

Response of marginal height costs and marginal height benefits to competition

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ABSTRACT

Height growth in trees is expensive in terms of the amount of stem tissue required to maintain productive tissue in sunlight. However, shifting allocation from stem support to leader growth and foliage production may allow trees to minimize shading effects on photosynthesis, especially for shorter trees within the population. This hypothesis was evaluated with data collected in competition studies for red alder (*Alnus rubra* Bong.), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), and red pine (*Pinus resinosa* Ait.). Stem allocation per unit height growth was defined as a marginal height cost, and foliage added per unit height growth was defined as marginal height benefit. A symmetry index was calculated as a simple function of the cumulative relative costs and benefits of the shorter half of trees within plots. Analyses of variance indicated that marginal height costs and benefits significantly increased with age at rates unique to the different levels of competition. It also indicated that marginal height costs were related to the square of initial height at levels also unique to the competition treatments. The effects of competition on the symmetry indexes for marginal height costs and marginal height benefits significantly interacted with age for red alder and Douglas-fir, but not for red pine; for red pine, the indexes only varied with age. The slope between the two indexes was nearly one for all three species, indicating that marginal height costs and benefits change congruently with competition. The results did not support the hypothesis that shorter trees in competing populations change stem allocation to favor foliage growth. The correspondence between the symmetry indexes for marginal height cost and marginal height benefit was apparently due to coordinated development where population effects on how much and where leaf area is added with height growth determine how much stems need to grow to counter the changes in mechanical forces created by the change in crown dimensions. The results provide additional evidence that tree form is the result of coordinated development, not allometry between trees foliage and structural components.

1. Introduction

Trees are self-designing plants constantly seeking tolerable space, vertically and horizontally. How they occupy new space depends on past explorations and genetics. Occupying the space above the tree is most beneficial due to unobstructed access to light in uniform canopies. Trees must continually grow into this space otherwise it could be used by neighboring trees. Acquiring this space is increasingly expensive in terms of the amount of support tissue needed to continually grow in height. Eichhorn (1902 as cited by Skovsgaard and Vanclay, 2008) noted systematic increases in stem production per hectare with tree height for

lightly thinned European silver fir (*Abies alba* Mill.). Vanninen and Mäkelä (2005) reconstructed allocation within Scots pine (*Pinus sylvestris* L.) stands ranging from 13 to 72 years old and plotted the allocation percentages in relation to height growth. They showed that total production increased with height consistent with Eichhorn's observations and that stem wood made up a growing percentage of total production up to 12 m in height, staying constant at around 45 % up to 28 m. These dynamics of increasing support cost can be explained on the basis of stem mechanics and the increasing amount of sapwood needed to support transpiration (Dean et al., 2013a, Valentine, 1988).

In simple economics, maximum profit occurs when marginal cost

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equals marginal benefit (Brue, 1993). In the case of competition for light, marginal cost is the stem volume required for each addition of height, and marginal benefit is the increase in productive tissue or leaf area with each increment in height. Theoretically, a height exists that maximizes photosynthetic tissue and thus overall tree growth. Game theoretics indicate that optimum height varies with degree of shading by neighboring trees (Falster and Westoby, 2003). Therefore, the amount of crowding within a population of trees should affect the balance between marginal height cost and marginal height benefit.

Crowding creates a hierarchy of sizes in plant populations where a portion of the members dominate the rest of the population through asymmetric competitive dynamics (*sensu* Schwinning and Weiner, 1998). The strongest effects of reducing height costs should be evident in the shorter trees and these effects should fade with increasing height rank. This should cause the distribution of height cost to skew to the shorter trees. Although the frequency distributions of height costs may change with crowding, they provide no information on how costs change with height rank.

Lorenz (1905) introduced a method of illustrating wealth inequity within a population by plotting cumulative relative wealth against the cumulative percentage of the population for wealth-sorted data. Equitable distribution would produce a diagonal from the origin to 100 % of both cumulative wealth and cumulative population. Inequitable distributions produce a convex curve with convexity of the curve indicative of the degree of inequality in the distribution. The area between the diagonal and the curve (Gini coefficient) has been adapted by plant ecologists to measure the effect of competition on size distribution (Weiner and Thomas, 1986). Binkley (2004) adapted the Gini coefficient to measure the disparity in size and growth that occurs in tree populations. He named this metric growth dominance because the Lorenz curve for these data indicates the degree of dominance of larger trees in acquiring resources as indicated by tree growth. The higher the growth dominance, the more the larger trees dominate resource uptake and utilization. In contrast to the Gini coefficient, growth dominance can take negative values, indicating that larger trees have lost their dominant position in the population. Although these indexes are the result of competition effects on the distribution of size or growth, they cannot measure competition-induced changes in the distributions of marginal height costs and marginal height benefits. The median of relative contributions to total growth or size for size-sorted data, however, does reveal how many trees have changed growth and size due to crowding. For a uniformly sized population all with the same growth rate, the median of relative contribution to total growth of individual trees will be 50 %. Competition and inherent genetic variation creates variation in the population, reducing the median value of cumulative relative tree growth to <50 %. The value will be further reduced as crowding increases. Medians for two variables can be directly compared if the values are based on a common tree order. If trees need to conserve stem growth for the sake of foliage growth, the median of cumulative relative stem growth per unit height growth will decrease at a faster rate than the median of cumulative relative foliage growth per unit height growth as crowding increases.

The objective of this study is to test the hypothesized effect of crowding on marginal height costs and marginal height benefits in even-aged, tree monocultures using data collected in three studies established to analyze effects of different initial spacings or thinning intensities on growth and tree dimensions. The hypothesis was analyzed by calculating the medians of the cumulative relative stem growth per unit height growth and cumulative relative foliage accumulation per unit height growth of individual trees within experimental plots. The medians were centered on zero to create a symmetry index S where $S = 0$ signified uniform distributions of cumulative relative cumulative values; $S < 0$ signified normal to positively skewed values; and $S > 0$ signified negatively skewed values. If shorter trees in the plots reduced stem growth relative to the net change in foliage, the symmetry index for marginal height costs would decrease more quickly than the symmetry

index for marginal height benefit as spacing decreased or growing-stock levels increased.

2. Materials and methods

2.1. Data

Three long-term data sets spanning up to three decades of repeated measurements were used for these analyses. These data sets are rare in that the data were collected across the range of developmental stages that can be statistically analyzed. The three data sets were collected from an initial planting density study for red alder (*Alnus rubra* Bong.) and two levels of growing stock studies: one established in three naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) stands and another in an artificially regenerated red pine (*Pinus resinosa* Ait.) plantation. For all, dendrometric data were collected repeatedly on trees growing at different spacing and levels of growing stocks. In the red alder study, trees were planted at four square spacings (1.8 m, 2.8 m, 4.2 m, and 6.4 m) and allowed to develop without interference. In the Douglas-fir and the red pine studies, trees were thinned to a series of growing-stock levels. The growing-stock levels in the Douglas-fir study were set to four, fixed percentages of plot growth relative to the unthinned control plots. These percentages were 10 %, 30 %, 50 %, and 70 %. In the red pine study, growing stock was defined as basal area per hectare after thinning, (7, 14, 21, 28, 35 m²/ha) plus an unthinned control.

2.1.1. Red alder

The biological characteristics of red alder are described by Harrington (1990). Red alder is a common hardwood species that is native to the coastal region of the northern Pacific coast in North America. It is relatively short lived, maturing between 60 and 70 years old, and it is intolerant to shade. It is unique in relation to the other species in this study in that it fixes nitrogen. Height growth is rapid when young, slowing significantly after the juvenile stages. Typical heights at 50 years old range between 18 and 37 m.

The red alder study was established by the Hardwood Silviculture Cooperative at Oregon State University. Details of the study were described by Weiskittel et al. (2009). Plantations were established in western Oregon, western Washington, and southwestern British Columbia. Plot size varied from 0.13 ha to 0.20 ha, and trees were measured every 3–5 years beginning at age 3 years. Within the 22 installations, each planting density was randomly assigned to one plot. Installations were individual plantations located in the western portion of the two states and Canadian province. Measurement protocols are also described by Weiskittel et al. (2009) and summarized by Dean et al. (2013b). The number of trees measured in each plot varied by planting density and age, ranging from a maximum of 688 at age 4 in the plots with the closest initial spacing to a minimum of 45 at age 13 in the plots with the widest spacing (Table 1). All diameters and all heights were measured at each remeasurement.

2.1.2. Douglas-fir

The biological characteristics of Douglas-fir are described by Hermann and Lavender (1990). The levels of growing stock study was established in coastal Douglas-fir (*P. menziesii*, var. *menziesii*) which is a different variety than *P. menziesii* var. *glauca* growing east of the Cascade Mountains in the northwest region of North America. Coastal Douglas-fir is considered intermediate in shade tolerance and is very long lived, commonly living for 500 years. Old trees can reach 76-m tall. Height increments culminate between 20 and 30 years of age.

The Douglas-fir data used in this study was collected in the three installations of the Levels of Growing Stock Study established on National Forests in the Pacific Northwest region of the United States (Harrington, 2018). These installations and others established by Weyerhaeuser Company, Oregon State University, and the Canadian

Table 1

Minimums, maximums, and means of numbers of trees per plot, total tree height, and diameter at breast height (dbh) for each measurement period by treatment. Only data from the Rocky Brook installation is shown for Douglas-fir because measurements were collected at different ages at the other 2 installations. Data shown for the Rocky Brook installation is typical of the other installations.

		Age												
		4			7			10			13			
Species	Spacing		Min	Median	Max	Min	Median	Max	Min	Median	Max	Min	Median	Max
Red alder	6.4 m	Trees/plot	32	51	86	32	50	83	32	51	82	45 ^S	49	53
		Height (m)	0.3	3.0	3.0	0.8	7.4	15.3	3.2	9.2	19.5	8.4	14.6	17.6
		dbh (cm)	0.5	1.8	6.6	0.5	7.1	18.5	2.0	11.7	26.9	9.1	20.8	30.5
	4.2 m	Trees/plot	65	97	138	59	94	136	57	96	133	80	94	110
		Height (m)	0.4	3.0	7.4	1.7	7.4	14.4	2.6	11.0	18.0	6.8	14.7	20.6
		dbh (cm)	0.5	1.8	7.1	0.5	7.1	17.8	1.3	11.9	23.9	5.6	17.0	27.9
	2.8 m	Trees/plot	129	203	296	129	200	294	139	204	292	189	192	195
		Height (m)	0.3	3.3	8.2	1.4	8.0	14.3	2.3	10.4	18.8	6.4	13.7	22.6
		dbh (cm)	0.5	1.8	7.4	0.5	7.1	17.5	1.0	10.4	22.1	3.6	14.7	24.9
	1.8 m	Trees/plot	195	388	688	192	374	683	218	367	658	287	310	332
		Height (m)	0.3	3.4	7.9	1.7	7.4	14.4	2.6	9.2	18.6	3.9	11.1	21.1
		dbh (cm)	0.5	2.0	7.1	0.5	6.3	14.7	1.3	8.4	18.3	2.3	11.2	20.3
		Age												
		28			39			45			58			
Douglas-fir	Growing stock													
	10%	Trees/plot	63	63	79	20	24	35	14	17	25	9	11	15
		Height (m)	5.6	9.2	13.4	9.8	15.2	19.8	11.6	19.1	23.2	18.7	25.7	32.0
		dbh (cm)	6.9	11.2	17.3	11.9	19.8	29.0	13.7	25.1	35.3	23.1	35.3	45.7
	30%	Trees/plot	73	74	78	37	49	51	32	45	45	25	32	35
		Height (m)	5.7	9.4	21.7	9.5	15.1	19.7	11.6	18.0	23.6	13.7	22.9	31.0
		dbh (cm)	5.3	11.2	18.8	8.6	17.8	25.9	10.4	20.8	31.2	14.2	27.4	39.4
	50%	Trees/plot	63	73	73	52	63	69	45	59	66	35	38	60
		Height (m)	5.0	9.5	14.4	7.9	14.8	21.1	9.2	17.6	25.0	10.4	22.0	30.3
		dbh (cm)	6.4	11.2	18.8	8.9	16.4	26.7	8.9	18.9	31.8	9.9	22.6	40.1
	70%	Trees/plot	78	78	80	72	75	75	69	72	75	56	65	72
		Height (m)	5.2	9.8	13.8	8.8	16.1	21.3	10.4	19.1	24.6	12.2	24.6	31.7
		dbh (cm)	5.6	11.2	19.1	9.4	17.1	28.4	9.7	20.1	33.0	11.2	24.6	41.7
100%	Trees/plot	168	178	212	158	158	207	134	138	187	95	100	127	
	Height (m)	4.4	8.7	16.1	5.8	13.0	23.5	6.8	15.3	26.5	9.2	20.7	33.7	
	dbh (cm)	4.1	8.6	22.9	3.8	11.4	31.0	4.1	13.5	34.0	4.8	17.8	40.4	
		Age												
		50			65			70			80			
Red pine	Basal area													
	7 m ² /ha	Trees/plot	8.0	12.0	23.0	8.0	12.0	23.0	7.0	12.0	23.0	7.0	12.0	23.0
		Height (m)	12.8	17.8	20.7	14.0	20.1	22.9	14.3	21.0	22.7	17.4	23.5	26.5
		dbh (cm)	10.9	22.6	32.3	14.5	30.5	40.6	16.3	33.9	44.5	19.6	39.1	50.3
	14 m ² /ha	Trees/plot	16.0	24.0	41.0	16.0	24.0	41.0	16.0	24.0	41.0	16.0	24.0	41.0
		Height (m)	15.9	18.0	20.1	16.2	20.9	23.2	18.9	22.1	23.5	20.7	23.9	26.2
		dbh (cm)	10.7	22.6	35.1	14.5	29.7	42.7	15.7	32.5	45.7	17.0	36.6	49.8
	21 m ² /ha	Trees/plot	30.0	42.5	66.0	21.0	30.0	48.0	16.0	24.0	39.0	13.0	16.5	31.0
		Height (m)	10.7	17.9	19.5	15.4	20.9	23.5	16.2	22.0	24.1	17.6	23.7	26.8
		dbh (cm)	9.4	21.6	31.5	10.2	27.1	38.4	10.2	29.2	41.4	11.2	32.5	45.7
	28 m ² /ha	Trees/plot	44.0	55.0	72.0	34.0	42.0	56.0	28.0	33.0	48.0	21.0	25.0	39.0
		Height (m)	15.7	18.0	20.1	18.4	20.9	23.9	19.4	22.0	26.8	20.9	23.8	26.8
		dbh (cm)	10.7	22.4	32.0	11.9	26.9	36.1	12.7	28.7	38.1	13.5	32.3	40.9
35 m ² /ha	Trees/plot	63.0	75.0	99.0	49.0	55.0	78.0	41.0	48.0	65.0	33.0	40.0	57.0	
	Height (m)	14.9	17.9	20.8	17.4	17.4	24.7	18.3	22.0	24.8	19.8	23.8	28.1	
	dbh (cm)	10.7	21.3	30.5	11.7	25.1	35.6	11.7	27.2	37.3	14.7	30.0	40.4	
Control	Trees/plot	76.0	89.0	118.0	73.0	84.5	109.0	69.0	82.0	105.0	66.0	74.5	91.0	
	Height (m)	14.3	18.0	22.0	18.6	20.9	25.6	19.8	22.0	27.1	22.1	23.8	29.9	
	dbh (cm)	9.9	22.5	32.3	12.2	25.4	36.3	12.2	26.9	37.8	16.3	29.0	40.1	

^SThe minimum number of trees increased from age 10 to 13 because some plots across the installations were not measured at age 13. The number of trees per plot decreased or remained the same through time for individual installations.

Forest Service comprised the Douglas-fir Levels of Growing Stock Study (LOGS) described by Curtis and Marshall (1986). The three USDA Forest Service installations were established in Washington and Oregon on the Olympic (Rocky Brook installation), Gifford Pinchot (Iron Creek installation), and the Umpqua (Stampede Creek installation) National Forests. Within each installation, levels of growing stock were randomly assigned to three, 0.08-ha plots. Trees in the plots had naturally regenerated. Measurement frequency varied by installation because thinning intervals were set according to height increment. The number of trees measured at the Rocky Brook installation varied from a maximum of 212 at age 28 years for the unthinned control to a minimum of 9 at age 58 years for the 10 % level of the growing stock (Table 1). These numbers are typical of the other two locations. Diameter at breast height (dbh) was measured for all trees, and total height and height to the base of the live crown were measured on a subsample of trees whose number depended on growing-stock level.

2.1.3. Red pine

The biological characteristics of red pine are described by Rudolf (1990). The range of red pine is in the northeastern and north central regions of North America. Red pine is intolerant to shade, but it does not seem to be as intolerant as red alder. Trees as tall as 43 m have been recorded, but heights of 21 to 24 m are more typical at maturity. Height increment slows significantly after 100 years of growth. The maximum life span of red pine is substantially shorter than that of Douglas-fir and is at least twice as long as that of red alder.

The red pine study was also designed to examine the effects of maintaining fixed levels of growing stock on tree and stand growth. This study was established in the Birch Lake plantation planted with 2,500 trees per hectare on the Superior National Forest in northern Minnesota, USA. The six basal area treatments were assigned at random to 18, 0.8-ha plots divided into three blocks. These plots were split into thirds to accommodate three thinning methods: low, crown, and combined. Analyses were conducted at the plot level, however. Plots were thinned about every 10 years, and trees were measured every 5–10 years. Diameter at breast height was measured on all trees greater than 8.9 cm, and height was measured on five trees per plot. Height to the base of the live crown was measured on an average of 57 percent of the trees. The number of trees measured at each measurement period varied from a maximum of 118 at age 45 in the unthinned plots to a minimum of 7 at age 80 for the 7 m²/ha basal area treatment (Table 1).

2.2. Variables

2.2.1. Marginal height cost

Stem volume increment per meter of height growth was calculated for each tree in the plot. Tree-volume equations for red alder, Douglas-fir, and red pine are described by Hibbs et al. (2007), Bruce and DeMars (1974), and Fowler (1997), respectively. Equations to calculate missing heights in the Douglas-fir and red pine data were developed using the procedure described by Dean et al. (2021). Volume increment per height increment was calculated for each tree that survived between measurement periods.

2.2.2. Marginal height benefit

Net leaf area added per meter of height increment was calculated for each tree that survived between measurement intervals. Leaf area per tree was calculated with regression equations based on combinations of dbh and height. The equation for red alder was developed by Helgerson et al. (1988) with 18, 10-year-old red alder trees collected in western Oregon. The equation based on dbh explained 91 % percent of the log-transformed values of leaf area. The equation was corrected for logarithmic bias. The equation for Douglas-fir was developed by Dean et al. (2021) based on data collected by Maguire and Bennett (1996). Leaf area per tree was regressed on power functions of dbh and total height with data from 20 trees ranging in age from 10 to 28-years old. Trees

were destructively harvested in Oregon, Washington, and British Columbia. The equation explained 82 % of the variation in leaf area. The equation for red pine was developed by Penner and Deblonde (1996). Twenty trees ranging in age between 21 and 57-years old were selected from three plantations within the Great Lakes – St. Lawrence region in Ontario province, Canada. Penner and Deblonde (1996) developed two sets of linear equations: one between sapwood cross-sectional area at breast height and leaf area and another between basal area at breast height and sapwood cross-sectional area. The authors stated that the fits were good. The leaf area for the red pine used in this study was calculated from basal area to sapwood cross-sectional area to leaf area.

2.3. Analyses

2.3.1. Symmetry index

The symmetry index created for this study applies to even-aged populations of trees and measures the vertical distance between the median value of cumulative sums of relative marginal height cost and benefits of trees in a plot and a horizontal line through the point where the shorter half of the trees are contributing 50 % of the growth (Fig. 1, diamond). Normal and positively skewed distributions produce convex Lorenz curves (Fig. 1, curves A and B). The median of points comprising a curve represents the proportion of total marginal height cost or total marginal height benefits contributed by the shorter half of the trees on a plot. It is possible that the shorter half of the population can contribute greater than half of the total costs and benefits on a plot (not shown). The cumulative proportion of the shorter half of the population will decrease as crowding increases (Fig. 1, A to B), resulting in the cumulative proportion of growth at the median height decreasing some amount. Subtracting 0.5 from the cumulative proportion of growth at the median tree height creates the symmetry index used in this study. Subtracting 0.5 from the cumulative value centers the index on zero bounded by -0.5 and 0.5 . The more negative, the greater the effect of competition on skewing the distributions to smaller values (Fig. 1, SA >

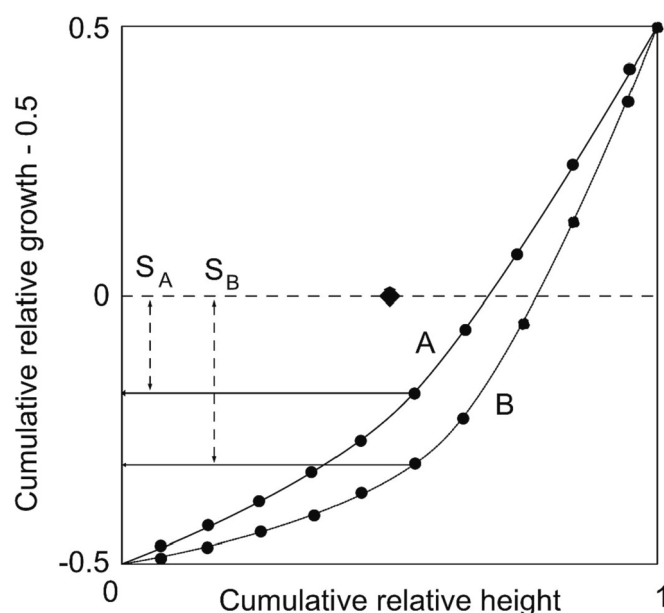


Fig. 1. Conceptualization of symmetry index. Index is the distance from a horizontal line through the theoretical median value of the cumulative relative growth attribute for a population where height is symmetrically distributed and height growth is proportional to height (diamond). Curves represent two tree populations with different distributions of a growth attribute. In population A, the shorter half of the trees contribute more to the total sum of the growth attribute than the shorter half of the trees in population B. The symmetry index for A (S_A) is greater (less negative) than the symmetry index for B (S_B). See text for more discussion.

S_B), and the more positive, the greater the effect of isolation (not shown).

2.3.2. Statistical analyses

The effects of initial spacing and level of growing stock on marginal height cost and benefits were analyzed with mixed, linear models for repeatedly measured data. The treatments were treated as fixed effects and age was included as a covariate to account for possible interactions between treatment effects and age. Repeated measures were treated as autoregressive type 1 effects. The number of different sites used in the red alder study allowed installations to be treated as a random effect. Random effects differed by study: for red alder and Douglas-fir, random effects were installations, and for red pine, the random effect was block. Similar analysis was conducted for evaluating treatment effects on the relation between initial height and marginal height costs; initial height replaced age in the model. All analyses were conducted using Proc Mixed with SAS (ver 9.4, Cary, NC) with the guidance from Littell et al. (2006).

3. Results

3.1. Competition effects on mean characteristics

The complete data set for the three species confirms the effects of planting density and level of growing stock on the mean dimensions of the trees reported for earlier stages of the studies. Evidence of competition was apparent by the last measurement in each study. Median values of diameter at breast height (dbh) for the closest spacing in the red alder study and the unthinned plots in the Douglas-fir and red pine studies were the smallest among the density treatments (Table 1). At the other end of the competition spectrum, median dbh values were the largest for the widest spacing and the lowest growing stock levels. The density treatments had similar effects on median height.

Competition effects on marginal height cost and benefits were confounded with age for all three species. Probabilities for a higher F value were all <0.011 for the interaction between initial spacing and age (Table 2). For all species, both marginal height cost and marginal height benefit generally increased with age in a radiating pattern from the origin (Fig. 2). The steepest ascent was seen for the most widely spaced trees and lowest growing stock levels with slope progressively declining as initial spacing decreases and growing-stock level increases. The lines for the closest spacings and the unthinned controls had the lowest slopes within each study. The radiating lines and the ordering of slopes within each study suggests that both marginal height costs and marginal height benefits decreased with competition, and the effects of competition on costs and benefits increased with age.

Table 2

Least-square means of marginal height cost ($\Delta v/\Delta h$) and marginal height benefit ($\Delta Al/\Delta h$) obtained from analyses of covariance for repeated measurements for the three species with measurement age as the covariate. Fixed effects: initial spacing or growing-stock level effects. Random effects: installation (red alder, Douglas-fir); block (red pine).

Fixed Effects	df		$\Delta v/\Delta h$		$\Delta Al/\Delta h$	
	num.	dem.	F	P > F	F	P > F
Red alder						
Spacing	3	256	5.36	0.001	1.73	0.162
Age	1	256	1043.10	<0.001	756.5	<0.001
Sp $\times$ Age	3	256	32.56	<0.001	28.9	<0.001
Douglas-fir						
% Growth	4	288	5.22	0.001	1.55	0.188
Age	1	288	376.20	<0.001	34.88	<0.001
% G $\times$ age	4	288	18.30	<0.0001	5.3	<0.001
Red pine						
Ba/ha	5	101	1.7	0.142	1.33	0.257
Age	1	101	80.19	<0.001	22.24	<0.001
Ba/ha $\times$ Age	5	101	5.38	0.002	3.17	0.011

Marginal height cost increased with height for all species (Fig. 3) with the widest spacings and the lowest levels of growing stock adding more stem volume per height increment than the closest spacing spacings and highest levels of growing stock. Linear-model fits to these data all included an interaction term between competition treatment and initial height squared as a simple transformation to account for curvilinearity evident in the relationship. The coefficients for each combination of treatment and height squared decreased with increasing competition within each study (Table 3).

3.2. Symmetry indexes

For both red alder and Douglas-fir, the symmetry indexes for both marginal height cost ($S_{\Delta v/\Delta h}$) and marginal height benefit ($S_{\Delta Al/\Delta h}$) interacted significantly with age (Table 4). The interaction of initial spacing or growing-stock level with age on the symmetry indexes was similar for both red alder and Douglas-fir (Fig. 4). The slopes between $S_{\Delta v/\Delta h}$ and age and between $S_{\Delta Al/\Delta h}$ and age were positive for the widest spacing, becoming systematically negative with increased spacing. For Douglas-fir, both $S_{dv/dh}$ and $S_{dAl/dh}$ increased with age in the lowest levels of growing stock. With increased growing-stock level, the change in the symmetry index with age became increasingly negative. The lines relating $S_{dv/dh}$ and $S_{dAl/dh}$ to age for the self-thinning plots were nearly horizontal but substantially lower than the bundle of lines describing the relationships for the lower levels of growing stock.

The symmetry indexes for the red pine plots exhibited marked variation, blending the effects of residual basal area on these variables. Age was the only factor that was related to the either $S_{\Delta v/\Delta h}$ or $S_{\Delta Al/\Delta h}$ with these data. The slope of the fitted lines was positive but quite shallow.

3.3. Relation between the symmetry indexes

For all four species, $S_{\Delta v/\Delta h}$ and $S_{\Delta Al/\Delta h}$ are closely correlated (Fig. 5). In addition, pairs of $S_{dv/dh}$ and $S_{dAl/dh}$ group together depending on the spacing or level of growing stock they represent moving from the center of the plot downward and to the left as spacing decreases or level of growing stock increases. The positive slopes indicate that both $S_{\Delta v/\Delta h}$ and $S_{\Delta Al/\Delta h}$ increase with wider initial spacing and decreasing level of growing stock.

Regressing $S_{dAl/dh}$ on $S_{dv/dh}$ shows that the slope between the two variables ranged from 0.9 for red alder to 1.0 for Douglas-fir and 1.2 for red pine (β_1 , Table 5). Competition treatment did not interact with the slope for any species. For red pine and Douglas-fir, the intercepts of the fitted lines were significantly affected by level of growing stock. No pattern between the intercepts and level of growing stock was evident.

4. Discussion

Although the effects of competition on mean marginal height cost per plot and on the distribution of marginal height cost among trees in a plot suggest that trees reduce stem support when competing with other trees, the nearly 1:1 relationship between the symmetry indexes is evidence against the hypothesis. Within each study, the slope of a line fit through the two symmetry indexes was not affected by competition level, although the intercept varied slightly with level of growing stock for Douglas-fir (Table 5). For each study, the data pairs grouped along different segments of the line according to treatment level, with the data from the closest spacings and highest levels of growing stock located at the bottom left of the line and the data from the widest spacings and lowest levels of growing stock located at the top right of the line (Fig. 5). Negative values of the symmetry indexes for marginal height costs and benefits indicate positively skewed data, which has been reported often for crowded tree stands; however, since the symmetry indexes are based on height-sorted data, competition-related changes in the symmetry index mean that marginal height cost and marginal height cost of

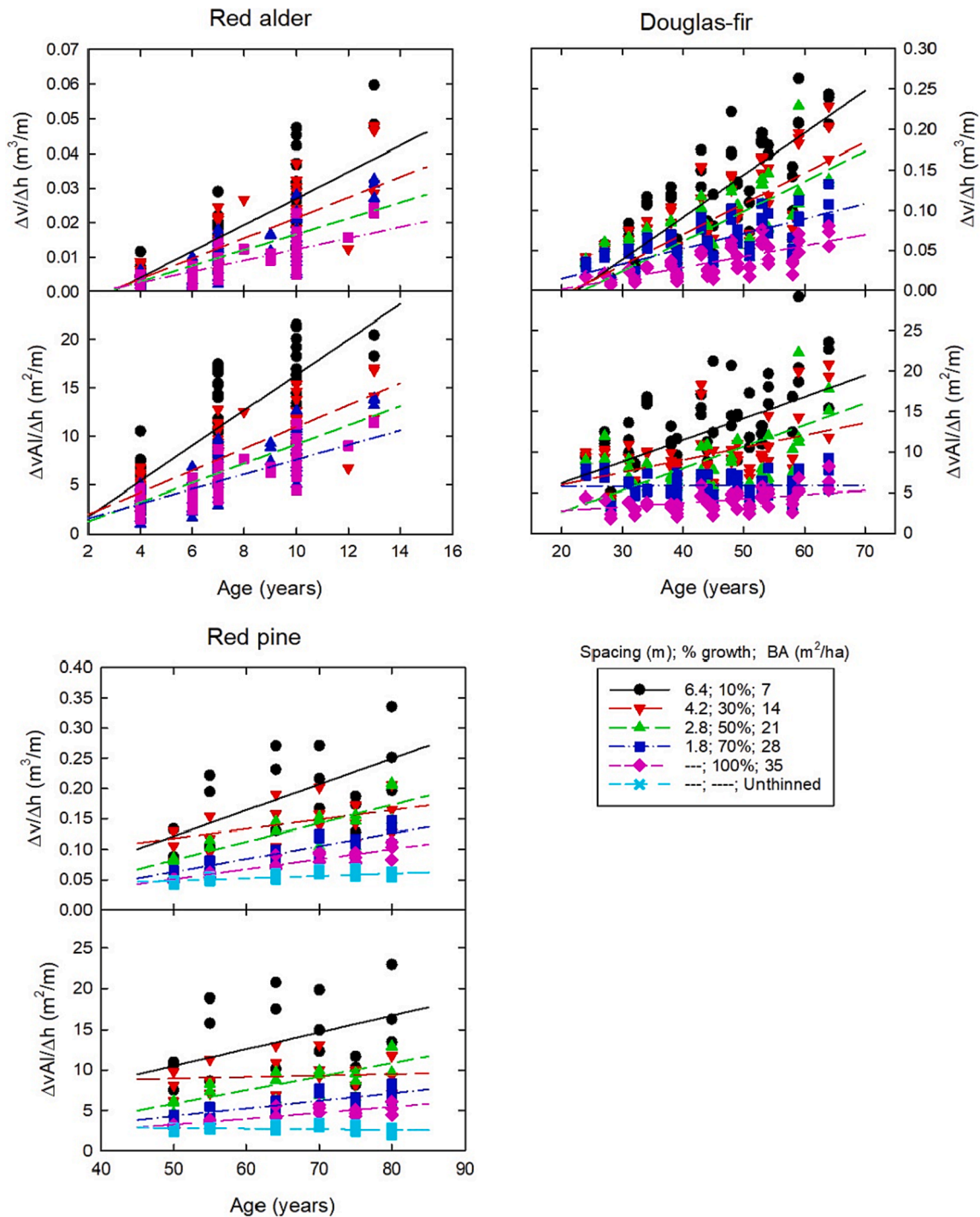


Fig. 2. Scattergrams of marginal height cost ($\Delta v/\Delta h$) and marginal height benefit ($\Delta AI/\Delta h$) by treatment and age. Each point is a plot mean. Lines for relating cost and benefit with age from linear mixed model analyses of all trees with age included as a continuous variable.

individual trees change up or down congruently.

The concurrent changes in stem volume growth and net foliage additions per unit height growth suggest that competition affects above-ground tree form. Dean et al. (2021) have shown that plot sums of marginal height cost increases with canopy foliage density and decreases with live-crown ratio using the same Douglas-fir and red pine data used in this study. Foliage density was calculated as the quotient between leaf area index and mean canopy depth. Both foliage density and mean live-crown ratio have been shown to co-occur with increasing level of competition (Long, 1985; Dean and Baldwin, 1996; Smith and Long, 1989). Increased foliage density and smaller live-crown ratios

indicate more foliage is held higher in the canopy as crowding increases, which increases the leverage or bending moment on the stem when subjected to wind. According to the constant-stress principle of stem formation, bending moment experienced in the stem is countered by basal area growth that varies by distance from the median of leaf area. In other studies, this model has been shown to describe stem dbh of all trees within temporary plots installed across a wide range of tree densities (Dean and Long, 1986; Meng et al., 2007; Lundqvist and Elfving, 2010). Dean (2001) and Dean (2004) derived production equations from the constant-stress model that described both stem volume growth and basal area growth from the plot sums of bending moments and the periodic

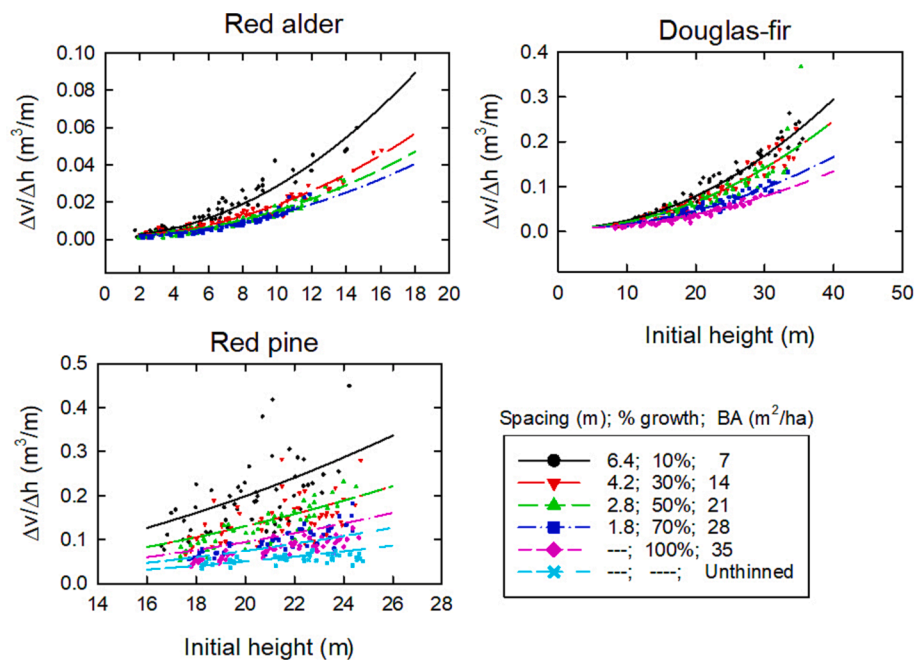


Fig. 3. Scattergrams of marginal height cost ($\Delta v/\Delta h$) and initial height by species and treatment. Each point is a plot mean. Lines for relating cost and initial height squared fit with a linear mixed model with spacing or growing stock as a fixed effect. Table 3 lists coefficients for individual curves.

Table 3

Estimated coefficients for the mixed, linear regression model. $y = [\beta_0 + \sum_{j=1}^{m-1} (E_j) i_j] + \beta_1 \bullet x + \gamma + \epsilon$ with repeated measures. $y = \frac{\Delta v}{\Delta h}$, $x = h^2$, β_0 and β_1 are regression parameters, E_j s are estimated treatment effects of treatment j on β_0 , and i_j s are indicator variables for treatment j , m is the number of treatments in each study, γ is a random effect, and ϵ is the error term. Random effect was installation for red alder and Douglas-fir and block for red pine. When all i_j s = 0, estimates of β_0 and β_1 are for the 1.8-m spacing treatment for red alder and unthinned treatments for Douglas-fir and red pine. For red alder, $E_{1...3}$ represent effects for the 6.4-m, 4.2-m, and 2.8-m spacing treatments, respectively. For Douglas-fir, $E_{1...4}$ represents effects of growing stock levels 10 %, 30 %, 50 %, 70 %, respectively, and for red pine, $E_{1...5}$ represents effects of residual basal areas 7, 14, 21, 28, and 35 m²/ha, respectively.

Species	Coefficient ($\times 10^{-4}$)		Effects on β_0 ($\times 10^{-4}$)				
	β_0	β_1	E_1	E_2	E_3	E_4	E_5
Alder	17.1	2.7	1.7	1.4	1.2		
Douglas-fir	67	1.8	1.5	1.5	1	0.8	
Red pine	-11.1	5	3.3	3.3	2.4	1.9	1.3

Table 4

Probabilities of greater values of F statistic from analyses of covariance of fixed and random effects on symmetry indexes of marginal height costs ($S_{\Delta v/\Delta h}$) and marginal height benefits ($S_{\Delta A/\Delta h}$) calculated with repeatedly measured data. Fixed effects are spacing and levels of growing stock. Random effects were installation for red alder and Douglas-fir studies and block for red pine. Measurement age is the covariant.

$S_{\Delta v/\Delta h}$					$S_{\Delta A/\Delta h}$				
Fixed Effects	df(n)	df(d)	F	P > F	Fixed Effects	df(n)	df(d)	F	P > F
Alder					Spacing	3	223	4.08	0.0076
Spacing	3	226	7.90	<0.001	Age	1	261	0.13	0.7192
Age	1	259	2.76	0.098	Sp $\times$ Age	3	256	16.09	<0.001
Sp $\times$ Age	3	256	32.87	<0.001					
Douglas-fir					% growth	4	117	5.16	0.001
% growth	4	128	4.62	0.002	Age	1	156	0.63	0.430
Age	1	189	19.83	<0.001	% G $\times$ age	4	126	4.58	0.002
% G $\times$ age	4	151	6.85	<0.001					
Red pine					BA/ha	5	298	0.51	0.766
BA/ha	5	298	0.79	0.559	Age	1	298	5.76	0.017
Age	1	298	6.05	0.014	Ba/ha $\times$ Age	5	298	0.77	0.575
Ba/ha $\times$ Age	5	298	0.63	0.680					

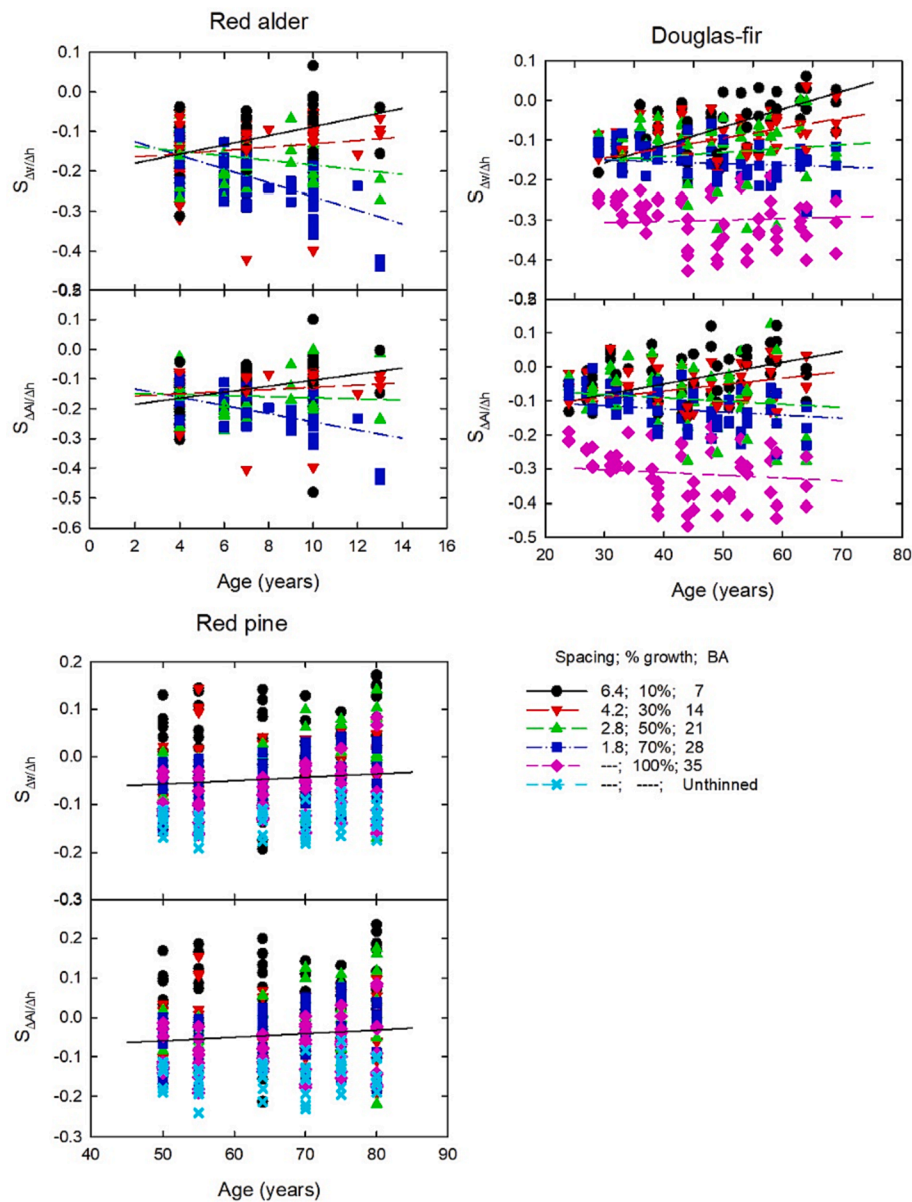


Fig. 4. Scattergrams of age and symmetry indexes for marginal height cost ($\Delta v/\Delta h$) and marginal height benefit ($\Delta Al/\Delta h$) by species and treatment. Each point is a plot mean. Lines for relating cost and benefit with age from linear mixed model analyses for all trees with age included as a continuous variable where a significant treatment $\times$ age interaction exists.

1984; Long and Smith, 1992; Hajek et al., 2015), which limits the proportion of crown surface area exposed to the sky (Cole and Lorimer, 1994). Since shoot growth is related to the degree of exposure to solar radiation (Kellomaki and Strandman, 1995), larger crowns should produce more leaf area per each unit of height growth. Therefore, the smaller crowns for trees planted closest together or in unthinned plots would not be able to produce as much leaf area as widely spaced trees leading to lower marginal height cost even for trees of the same initial height. Dean (2004) demonstrated how the change in the product of leaf area and height to median leaf area could predict basal area increment for a number of coniferous species with a regression model based on the constant-stress principle.

The upper range of symmetry index pairs moved into the first quadrant of the Cartesian Coordinate plane as the average age of the trees in the studies increased. None of the symmetry indexes were positive for plots in the red alder spacing study. Trees in the Douglas-fir study were much older than the red alder trees, and many values for both indexes were positive for plots subjected to the most intensive

thinning treatments. The red pine trees in the Birch Lake Plantation study were older than the Douglas-fir trees, and upper range of data pairs red pine extended further into the first quadrant than those for Douglas-fir plots. For this analysis, positive symmetry indexes indicate that the shorter half of the trees contributed greater than 50 % of either stem growth or leaf area accumulation when all trees grow taller by the same amount. This could occur when the height distribution is negatively skewed. In the older, lowest density plots, shorter trees could have caught up with the taller trees or died, truncating the shorter portion of the height distribution.

Working with the same red pine data set used in this study, Bradford et al. (2010) tested the effects of the various residual basal areas and thinning methods on Binkley's growth dominance coefficient to gain insight on the distribution of tree growth. Averaged across sampling dates, the growth dominance coefficient was not significantly different from zero for any of the thinned plots. However, the growth dominance coefficient for crown thinning was significantly different than zero for the lowest and two highest residual basal areas; changed sign from the

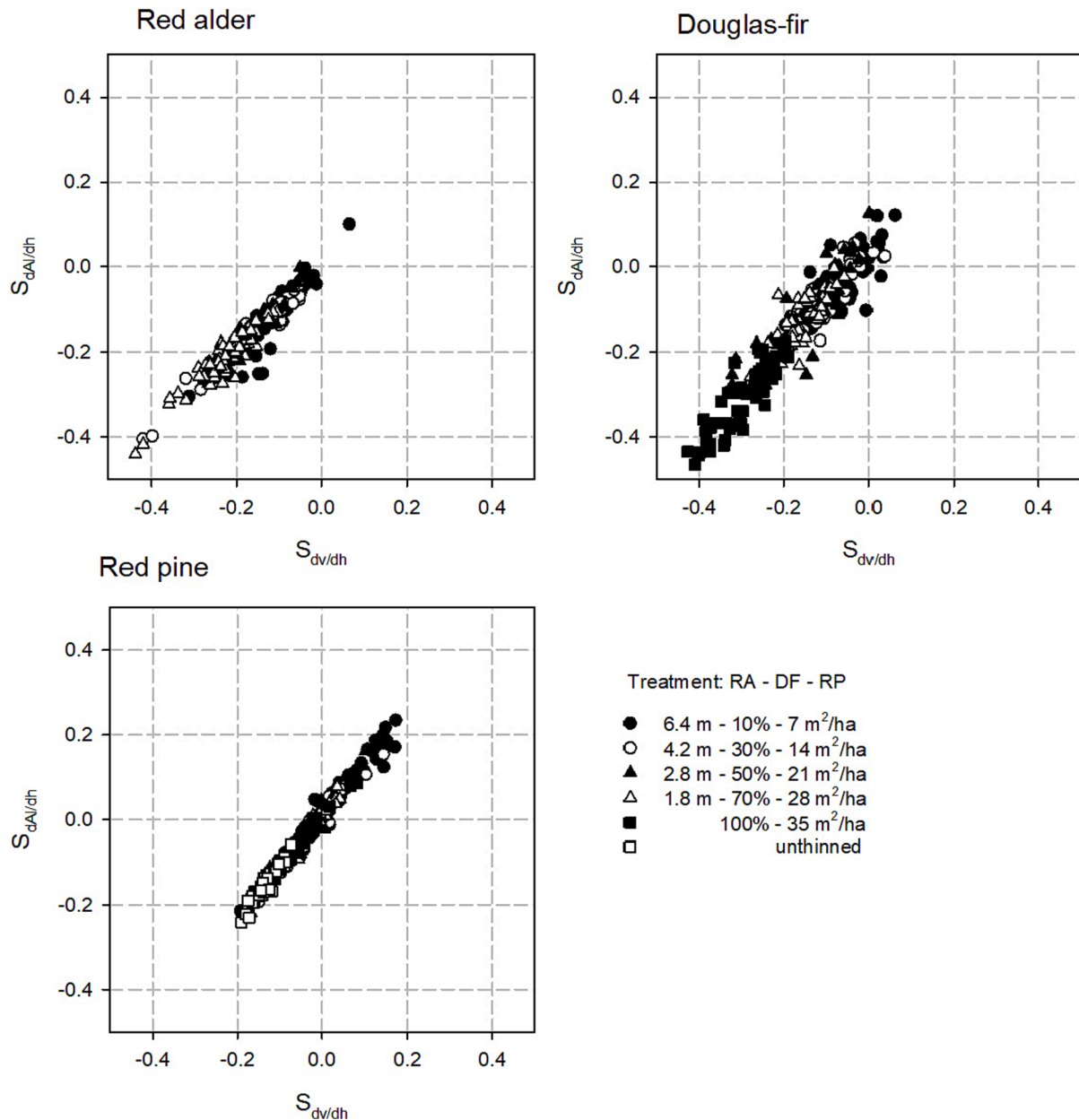


Fig. 5. Scattergram of symmetry index for marginal height cost ($\Delta v/\Delta h$) and marginal height benefit ($\Delta Al/\Delta h$) by species and treatment. Each point is a plot value. [Table 6](#) list regression coefficients for separate line fits through the data.

Table 5

Estimated coefficients and probabilities of greater F statistics for the mixed, linear regression model $y = [\beta_0 + \sum_{j=1}^{m-1} (E_j) i_j] + \beta_1 \bullet x + \gamma + \epsilon$ with repeated measures. $y = S_{\Delta v}$, $x = S_{\Delta Al}$, β_0 and β_1 are regression parameters, E_j s are estimated treatment effects of treatment j on β_0 , and i_j s are indicator variables for treatment j , m is the number of treatments in each study, γ is a random effect, and ϵ is the error term. Random effect was installation for red alder and Douglas-fir and block for red pine. When all i_j s = 0, estimates of β_0 and β_1 are for the 1.8-m spacing treatment for red alder and unthinned treatments for Douglas-fir and red pine. For red alder, $E_{1...3}$ represent effects for the 6.4-m, 4.2-m, and 2.8-m spacing treatments, respectively. For Douglas-fir, $E_{1...4}$ represents effects of growing stock levels 10 %, 30 %, 50 %, 70 %, respectively, and for red pine, $E_{1...5}$ represents effects of residual basal areas 7, 14, 21, 28, and 35 m²/ha, respectively.

Species	Fitted coefficient		Effect on β_0					P > F		
	β_0	β_1	E_1	E_2	E_3	E_4	E_5	β_1	Treatment	$T \times \beta_1$
Alder	-0.01134	0.9024						<0.001	0.1965	0.839
D-fir	0.02961	1.0145	0.03471	0.0412	0.03291	-0.00796		<0.001	<0.001	0.135
RP	0.01392	1.1894	0.007128	0.0148	0.01122	0.01024	0.008803	<0.001	<0.001	0.248

Table 6

Estimated coefficients for the mixed, linear regression model $y = [\beta_0 + \sum_{j=0}^{m-1} (\delta_{j+1})i_j] + [\beta_1 + \sum_{j=0}^{m-1} (\theta_{j+1})i_j] \bullet x + \gamma + \epsilon$ with repeated measures. $y = \frac{\Delta v}{\Delta h}$, $x = \frac{\Delta M}{\Delta h}$, $M =$ leaf area $\times$ height to median leaf area, β_0 and β_1 are estimated coefficients for the intercept and slope, respectively, δ_j and θ_j are treatment effects for the j^{th} treatment, m is number of treatments in each study, γ is a random effect, and ϵ is the error term. When all δ_j and $\theta_j = 0$, β_0 and β_1 refer to fits to the closest spacing for the red alder study and the two unthinned treatments for the Douglas-fir and red pine studies. The random effect for red alder and Douglas-fir were installations, and for red pine, it was block.

Red alder			Douglas-fir			RP		
Treatment	β_0	β_1	Treatment	β_0	β_1	Treatment	β_0	β_1
1.8	-8.509	0.897	100 %	-7.661	0.9193	Unthinned	-6.062	0.709
Effects	δ	θ	Effects	δ	θ	Effects	δ	θ
6.4	-0.048	0.085	10 %	0.559	-0.073	7	-0.517	0.167
4.2	-0.004	0.045	30 %	0.543	-0.08	14	-0.618	0.164
2.8	-0.044	0.03	50 %	0.467	0.076	21	-0.304	0.11
			70 %	0.268	0.046	28	-0.24	0.082
						35	0.144	0.005

lowest to highest residual density; and were significantly affected by this thinning treatment. The growth dominance coefficient for the unthinned plots was significantly greater than zero and significantly different from the coefficients for the thinned plots. The symmetry indexes responded differently to these growing-stock treatments than growth dominance coefficients. Growth dominance in the Bradford et al. (2010) study was calculated for tree biomass increment, whereas the symmetry index is calculated just for stem and foliage changes. Also, the present analysis lumped the thinning methods together and analyzed the indexes with age taken into account. Although the two symmetry indexes closely covaried, individual plot values varied substantially within a treatment such that treatment effects could not be detected even with a Type I error rate set to 10 %.

The correspondence between the distributions of marginal height costs and benefits may appear to be a forgone conclusion because stem volume and leaf area are calculated with common stem dimensions. Results from Dean and Cao (2003) demonstrate that the possibility of spurious correlations between marginal height costs and benefits is unlikely, however. In their analysis, they determined null correlation coefficients between structural components and periodic increments in the component by randomly selecting dbhs and heights from distributions derived from plot data and calculating the components with prediction models with varying degrees of terms and factors in both linear and nonlinear equation types. They found that the null correlation coefficient between foliage mass and stem mass was quite high (0.88) when foliage and stem mass were calculated with simple power functions of dbh. Using these same equations, the null correlation changed considerably when foliage mass was correlated with periodic increment of stem mass; it changed signs and declined by half. This indicates that the observed relationship between marginal height increment and marginal height costs are not the inherent result of using DBH and height to calculate stem volume and leaf area.

The congruence between $S_{\Delta v/\Delta h}$ and $S_{\Delta A/\Delta h}$ across all initial spacings and levels of growing stock indicates that height growth and survival of competing trees do not require increasing the risk of mechanical or hydraulic failure in exchange for foliage growth. According to these results, stem growth and foliage additions associated with a unit of height growth follow the same distribution patterns among trees regardless of competitive status. In addition to contradicting the basic assumption in game theoretics (e.g., King, 1990), this result also contradicts predictions of an ordering of allocation priorities within trees. For instance, the priority allocation hypothesis of Waring and Pitman (1985) assume that foliage has highest priority for the distribution of carbohydrate and that stem growth has the lowest priority. The transport-resistance model of Thornley (1991) suggests a cascade of allocations starting with foliage then to stem growth further down the chain. The matching distributions of marginal height cost and benefits suggests that allocation priorities remain constant regardless of degree of crowding; crowding affects crown properties, and the stem changes

accordingly.

The coordination between crown and stem growth has physiological support. Indole acetic acid (IAA) is produced in the rib meristem of elongating twigs and is translocated to and down the stem. The amount of IAA produced is related to amount of new tissue produced by the crown (Zimmermann and Brown, 1980, p.15). Poorter et al. (2012) reviewed the literature on biomass allocation and concluded that competition-induced changes in aboveground architecture explained growth responses better than strategic changes in allocation. Ford (2014) argued that competition effects on architecture must be considered in addition to effects on relative growth rates. Within an even-aged, single-species population, crowns will fit into the overall canopy where they can, and due to intercrown abrasion, a large majority of the crowns will be exposed to the sky. When the population is crowded, small spaces outnumber large spaces, which translates into greater numbers of small trees with corresponding lower marginal height costs and benefits. Coordinated development that enables the crown to at least reside in the canopy may be a better definition of competitiveness. In addition, coordinated development seems to explain tree growth under competitive conditions better than strategic changes in allocation.

From a practical perspective, these results reinforce the importance of height to tree and stand production. Although the importance of height is tacitly acknowledged when quantifying site quality by height attained at a standard given age, these results show that the dynamics of height growth during the rotation directly affect production rates since marginal height costs increase with the square of height (Fig. 3). These results also show that marginal height benefits (net foliage added per unit height increment) are closely tied to height increment (Fig. 5). Consequently, although stand production is usually ascribed to leaf area index, stand production can be equally related to periodic height increment. Long-term studies with loblolly pine (*Pinus taeda* L.) on the effects of weed control, fertilization, and irrigation on stand production have verified the relationship between stand production and leaf area index (Albaugh et al., 1998; Albaugh et al., 2004; Borders et al., 2004; Martin and Jokela, 2004; Samuelson et al., 2004; Albaugh et al., 2018). However, in each of these studies, where cultural treatments positively affected production, the treatments also positively affected height increment.

Process-based growth models would benefit from incorporating process-based routines for simulating height increment. Currently, height increment is based on age or diameter-height relationships (e.g., Sands and Landsberg, 2002). Branch studies have identified some of the factors affecting stem elongation, which should apply to the process of height growth (Remphrey and Powell, 1984; Kellomaki and Strandman, 1995; Deleuze et al., 1996). Given the interrelationships between competition, growth, and form, incorporating developmental processes involved in crown architecture is a logical addition to process-based forest growth models.

CRediT authorship contribution statement

Thomas J. Dean: Conceptualization, Formal analysis, Writing – original draft. **Constance A. Harrington:** Methodology, Data curation, Writing – review & editing. **Anthony D’Amato:** Methodology, Data curation, Writing – review & editing. **Brian J. Palik:** Methodology, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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