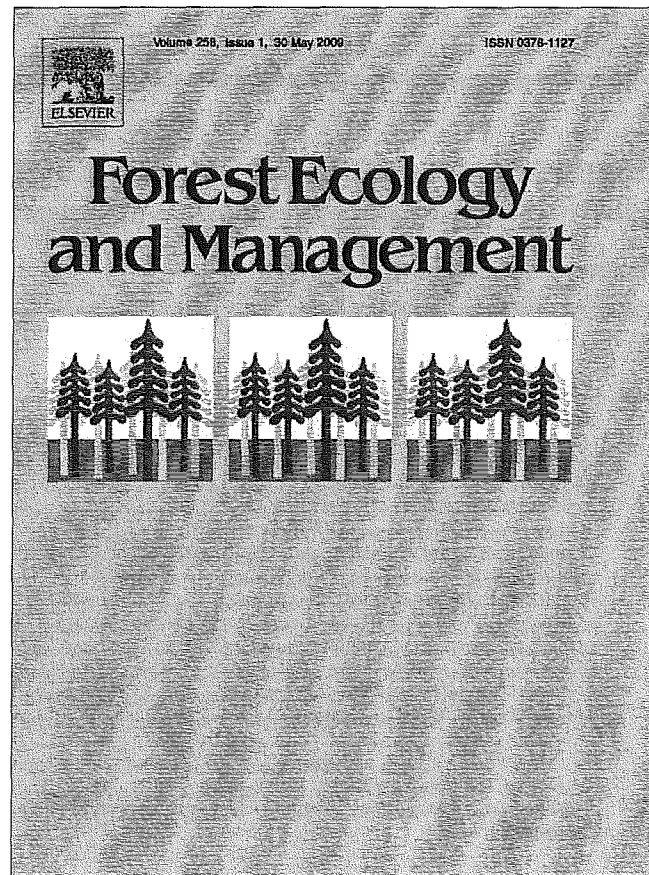


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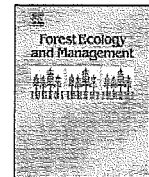
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ABSTRACT

Growth and mortality of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) were studied for 25 years after planting seedlings at 1–6-m spacings on a site of moderate quality in the western Cascade Mountains of Washington. Responses were compared to those from two other studies representing high and low site qualities. Third-year height did not differ among spacings ($P = 0.80$), providing no evidence that close spacing stimulated early growth. Piecewise regression identified the onset of competition-induced mortality when stand density index (SDI [Reineke, L.H. 1933. Perfecting a stand density index for even-aged forests. Journal of Agricultural Research 46, 627–638]) exceeded 52% (S.E. = 4.6) of the species' maximum or when average crown ratio (CR) declined below 52% (S.E. = 0.9). For a range of SDI values, CR averaged 2–7% points greater at the high-quality site than at the moderate-quality site. In a regression analysis of combined data from the moderate- and high-quality sites, relative values of average stem diameter and stand volume (% of maximum values observed per site) 23–25 years after planting increased and decreased with planting spacing, respectively ($R^2 = 0.97$ and 0.91 , respectively). Intersection of these relationships at 3 cm spacing indicated a point of equivalent relative development of tree size and stand yield. For a range of site qualities, stands planted at 3-m spacing: (1) maintained tree vigor (CR > 50%) and stability (average height:dbh ratio < 90), (2) experienced little or no competition-induced mortality through age 25 years, and (3) allocated 25-year growth equitably to development of tree size and stand yield, thereby providing a desirable starting point for subsequent management.

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1. Introduction

Spacing is a critical feature to consider when establishing forest plantations because it determines the timing and intensity of resource competition among individual trees. Given the limited pool of resources available to support tree growth on a forest site, competition among individual trees intensifies as they grow in size and their resource requirements increase. Trees become dominant within a stand when their initial size, genetic characteristics, or resource availability enable them to grow faster, suppress their neighbors, and occupy additional growing space. Spacing affects the timing, and therefore tree size, at which these competitive interactions occur (Long et al., 2004). In this way, spacing directly influences stand dynamics associated with differentiation in tree size and onset of competition-induced mortality.

Typical planting spacings for coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) are based on a variety of criteria, including forecasts of tree survival, growth, and stability

(Talbert and Marshall, 2005). These criteria often are viewed as components of stand vigor, and one goal of selecting the proper spacing is to enable crop trees to maintain their vigor until a subsequent thinning or other treatment. Maintaining crown ratio (live crown length:tree height ratio) at 40% or greater is considered desirable for sustaining vigorous growth (Smith, 1986, p. 83), although few studies have experimentally manipulated this variable or related it to stand density to identify critical values for stand management (Young and Kramer, 1952; Long, 1985; Dean and Baldwin, 1996a). Likewise, maintaining the ratio of height:stem diameter (i.e., slenderness ratio) below 80–100 is considered desirable for reducing susceptibility to wind-throw and stem breakage, especially when stand height exceeds 25 m (Cremer et al., 1982; Lohmander and Helles, 1987; Wilson and Oliver, 2000). As initial spacing decreases, risk of declining vigor from accelerated crown recession (i.e., mortality of lower branches) or loss of stability from development of a high slenderness ratio occurs earlier in stand development. Declining vigor from intense competition increases the probability that an individual tree will die. The onset of competition-induced mortality in stands of coast Douglas-fir has been estimated to occur when stand density index (SDI; Reineke, 1933) exceeds a

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threshold of 55% of the species' maximum value (Drew and Flewelling, 1979).

Although resource competition characterizes many of the interactions that occur among trees, variable-density studies of coast Douglas-fir (Scott et al., 1998; Woodruff et al., 2002), red alder (*Alnus rubra* Bong.) (Knowe and Hibbs, 1996; Hurd and DeBell, 2001), and cottonwood (*Populus* spp.) (Krinard, 1985; DeBell et al., 1996) have demonstrated that peak growth of individual trees occurs at close spacings early in stand development (<10 years old) and at progressively wider spacings as the stand develops. Potential explanations for this phenomenon are related to characteristics of high-density stands: greater probability of seedlings occurring on superior micro-sites, reduced abundance of competing vegetation, reduced browsing pressure, and changes in light quality that affect seedling allometry (Ritchie, 1997).

To facilitate selection of appropriate initial spacings for forest plantations given specific management objectives, an improved understanding is needed that accounts for effects of site quality and planting spacing on subsequent stand dynamics. In general, site quality does not influence the maximum size-density limit of conifer species, but rather it has a positive influence on the rate of increase in average tree size as stands develop, and subsequently, the rate of decrease in stem density as they undergo competition-induced mortality (Harms et al., 2000; Pittman and Turnbull, 2003; VanderSchaaf and Burkhardt, 2008). Although stand dynamics of Douglas-fir have been the subject of considerable research (Oliver and Larson, 1996), and prominent growth and yield models for the Pacific Northwest region (e.g., ORGANONFVS, and CONIFERS) include empirical functions for predicting growth and mortality of individual trees from variables such as crown ratio and SDI (Ritchie, 1999; Ritchie and Hamann, 2008), several fundamental relationships have yet to be quantified. For example, the relationship of mortality rate to crown ratio could be analyzed for a potential threshold response that signals the onset of competition-induced mortality. Likewise, the relationship of crown ratio to SDI could be investigated to see if it varies with site quality. Relationships of relative tree size and relative stand volume (i.e., % of maximum values observed on a given site) to planting spacing could be analyzed jointly to identify a compromise spacing that supports equivalent development of both variables.

In this study (hereafter referred to as the 1981 study), growth and mortality rates were monitored for 25 years on Douglas-fir planted at 1–6-m spacings on a site of moderate quality in the western Cascade Mountains of Washington. Study objectives were to characterize relationships of growth and mortality rate to planting spacing and SDI and to compare these responses to those observed on a low-quality site (1925 Wind River study; Eversole, 1955) and a high-quality site (Maple Ridge study, 49-tree-plot trial; Reukema and Smith, 1987). The research also tested the following null hypotheses: (1) early growth in height does not differ among planting spacings, and (2) average top height does not differ among planting spacings.

2. Methods

2.1. Study site and treatments

The 1981 study was conducted in the Trout Creek Unit (T4NR7E S18) of the Wind River Experimental Forest, Gifford Pinchot National Forest, about 20 km north and slightly west of Carson, WA (lat. 45°50'N, long. 122°0'W). The soil is classified as a dark brown loam of the Stabler series, a medial, amorphic, mesic, Vitric Hapludand with a solum thickness of 76–127 cm. Vegetation is intermediate between the western hemlock (*Tsuga heterophylla*

(Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) zones (Franklin and Dyrness, 1973). Elevation ranges from 512 to 557 m, slopes are less than 10%, and aspect is south. The average frost-free growing season is 120 days and average annual precipitation for the study period (1981–2005) is estimated to be 2748 mm (Daly et al., 1994).

The pre-harvest old-growth stand was dominated by Douglas-fir (site class III–IV, McArdle et al., 1961) and western hemlock, with occasional western redcedar (*Thuja plicata* Donn ex D. Don) and Pacific silver fir. The understory was dominated by vine maple (*Acer drdnatum* Pursh), salal (*Gaultheria shallon* Pursh), Oregon-grape (*Mahonia nervosa* Pursh), vanilla-leaf (*Achlys triphylla* (Smith) DC), beargrass (*Xerophyllum tenax* (Pursh) Nut.), red huckleberry (*Vaccinium parvifolium* Smith), spreading dogbane (*Apocynum androsaemifolium* L.), and saplings of western hemlock and Pacific silver fir. The site was clearcut harvested in 1977 and woody debris was piled and burned in summer 1978. Remaining debris was scattered and areas dominated by residual understory vegetation were scarified with a brush rake in 1979.

In summer 1980, 34 plots of dimension 63.2 m x 63.2 m (0.4 ha) were located on the 26-ha study site. Four plots were randomly assigned for planting Douglas-fir seedlings at 1-m spacing and six plots were randomly assigned for planting at each of 2-, 3-, 4-, 5-, and 6-m spacings resulting in a completely randomized experimental design. Because costs for establishing the closest spacing (1-m) were very high and the area available for plot location was finite, only four replications of the 1-m spacing were installed. Individual planting spots were marked with stake flags, and in March 1981, 2 + 0 bare-root Douglas-fir seedlings were hand planted. A 5% solution of Roundup (glyphosate) herbicide in water was applied as a directed application in August 1981 to suppress beargrass and salal. Seedling mortality surveys were performed several times during the first few years, and seedlings that died or had poor vigor were replaced to ensure that assigned spacings were maintained. Volunteer seedlings of Douglas-fir and other tree species were removed in 1986, 1990, and 1998.

2.2. Measurements and statistical analyses

In July 1984, third-year height (nearest 0.01 m) was measured on 10–30% of seedlings per plot located in systematically selected rows. In 1989 (year 9), measurement trees were assigned and tagged within each plot. The 1- and 2-m spacings each had 200 measurement trees per replication, and the 3-, 4-, 5-, and 6-m spacings had 196, 100, 64, and 49 measurement trees per replication, respectively. In 2001 (year 21) and 2005 (year 25), dbh (stem diameter at 1.3-m height; nearest 0.1 cm) was measured on each tagged tree and height (nearest 0.1 m) was measured on a systematic sample of 48–50 tagged trees per plot for the 1-, 2-, 3- and 4-m spacings and on each tagged tree in the 5- and 6-m spacings. Crown base height (i.e., defined as the height at which whorl branches are present on at least three of four cardinal-direction quadrants of the crown; nearest 0.1 m) was measured on each height measurement tree. Average crown width (nearest 0.1 m; average of two directions perpendicular to each other) was measured on a systematic sample of 10–22 height measurement trees per plot.

All statistical analyses were conducted in SAS (SAS Institute Inc., 2005) with a significance level of $\alpha = 0.05$. Specific responses in the 1981 study, the 1925 study, and the Maple Ridge study refer to years since planting 2-year-old seedlings. Plot averages for year 25 were calculated for the following variables: height, quadratic mean diameter (square root of the mean squared dbh, hereafter referred to as average dbh), slenderness ratio (height:dbh, expressed in the same units for both variables), crown base height, crown width,

crown length (height-crown base height), and crown ratio (% $100 \times \text{crown length/height}$). Stand basal area (m^2ha^{-1}) per plot was calculated as the total cross-sectional area of trees at breast height in year 25. Stand density index (SDI) was calculated in metric units (Daniel et al., 1979) and converted to a percentage of the species' maximum (SDI%) using the value for Douglas-fir presented in Dean and Baldwin (1996b): 1470 trees ha^{-1} having a quadratic mean diameter of 25 cm. To predict height of trees for which only dbh was measured, the following equation recommended by Curtis (1967) was fitted to each plot by applying non-linear regression to the combined data from all measurement years:

$$H = 1.3 + \exp(a_0 + a_1 D^{a_2}) \quad (1)$$

where H is total height (m), D is dbh (cm), and a_0 , a_1 , and a_2 are coefficients to be estimated. The variables, dbh, height, and predicted height, were applied to the equations of Bruce and DeMars (1974) to calculate stem volume per tree, and these values were summed for each plot and expanded to a per-hectare basis (m^3ha^{-1}). Net periodic annual increment (PAI) in stand volume ($\text{m}^3\text{ha}^{-1}\text{year}^{-1}$) and volume mortality ($\text{m}^3\text{ha}^{-1}\text{year}^{-1}$) were calculated for the period of years 21–25.

Using data from year 25, breast height age and average height of the 100 trees of largest dbh ha^{-1} (i.e., top height) were calculated per plot (as per Miller et al., 2004) and applied to the procedures in King (1966) to calculate an average site index. The age at which trees reached breast height (1.37 m in King, 1966) was determined by fitting plot-specific regression models of age as a quadratic function of top height using combined data from all measurement years.

Values of each tree and stand variable from year 25 were subjected to analysis of variance (ANOVA) in SAS Procedure GLM to test for significant differences among planting spacings. Prior to ANOVA, an arc-sine, square-root transformation was applied to proportionate values of crown ratio, cumulative mortality (% of trees), and SDI% to homogenize their residual variances (Sokal and Rohlf, 1981, pp. 427–428). When ANOVA detected significant differences due to planting spacing, multiple comparisons of means were conducted with the Ryan-Einot-Gabriel-Welsch Multiple Range Test (SAS Institute Inc., 2005). To test Hypothesis 1 (i.e., early growth in height does not differ among planting spacings), average third-year height was calculated for each plot based on 30 randomly selected trees (similar to the approaches used by Scott et al., 1998 and Woodruff et al., 2002), and the means were subjected to ANOVA. To test Hypothesis 2 (i.e., average top height does not differ among planting spacings), plot means for top height in year 25 were subjected to ANOVA. An initial analysis confirmed that top height by plot did not exhibit any spatial pattern across the study site that potentially would confound responses associated with spacing.

Piecewise regression in SAS Procedure NUN was used to identify threshold values of SDI% and average crown ratio from year 21 at which volume mortality accelerated during years 21–25, indicating the onset of competition-induced mortality. The model was constrained to have linear and quadratic portions corresponding to before and after the onset of competition-induced mortality, respectively. Starting values for the mortality threshold parameter were 55% and 50% for SDI% and average crown ratio, respectively, based on information presented in Drew and Flewelling (1979) and Long (1985). Values of the predictor variables (SDI% and average crown ratio) from year 21 were used to test the potential of predicting subsequent mortality rate during years 21–25. The best polynomial models (i.e., potentially containing linear, quadratic, and cubic terms) for describing relationships of stand volume PAI and crown ratio to SDI% were selected with stepwise regression.

To identify the planting spacing that resulted in equivalent relative development in average tree size and stand volume by year 25, treatment means of dbh and stand volume for similar spacings (1–5 m) in the 1981 study (year 25) and the Maple Ridge study (year 23) were expressed as a percentage of the maximum value observed in each respective study. The relative values of dbh and stand volume were subjected to stepwise regression to select the best polynomial models of spacing. The intersection of relationships for relative dbh and volume identified the spacing at which equal relative development had occurred. Residuals for each ANOVA and regression were plotted against predicted values to assess homogeneity of their distribution. Models selected with stepwise regression were those having the highest values for the coefficient of determination (R^2) after adjusting for degrees of freedom.

3. Results

In the 1981 study, average third-year height did not differ among planting spacings ($P = 0.795$), providing no evidence for rejecting Hypothesis 1 (i.e., early growth in height does not differ among planting spacings) (Tables 1 and 2). Site index averaged 34.1 m ($n = 34$ plots; $S.E. = 0.4$). Average top height of the stand in year 25 averaged 17.3 m ($n = 34$ plots; $S.E. = 0.2$) and did not differ among spacings ($P = 0.244$; Hypothesis 2). Each of the other tree and stand variables differed ($P < 0.004$) among spacings in year 25. Average height in the 1-m spacing (10.0 m) was less than values observed in the other spacings (12.8–15.2 m). Similarly, cumulative mortality and volume mortality were greater in the 1-m spacing than in the other spacings. Average dbh differed strongly among close spacings (8.5–17.0 cm for 1–3-m spacings) but less so among wide spacings (19.8–22.7 cm for 4–6-m spacings). Relative differences among spacings for slenderness ratio, crown width, crown length, crown ratio, basal area, and SDI% were similar to those observed for dbh. In contrast, crown base height had similar values for the close spacings (4.3–5.2 m) and they differed from those for the wide spacings (1.0–2.4 m). Average values for stand volume were similar for the 1- and 2-m spacings and they differed from those for the other spacings.

Compared to the 1981 study, Douglas-fir planted at similar spacings in the Maple Ridge study (site index = 43.0 m; Reukema and Smith, 1987) averaged 5–9 m taller in height, whereas those planted in the 1925 study (site index = 30.4 m; Miller et al., 2004) averaged 1–3 m shorter (Table 2). For similar planting spacings, Douglas-fir at Maple Ridge averaged 3–8 cm larger in dbh than in the 1981 study, while in the 1925 Wind River study they averaged

Table 1

Analysis of variance results for tree and stand variables of Douglas-fir planted at 1–6-m spacings in the 1981 study. All variables are for year 25 except where noted.

Variable	Model df	Error df	Model MS	Error MS	Prob. > F
Height ^{third-year}	5	28	0.001	0.002	0.795
Height	5	28	15.4	2.4	<0.001
Dbh	5	28	143.6	2.9	<0.001
Slenderness ratio	5	28	2560.9	8.5	<0.001
Top height	5	28	2.5	1.7	0.244
Crown base height	5	28	20.4	0.9	<0.001
Crown width	5	28	7.0	0.2	<0.001
Crown length	5	28	65.3	0.6	<0.001
Crown ratio	5	28	0.3	0.002	<0.001
Basal area	5	28	659.6	17.7	<0.001
Volume	5	28	22736.1	1300.6	<0.001
Volume PAI ^a	5	28	137.9	11.0	<0.001
SDI%	5	28	0.4	0.005	<0.001
Cumulative mortality	5	28	0.08	0.02	0.004
Volume mortality ^a	5	28	1.3	0.2	0.002

^a Volume mortality and volume PAI are for the period of years 21–25.

Table 2

A comparison of tree variables for Douglas-fir planted at various spacings in the 1981 study, the 1925 study, and the Maple Ridge study. Means from the 1981 study followed by the same letter do not differ significantly ($P \geq 0.05$).

Data source	Spacing (m)	Height ^{third-year} (m)	Height (m)	Dbh (cm)	Slenderness ratio (cm cm ⁻¹)	Crown base height (m)	Crown width (m)	Crown length (m)	Crown ratio (%)
1981 study (year 25, except where noted)	1.0	0.46 a	10.0 b	8.5 e	127 a	5.2 a	2.2 e	4.3 d	40 e
	2.0	0.47 a	12.8 a	13.8 d	101 b	5.6 a	3.1 d	7.5 c	56 d
	3.0	0.50 a	13.7 a	17.0 c	84 c	4.3 a	3.7 c	10.1 b	69 c
	4.0	0.48 a	14.3 a	19.8 b	73 d	2.4 b	4.6 b	12.4 a	84 b
	5.0	0.47 a	15.2 a	22.0 ab	70 de	1.7 b	4.9 ab	13.2 a	88 ab
	6.0	0.48 a	14.3 a	22.7 a	66 e	1.0 b	5.3 a	13.4 a	92 a
1925 study (year 27)	1.2	–	10.1	9.3	108	–	–	–	–
	1.5	–	9.2	9.6	96	–	–	–	–
	1.8	–	10.2	11.0	93	–	–	–	–
	2.4	–	11.6	13.6	85	–	–	–	–
	3.0	–	13.0	16.4	80	–	–	–	–
	3.7	–	13.5	18.2	74	–	–	–	–
Maple Ridge study (year 23)	0.9	–	19.2	13.3	139	11.9	2.6	7.3	38
	1.8	–	19.8	16.7	120	11.6	2.6	8.2	41
	2.7	–	21.2	22.1	93	10.7	3.1	10.5	49
	3.7	–	21.4	26.3	80	9.3	3.8	12.1	56
	4.6	–	20.4	28.3	70	7.2	4.6	13.2	64

2–4 cm smaller. Average values for slenderness ratio and crown width at Maple Ridge were similar to those observed in the 1981 study. However, crown ratio was 2–28% points lower and crown base height was 6–7 m greater at Maple Ridge. At the closest spacing, crown length at Maple Ridge averaged 3 m greater than in the 1981 study.

Comparisons with the Maple Ridge study suggest that competition intensity and associated mortality increased with site quality, resulting in less variability in tree size by years 23–25. For similar spacings at Maple Ridge, greater values of SDI% developed than those observed in the 1981 study, and concomitantly, they were associated with lower values of crown ratio (Tables 1 and 2). Considerable competition-induced mortality at the closest spacing of Maple Ridge (55% by year 23) resulted in average height values that varied only about 2 m among the five spacings of the study; whereas, average height in the 1981 study varied over 5 m. Likewise, average crown width varied less among spacings at Maple Ridge (2 m) than in the 1981 study (3.1 m). Greater intensity of competition at Maple Ridge also resulted in

significant crown recession in the 4.6-m spacing by year 23 (average crown ratio = 64%); however, very little recession had occurred by year 25 in the 5-m spacing of the 1981 study (average crown ratio = 88%).

Stand characteristics varied strikingly among the three studies. For approximate spacings of 1–4 m, the cumulative mortality rate at Maple Ridge averaged 10–26% points higher than in the 1981 study and the 1925 study (Table 3). Despite the lower stem densities resulting from mortality at Maple Ridge, stand basal area and volume averaged 2–3 times that observed in the other two studies. For similar spacings, stand basal area and volume in the 1981 study averaged 6–81% greater than in the 1925 study, with the largest differences occurring at the closest spacings. At Maple Ridge, the two plots representing the 0.9-m spacing had an SDI% value that exceeded 100%, suggesting an irregularity in stand structure (Reineke, 1933).

During years 21–25, volume mortality in the 1981 study increased exponentially as SDI% in year 21 increased above 52% (S.E.=4.6) or as crown ratio in year 21 decreased below 52%

Table 3

A comparison of stand variables for Douglas-fir planted at various spacings in the 1981 study, the 1925 study, and the Maple Ridge study. Means from the 1981 study followed by the same letter do not differ significantly ($P > 0.05$). Precision for stand volume estimates at Maple Ridge is 1 m³ ha⁻¹ because values were estimated from a graphical plotting of the data (Reukema and Smith, 1987).

Data source	Spacing (m)	Top height (m)	Basal area (m ² ha ⁻¹)	Volume (m ³ ha ⁻¹)	Volume PAI (m ³ ha ⁻¹ year ⁻¹)	SDI%	Cumulative mortality (%)	Volume mortality ^a (m ³ ha ⁻¹ year ⁻¹)
1981 study (year 25, except where noted)	1.0	18.4 a	39.9 a	221.6 a	18.1 a	85 a	29 a	1.4 a
	2.0	17.5 a	33.1 b	213.7 a	20.0 a	58 b	12 b	0.4 b
	3.0	17.4 a	23.2 c	149.9 b	14.8 ab	37 c	7 b	0.1 b
	4.0	17.4 a	17.7 cd	111.6 bc	12.0 bc	27 d	8 b	0.1 b
	5.0	17.0 a	14.0 de	88.8 c	9.7 bc	20 de	6 b	0.0 b
	6.0	16.2 a	10.7 e	65.2 c	7.2 c	15 e	4 b	0.1 b
1925 study (year 27)	1.2	–	30.3	156.9	11.2	62	36	0.2
	1.5	–	24.6	117.2	9.4	50	23	0.1
	1.8	–	23.0	118.1	10.0	44	21	0.1
	2.4	–	17.3	87.2	8.5	32	18	0.0
	3.0	–	21.0	128.8	13.1	34	10	0.0
	3.7	–	17.4	105.9	10.6	27	9	0.1
Maple Ridge study (year 23)	0.9	–	78.0	427	–	138	55	–
	1.8	–	44.7	354	–	73	34	–
	2.7	–	40.6	350	–	59	23	–
	3.7	–	32.3	236	–	44	19	–
	4.6	–	26.7	206	–	35	10	–

^a Volume PAI and volume mortality were calculated for the period of years 21–25 (1981 study) or years 21–27 (1925 study).

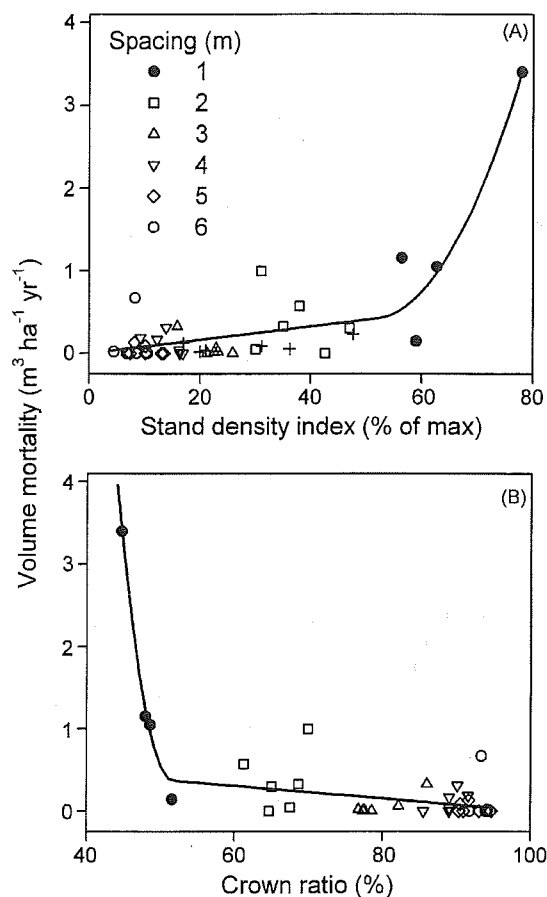


Fig. 1. Piecewise linear regression relationships of Douglas-fir volume mortality during years 21–25 versus (A) stand density index (Reineke, 1933) and (B) crown ratio in year 21 in the 1981 and 1925 studies (equations are listed in Table 4). Stands were planted at the spacings indicated in the legend ('+' symbol indicates volume mortality during years 21–27 for 1.2–3.7-m spacings in the 1925 study; those values were not included in the regression).

(S.E. = 0.9) (Fig. 1; Table 4). These values for SDI% and crown ratio can be interpreted as thresholds for the onset of competition-induced mortality. In the 1925 study, volume mortality was minor during years 21–27 ($<0.02 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) perhaps because, even

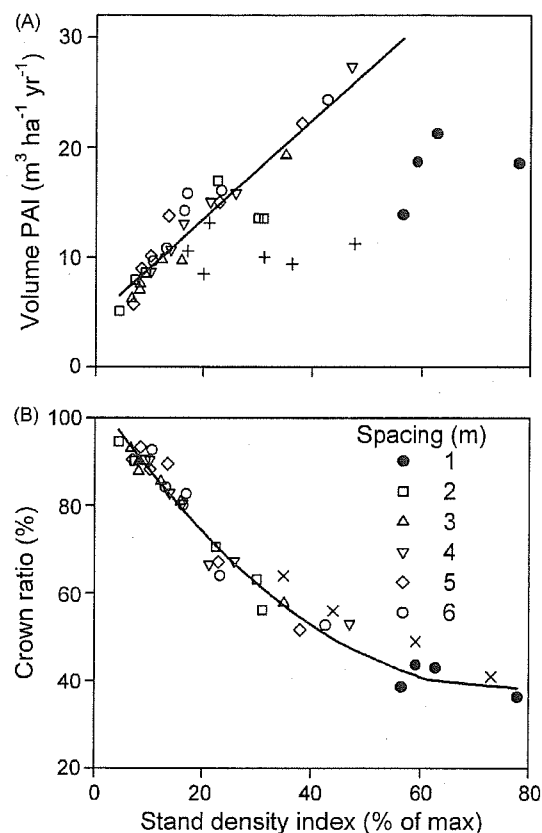


Fig. 2. Regression relationships of Douglas-fir average (A) net periodic annual increment (PAI) in stand volume during years 21–25 and (B) crown ratio in year 25 versus stand density index (Reineke, 1933) in year 21 in the 1981 study (equations are listed in Table 4). The regression for (A) excludes data for the 1-m spacing of the 1981 study and for the 1925 study ('+' symbol indicates PAI during years 21–27 for 1.2–3.7-m spacings in the 1925 study; 'x' symbol indicates crown ratio from year 23 for 1.8–4.6-m spacings in the Maple Ridge study).

at the closest spacing (1.2 m), SDI% in year 21 did not exceed the threshold value of 52% (Fig. 1).

Net PAI in stand volume for years 21–25 was strongly related to SDI% in year 21 for the 2–6-m spacings in the 1981 study ($R^2 = 0.88$) (Fig. 2a; Table 4). However, volume PAI in the 1-m spacing was considerably less than predicted for the other spacings

Table 4

Regression equations for characterizing mortality and growth of Douglas-fir during 23–27 years after being planted at various spacings. Graphical depictions of these models are given in listed figures.

Data source	Equation ^b	Fig.	Goodness of fit ^a		
			R^2	$S_{y,x}$	n
1981 study	$\text{SDI}\% \leq 52.1: M = 0.008(\text{SDI}\%)$	1a	0.87	0.3	34
	$\text{SDI}\% > 52.1: M = 0.008(\text{SDI}\%) + 0.004(\text{SDI}\% - 52.1)^2$				
	$\text{CR} \geq 51.5: M = 0.008(100 - \text{CR})$	1b	0.91	0.2	34
	$\text{CR} < 51.5: M = 0.008(100 - \text{CR}) + 0.062((100 - \text{CR}) - 51.5)^2$				
1981 study	$\text{PAI} = 4.54 + 0.449(\text{SDI}\%)$	2a	0.88	1.9	30 ^c
	$\text{CR} = 105 - 1.78(\text{SDI}\%) + 0.012(\text{SDI}\%)^2$	2b	0.97	3.2	34
1981 study & Maple Ridge study	$D\% = 38.1 + 7.94(S)^2 - 1.10(S)^3$	3	0.97	3.9	10
	$V\% = 98.4 - 2.58(S)^2$		0.91	6.9	10

^a R^2 is the coefficient of determination adjusted for degrees of freedom, $S_{y,x}$ is the standard error of estimate, and n is the sample size. Each regression was highly significant ($P < 0.001$).

^b Variables: SDI% is stand density index (Reineke, 1933) in year 21 expressed as a percentage of the maximum value for Douglas-fir; M is volume mortality during years 21–25 ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$); CR is crown ratio (%) in year 21; S is planting spacing (m); PAI is periodic annual increment of volume ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) during years 21–25; and $D\%$ and $V\%$ are dbh and stand volume, respectively, expressed as a percentage of maximum values observed in the 1981 study (year 25) or Maple Ridge study (year 23).

^c Regression does not include the 4 plots for the 1-m planting spacing.

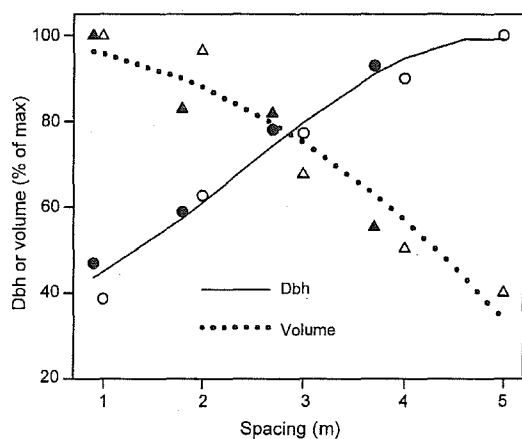


Fig. 3. Regression relationships of percentage of maximum values for dbh (circles) and stand volume (triangles) to planting spacing for Douglas-fir in the 1981 study (year 25; open symbols) and in the Maple Ridge study (year 23; filled symbols) (equations are listed in Table 4).

because of competition-induced growth reductions and mortality. The disproportionately low values of volume PAI observed in the 1-m spacing were associated with average crown ratios of 36–44%—values below the threshold at which competition-induced mortality was detected (crown ratio = 52%). With increasing SDI%, volume PAI in the 1981 study diverged from that observed in the 1981 study—a response that may be attributable to growth stagnation because only minor amounts of volume mortality occurred during years 21–27 ($\leq 0.2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$).

In the 1981 study, average crown ratio in year 25 was closely related to SDI% in year 21 for all spacings ($R^2 = 0.97$) (Fig. 2b; Table 4). In this quadratic relationship, crown ratio varied little (36–44%) for values of SDI% above the threshold of 52% perhaps because competition-induced mortality during years 21–25 claimed those trees having lower values of crown ratio. For a range of SDI% values, crown ratio of trees at Maple Ridge averaged 2–7% points greater than observed in the 1981 study (Fig. 2b).

Based on combined data from the 1981 study and the Maple Ridge study, the relationships of average dbh and stand volume in year 25 to planting spacing intersected when spacing equaled 2.9 m, indicating equivalent relative development for the two variables (77% of maximum) (Fig. 3; Table 4). Therefore, a planting spacing of about 3 m resulted by year 25 in an equitable compromise between allocation of growth to tree size and stand yield. Although a statistical comparison was not possible because of the small sample size of each regression ($n = 10$), the relationships differed little between the two sites.

4. Discussion

This research has identified several fundamental relationships regarding effects of planting spacing and site quality on growth and mortality rate of Douglas-fir. It is important to emphasize that planting spacing should be viewed as a surrogate for the timing at which competitive interactions among trees began, and therefore, its effects should be interpreted as indirect. As noted in the results above, a given planting spacing common to the three study sites often resulted 23–27 years later in very different SDI% values because of variation in site quality and its associated effects on timing and intensity of inter-tree competition.

The tree and stand variables responded to planting spacing in two ways: (1) a difference between the closest spacing and the other spacings, as observed for average height, cumulative mortality, and volume mortality, and (2) large differences among

close spacings and small differences among wide spacings, as observed for stem diameter, slenderness ratio, crown size, and stand growth variables. The two response types can be attributed to the greater tolerance of height growth and survival of young conifers to competition compared to that of variables derived primarily from growth in stem diameter or crown size (Wagner, 2000).

In contrast to results presented by Scott et al (1998) and Woodruff et al. (2002), early growth in height did not differ among planting spacings (Hypothesis 1). The growth increases reported by Scott et al and Woodruff et al probably resulted from increased allocation to aboveground biomass in response to changes in the light environment (i.e., reductions in the red/far red ratio) in high-density stands (Ritchie, 1997). The closest spacings in the studies by Scott et al (1998) and Ritchie (1997) had height: spacing ratios that exceeded 1.0 and 2.3, respectively, indicating that seedlings were tall enough to influence the light environment of their neighbors. However, seedlings growing at the closest spacing (1 m) in the 1981 study probably had little influence on the light environment of their neighbors because their height averaged 0.46 m in year 3, resulting in a height: spacing ratio of 0.5.

As expected, average top height in year 25 did not differ among planting spacings in the 1981 study (Hypothesis 2) because of its invariance to a broad range of stand densities (Larmer, 1985). However, average height in the 1-m spacing was 3–5 m less than in each of the other spacings because the closest spacing included a significant number of trees from the intermediate and suppressed crown classes (data not shown).

Combined effects of reductions in tree growth and onset of competition-induced mortality explain the lower values of volume PAI observed for the 1-m spacing versus the 2–6 m spacings in the 1981 study. Volume PAI in the 2-m spacing during years 21–25 was approximately $2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ greater than in the 1-m spacing, and volume mortality in the 1-m spacing ($1.4 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) accounted for 70% of this difference. Although reductions in stem density from competition-induced mortality are likely to stimulate growth of surviving trees, such growth increases can only partially compensate for losses in growing stock due to mortality. As a result, volume increment of stands established at close spacings generally declines and is eventually surpassed by stands established at wider spacings (Reukema, 1979; Peet and Christensen, 1987)—a phenomenon referred to as the "crossover effect" by Oliver and Larson (1996). Therefore, the 2-m spacing will likely exhibit superior stand growth until it, too, succumbs to growth reductions and competition-induced mortality.

Stands in the Maple Ridge study had a smaller range of average heights and lower average crown ratios than those in the 1981 study, yet for a given value of SDI%, crown ratio at Maple Ridge averaged 2–7% points greater than in the 1981 study. In addition, at the closest spacing, crown length at Maple Ridge was 3 m greater than in the 1981 study. The larger crown sizes for a given stand density can be viewed as both a symptom and a cause of the high productivity of stands at Maple Ridge. Greater site productivity, often attributed to higher levels of resource availability, may have enabled trees at Maple Ridge to retain longer crowns for a given level of stand competition, and the larger crowns, and therefore higher leaf areas, contributed more to net production (Long et al., 2004). In addition, competition-induced mortality at Maple Ridge probably eliminated many of the trees that had low crown ratios, resulting in both an increase in mean crown ratio and additional growing space for surviving trees, enabling them to retain longer crowns.

The onset of competition-induced mortality was associated with values of SDI% that exceeded 52% (similar to the 55% threshold identified by Drew and Flewelling, 1979) or values of crown ratio less than 52%. Crown ratio has been interpreted as an

index of the ratio of photosynthesizing tissue to respiring tissue in a tree (Oliver and Larson, 1996, p. 77); thus, a low value indicates that a tree is less able to support its energy demands of growth and respiration, making it increasingly susceptible to mortality. The minimal mortality, observed in the 1925 study during years 21–27 may be attributable to delayed stand development, or possibly growth stagnation (Fig. 1). In the Maple Ridge study, the cumulative mortality rate averaged 2–4% per year during years 19–23 for trees planted at 0.9-, 1.8-, and 2.7-m spacings versus 1% per year or less for trees planted at 3.7- and 4.6-m spacings (Reukema and Smith, 1987). In the three closest spacings at Maple Ridge, this mortality is probably a result of intraspecific competition because, by year 19, values of SDI for these spacings equaled or exceeded the threshold value of 52%.

Slenderness ratios of 100 or greater were observed in the closest spacings of each of the three studies, indicating a limitation in stand stability (Wilson and Oliver, 2000). This instability is symptomatic of the competitive environment of close spacings wherein diameter growth is more restricted than height growth, decreasing stem taper (Larmer, 1985; Waring and Schlesinger, 1985, pp. 34–37), and crown recession is accelerated, elevating a tree's center of gravity.

Analysis of combined data from the 1981 study and the Maple Ridge study indicated that a planting spacing of 3 m allowed equivalent development of dbh and stand volume by 23–25 years of age. This finding confirms what many regeneration foresters have been practicing intuitively for years: an intermediate spacing of 3 m provides the best compromise for development of average tree size and stand yield of coast Douglas-fir. In general, gross production of biomass is maximized when forest stands are grown at close spacings (Assmann, 1970; Curtis et al., 1997). However, biomass of individual trees is maximized at wide spacings that promote crown development and thereby maintain individual tree growth. Thus, net production of stand biomass (gross production minus mortality) is maximized by establishing and managing stands at an intermediate spacing that sacrifices some stand growth to maintain growth of individual trees (Long, 1985; Peet and Christensen, 1987).

5. Conclusions

During the 25 years of the 1981 study, Douglas-fir planting spacings of 3 m or greater were associated with maintenance of crown ratios above 50%, slenderness ratios less than 90, and no evidence of competition-induced mortality. Competition-induced mortality accelerated as stand density exceeded 52% of the maximum SDI and as average crown ratio declined below 52%—conditions which developed by year 21 in stands planted at 1-m spacing.

Measures of crown size, such as crown ratio, can serve as indicators of potential productivity because they estimate relative access to resources for individual trees (Long et al., 2004). Results from this research suggest that, for a given value of SDI, average crown ratio will be greater on sites of higher quality. The higher values of crown ratio observed at Maple Ridge may have resulted from greater availability of resources, competition-induced mortality of trees with smaller crown ratios, greater retention of crown length from additional growing space for surviving trees, or a combination of these processes. Regardless of the mechanism, a larger average crown size indicates that high rates of stand production are likely to be sustained.

Choice of the spacing at which to establish forest plantations is a critical silvicultural decision because it determines the timing and intensity of resource competition among trees. Results of this research indicate that establishing Douglas-fir plantations at a 3-m spacing will, by age 25 years, provide a desirable starting point for

subsequent management because its effects on subsequent stand dynamics: (1) allow trees to develop and maintain large crown sizes for sustaining stand growth, (2) maintain stand stability by keeping slenderness ratios below 90, (3) delay the onset of competition-induced mortality and thereby support continued acceleration of volume production through age 25 years, and (4) promote equal relative development of average tree size and stand yield. Future management decisions regarding thinning regimes and rotation lengths also should be considered when choosing the appropriate spacing for plantation establishment.

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