerant *Pinus contorta* Dougl. ex Loud. on drier sites at low elevations, while on moister sites, *P. ponderosa* can mix with the shade-tolerant *Abies grandis* (Dougl. ex D. Don) Lindl., often but not always forming a stratified mixture (Oliver and Larson 1996; Cobb et al. 1993; Garber and Maguire 2004). The *Pinus* species have strong apical control and little plasticity in crown structure, even under shaded conditions (O'Connell and Kelty 1994; Williams et al. 1999). In contrast, *Abies* species can shift growth from leader to laterals in shady conditions (Klinka et al. 1992). The primary objectives of this study were (*i*) to verify the usual effect of spacing on branch diameter in these three species; (*ii*) to test whether the effect of spacing on maximum branch diameter at a given height in the crown differs by competitor species; and (*iii*) to outline the silvicultural implications of these spacing trial results for managing stand structure through spacing and species composition. To test the effect of spacing and species composition at multiple levels within a given crown, the statistical model had to address within-tree autocorrelation and (or) random tree effects. Likewise, it was of biological and practical significance to know whether the effects of spacing and species composition were imposed solely through their influence on tree diameter, height, and live crown length, that is, whether allometric relationships were preserved. Therefore, two secondary objectives were (*i*) to test whether random tree effects were sufficient to account for within-tree autocorrelation of branch diameters; and (*ii*) to test for any residual spacing and species composition effect on branch diameter profiles beyond that accounted for by introducing tree diameter, height, and crown length as covariates.

Materials and methods

Study sites

The study was conducted at two sites. The first site, Pringle Butte, is a mixture of *P. ponderosa* and *P. contorta*. The sec-

ond site, Lookout Mountain, is a mixture of *P. ponderosa* and *A. grandis*. Both sites are east of the Cascade Range crest, 45 km southwest of Bend, in the Pringle Falls Experimental Forest, within the Bend – Fort Rock Ranger District of the Deschutes National Forest, Deschutes County, Oregon. Growth and development on both sites were described in detail by Garber and Maguire (2004).

Pringle Butte site

The Pringle Butte study site is located on the northwest-facing slope of Pringle Butte at an elevation of 1400 m (43°44′N, 121°37′W). Slopes range from 10% to 20%, with an average of 15%. Mean annual precipitation is only 61 cm and falls predominantly between the months of October and April, with a 0.5-m snow pack common between January and March. Maximum temperatures occur in July, averaging 26 °C, and frosts can occur at any time during the year (Cochran and Barrett 1999*a*). The soils in this area are well drained and have been typed as a Typic Cryorthent, developed in 90 cm of dacite pumice from the eruption of Mount Mazama (Seidel 1989). This pumice layer overlays a sandy loam paleosol, developed in older volcanic ash with cinders and basalt fragments.

The spacing study was established in a 4.8-ha stand that was clear-cut in 1967. The initial stand was characterized as a ponderosa pine / bitterbrush–snowbrush / sedge plant community (Seidel 1989). The ground cover consisted of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), long-stolon sedge (*Carex pensylvanica* Lam.), scattered Ross sedge (*Carex rossi* Boott), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and western needle grass (*Stipa occidentalis* Trub. ex Wats.). The *P. ponderosa* site index (base age 100; Barrett 1978), estimated from height data collected in 2001, is about 30 m.

The site was planted with 2-0 bare root stock grown at the USDA Forest Service nursery in Bend, Oregon. Seedlings were planted by auger in the spring of 1967. In addition, the *C. velutinus* was sprayed twice in the first 5 years with herbicides to reduce competition (Seidel 1989). Current plot attributes for Pringle Butte are given in Table 1.

Lookout Mountain site

The Lookout Mountain study site is located on the northeast-facing slope of Lookout Mountain at an elevation of 1550 m (43°49′N, 121°41′W). Slopes average close to 20%. Average annual precipitation is approximately 100 cm, most of which falls as snow between the months of September and May. Summers are hot and dry, with temperatures ranging from 21 to 32 °C. Nights are predominantly cool, with the chance of frost occurring any time during the year (Cochran and Barrett 1999*b*). Soils are deep, well-drained Typic Cryorthents, developed from dacite pumice originating from the eruption of Mount Mazama, overlaying a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments (Seidel 1985, Cochran and Barrett 1999*b*).

This spacing study was established in a 8.1-ha stand that was clear-cut in 1974. The original vegetation was characterized as a mixed-conifer/snowbrush–chinkapin plant community (Seidel 1985). The ground cover consisted primarily of *C. velutinus*, *Arctostaphylos patula*, and golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.) (Seidel 1985).

Table 1. Mean plot tree attributes by study site, spacing, and species composition.

Study site	Spacing (m)	Composition	Quadratic mean stand diameter (cm)	Mean tree height (m)	Stems (no./ha^{-1})
Pringle Butte	1.8	Pure *Pinus contorta*	11.41	8.59	2786.11
		Mixture	11.91	7.58	2650.21
		Pure *Pinus ponderosa*	12.67	6.79	2123.56
	2.7	Pure *Pinus contorta*	15.03	8.93	1267.36
		Mixture	16.36	8.63	1242.75
		Pure *Pinus ponderosa*	15.66	7.67	1242.75
	3.7	Pure *Pinus contorta*	16.98	9.30	747.49
		Mixture	17.25	8.19	677.42
		Pure *Pinus ponderosa*	16.74	7.13	607.34
	4.6	Pure *Pinus contorta*	19.42	9.21	468.83
		Mixture	21.44	9.79	411.42
		Pure *Pinus ponderosa*	22.05	9.39	430.56
	5.5	Pure *Pinus contorta*	20.46	9.61	318.93
		Mixture	22.06	9.34	318.93
		Pure *Pinus ponderosa*	23.57	9.29	325.58
Lookout Mountain	1.8	Pure *Abies grandis*	7.43	6.33	2823.87
		Mixture	9.88	7.70	2989.98
		Pure *Pinus ponderosa*	10.55	8.56	2865.39
	3.7	Pure *Abies grandis*	11.05	8.75	716.35
		Mixture	13.92	9.58	685.20
		Pure *Pinus ponderosa*	15.05	9.68	737.11
	5.5	Pure *Abies grandis*	11.46	8.66	318.38
		Mixture	16.01	9.36	327.61
		Pure *Pinus ponderosa*	18.62	10.39	332.22

Ceanothus velutinus ground cover was very dense over much of the study site. The late-successional plant community association is *Abies concolor / Ceanothus velutinus* (Franklin and Dyrness 1973). The site index (base age 100, Barrett 1978) for *P. ponderosa*, estimated from height data collected in 1999, is about 34 m.

The site was planted with 2-0 bare root *P. ponderosa* stock from the USDA Forest Service nursery in Bend, Oregon, and 2-0 *A. grandis* containerized stock. Seed of each species was collected in 1971 from near the study site. Planting took place in the spring of 1974, and during the first 2 years any seedlings that died were replaced by transplanted seedlings from outside the plots. In addition, the *Ceanothus velutinus*, *Arctostaphylos patula*, and *Castanopsis chrysophylla* were sprayed in June 1976 and 1979 with herbicides to reduce competition (Seidel 1985). Current plot attributes for Lookout Mountain are given in Table 1.

Experimental design

Each study was established under a completely randomized split-plot design in which the whole-plot factor was tree spacing and the split-plot factor was species composition. Pringle Butte was composed of five initial square tree spacings: 1.8, 2.7, 3.7, 4.6, and 5.5 m (6, 9, 12, 15, and 18 feet). Species composition included pure *P. ponderosa*, pure *P. contorta*, and a 50:50 replacement-series mix of both species. Treatment combinations were replicated twice, so each of the five spacings were randomly assigned to 10 whole plots, and subplots within each whole plot were randomly assigned a species mix. The size of the whole plots varied by spacing but each contained from 25 to 88 measured trees.

Lookout Mountain was composed of three initial square tree spacings: 1.8, 3.7, and 5.5 m (6, 12, and 18 feet). The three species combinations in the subplots included pure *P. ponderosa*, pure *A. grandis*, and a 50:50 replacement-series mix of both species. Each whole plot consisted of three subplots of the same spacing. The whole plots were of variable size, depending on spacing, and were designed so that each subplot had 24 measured trees. Three replications produced a total of 9 whole plots and 27 subplots.

Data collection

In June and July 2001, a sample tree, one from each of the two larger thirds of the diameter range, was selected at random from each pure subplot at Pringle Butte and Lookout Mountain. On mixed subplots, one tree of each species from the upper two-thirds of the diameter distribution was also selected. Of these 114 trees, 27 were *A. grandis*, 30 were *P. contorta*, and 57 were *P. ponderosa*. For each sample tree, four attributes were recorded (Table 2): (*i*) diameter at breast height, DBH (to the nearest 0.1 cm); (*ii*) total tree height, HT (to the nearest 0.01 m); (*iii*) height to the lowest live branch, HLB (to the nearest 0.01 m); and (*iv*) two perpendicular crown widths (to the nearest 0.1 m). Crown width was defined as the distance through the stem between the largest branch extensions. On every whorl from ground level to the tree tip, height of attachment (nearest 0.01 m) and basal diameter (nearest millimetre) of the thickest branch were measured. Basal branch diameters were measured by caliper at horizontal and vertical axes relative to the standing tree, at a distance from the bole approximately equal to one branch diameter. Ramicorn branches were included in the analysis, while fork elements were not. Branch diameter and crown

Table 2. Mean tree characteristics from sample trees by study site and species.

| Parameter | Pringle Butte | | Lookout Mountain | |
	Pinus contorta	*Pinus ponderosa*	*Abies grandis*	*Pinus ponderosa*
Sample size				
Trees	30	30	27	27
Total branches	5180	2899	10 170	2718
Branch diameter (mm)				
Min.	1.0	1.0	1.0	2.0
Mean	16.4	25.0	8.9	30.6
Max.	57.0	69.0	55.0	77.0
Depth into crown (m)				
Min.	0.08	0.10	1.39	0.23
Mean	6.48	5.88	7.85	7.73
Max.	12.96	11.04	14.96	13.07
DBH (cm)				
Min.	8.5	11.0	9.0	13.6
Mean	18.6	20.7	18.2	26.2
Max.	26.6	33.1	26.8	41.7
Total Height (m)				
Min.	7.52	6.93	6.05	10.04
Mean	10.66	9.91	11.34	12.43
Max.	13.80	14.11	15.68	15.60
Height to lowest live branch (m)				
Min.	0.24	1.43	0.00	1.07
Mean	1.90	2.98	0.59	3.79
Max.	5.07	4.65	1.36	6.09
Crown length (m)				
Min.	2.46	4.20	5.25	5.12
Mean	8.76	6.93	10.75	8.64
Max.	12.96	11.04	14.96	13.07
Crown width (m)				
Min.	1.41	2.35	1.95	1.80
Mean	4.09	3.92	3.05	4.21
Max.	6.01	6.43	4.75	6.45

width used in the analysis was the geometric mean of the two perpendicular measurements.

Model development and statistical analysis

Maximum branch diameter

Various regression models were explored for describing the trend in maximum branch diameter per whorl (BD) over depth into crown (DINC). In addition, other tree, stand, and treatment variables were added to the models to account for the influence of each on the shape of the maximum branch diameter profile.

Several basic model forms were tested by Maguire et al. (1999) for describing maximum branch diameter trends in young coastal *Pseudotsuga menziesii* (Mirb.) Franco. Reasonable biological behavior and unbiased residuals were obtained from a variable exponent equation originally introduced for describing stem taper (Kozak 1988):

[1] $Y = X^C$

where Y is a ratio of diameter inside bark at some height h to diameter inside bark at reference point p, $X = [1 - (Z)^{0.5}] / [1 - (p)^{0.5}]$, $Z = h / HT$, and $C = f$ (Z and other tree and site variables). This model was formulated so that the ratio X ranges from zero at the tree tip and one at reference point p (Kozak 1988). This equation was modified by Maguire et al. (1999) so that BD's of a particular whorl were expressed as proportion of the predicted largest BD within a tree (MBD) for a tree of a given diameter, height, and crown length (CL). BD was constrained to equal zero at tree tip and predicted MBD at relative height p. Maguire et al. (1999) assumed p varied as a function of crown ratio (CR), yielding the following modification of [1]:

[2] $\dfrac{BD}{MBD} = X^C + \varepsilon$

where $X = [1 - (Z)^{0.5}] / [1 - (p)^{0.5}]$; $Z = h/CL$; $p = f$ (CR); $h = CL - DINC$ = height of the branch above crown base (metres); C is a function of branch position (Z) and other tree and stand predictors such as DBH, HT, CL, CR, HLB, spacing (SPACE), and species composition (SPPCOMP); and $\varepsilon \sim N(0, \sigma^2)$. Expressing MBD as a nonlinear function of empirical stand-grown crown width (CW) and multiplying it into both sides, [2] can be rewritten as:

[3] $BD = \gamma_1(CW)^{\gamma_2} X^C + \varepsilon$

where BD, X, C, and ε are as defined previously and γ_1 and γ_2 are parameters to be estimated from the data (Maguire et al. 1999). In this model, trends in relative branch diameter represented by X^C are scaled to the maximum branch diameter represented in the nonlinear function of CW.

Multiple observations of branch diameter were collected from each of the 114 sample trees; therefore, the data violated the assumption of independence (Neter et al. 1996). Moreover, preliminary residual analysis indicated the presence of autocorrelation. Some success in reducing the impact of autocorrelation in longitudinal forestry data using mixed-effects models has been demonstrated (Garber and Maguire 2003). Mixed models have also been implemented for modeling branch diameters (Meredieu et al. 1998; Mäkinen and Colin 1998, 1999; Maguire et al. 1999), so a nonlinear mixed-effects model with a random tree effect was selected:

[4] $\mathbf{BD}_i = f_i(\boldsymbol{\theta}_i; \mathbf{X}_i) + \boldsymbol{\epsilon}_i$

where $\mathbf{BD}_i$ is a $n_i \times 1$ vector of branch diameters observed on a subject tree i, f_i can be any nonlinear function, $\boldsymbol{\theta}_i$ is a $n_i \times p$ vector of fixed and random effects, and $\boldsymbol{\epsilon}_i$ is a $n_i \times 1$ vector of within-subject errors. Lindstrom and Bates (1990) suggest formulating $\boldsymbol{\theta}_i$ by specifying design matrices $\mathbf{A}_i$ and $\mathbf{B}_i$ ($n_i \times p$ and $n_i \times q$, respectively): $\boldsymbol{\theta}_i = \mathbf{A}_i \boldsymbol{\alpha} + \mathbf{B}_i \boldsymbol{\delta}_i$, where $\boldsymbol{\alpha}$ is a $p \times 1$ vector of fixed effects parameters and $\boldsymbol{\delta}_i$ is $q \times 1$ vector of random-effects parameters. These design matrices contain zeros and ones to turn fixed effects and random effects off and on, respectively. For example, if all the covariates specified in $\mathbf{X}_i$ are to have a single fixed and random effect, $\mathbf{A}_i = \mathbf{B}_i = \mathbf{I}_i$. For this application a single random tree effect was introduced, therefore, $q = 1$.

To complete the specification of [4], it is necessary to characterize the distribution of δ_i and $\boldsymbol{\epsilon}_i$. It was assumed that

Table 3. Variables associated with modeling branch diameter.

Variable	Definition
BD	Diameter of largest whorl branch (mm)
MBD	Diameter of the largest branch on a tree (mm)
SPACE	Tree spacing (m)
SPPCOMP	Plot species composition (pure = 0, mixed = 1)
DBH	Diameter at breast height (cm)
HT	Total tree height (m)
HLB	Height to lowest living branch (m)
CL	Crown length (m, HT – HCB)
CR	Crown ratio (CL/HT)
CW	Crown width (m)
RDBH	DBH relative to largest DBH on subplot
h	Branch height of above crown base (m)
DINC	Branch depth into crown (m)
RDINC	Branch relative depth into crown (DINC/CL)

δ_i and ϵ_i were univariate and multivariate normal, respectively, and have variance and covariance

$$\begin{bmatrix} \delta \\ \epsilon \end{bmatrix}_i \sim N\left(\begin{bmatrix} 0 \\ \boldsymbol{0} \end{bmatrix}_i, \begin{bmatrix} \sigma^2 \Lambda & \boldsymbol{0}_{\epsilon\delta} \\ \boldsymbol{0}_{\delta\epsilon} & \sigma^2 \mathbf{I} \end{bmatrix}_i \right)$$

where 0 is a null scalar, $\boldsymbol{0}$ is a $n_i \times 1$ null mean vector, $\boldsymbol{0}_{\delta\epsilon}$ and $\boldsymbol{0}_{\epsilon\delta}$ are the null covariance matrices, Λ_i is a $q \times q$ correlation matrix for the random tree effects, $\mathbf{I}_i$ is an $n_i \times n_i$ within-tree correlation identity matrix, and σ^2 is a scalar representing the mean square error.

Relative performance of different predictor variables was assessed by running an all-subsets regression on a logarithmic transformation of [3], assuming a multiplicative rather than an additive error term. The best subsets, with and without the treatment covariates SPACE, SPPCOMP, and SPACE × SPPCOMP, were then refitted in nonlinear form with additive random effects using maximum likelihood. Only variables significant at $\alpha = 0.05$ were retained in the final model. Assumptions essential for valid tests on parameters were assessed using empirical autocorrelation plots (Monserud 1986; Pinheiro and Bates 2000). Models with alternative sets of fixed covariates and random tree effects were compared using Akaike's (1969) information criterion (AIC):

$$\text{AIC} = -2l(\theta) + 2k$$

where $l(\theta)$ is the log likelihood and k is the number of parameters in the model. Nested models, including tests on random effects and covariates, were compared using likelihood ratio tests (Pinheiro and Bates 2000). All models were also evaluated on the basis of residual plots, bias, standard errors of estimates, and biological behavior. Analyses were done using the nlme3 library (Pinheiro and Bates 2000) within S-PLUS 2000 (MathSoft, Inc., Seattle, Washington).

Crown width

The maximum branch diameter model was used to test the effects of spacing and species composition on the relative shape of the BD profile. However, this provided no information on the influence of spacing and species composition on the

magnitude of BD. Since BD in [3] was mathematically constrained by the largest branch diameter on the trees located near crown base, which in turn is a function of the tree's empirical crown width, the effects of SPACE and SPPCOMP on the absolute BD was assessed by modeling CW as a function of spacing and species composition:

[5] $\text{CW} = (\beta_0 + \beta_1 \text{SPPCOMP}) \times \text{SPACE}^{\beta_2}$

$$\times \{1 - \exp[-(\beta_3 \text{RDBH})]\} + \epsilon$$

where β_i are parameters to be estimated from the data, RDBH is the subject tree's diameter relative to the diameter of the largest tree on the subplot, and $\epsilon \sim N(0, \text{SPACE}^W \sigma^2)$ (see Table 3 for variable definitions). This model assumes tree stand-grown crown width is an asymptotic function of relative tree size within the plot. Moreover, it assumed the asymptote was defined by spacing at close spacings and species genotype at wider spacings that have not yet attained crown closure. Parameters were estimated by weighted and unweighted nonlinear least squares, where $W = -0.5, -1.0, \dots,$ or -3.0. Final models were selected on the basis of residual analysis and Furnival's (1961) index of fit.

Results

Crown width models

All models accounted for greater than 50% of the variation in CW, with better fits in the *Pinus* species. Spacing was significant in each species (Fig. 1). The effect of species composition was significantly positive in *A. grandis* and *P. contorta* (Table 4). The models confirmed that the maximum stand-grown crown width was related to spacing, increasing with spacing at a decreasing rate.

Maximum branch diameter models

Overall, the variable-exponent model for branch diameter fit well, with coefficients of determination ranging from 0.71 for *A. grandis* ([6c]) to 0.88 for *P. ponderosa* at Pringle Butte ([6b]). Final models had well-distributed, homogeneous residuals and therefore did not require weighting. A single random tree effect in each species on the CW term was adequate for reducing the significant impact of autocorrelation on standard error estimation ($\alpha \leq 0.05$). The most dramatic example of this was *P. ponderosa* at Pringle Butte, where the single random tree effect rendered the effects of autocorrelation, evident in the nonlinear least squares fit, insignificant at an α level of 0.05 (Fig. 2).

All models were curvilinear, peaking just above the base of the live crown, but covariates differed by species and location (Table 5):

Pinus contorta, Pringle Butte:

[6a] $\text{BD} = \gamma_{11} \text{CW}$

$$\times \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\gamma_{12}}} \right)^{\gamma_{13} e^{-z} + \gamma_{14} \text{HT} + \gamma_{15} \text{CL} + \gamma_{16} \text{SPACE} + \gamma_{17} \text{SPPCOMP}} + \epsilon$$

Pinus ponderosa, Pringle Butte:

Fig. 1. Plots of crown width versus relative stem diameter for three spacings (1.8-, 3.7-, and 5.5-m) and two species compositions (pure (P) and mixed (M), when significant) for (*a*) *Pinus contorta*, (*b*) *Pinus ponderosa* at Pringle Butte, (*c*) *Abies grandis*, and (*d*) *Pinus ponderosa* at Lookout Mountain.
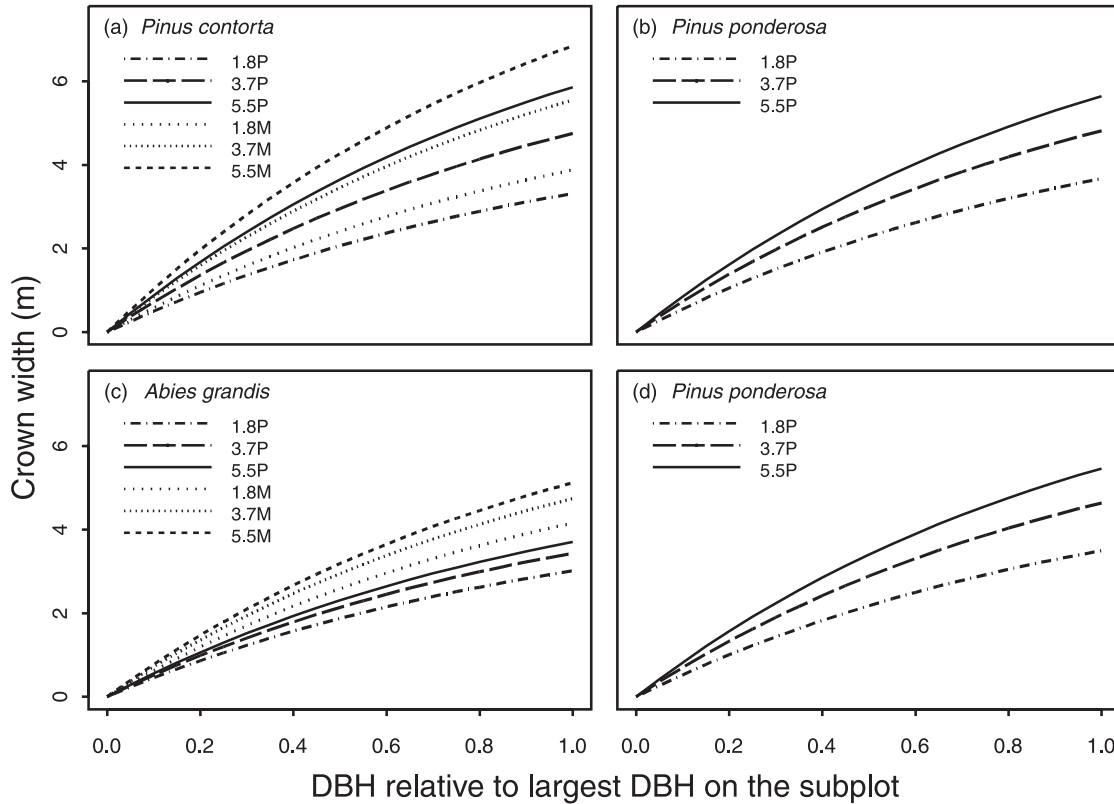

Table 4. Parameter estimates, mean square errors, and coefficients of determination for [5].

Species	Parameters and estimated values[a]				Fit statistics	
	β_0	β_1	β_2	β_3	MSE	R^2
Pringle Butte						
Pinus contorta	3.8313	0.6474	0.5191	ns	0.5182	0.83
Pinus ponderosa	4.5744	ns	0.3928	ns	0.4689	0.77
Lookout Mountain						
Abies grandis	4.2416	1.6146	0.1901	ns	0.4758	0.59
Pinus ponderosa	4.3219	ns	0.4071	ns	0.7008	0.65

[a]ns, not significant at the $\alpha = 0.05$ level.

$$[6b] \quad BD = \gamma_{21}CW$$
$$\times \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\gamma_{22}CR}} \right)^{\gamma_{23}Z^{\gamma_{24}} + \gamma_{25}CL + \gamma_{26}SPACE \times SPPCOMP} + \varepsilon$$

Abies grandis, Lookout Mountain:

$$[6c] \quad BD = \gamma_{31}CW$$
$$\times \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\gamma_{32}CR}} \right)^{\gamma_{33}Z^{\gamma_{34}} + \gamma_{35}SPPCOMP + \gamma_{36}SPACE \times SPPCOMP} + \varepsilon$$

Pinus ponderosa, Lookout Mountain:

$$[6d] \quad BD = \gamma_{41}CW^{\gamma_{42}} \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\gamma_{43}CR}} \right)^{\gamma_{44}Z + \gamma_{45}\frac{HT}{DBH} + \gamma_{46}CL} + \varepsilon$$

The overall average bias was below 0.4 mm in all species. Average bias among crown positions was also small, generally below 1.0 mm (5.0%), with standard errors of estimates near 6.0 mm. There was a consistent positive bias of less than 1.0 mm near crown base and between 0.6 and 0.7 relative height above crown base. There were no obvious patterns in bias among the spacing or species composition treatments.

For all but *P. ponderosa* at Lookout Mountain, the scalar representing MBD was a linear function of CW (i.e., the exponent was not significantly different from unity). The value *p* was modeled as a linear function of CR for each species except *P. contorta* ([6a]), which was reparameterized as a constant estimated from the data. The variable exponent was slightly different for each species. All equations contained a single function of Z, allowing the exponent to change with height in the crown. In addition, tree-level variables, including HT, CL, and DBH/HT, significantly influenced some relative branch diameter profiles. At Pringle Butte, HT and CL had a positive and negative effect, respectively, on relative maximum branch diameter in *P. contorta* ([6a]). In contrast, CL had a significant positive effect in *P. ponderosa* at Pringle Butte, because no other surrogate for tree size was significant. At Lookout Mountain, *P. ponderosa* had significant positive and negative effects of CL and DBH/HT, respectively, on relative branch diameter profiles. No tree variables explained
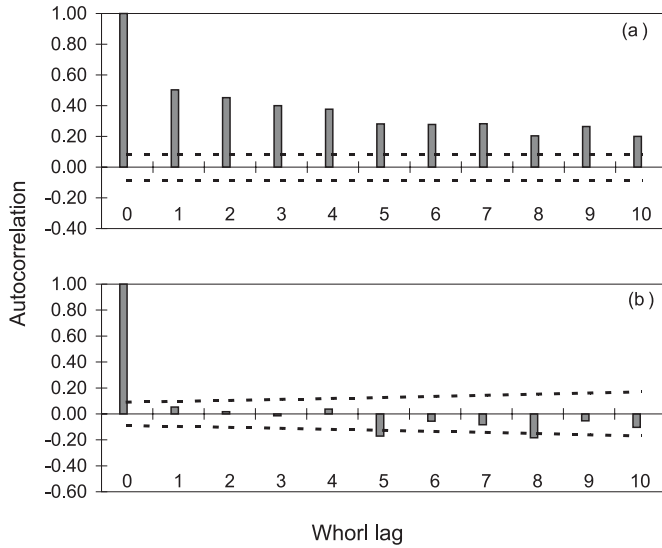
Fig. 2. Autocorrelation plots for the two different runs for *Pinus ponderosa* at Pringle Butte ([6b]): (a) generalized nonlinear least-squares run (GNLS, no random effect); (b) nonlinear mixed-effects model run with a random tree effect (NLME). Estimates of the parameters for each run were obtained using the method of maximum likelihood. Dotted lines represent 95% confidence region.

Table 5. Parameter estimates and asymptotic standard errors of the best variable exponent maximum branch diameter model for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa* at Pringle Butte and Lookout Mountain.

Parameter	Estimated value	SE
***Pinus contorta*, [6a]**		
γ_{11}	7.4646	0.3808
γ_{12}	0.0772	0.0490
γ_{13}	−1.8563	0.1202
γ_{14}	0.1537	0.0136
γ_{15}	−0.0668	0.0150
γ_{16}	0.0564	0.0117
γ_{17}	0.0696	0.0248
SD(δ_{11})	0.5766	0.2407
SD(ε)	4.7212	0.0397
***Pinus ponderosa* (Pringle Butte), [6b]**		
γ_{21}	8.3974	0.6295
γ_{22}	0.6854	0.0947
γ_{23}	0.4945	0.0437
γ_{24}	0.5557	0.0871
γ_{25}	0.0153	0.0058
γ_{26}	0.0139	0.0052
SD(δ_{21})	1.1187	0.1940
SD(ε)	4.2315	0.0462
***Abies grandis*, [6c]**		
γ_{31}	5.4002	0.2794
γ_{32}	0.7776	0.0351
γ_{33}	0.4575	0.0511
γ_{34}	0.5102	0.0885
γ_{35}	−0.3210	0.0745
γ_{36}	0.0589	0.0047
SD(δ_{31})	0.7080	0.2177
SD(ε)	3.0220	0.0477
***Pinus ponderosa* (Lookout Mountain), [6d]**		
γ_{41}	13.7854	1.3385
γ_{42}	0.7210	0.0758
γ_{43}	0.7949	0.0447
γ_{44}	0.4105	0.0380
γ_{45}	−0.2603	0.0873
γ_{46}	0.0261	0.0039
SD(δ_{41})	0.8851	0.2585
SD(ε)	4.9732	0.0554

any additional variation in the relative branch diameter profiles of *A. grandis*.

Spacing had a positive effect on all species through its influence on predicted CW ([5]). However, spacing also had a significant positive effect on relative branch diameter profiles on *P. ponderosa* and *P. contorta* at Pringle Butte. Although CL was chosen for the final model, SPACE and CL were interchangeable in [6b], with identical AIC's. Mixed species composition resulted in a significant positive effect on the overtopping *P. contorta*, but a significant negative effect on the subordinate *A. grandis* at Lookout Mountain. The interaction between spacing and species composition was significant in the two subordinate species, *P. ponderosa* at Pringle Butte and *A. grandis* at Lookout Mountain, indicating a positive effect of spacing on relative branch size only in mixed-species plots.

Data for models [6a]–[6c] were reanalyzed without explicit treatment variables SPACE and SPPCOMP in the variable exponent, thereby restricting relative branch profile to vary by only tree-level covariates. The resulting models contained exactly the same tree-level variables as in [6a], [6b], and [6c]. Overall fits of these reduced models, however, were inferior to the full models (Table 6).

Predicted trends in maximum branch diameter profiles

Vertical profiles of maximum branch diameter indicated that each species exhibited a peak between 0.1 to 0.4 relative height above crown base. The location of this peak varied by species, spacing, and the tree's social position. In *P. ponderosa*, maximum branch diameter peaked at a slightly higher relative height above crown base than its competitor, *P. contorta* at Pringle Butte (Fig. 3a vs. 3b), but lower than its competitor *A. grandis* at Lookout Mountain (Fig. 3c vs. 3d).

Progressively wider spacings resulted in larger branches on pure plots for all species (Fig. 3). This was most evident

for *P. ponderosa* (Fig. 3b, 3d). In contrast, there was dramatically less response in branch size for *A. grandis* at spacings greater than 3.7 m (Fig. 3c).

Effects of species composition across spacing were also evident (Fig. 4). While maximum branch diameter profiles increased with spacing in mixtures, responses were different than in monocultures. In the subordinate species, *P. ponderosa* at Pringle Butte (Fig. 4a–4c) and *A. grandis* (Fig. 4d–4f), pure plots had wider maximum branch diameter profiles at tighter spacings than mixed plots. As spacing increased, the difference between pure and mixed plots diminished; that is,

Table 6. Akaike's information criterion, log likelihood, and likelihood ratio tests comparing full models with tree and site variables ([6a]–[6c]) to reduced models with only tree-level variables.

Equation	No. of estimated parameters	AIC	Log likelihood	Likelihood ratio statistic	p value
Abies grandis					
6a, full	8	2447.84	−1215.92	20.87	0.000 029
Reduced	6	2464.71	−1226.35		
Pinus contorta					
6b, full	9	4005.29	−1993.65	24.20	0.000 006
Reduced	7	4025.49	−2005.74		
Pinus ponderosa (**Pringle Butte**)					
6c, full	8	2957.14	−1470.57	7.74	0.005 413
Reduced	7	2962.88	−1474.44		
Pinus ponderosa (**Lookout Mountain**)					
6d	8	2179.69	−1081.85		

Fig. 3. Profiles of maximum branch diameter versus relative height above crown base for a tree of average height and corresponding diameter and crown length at 1.8-, 3.7-, and 5.5-m spacing for pure plots of (*a*) *Pinus contorta*, (*b*) *Pinus ponderosa* at Pringle Butte, (*c*) *Abies grandis*, and (*d*) *Pinus ponderosa* at Lookout Mountain.
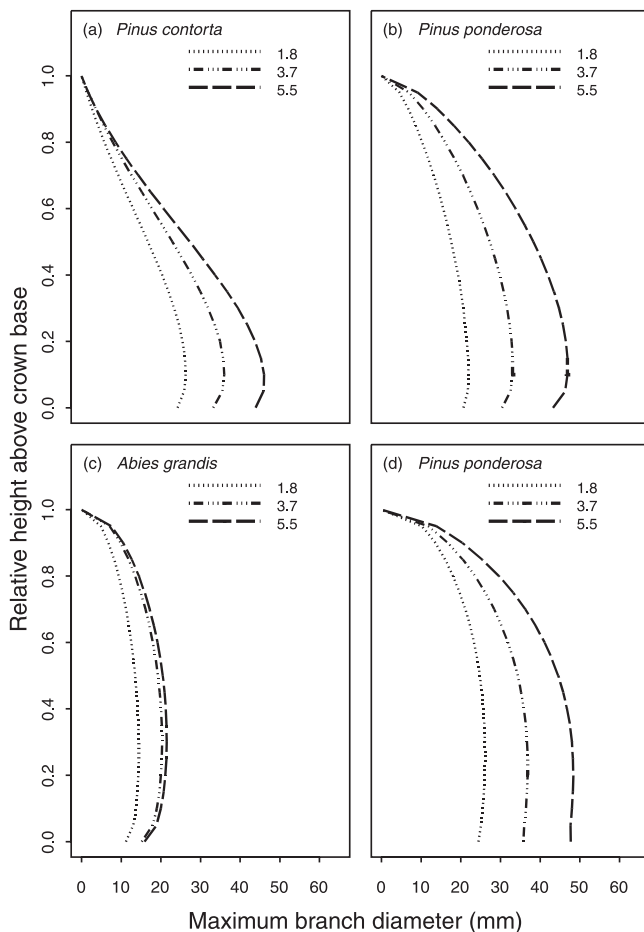
the subordinate trees in mixtures had a greater response to the increase in spacing than trees in pure plots. In contrast, the dominant species, *P. contorta* at Pringle Butte and *P. ponderosa* at Lookout Mountain, had wider branch diameter profiles in mixture than in pure plots at the closest spacing. As spacing increased, differences became smaller in *P. contorta* but not in *P. ponderosa* at Lookout Mountain (Fig. 4). In this latter case, branches near crown base in mixed plots exceeded those on pure plots by greater than 4 mm at all spacings.

Trees in a superior social position, here defined as greater relative height or height of the subject tree relative to the tallest tree in the subplot, were predicted to have greater maximum branch diameter in all species (Fig. 5). This response was most pronounced in *P. ponderosa* at Pringle Butte and least pronounced in *P. contorta*.

Discussion

Response of crown width

As expected, crown width increased asymptotically with increasing relative DBH in all species, with the asymptote as a function of spacing and, in the case of *P. contorta* at Pringle Butte and *A. grandis* at Lookout Mountain, species composition. Spacing – crown width relationships have been previously demonstrated (Curtis and Reukema 1970; Cochran and Dahms 1998, 2000). The width that crowns attain ultimately depends on competition for growing space, primarily aerial space in closed stands. Increasing spacing clearly allows crowns to expand up to the spacing corresponding to maximum potential crown width for that species. Likewise, when a faster growing species is interplanted with a slower growing species, the net effect is similar to that of increasing spacing, since the species of lower stature will not afford the same level of lateral competition as other individuals of the same species. Therefore, at Pringle Butte, *P. contorta* had significantly greater crown widths for a given spacing in mixtures relative to pure stands. *Pinus contorta* overtopped its associate *P. ponderosa* on the mixed plots and therefore

Fig. 4. Profiles of maximum branch diameter with relative height above crown base for two trees of average diameter, height, and crown length for each species on pure (Pure) and mixed (Mix) plots for *Abies grandis* (GF), *Pinus contorta* (LP), and *Pinus ponderosa* (PP): (*a*) 1.8-, (*b*) 3.7-, and (*c*) 5.5-m spacings at Pringle Butte and (*d*) 1.8-, (*e*) 3.7-, and (*f*) 5.5-m spacings at Lookout Mountain.
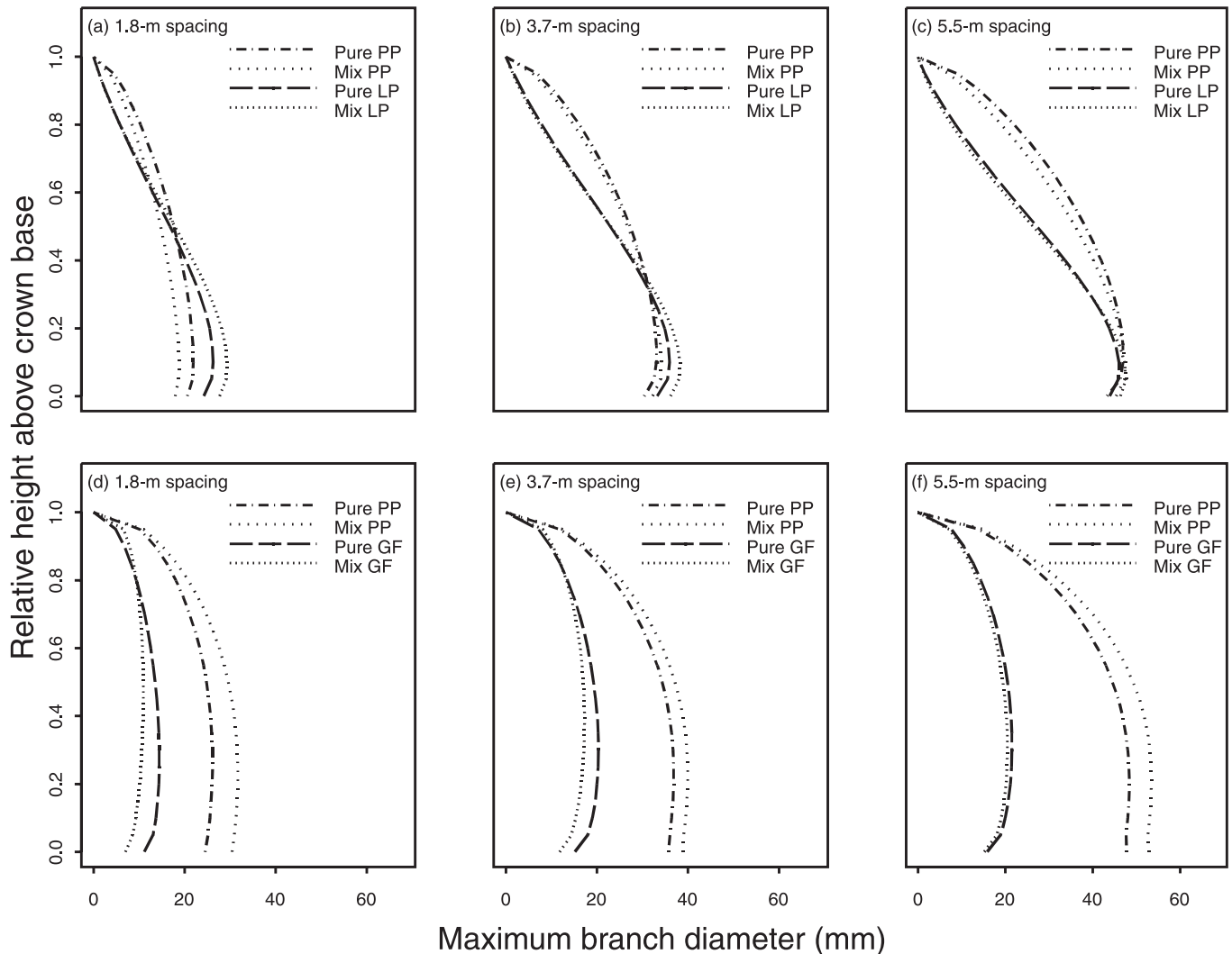
had greater opportunity to expand its crowns than in pure *P. contorta* plots at the same spacing.

Maximum branch diameter

Maguire et al. (1999) speculated that a random tree effect would eliminate any significant autocorrelation among branches within trees and verified this assumption qualitatively by residual analysis. Similar assumptions were apparently made in modeling branch diameters on *Pinus sylvestris* L. and *Pinus nigra* Arnold subsp. *laricio* (Poiret) Maire, but without mention of the residual analysis (Meredieu et al. 1998; Mäkinen and Colin 1998). Results in central Oregon suggest a random tree effect is adequate in accounting for autocorrelation among branch diameters on a single tree, even in cases where multiorder autocorrelation is initially present (Fig. 2). In contrast, recent work on *Pseudotsuga menziesii* in the Oregon Coast Range indicated random effects were not enough to account for within-tree autocorrelation in modeling maximum branch diameter profiles (Weiskittel 2003). The inconsistencies among these studies may stem from dif-

ferences in the hierarchical structure of the sampling scheme, sampling size, geographical scope, range and number of covariates, and other factors.

Selection of covariates is an important process for the development of predictive models. Ideally, tree-level variables would be most useful in predicting crown architecture of trees grown under varying stand structures, especially for incorporation into growth models (e.g., Houllier et al. 1995). The models developed in the present study have some potential for prediction across the range in spacing and tree size represented in the data. However, the primary objective was to test the effect of spacing and species composition on maximum branch diameter profiles. Most previous efforts at modeling branch diameter have relied on tree-level variables exclusively (Colin and Houllier 1992; Doruska and Burkhart 1994; Maguire et al. 1994; Gilmore and Seymour 1997; Roeh and Maguire 1997; Maguire et al. 1999). Stand variables such as site index and competition index have been included, but have not contributed much additional predictive power to the models (Maguire et al. 1991; Mäkinen and Colin 1998).

Fig. 5. Profiles of maximum branch diameter versus relative height above crown base for three trees in different social positions (RHT = total height / total height of tallest tree on subplot) and corresponding diameters, heights, and crown lengths in pure plots at 3.7-m spacing: (*a*) *Pinus contorta*, (*b*) *Pinus ponderosa* at Pringle Butte, (*c*) *Abies grandis*, and (*d*) *Pinus ponderosa* at Lookout Mountain. The three social positions represented were the tallest tree, average subplot RHT, and one standard deviation below average subplot RHT.
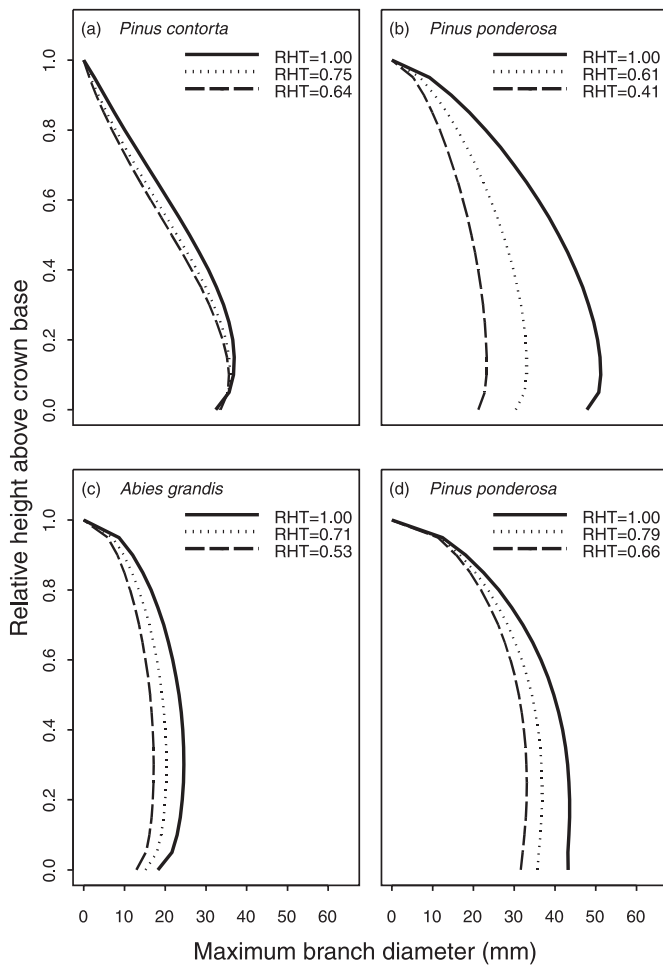
Variables representing tree size (e.g., diameter, height, and crown length) have adequately represented the effects of relative canopy position, stand density, and site quality on tree allometrics, including branch size (Roeh and Maguire 1997; Mäkinen and Colin 1998; Maguire et al. 1999). However, data for these studies have been collected from even-aged, single-species stands, where stand structures are relatively simple and homogeneous. In this context, total height serves as an indicator of relative tree height within the canopy, while crown length reflects local stand density and spacing.

In more complex stand structures, similar-sized trees grown under different conditions have different crown architectures (O'Connell and Kelty 1994). Consequently, tree size variables would not as effectively reflect relative position and cumulative effects of past competition. Accounting for the effects of growing conditions with tree variables proved to be difficult at Pringle Butte and Lookout Mountain. In some cases, such as in *P. ponderosa* at both sites, crown length

was able to account for the same or greater variation in relative branch profiles as spacing. In *P. contorta*, crown length and spacing were significant in the model, but had opposite effects; that is, the marginal effect of increasing crown length was a decrease in relative branch diameter, but the marginal effect of spacing was an increase. This relative effect should not be confused with the net absolute effect on branch diameter, as crown length generally has a positive effect on crown width (Hann 1997; Marshall et al. 2003), and that effect in the present study is largely accounted for by the spacing effect in CW ([5]).

Species composition was harder to account for using tree size variables exclusively. Explicit treatment variables were necessary in all species except *P. ponderosa* at Lookout Mountain. The need to represent species composition was especially true in the subordinate species, where increased spacing resulted in more equal height and volume contribution between the species in the mixed stands (Garber and Maguire 2004). For the dominant species, relative branch diameter profiles in mixed stands behave more like those in pure stands at wider spacing, since they are growing, to some extent, as if the subordinate species were absent.

Implications for branch diameter development

Current branch diameter depends on the rate and duration of past branch growth. Growth of a branch depends on position of the branch within the crown, tree social position, and stand structure (Mäkinen 1999*a*). In general, branch diameter growth begins rapidly, then decreases markedly as a negative exponential function of branch age (Kershaw et al. 1990; Mäkinen 1999*b*). As a result, older branches, such as those deeper in the crown, are generally growing slower than younger branches at the top of the tree. Branch growth at a given height is also positively correlated with growth of the main stem (Mäkinen 1999*a*). Faster tree growth suggests better social position within a stand. Lower social positions, and consequently lower relative heights, can result in rapid deceleration of branch growth (Fujimori 1993; Mäkinen 1999*a*; Mäkinen and Colin 1999). As a result, branches attain smaller diameters with decreasing social position (Fig. 5; Colin and Houllier 1991; Gilmore and Seymour 1997).

The decline in branch growth with depth into crown is expected to result in branches of maximum diameter at the base of the live crown. However, the peak in branch diameter above the base of the live crown has been reported in several other species besides the three in this study and across a range in shade tolerance. These other species include *P. nigra* (Meredieu et al. 1998), *P. sylvestris* (Mäkinen and Colin 1998), *Picea abies* (L.) Karst. (Colin and Houllier 1991), *Abies balsamea* (L.) Mill. (Gilmore and Seymour 1997), and *Pseudotsuga menziesii* (Maguire et al. 1994; Maguire et al. 1999). Although the decrease in branch size near the base of the live crown has been attributed to a poorer light environment (Kershaw et al. 1990; Mäkinen 1999*b*), this growth pattern was also evident in the widest spacings at Pringle Butte and Lookout Mountain, where crown closure has not occurred. Likewise, Roeh and Maguire (1997) reported a decrease in branch diameter at the base of the live crown in stands of young *Pseudotsuga menziesii* that have not reached crown closure. These results suggest that branch growth slows before crown closure, due in part to self-shading and shading

by adjacent trees. Other factors may include increasing hydraulic resistance with increasing branch length (Waring and Sylvester 1994), increasing branch diameter growth as tree diameter growth increases at early stages of stand development (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998), and the higher number of whorl branches found at the base of the crown, increasing competition among branches (Maguire et al. 1994).

Although the decline in branch growth with increasing age is rapid, the branch continues to grow or at least survive for many years (Andrews and Gill 1939; Mäkinen 1999b). As branches develop, they are quickly relegated to lower positions in the crown and hence poorer light conditions (Brooks et al. 1991; Sampson and Smith 1993). Branch growth declines proportionately, with a noticeable reduction in earlywood production (Kershaw et al. 1990; Mäkinen 1999a; Mäkinen and Colin 1999; Protz et al. 2000). Most water transport occurs in earlywood tracheids because of their greater diameter. Consequently, as earlywood production decreases branch hydraulic resistance increases (Pothier et al. 1989; Protz et al. 2000). The heightened water stress reduces stomatal conductance and total photosynthesis of branches in lower canopy positions, promoting foliage senescence. Despite increasing stress, these branches can persist for long periods, with half or more of the life of a branch spent without perceivable increment (Andrews and Gill 1939; Kershaw et al. 1990; Mäkinen 1999a). Senescent branches are assumed to satisfy their own maintenance costs, but do not contribute to net tree production (Sprugel et al. 1991; Fujimori 1993). Eventually, the branch dies when it no longer fixes enough carbon to meet its needs.

Effects of stand density on branch diameter have been observed in many previous studies (Grah 1961; Magnussen and Yeatman 1987; Ballard and Long 1988; Colin and Houllier 1991; Maguire 1994). In central Oregon, *P. ponderosa* responded more dramatically to spacing than the other two species. A recent study on these same plots reported a positive height and volume response to increased spacing by *P. ponderosa* at Pringle Butte (Garber and Maguire 2004). Clearly, spacing has a profound effect on the development of *P. ponderosa* on these moisture-limited sites. Only *A. grandis* did not show a pronounced increase in maximum branch diameter between the two widest spacings at Lookout Mountain (Fig. 4c). Crown closure has not occurred on either one of these two spacings for *A. grandis*, and the live crowns extend to the ground. Consequently, the trees at both spacings were essentially open grown. Effects of stand density on branch growth have also previously been shown to vary with height in the crown. In the *Pinus* species in central Oregon, relative increases in branch diameter were smaller at higher positions in the crown with progressively wider spacings. Branch growth in the upper crown is influenced more by regional conditions, whereas local stand conditions affect the lower portion of the crown (Mäkinen 1999b).

In contrast to single-species stands, canopies in mixed-species stands not only differentiate on the basis of microsite and genetic variation within a species, but they also stratify by species grouping (Cobb et al. 1993; Oliver and Larson 1996; Smith et al. 1997). The process of stratification is a function of many silvical attributes, including shade tolerance and height growth. Consequently, when different species are well interspersed as individuals, multiple strata can form (Cobb et al. 1993), resulting in deeper vertical foliage profiles (Yang et al. 1999), different light environment, and an alteration of tree growth dynamics, as manifested in crown architectural changes. At Pringle Butte and Lookout Mountain, branch diameter profiles depended on competing species. For the dominant species, such as *P. contorta* at Pringle Butte and *P. ponderosa* at Lookout Mountain, greater branch diameters were found in mixtures owing to the lower stature and competitive effect of the subordinate species. In contrast, the subordinate species (*P. ponderosa* at Pringle Butte and *A. grandis* at Lookout Mountain) had smaller maximum branch diameter in mixtures than in pure plots. Stratification has therefore influenced branch diameter development over time, causing prolonged or enhanced branch growth in the overtopping species and suppressed growth in subordinate species. In addition, the effects of competing species varied with increasing spacing, resulting in smaller differences in branch diameters between trees in pure and mixed plots. Spacing effects on stand development in these plots suggested that increasing spacing in mixed plots accelerates growth for individuals of both the superior and the subordinate species, but the acceleration was more marked for the subordinate species, in parallel with the increased light availability from understory to open-grown conditions (Garber and Maguire 2004). Wider spacing resulted in less stratification in both spacing trials, and maximum branch diameter responded in a similar way.

Management implications

Stand structure influences crown structure (Curtis and Reukema 1970; Cochran and Dahms 2000), which in turn affects wood quality, for example, juvenile wood core, knot size, and earlywood/latewood ratio (Maguire et al. 1991; Agestam et al. 1998; Björklund and Moberg 1999; Moberg 2001; Gartner et al. 2002). Two general strategies have been adopted in the past to improve wood quality in single-species stands. The first is to maintain high densities, smaller crowns (Curtis and Reukema 1970), and longer crown-free boles. The second is to grow at wide initial spacing and prune (Smith et al. 1997). An alternative strategy to improve wood quality involves cultivation of stratified, mixed-species stands in which subordinate species serve as trainers, accelerating the growth reduction and self-pruning of branches on the overtopping species (Smith et al. 1997). This approach can also yield wood of high quality in the subordinate species, analogous to uneven-aged stands, where younger cohorts develop under partial shade (Singleton and Maguire 2002). Moreover, with greater knowledge of species-specific branch dynamics, species, spacing, and the species proportion can be fine-tuned to obtain the desired log size, log quality, and stand volume. For example, if 3.7-m spacing provides desired log size by age 50, but crowns and branches are too large to meet wood quality objectives, interplanting a slower growing tolerant species may inhibit growth and persistence of lower branches with little sacrifice in log size.

Another use of such models is in growth simulators. Many simulators use gross crown dimensions as predictor variables in dynamic growth equations. However, there is greater interest in modeling the finer elements of tree crowns (D.W. Hann, personal communication). Although these equations are not

dynamic in nature, stand inventories do not include crown measurements; therefore, static models would be necessary for predicting initial conditions in the foreseeable future.

Acknowledgments

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