

# Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon<sup>1</sup>

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**Abstract:** Mixed conifer and hardwood stands in southwestern Oregon were studied to explore the hypothesis that competition effects on individual-tree growth and survival will differ according to the species comprising the competition measure. Likewise, it was hypothesized that competition measures should extrapolate best if crown-based surrogates are given preference over diameter-based (basal area based) surrogates. Diameter growth and probability of survival were modeled for individual Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees growing in pure stands. Alternative models expressing one-sided and two-sided competition as a function of either basal area or crown structure were then applied to other plots in which Douglas-fir was mixed with other conifers and (or) hardwood species. Crown-based variables outperformed basal area based variables as surrogates for one-sided competition in both diameter growth and survival probability, regardless of species composition. In contrast, two-sided competition was best represented by total basal area of competing trees. Surrogates reflecting differences in crown morphology among species relate more closely to the mechanics of competition for light and, hence, facilitate extrapolation to species combinations for which no observations are available.

**Résumé :** Des peuplements mélangés de conifères et de feuillus du sud-ouest de l'Oregon ont été étudiés afin de vérifier l'hypothèse selon laquelle les effets de la compétition sur la croissance et la survie d'un arbre diffèrent selon l'espèce compétitrice. Par conséquent, nous avons posé l'hypothèse que les mesures de compétition seraient mieux extrapolées si la préférence est donnée à des variables substitutives basées sur la cime plutôt que sur le diamètre (surface terrière). La croissance en diamètre et la probabilité de survie ont été modélisées pour des tiges de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) en peuplements purs. D'autres modèles qui tiennent compte du fait que la compétition s'exerce d'un seul ou des deux côtés en fonction de la surface terrière ou de la structure de la cime ont ensuite été appliqués à d'autres parcelles où le douglas de Menzies était mélangé avec d'autres espèces résineuses ou feuillues. Dans le cas de la compétition qui s'exerce d'un seul côté, les variables basées sur la cime ont donné de meilleurs résultats que les variables basées sur la surface terrière pour traduire l'effet de la compétition tant sur la croissance en diamètre que sur la probabilité de survie et cela peu importe la composition en espèces. Au contraire, la compétition qui s'exerce des deux côtés était mieux représentée par la surface terrière totale des arbres compétiteurs. Les variables substitutives qui traduisent des différences dans la morphologie de la cime sont plus étroitement reliées aux mécanismes de compétition pour la lumière et, par conséquent, facilitent l'extrapolation à des combinaisons d'espèces pour lesquelles aucune observation n'est disponible.

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## Introduction

As societies have demanded more and different products and amenities from the forest, mixed-species stands have be-

come more appealing. In addition to furnishing wood products, they can provide a more diverse habitat for some wild-life species, they can be more aesthetically satisfying to some people, and they are considered by others to be more "natural" in structure than even-aged plantations of a single species. Even from a strictly timber-production point of view, some mixes of species were thought to provide certain tending advantages over monocultures (West 1991), and the perception persists that mixed-species stands are more pest resistant, risk averse, or both (Ashton 2000). However, managing mixed-species stands is more complex than managing pure even-aged stands, largely because the competition processes, development patterns, and treatment options of mixed-species stands are more variable than those of pure-species stands (Oliver and Larson 1996).

Accounting for the differential effects of competing species on the growth of individuals has received much less attention than has the yield of mixed-species stands and

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plantations relative to the yields of the component species when grown in monocultures (e.g., Kelty 1992, 2000; Burkhardt and Tham 1992). Yet, these comparative yields are essentially the integrals of growth of the component species under similar total stand densities but differing species composition; hence, they imply differential competitive effects for a given unit of stand density. More difficult to assess is the measure of stand density applied in each study, but few, if any, of the cases reviewed by Kelty (1992, 2000) or Burkhardt and Tham (1992) apparently employed density measures that would serve well as surrogates for crown structure and shading effects. Various types of experimental designs have been implemented to test mixed-species yields (Firbank and Watkinson 1990), but it is widely conceded that it would be physically impossible to test all species combinations of potential interest. It is encouraging that in the few cases for which observational field studies have been compared with controlled experiments, the relative competitive abilities among species are in close agreement (Keddy 1990). This result would suggest that much potentially valuable information could be collected from observational studies in naturally regenerated mixed species forests. Plant-to-plant competition has been divided into two parts (Weiner 1990): (i) the influence of plant competitors on resource availability (competitive effects) and (ii) the response of plants to available resources in an environment modified by the competitor plants (competitive response). The term "competition" most often refers to direct interference (e.g., physical abrasion) or to exploitative competition (competition for light, water, or nutrients); however, "apparent competition" can result from interactions with natural enemies or be mediated by interactions with other species on the same trophic level (Connell 1990). On the basis of observations from a number of different plant communities, Keddy (1990) noted that a large portion of the competitive ability of a species was predictable from relative heights. All else being equal, taller individuals will capture more light, although the level of light competition imposed by larger trees, or one-sided competition, also depends on the pattern in vertical light extinction controlled by each species' crown structure (Vanclay 1994).

Two-sided competition results from competition for belowground resources, such as nutrients and moisture (Vanclay 1994). The intensity of two-sided competition can be affected by differences between species in their ability to absorb and efficiently utilize both moisture and nutrients and in their ability to tolerate deficiencies or excesses in both moisture and nutrients (Minore 1979; Tilman 1990). One- and two-sided competition have asymmetric effects on tree development. One-sided competition amplifies the variation in relative growth rate, whereas two-sided competition acts to slow the growth of all plants; that is, competition for light exaggerates relative differences in plant size, whereas competition for nutrients and water dampens the divergence in plant size (Weiner 1990).

In operational stands, species mixtures can occur in an almost infinite array of combinations, and as a result, it is unreasonable to expect that all possible combinations could be

sampled when developing models of diameter growth ( $\Delta D$ ) and survival probability (PS). Because interspecific competition can differ from intraspecific competition, failure to quantify these differences could be a major weakness both in extrapolating to mixed species stands and in specifying models to simulate mixed species dynamics (Burkhardt and Tham 1992). As a result, some modelers have questioned the ability of "empirical" models to characterize the development of mixed species stands (e.g., Bartelink 2000).

The objective of this study was to evaluate whether the effect of a given unit of tree competition depends on its species composition. Specifically, Douglas-fir  $\Delta D$  and PS equations incorporating alternative measures of one- and two-sided competition were developed for one-species mixture ("pure" stands) to predict Douglas-fir  $\Delta D$  and PS for stands with other mixtures of species. We chose to develop the Douglas-fir  $\Delta D$  and PS equations on pure-species stands for two primary reasons: (i) to represent a "control" situation in which competitive effects are not complicated by differential species effects, thereby providing a basis of comparison to mixed species stands, and (ii) to simulate the consequences of the common practice of applying equations developed from single-species research plots to multispecies inventory plots. The  $\Delta D$  and PS equations examined in this study are two of several equations needed in a model for projecting stand development. Equations for predicting height growth, crown recession, and regeneration also include measures of competition and, therefore, could be impacted by the species composition of the competitors.

### Past work on quantifying competitive effects on growth and survival

Because  $\Delta D$  (or basal area growth rate,  $\Delta BA$ )<sup>4</sup> and PS (or the probability of mortality, PM)<sup>5</sup> are key elements in modeling the development of mixed-species stands, many studies have explored ways to predict these attributes for a given tree. In general, these studies have found that  $\Delta D$  (or  $\Delta BA$ ) and PS (or PM) depend upon the following five classes of tree and stand attributes (Hann and Wang 1990; Hann and Larsen 1991): (i) the size of the tree; (ii) the vigor of the tree; (iii) the competitive status of the tree in the stand with regard to both one- and two-sided competition; (iv) the level of one-sided and (or) two-sided competition that a tree experiences within the stand; and (v) the productivity of the stand.

The following attributes have been the most common predictors in  $\Delta D$  (or  $\Delta BA$ ) and PS (or PM) equations:  $D$  for tree size (e.g., Monserud 1976; Hann and Wang 1990; Hann and Larsen 1991; Cao 2000), crown ratio (CR) for tree vigor (e.g., Wykoff et al. 1982; Hann and Wang 1990; Hann and Larsen 1991; Monserud and Sterba 1999), and site index (SI) for stand productivity (e.g., Holdaway 1984; Hann and Wang 1990; Hann and Larsen 1991; Hynynen 1995). A wider variety of competition attributes have been incorporated into  $\Delta D$  and PS equations to represent one-sided competition, including basal area in trees with larger  $D$  than the subject tree (BAL) (e.g., Wykoff et al. 1982; Hann and Wang

<sup>4</sup>By definition  $\Delta BA = \pi/2(2\Delta DD + \Delta D^2)$ .

<sup>5</sup>By definition  $PM = 1.0 - PS$ .

1990; Hann and Larsen 1991; Monserud and Sterba 1999) and crown closure at the top of the subject tree (CCH) (e.g., Hann and Wang 1990; Biging and Dobbertin 1995). Two-sided competition has often been represented by BA of the stand (e.g., Hamilton and Edwards 1976; Hann and Larsen 1991; Cao 2000). A combination of both a one-sided and a two-sided competition measure reflects the subject tree's social position, as well as the level of total competition.

Predicting  $\Delta D$  (or  $\Delta BA$ ) or PS (or PM) in mixed-species stands has usually been accomplished by developing separate equations for each species because of expected differences in both inherent growth potential for a given size and response to one-sided and two-sided competition (e.g., Hamilton and Edwards 1976; Wykoff et al. 1982; Buchman et al. 1983; Holdaway 1984; Wensel et al. 1987; Hann and Wang 1990; Wykoff 1990; Hann and Larsen 1991; Biging and Dobbertin 1995; Monserud and Sterba 1999). Some of the one- and two-sided competition attributes used in these equations do incorporate species differences to some extent (e.g., CCFL, CCH,  $CC_{66}$ , and CCF) by way of species-specific crown width equations, while others do not (e.g., BAL and BA). For a given species, the apparent assumption behind the former set of competition attributes is that differences in crown attributes (potential or actual crown width (CW) at different heights) will adequately explain the differential impact of competitor species on responses of the subject tree. The apparent assumption behind the latter set of attributes is that all species affect  $\Delta D$  (or  $\Delta BA$ ) or PS (or PM) uniformly in direct proportion to the square of diameter (i.e., that a unit of competitor basal area will affect the  $\Delta D$  (or  $\Delta BA$ ) or PS (or PM) of the subject tree in exactly the same manner, regardless of species). Therefore, two trees of different species but with the same  $D$  would provide the same contribution to BAL and BA but not necessarily the same contribution to CCFL, CCH,  $CC_{66}$ , or CCF. While alternative measures of competition have been explored in mixed-species stands (Hann and Wang 1990; Hann and Larsen 1991; Biging and Dobbertin 1995), apparently no studies have directly explored the validity of these implicit assumptions when predicting  $\Delta D$  (or  $\Delta BA$ ) and PS (or PM) for mixtures of species not represented in the original modeling data set.

## Data

Data were collected from plots located in the southwestern Oregon region of the Pacific Northwest, U.S.A. This area extends from near the California border in the south ( $42^{\circ}10'N$ ), to Cow Creek in the north ( $43^{\circ}00'N$ ), and from the Cascade crest on the east ( $122^{\circ}15'W$ ) to approximately 24 km west of Glendale ( $123^{\circ}50'W$ ). Because of its unique combination of weather conditions and geologic features, this area contains some of the more productive and ecologically complex coniferous forests in the world (site indices of up to 50 m at a breast height age of 50 years). Southwestern Oregon forests also have the distinction of growing on the widest range of soil and climatic conditions of any region within the Pacific Northwest, and it is here that a number of different floras merge to produce the most complex forests in the Pacific Northwest (Franklin and Dyrness 1973). A total of 27 coniferous species and over 17 hardwood species

are found within southwestern Oregon (Burns and Honkala 1990a, 1990b), and they often grow in mixed-species stands.

Permanent plots in the study area are very scarce and are limited to pure stands of Douglas-fir; therefore, the data were collected using backdated temporary plots located in 529 randomly selected stands. Such data provide unbiased estimates of permanent plot growth components (Wykoff 1990), and they have been applied widely both in the evaluation of alternative measures of competition (Biging and Dobbertin 1992, 1995) and in the development of the CACTOS (Wensel et al. 1987), FVS/Prognosis (Wykoff 1990), and ORGANON (Hann and Ritchie 1988; Hann and Larsen 1991) stand-development models. None of the sampled stands had been treated silviculturally in the past 5 years.

In total, 30 tree species were found on these 529 plots. The most common coniferous species was Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; found on 527 plots), followed by incense-cedar (*Libocedrus decurrens* Torr.; 244 plots), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.; 235 plots), ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws.; 191 plots), sugar pine (*Pinus lambertiana* Dougl.; 191 plots), and white fir (*Abies concolor* (Gord. & Glendl.) Lindl. ex Hildebr.; 161 plots). The most common hardwood species was Pacific madrone (*Arbutus menziesii* Pursh; found on 270 plots), followed by golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.; 156 plots), California black oak (*Quercus kelloggii* Newb.; 88 plots), canyon live oak (*Quercus chrysolepis* Liebm.; 82 plots), Pacific dogwood (*Cornus nuttallii* Audubon; 81 plots), and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.; 75 plots).

Only data from those plots containing Douglas-fir were analyzed in this study. The number of species on a plot in this subset of the data ranged from 1 to 12 per plot and averaged almost 5 species. A pure Douglas-fir plot was defined as containing at least 80% of its basal area in Douglas-fir, a definition commonly used in the Pacific Northwest (e.g., Curtis et al. 1981). Of the total number available, 162 plots were defined as pure Douglas-fir and 365 plots were defined as mixed-species composition.

Measurements taken at the end of the previous 5-year growth period on every tree included a mortality indicator of whether the tree died in the past 5 years or not,  $D_f$  (where an "f" in the subscript indicates the final measurement taken at the end of the growth period and an "i" indicates the initial measurement taken at the start of the growth period), total height ( $H_f$ ), and height to live-crown base ( $HCB_f$ ). Backdating to the start of the 5-year growth period was accomplished by coring every live tree capable of admitting an increment borer, dating every dead tree based on its physical features (USDA Forest Service 1978; Cline et al. 1980), and conducting stem analyses for past height growth on a subset of felled trees. Details of the sampling design, measurement techniques, and backdating procedures can be found in Hann and Hanus (2001).

After the basic tree variables had been backdated, a number of tree and stand variables were calculated for the start of the growth period, including  $CR_i$ ,  $BAL_i$ ,  $CCH_i$ ,  $BA_i$ , the total crown surface area of the plot ( $TCSA_i$ ), and Douglas-fir SI.  $CCH_i$  and  $TCSA_i$  were calculated from the crown profile

equations of Hann (1999) and Hann and Hanus (2001), and Douglas-fir SI was calculated from the equations of Hann and Scrivani (1987).

The resulting pure data set contained 6620 live Douglas-fir trees with measurements of  $\Delta D$ , 473 live Douglas-fir trees without measurements of  $\Delta D$ , and 346 dead Douglas-fir trees. The mixed-species data set contains 8811 live Douglas-fir trees with measurements of  $\Delta D$ , 1532 live Douglas-fir trees without measurements of  $\Delta D$ , and 491 dead Douglas-fir trees. The mixed-species data set was further divided into two subsets: (i) those mixed-species plots in which the non-Douglas-fir species on the plot were dominated by conifers and (ii) those mixed species plots in which the non-Douglas-fir species on the plot were dominated by hardwoods. The main characteristics of the pure-species plots, mixed-species, mixed-conifer, and mixed-hardwood plots are shown in Tables 1 and 2.

## Data analysis

### Diameter growth rate

The basic equation form used to model the  $\Delta D$  of Douglas-fir was taken from the previous work of Hann and Larsen (1991) and Zumrawi and Hann (1993):

$$[1] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right) + a_5 \times COMA + a_6 \times COMAB$$

where COMA is a measure of the effect of one-sided competition, i.e., competition from above, and COMAB is a measure of the effect of two-sided competition, i.e., competition from above and below.

The log transformation homogenized the variance about the regression surface and linearized the parameters of the equation to meet the assumptions of linear regression techniques.

In the initial step, COMA and COMAB were formed from  $D$ 's alone:

$$[2] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right) + a_5 \times COMA_D + a_6 \times COMAB_D$$

$$[3] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right) + a_5 \times COMA_C + a_6 \times COMAB_C$$

$$[4] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right) + a_5 \times COMA_D + a_6 \times COMAB_C$$

$$[5] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right) + a_5 \times COMA_C + a_6 \times COMAB_D$$

All fitted models were evaluated to assure that the size and signs of the parameter estimates met expected behavior, the parameter estimates were significantly different from

**Table 1.** Summary of the plot attributes at the start of the growth period in the modeling data sets.

	BA <sub>i</sub>	SI	TCSA <sub>i</sub>
<b>Pure stands (n = 162)</b>			
Mean	47.91	31	68.24
SD	20.08	5	28.12
Minimum	0.01	15	0.37
Maximum	124.4	44	163.28
<b>Mixed-conifer stands (n = 223)</b>			
Mean	40.75	30	65.24
SD	19.95	4.8	27.61
Minimum	2.44	13	7.33
Maximum	92.49	45	157.14
<b>Mixed-hardwood stands (n = 142)</b>			
Mean	35.07	30	85.19
SD	17.57	8.8	35.56
Minimum	0.02	14	3.02
Maximum	71.86	42	184.59

**Note:** Abbreviations are as follows: BA<sub>i</sub>, basal area; SI, site index; TCSA<sub>i</sub>, tree crown surface area; n, number of plots.

$$COMA_D = \frac{BAL_i^2}{\ln(D_i + 12.7)}$$

$$COMAB_D = BA_i^{0.5}$$

CCH<sub>i</sub> and TCSA<sub>i</sub> were selected as the crown-based competition attributes to form alternative representation of COMA and COMAB, respectively. After several alternatives had been explored, the following formulations for COMA and COMAB proved best for characterizing the relationship between CCH<sub>i</sub>, TCSA<sub>i</sub>, and  $\ln(\Delta D)$ :

$$COMA_C = CCH_i^{0.5}$$

$$COMAB_C = TCSA_i^{0.33}$$

The following four equation forms were fit to the five data sets (i.e., all plots, pure Douglas-fir plots, all mixed-species plots, mixed-conifer plots, and mixed-hardwood plots):

zero ( $\alpha = 0.05$ ), and multicollinearity was small. The following "reduced" equation (i.e., without the competition attributes) was also fit to each of the five data sets:

**Table 2.** Summary of the tree attributes at the start of the growth period in the modeling data sets.

Data set, stand type, and attribute	DBH <sub>i</sub>	CR <sub>i</sub>	CCH <sub>i</sub>	BAL <sub>i</sub>
<b>Diameter growth data set</b>				
Pure stands ( <i>n</i> = 6620)				
Mean	45.8	0.43	24.1	26.55
SD	29.5	0.17	36.1	18.53
Minimum	1.1	0.1	0	0
Maximum	203.4	1	253.4	118.47
Mixed-conifer stands ( <i>n</i> = 5201)				
Mean	42.1	0.49	54.5	24.11
SD	31.3	0.18	33.5	16.05
Minimum	0.6	0.1	0	0
Maximum	205.3	1	242.4	90.27
Mixed-hardwood stands ( <i>n</i> = 3610)				
Mean	30.4	0.5	30.5	21.7
SD	23.9	0.2	40.5	14.75
Minimum	0.3	0.1	0	0
Maximum	181.5	1	285.5	70.84
<b>Survival data set</b>				
Pure stands ( <i>n</i> <sub>alive</sub> = 7093; <i>n</i> <sub>dead</sub> = 346)				
Mean	41.4	0.43	36.2	27.62
SD	30.7	0.17	54.1	18.99
Minimum	0.3	0.1	0	0
Maximum	203.4	1	363.7	118.47
Mixed-conifer stands ( <i>n</i> <sub>alive</sub> = 5864; <i>n</i> <sub>dead</sub> = 243)				
Mean	36.5	0.48	42	25.6
SD	32.1	0.19	60.3	15.58
Minimum	0.3	0	0	0
Maximum	205.3	1	368.9	92.48
Mixed-hardwood stands ( <i>n</i> <sub>alive</sub> = 4475; <i>n</i> <sub>dead</sub> = 248)				
Mean	24	0.49	57.6	24.1
SD	24	0.21	70.9	15.8
Minimum	0.3	0.1	0	0
Maximum	181.5	1	356.2	70.8

**Note:** Abbreviations are as follows: DBH<sub>i</sub>, diameter at breast height; CR<sub>i</sub>, crown ratio; CCH<sub>i</sub>, crown competition factor at height; BAL<sub>i</sub>, basal area in larger trees; *n*, number of trees.

$$[6] \quad \ln(\Delta D) = a_0 + a_1 \times \ln(D + 2.54) + a_2 \times D^2 + a_3 \times \ln(SI - 1.37) + a_4 \times \ln\left(\frac{CR + 0.2}{1.2}\right)$$

The fit of eqs. 2–5 to each data set was evaluated by taking the mean square error for the “full” equation fit to a particular data set (F-MSE<sub>F</sub>) that included the competition attributes, dividing it by the mean square error for the “reduced” equation fit to the same data set (F-MSE<sub>R</sub>), and expressing the quotient as a percentage (Biging and Dobbertin 1995). A reduced equation without competition attributes as a basis of comparison has been widely applied in prior evaluations (e.g., Opie 1968; Alemdag 1978; Smith and Bell 1983; Martin and Ek 1984; Daniels et al. 1986; Biging and Dobbertin 1992, 1995).

To evaluate the ability of the  $\ln(\Delta D)$  equations to extrapolate to mixed-species stands, eqs. 2–5 fitted to the pure Douglas-fir data set were then used to predict the  $\ln(\Delta D)$  for

the three mixed-species data sets. The residual of predicted  $\ln(\Delta D)$  minus actual  $\ln(\Delta D)$  for each equation was formed for each tree, and these data were used to compute the mean of the extrapolated residuals ( $\hat{R}$ ), the mean square error of the extrapolated residuals [E-MSE<sub>F</sub>], and the standard deviation of the extrapolated residuals [SD(R)] for the overall mixed-species data set and its conifer-dominated and hardwood-dominated subsets. The extrapolation properties of the models were evaluated in two ways: (i) extrapolation of the models was evaluated for each separate data set, by dividing the E-MSE<sub>F</sub> for a particular data set by the F-MSE<sub>R</sub> for the same data set; and (ii) extrapolation of the models was evaluated across the three mixed species data sets, by dividing the E-MSE<sub>F</sub> for a particular data set by F-MSE<sub>R</sub> for the pure Douglas-fir data set. In both cases the quotient was expressed as a percentage.

The residual data for each equation were also divided into classes by the percentage of the BA<sub>i</sub> in non-Douglas-fir species (with each class covering a range of 10%), and the  $\hat{R}$  and the upper and lower bounds defined by  $\hat{R} \pm SD(R)$  were plotted across the mean percentage of each class for the overall mixed-species data set and its conifer-dominated and hardwood-dominated subsets. For the conifer-dominated data subsets, the classes were defined by the percentage of BA<sub>i</sub> in non-Douglas-fir conifers alone; for the hardwood-dominated data subsets, the classes were defined by the percentage of BA<sub>i</sub> in hardwoods alone.

### Survival rate equation

The nonlinear logistic equation form was chosen to model the probability of Douglas-fir survival through the next 5 years:

$$[7] \quad PS = (1.0 + e^{-Z})^{-1}$$

where *Z* is a linear function of parameter estimates and explanatory variables,  $Z = b_0 + b_1(X_1) + b_2(X_2) + \dots + b_k(X_k)$ .

The logistic equation can be formulated to accept a binary dependent variable, such as a survival indicator, and the parameters can be estimated by either weighted nonlinear regression or by maximum-likelihood methods (Monserud and Sterba 1999). The resulting predictions are bounded by 0 and 1. The logistic equation form has been widely applied over the past 25 years for modeling either PM (e.g., Hamilton and Edwards 1976; Hamilton 1986; Hann and Wang 1990; Monserud and Sterba 1999; Hann and Hanus 2001) or PS (Monserud 1976; Buchman et al. 1983; Vanclay 1991; Zhang et al. 1997; Cao 2000).

The following *Z* functions were used by Hann and Wang (1990) to model PM in the same study area:

$$Z = -[b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(BAL_i)]$$

$$Z = -[b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(CCH_i)]$$

By reversing the signs on the parameters, these *Z* functions for PM can be transformed into functions for PS. Both models include attributes related to tree size, tree vigor, stand productivity, and one-sided competition. To add a measure of two-sided competition, BA<sub>i</sub> was added to the first function to form a *D*-dependent combination of attributes, and TCSA<sub>i</sub> was added to the second function to form a crown-dependent combination of attributes:

$$[8] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(BAL_i) + b_5(BA_i)$$

$$[9] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(CCH_i) + b_5(TCSA_i)$$

As with the diameter growth rate equations, two additional  $Z$  functions were evaluated in which the  $D$ - and crown-dependent attributes were mixed:

$$[10] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(BAL_i) + b_5(TCSA_i)$$

$$[11] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(CCH_i) + b_5(BA_i)$$

The parameters of eq. 7 with functions 8–11 were estimated for the five data sets (i.e., all plots, pure Douglas-fir plots, all mixed-species plots, mixed-conifer plots, and mixed-hardwood plots) by the maximum-likelihood method (Young and Young 1998). The alternative fits were evaluated based on the expected behavior as indicated by the signs on the parameter estimates and upon the Akaike information criterion (AIC) for each fit (Zhang et al. 1997). The following reduced function for eq. 7 (i.e., without the competition attributes) was also fit to each of the five data sets:

$$[12] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI)$$

The fit of eq. 7 with functions 8–11 to each data set was evaluated by taking the AIC for the “full” equation fit to a particular data set ( $AIC_F$ ) that includes the competition attributes, dividing it by the AIC for the reduced equation fit to the same data set ( $AIC_R$ ), and expressing the quotient as a percentage.

To evaluate the ability of the survival equations to extrapolate to mixed-species stands, eq. 7 with functions 8–11 fitted to the pure Douglas-fir data set were used to predict the 5-year survival rates, in percent, for the three mixed-species data sets. The predicted survival rates were then compared with the observed survival rates for the same data sets. Each equation–function combination was also used to calculate the percent correct classification for all trees in each of the three mixed-species data sets (Monserud and Sterba 1999). If the predicted probability of survival was greater than or equal to a threshold, the tree was considered alive; otherwise, it was considered dead. The mean survival rate for each data set was used as the threshold value (Monserud and Sterba 1999).

## Results

### Diameter growth

Mean square errors for eq. 6 (i.e.,  $F\text{-MSE}_R$ ) and the reduction in MSEs for eqs. 2–5 (both fitted and extrapolated) by stand type are reported in Table 3. In all cases, the use of one- and two-sided competition variables reduced the MSE by more than 11% over eq. 6. All parameters in all models were significantly different from 0. Surprisingly, the equation with the best fit was not eq. 3, which used the crown-related attributes of  $CCH_i$  and  $TCSA_i$  to form competition variables. Equation 5 with  $CCH_i$  and  $BA_i$  was the best for all

the stand types except the mixed hardwoods, where eq. 3 performed better. The reduction in MSE over the reduced model ranged from 18% for the pure Douglas-fir plots to 14% for the mixed-hardwood plots. The equations that included  $CCH_i$  as the one-sided competition variable (eqs. 3 and 5) showed the largest reduction in MSE. The use of  $TCSA_i$  (eq. 3) versus  $BA_i$  (eq. 5) as the two-sided competition variable in combination with  $CCH_i$  did not cause a large difference in MSE reduction (Table 3). The increased reduction in MSE from using  $CCH_i$  instead of  $BAL_i$  as the one-sided competition variable was always more than 2%.

Extrapolations from the equations fit to the pure Douglas-fir data alone also reduced the MSE over the value for eq. 6. Equation 3 was always best for extrapolating to other species mixes when compared with fitting eq. 6 directly to the data (Table 3). This result suggests that equations whose competition attributes are based on crown attributes will extrapolate better than equations whose competition attributes are based on  $D$  alone. The reduction in MSE was 13% for mixed-conifer stands and 8% for mixed-hardwood stands, with an average reduction of 12% for the combined data. The poorer performance obtained by extrapolating the equation fit to the pure Douglas-fir data versus the equations fit to the three mixed-species data sets was reflected in the 2.4% higher MSE for mixed conifer stands. The first set of extrapolation results in Table 3 uses  $F\text{-MSE}_R$  for each data set as the denominator when computing the reduction in MSE. Because these values change among data sets, it is difficult to use them to examine which equation extrapolates best across the data sets. The second set of extrapolation results in Table 3, therefore, presents the reductions in MSE resulting from extrapolation from the  $F\text{-MSE}_R$  resulting from the fit to the pure Douglas-fir data set as the denominator. The results confirm that eq. 3 would extrapolate the best across the data sets.

Extrapolating any of the equations fit to the pure Douglas-fir data to the mixed-species data sets produced residuals that were consistently unbiased as the percentage of the  $BA_i$  in the other species increased (Fig. 1). For all equations, precision decreased in mixed-conifer plots when other conifers represented at least 90% of the plot's  $BA$ , and it increased when the proportion of hardwoods on the plot was over 90%.

### Survival

Examination of the signs on the parameters for functions 8–11 when used in eq. 7 indicated problems with functions 8 and 9. The sign on the  $BA_i$  parameter in function 8 was incorrect for all data sets, and the sign on the  $TCSA_i$  parameter in function 9 was incorrect for the fits to the whole data set and to the pure Douglas-fir data sets. Therefore, the following simplified functions were used in the remainder of the analysis for those data sets with behavioral problems:

$$[13] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(BAL_i)$$

$$[14] \quad Z = b_0 + b_1(D_i) + b_2(CR_i) + b_3(SI) + b_4(CCH_i)$$

The AIC for the use of function 12 in eq. 7 ( $AIC_R$ ) and the reduction in AIC when using different functions in eq. 7 fit to each data set are given in Table 4. For all data sets, the use of function 11 in eq. 7 showed the best performance. Re-

**Table 3.** Diameter-growth statistics used to evaluate the fit and extrapolation performance for each equation.

Equation No.*	Stand type				
	Pure Douglas-fir	Whole data set	All mixed	Mixed conifer	Mixed hardwood
F-MSE <sub>R</sub> for eq. 6	0.418 14	0.403 52	0.389 43	0.407 61	0.354 94
<b>Fit MSE for each data set as a percentage of the reduced equation MSE for each data set (100 × (F-MSE<sub>F</sub>)/(F-MSE<sub>R</sub>))</b>					
Equation 6	100	100	100	100	100
Equation 2	86.51	87.96	88.11	88.02	88.6
Equation 3	82.36	84.04	85.26	84.42	85.82 <sup>†</sup>
Equation 4	86.35	87.97	88.12	88.08	88.32
Equation 5	81.76 <sup>†</sup>	83.78 <sup>†</sup>	84.14 <sup>†</sup>	84.17 <sup>†</sup>	86.34
<b>Extrapolated MSE for each data set as a percentage of the reduced equation MSE for each data set (100 × (E-MSE<sub>F</sub>)/(F-MSE<sub>R</sub>))</b>					
Equation 2			93.22	91.87	97.66
Equation 3			87.88 <sup>†</sup>	86.55 <sup>†</sup>	92.16 <sup>†</sup>
Equation 4			93.59	91.6	99.08
Equation 5			88.35	86.7	93.17
<b>Extrapolated MSE for each data set as a percentage of the reduced equation MSE for the pure Douglas-fir (100 × (E-MSE<sub>F</sub>)/(0.41814))</b>					
Equation 6	100				
Equation 2			86.82	89.55	82.9
Equation 3			81.85 <sup>†</sup>	84.37 <sup>†</sup>	78.23 <sup>†</sup>
Equation 4			87.16	89.3	84.1
Equation 5			82.28	84.52	79.09

\*MSE, mean square error.

<sup>†</sup>Best equation for a given data set.

duction in AIC over the use of function 12 in eq. 7 ranged from 16% for Douglas-fir pure stands to 6% for mixed-conifer stands. The addition of BA<sub>i</sub> to CCH<sub>i</sub> (i.e., the use of function 11 instead of function 14 in eq. 7) did not dramatically increase the reduction of AIC. In most data sets, using CCH<sub>i</sub> to form the one-sided competition variable resulted in an improvement of over 3% on functions with BAL<sub>i</sub>. The exception was in mixed hardwoods, where CCH<sub>i</sub> resulted in just a 1% improvement over BAL<sub>i</sub>.

The observed and predicted overall survival rates, in percent, and the predicted rates of correctly classifying each sample tree as dead or alive, in percent, are also presented in Table 4 to show which function fit to the pure Douglas-fir data would best extrapolate to the mixed-species data sets. For all data sets, the use of function 13 in eq. 7 produced the closest agreement between predicted and observed survival, with the differences always smaller than 2.3% (Table 4).

On the other hand, the use of function 9 or 14 in eq. 7 always produced the highest rate of correct classification, with values ranging from 72.02% for the mixed-hardwood stands to 76.43% for the mixed-conifer stands (Table 4). This result agrees with our finding for diameter growth, which indicated that crown-based measures of competition provide better extrapolations at the single-tree level that diameter-based measures of competition.

**Discussion**

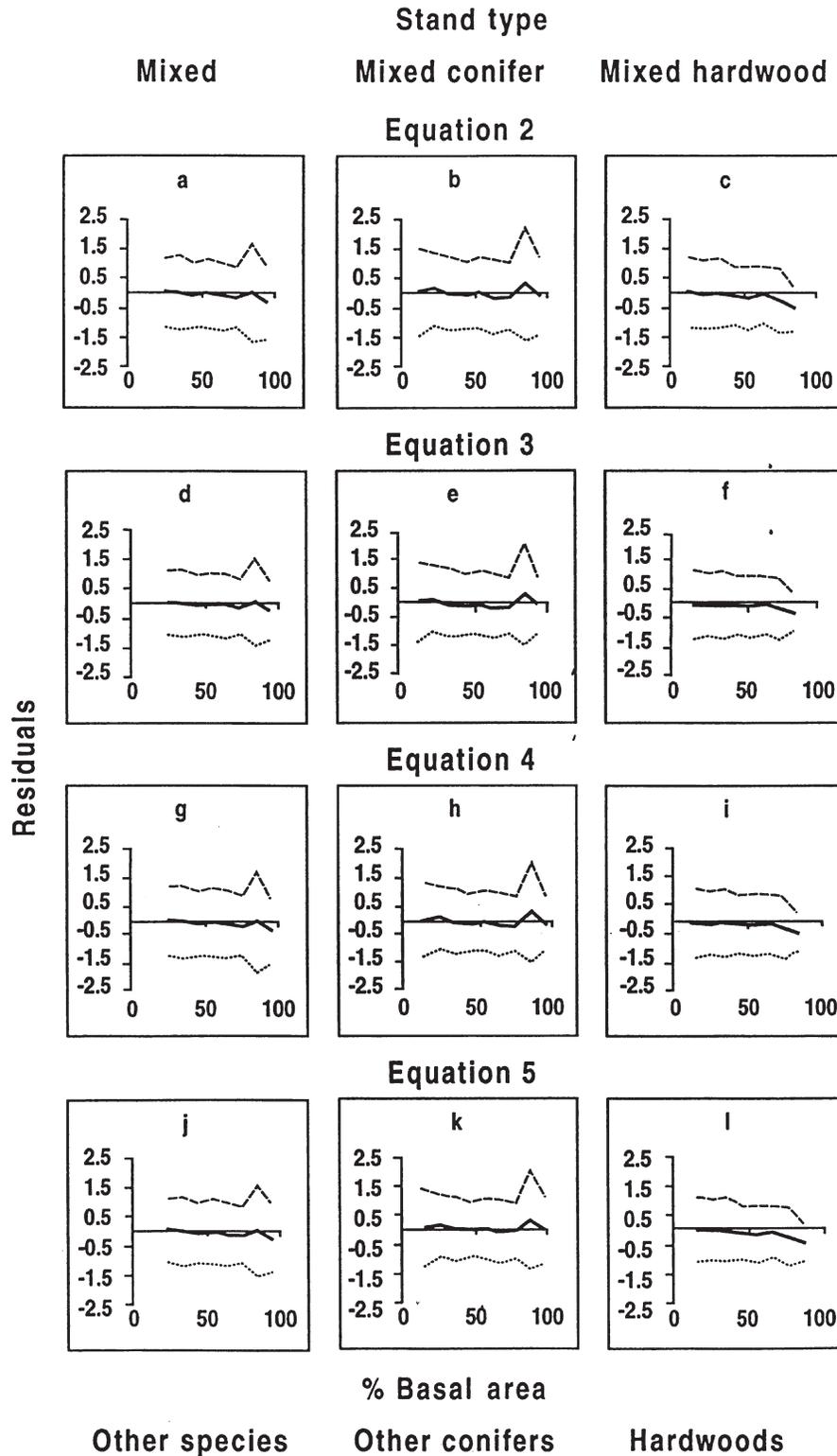
Results of the analysis indicated that the form of the variables representing one- and two-sided competition did sig-

nificantly influence the ability of the models to extrapolate from pure Douglas-fir stands to mixed-species stands, including mixtures of other conifers and hardwood species. One-sided competition was best characterized by a crown-based variable, CCH, when extrapolating both the ΔD and PS equations to stands of widely varying composition of competing species. Surprisingly, the crown-based indicator of two-sided competition, TCSA, was best in the ΔD equations for the mixed-hardwood stands only. The diameter-based variable for two-sided competition, BA<sub>i</sub>, was superior to crown-based variables for describing Douglas-fir ΔD in all other species mixes and for predicting Douglas-fir PS, regardless of the species mix.

Both crown-based measures of competition (CCH<sub>i</sub> and TCSA<sub>i</sub>) were present in the equations that extrapolated best for ΔD (Table 3) and for correctly classifying trees as to either alive or dead (Table 4). Although the model including only BAL<sub>i</sub> (function 13 in eq. 7) provided the best extrapolations for predicting average survival rate, the best fitting equations (eq. 5 and function 11 in eq. 7) for most data sets combined CCH<sub>i</sub> with BA<sub>i</sub> and also provided acceptable extrapolations to the mixed-species data sets (Table 4).

Extrapolation of the Douglas-fir survival rate equations from pure Douglas-fir to mixed-species stands resulted in approximately 75% overall correct classification of the trees (Table 4). This value is lower than the 86% reported by Monserud (1976) and the 89% reported by Monserud and Sterba (1999) using data from permanent plots. Because mortality can be highly variable in a stand (Monserud 1976), the estimation of survival (or mortality) rate is often the

**Fig. 1.** Residuals of equations extrapolated from pure Douglas-fir stands to mixed-species stands plotted across the proportion of basal area in other species by equation and stand type. The broken lines represent the lower and upper 95% confidence limits of the mean residuals.



weakest component of stand-development models. The difficulties of modeling survival rate are particularly acute when using data from temporary plots in which the date of death must be estimated (Hann and Wang 1990).

Crown closure at different heights has been tested as a one-sided competition variable in several species. Hann and Ritchie (1988) compared CCH and  $CC_{66}$  (crown closure at 66% or the subject tree's height) for modeling height growth

**Table 4.** Probability of survival statistics used to evaluate the fit and extrapolation performance for each function of eq. 7.

Function	Stand type				
	Pure Douglas-fir	Whole data set	All mixed	Mixed conifer	Mixed hardwood
AIC <sub>R</sub> for function 12*	53 114	156 658	101 811	47 107	57 726
<b>Fit AIC for each data set as a percentage of the reduced equation AIC for each data set (<math>100 \times (\text{AIC}_F)/(\text{AIC}_R)</math>)</b>					
Function 12	100	100	100	100	100
Function 13	96.65	98.11	99	99.99	90.66
Function 14	84.58	91.41	94.13	94.52	88.07
Function 10	92	95.85	97.18	97.56	89.43
Function 11	83.55 <sup>†</sup>	91.04 <sup>†</sup>	94.09 <sup>†</sup>	94.46 <sup>†</sup>	87.71 <sup>†</sup>
<b>Observed and predicted survival rates (%) when extrapolating equations for pure Douglas-fir to other species mixes</b>					
Observed survival rate			89.19	88.37	89.97
Extrapolated survival rate					
Function 13			87.52 <sup>†</sup>	87.33 <sup>†</sup>	87.69 <sup>†</sup>
Function 14			84.4	84.03	84.71
Function 10			83.81	84.79	82.99
Function 11			84.85	84.54	85.12
<b>Percent correct classifications when extrapolating equations for pure Douglas-fir to other species mixes</b>					
Function 13			66.91	67.51	66.45
Function 14			73.93 <sup>†</sup>	76.43 <sup>†</sup>	72.02 <sup>†</sup>
Function 10			67.59	69.85	66.83
Function 11			73.79	76.15	71.72

\*AIC, Akaike's information criterion.

<sup>†</sup>Best equation for a given data set.

rate in Douglas-fir and concluded that CCH was superior. Biging and Dobbertin (1995) found that CCH was superior to  $CC_{66}$  for modeling both diameter and height growth rate in ponderosa pine, but that  $CC_{66}$  was superior to CCH for modeling diameter and height growth of white fir. Of particular relevance to the present study, either CCH or  $CC_{66}$  was superior to BAL for both species. In fact, crown-based, one-sided, distance-independent competition indices performed as well as or better than the best distance-dependent competition index. Understanding the spatial and size relationships between neighbors has been regarded as essential to quantifying intertree competition (Tomé and Burkhart 1989); however, no clear superiority of distance-dependent indices of competition has yet been proved (e.g., Biging and Dobbertin 1995; Daniels et al. 1986).

The use of crown attributes such as  $CCH_i$  and  $TCSA_i$  does require the development of crown-profile equations (e.g., Biging and Wensel 1990; Hann 1999; Hann and Hanus 2001) for each of the species that might be encountered, and their application would require the measurement of  $H$  and HCB on every sample tree. These tasks can be both time consuming and expensive. However, with appropriate additional information,  $CCH_i$  can be related to light extinction through the stand canopy, and  $TCSA_i$  can be related to the amount of leaf area in the stand (Maguire and Hann 1989). Overall, extrapolation of the  $\Delta D$  equations developed in pure Douglas fir-stands to mixed-conifer stands resulted in low bias and high precision (Fig. 1). However, the bias was higher and the precision lower in mixed-hardwoods stands

(7.39% in loss of MSE versus a 2.83% loss in mixed-conifer stands).

Differences in tree morphology, allometrics, and resulting crown structure among the conifer and hardwood species in southwestern Oregon explain the superior performance of crown-based indices for one-sided competition in  $\Delta D$  equations. A comparison of maximum  $D$ ,  $H$ , CL, and LCW values for the southwestern Oregon conifer species indicates that they achieve similar maximum sizes (Table 5). The hardwoods, on the other hand, exhibit much smaller maximum  $D$ ,  $H$ , and CL values than the conifers and, as a result, they only achieve dominance over smaller, and usually younger, conifers. In addition, their relative crown widths, as indicated by the ratio of  $LCW/D$ , are larger than those of the conifer species. Therefore, it is understandable that  $TCSA_i$ , which incorporates information about each tree's  $D$ ,  $H$ , CL, and LCW, would be superior to  $BA_i$  as a surrogate for two-sided competition in the  $\Delta D$  equations for hardwood-dominated stands.

The fact that CCH recognizes species differences in crown profile (Biging and Wensel 1990; Hann 1999; Hann and Hanus 2001) lends biological appeal to this measure, since the total crown cross-sectional area of competitors at the top of the subject tree should represent the shading effect of the competing trees. Similarly, crown size and shape integrate past growth dynamics (Courbaud 2000). Because leaf area density (foliage bulk density) differs tremendously even among coniferous species (Brown 1978), a given unit of crown cross-sectional area of one species would be expected

**Table 5.** Maximum measured tree attributes (m) for major conifer and hardwood species in southwestern Oregon as reported by Hann (1997).

Species	<i>D</i>	<i>H</i>	CL	LCW	LCW/ <i>D</i>
<b>Conifers</b>					
Douglas-fir	2.065	74.5	49.7	19.3	9.35
White and grand firs	1.275	67.3	45.6	11.0	8.66
Incense-cedar	1.748	56.0	29.5	12.0	6.84
Ponderosa pine	1.224	61.9	31.1	12.0	9.76
Sugar pine	1.770	51.1	26.6	15.5	9.89
<b>Hardwoods</b>					
California black oak	0.88	27	15	12.6	14.32
Canyon live oak	0.574	17.1	10.8	10.9	19.07
Golden chinkapin	0.536	26.4	19.3	7.4	13.77
Pacific madrone	0.826	31.4	15.9	15.9	19.30
Tanoak	0.759	30.7	15.4	11.7	15.46

to impose a different shading effect than a unit of another species. However, nonphotosynthetic tissues also absorb solar radiation, and differences in leaf area density among species are counterbalanced by differences in branch bulk density. For example, the bulk density of foliage within the crown is about 30% higher in grand fir than in Douglas-fir, and foliage bulk density in Douglas-fir is about 20% higher than in ponderosa pine (Brown 1978). Yet, bulk density of the entire live crown (branches + foliage) varies little among these three species (Brown 1978).

Representation of two-sided competition with  $BA_i$  assumes that there are no differences between species in their level of competition for water and nutrients per unit basal area. Belowground processes in forests are still poorly understood, and hence, the relationship between basal area and fine root amount or turnover, for example, is not known. However, the amount of foliage per unit basal area varies widely among species (Brown 1978), as would be expected given the varying proportion of tree basal area consisting of sapwood and the relatively constant ratio of leaf area to sapwood area within a species (Waring et al. 1982). Therefore,  $BA_i$  does not provide a conceptually satisfying representation of belowground competition, although differences among species in the spatial occupation of roots, efficiency of water and nutrient use, and allocation of resources may complicate its interpretation. We conclude that by incorporating the influence of tree size (*D*), tree vigor (CR), historic site productivity (SI), and one- and two-sided competition variables (CCH, TCSA, BA, BAL) into the equations, it is possible to simulate the development of different stand structures and to study the influence of different silvicultural treatments from equations developed for pure stands. These results suggest that differences in crown structure and competitive effects among species make it more difficult to extrapolate diameter growth from pure Douglas-fir stands to mixed-hardwood stands without accounting for these differences.

Likewise, we conclude that the relative performance of model constructs representing competitive effects among species largely depends on the variables selected and how well they represent the relative amount of each species present. The closer the selected dimensions are to the functions

or processes by which a tree secures light, water, and nutrient resources, the better they will improve our understanding of mixed species stand growth and dynamics.

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