



## Evaluation of field performance of poplar clones using selected competition indices

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**Abstract.** Use of competition indices in the analysis of forestry experiments may improve detection and understanding of treatment effects, and thereby improve the application of results. In this paper, we compared the performance of 8 indices in an analysis of a spacing trial of four *Populus* clones planted in pure and mixed clonal plots. Indices were included as covariates in analyses of variance and evaluated on their ability to decrease mean square error. Indices that were simple to calculate (i.e., required only diameter and spacing or distance information) decreased mean square error by as much as 32%. We then illustrate the use of a simple index to assess clonal response to intra- and inter-genotypic competition and to interpret treatment effects confounded by different levels of competition. In pure clonal plots (intra-genotypic competition), all the clones tested reacted similarly to competition, while the same clones tested in mixed plots (inter-genotypic competition) reacted differently to varying levels of competition. The use of a competition index to assess clone rankings within a mixed clonal plot can be an effective way to predict clonal performance within a mono-clonal planting.

### Introduction

Competition indices have been used in analyses and prediction of individual tree growth for a wide variety of species and growing conditions, including naturally regenerated Douglas-fir and western hemlock (Wimberly and Bare 1996), a red pine plantation (Martin and Ek 1984) and a jack pine plantation with trembling aspen ingrowth (Mugasha 1989). Many studies have compared distance-dependent (spatially explicit) indices with distance-independent indices as components of tree growth models (Martin and Ek 1984; Daniels et al. 1986; Mugasha 1989; Biging and Dobbertin 1995; Wimberly and Bare 1996). Most concluded that in relatively uniformly-spaced plantations and natural stands, the additional modeling accuracy obtained with distance-dependent indices is small and the extra effort and expense of collecting distance information is not warranted. Several researchers have used or advocated use of indices in the interpretation of genetic tests (Tuskan and McKinley 1984; Magnussen and Yeatman 1987; Land and Nance 1987; Mäkinen 1997) and silvicultural trials where treatment effects have been confounded or exaggerated by differences in levels of competition.

Although the efficacy of both simple and complex indices has been established, their use in the analysis and interpretation of genetic and silvicultural trials has not become commonplace. A short-rotation intensive culture poplar plantation at the Meridian Seed Orchard near Yelm, Washington provided a unique opportunity to compare response to both intra- and inter-clonal competition using indices. In this paper, we examine the effectiveness of 8 indices in decreasing mean square error in a covariance analysis testing treatment effects on height and diameter growth. We also assess growth response of the four clones to intra- and inter-clonal competition, and demonstrate how a competition index can be used to interpret and apply results of this experiment.

## Materials and methods

### *Site description*

A poplar research trial was established in the early spring of 1990 at the Department of Natural Resources Meridian Seed Orchard, 12 km east of Olympia, Washington (lat. 47° 0' N, long. 122° 44' W). The site and experimental methods were described fully in DeBell and Harrington (1997). Briefly, the trial was a randomized complete block design testing 4 clones: 3 of the clones were *Populus trichocarpa* × *P. deltoides* hybrids (11–11, 47–174, 49–177) and one was a local *Populus trichocarpa* clone (CL). Each clone was planted at 3 square spacings (0.5-m, 1.0-m and 1.5-m) in 2 types of plots (pure clonal plots and mixed clonal plots with equal representation of the 4 clones) with 3 replicate blocks. A minimum of 3 buffer rows surrounded 100-tree interior measurement plots. The study area was uniformly irrigated via drip lines and was maintained in a weed-free condition by applying herbicides and hoeing.

Survival, diameter at 1.3 m, and height were measured after the first growing season in fall 1990 and in fall 1992 (Table 1). Only live, undamaged trees in the inner 8 rows × 8 columns were used as subject trees in our evaluation of competition indices, so that all the nearest competitors were within the measurement plot. Because these 64 trees represent a sub-sample of the 100-tree measurement plot, summary statistics listed in Table 1 differ slightly from those previously published from the entire trial (DeBell and Harrington 1997). Variation in size 1 year following planting and subsequent growth of individual subject trees was substantial. Diameters ranged from 0.2 to 4.2 cm (with a coefficient of variation ( $C_v$ ) of 24.9) and heights from 1.3 to 5.2 m ( $C_v = 14.4$ ) after the first growing season. After the third growing season, diameters ranged from 0.8 to 11.1 cm ( $C_v = 38.5$ ) and heights from 2.25 to 13.2 m ( $C_v = 25.4$ ). Survival in the fall of 1990 was 100 percent; and at the end of the third year (1992) it exceeded 75 percent in all clonal, spacing, and mixed/pure plot type combinations except for CL in the mixed clonal plots at 0.5-m spacing (44%). All competition indices were calculated from the 1990 measure-

Table 1. Mean tree and stand characteristics of intensively cultured short-rotation *Populus* at one and three growing seasons after planting

	Survival (%)				Height (m)				Diameter (cm)			
	Mixed		Pure		Mixed		Pure		Mixed		Pure	
	Year 1	Year 3	Year 1	Year 3	Year 1	Year 3	Year 1	Year 3	Year 1	Year 3	Year 1	Year 3
0.5-m spacing												
11-11	100	100	100	91	3.4	6.1	3.3	6.5	1.8	3.2	1.8	3.2
47-174	100	90	100	93	3.2	6.3	3.4	6.7	1.5	2.9	1.5	3.1
49-177	100	90	100	80	3.7	7.8	3.7	6.8	2	4.2	1.9	3.4
CL	100	44	100	76	2.6	3.7	3.3	6.4	1.1	1.4	1.7	3.1
1.0-m spacing												
11-11	100	100	100	100	3.6	10.3	3.7	9.8	2.5	6	2.5	5.6
47-174	100	98	100	98	3.6	9.7	3.6	10	2.1	5.3	2.1	5.6
49-177	100	88	100	91	3.8	10.8	3.8	9.5	2.6	7	2.6	5.7
CL	100	100	100	99	3.1	6.7	3.2	9.2	1.8	3.3	2.1	5.2
1.5-m spacing												
11-11	100	100	100	100	3.2	11.2	3.4	11	2.3	8.3	2.4	7.5
47-174	100	94	100	100	3.1	10.4	3.3	11	1.9	6.6	2	7.4
49-177	100	94	100	93	3.2	11.2	3.5	11.3	2.2	8.9	2.7	7.9
CL	100	100	100	100	2.9	9.4	2.8	10.5	1.8	5.5	1.9	7.0

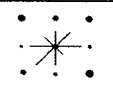

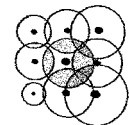
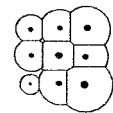
ments and were related to cumulative height and diameter growth during the 1991 and 1992 growing seasons.

#### *The indices*

Our intention was not to develop and test new indices, but to find one that was well correlated with our growth data and then use it as a tool to help interpret results. Many of the indices we evaluated have appeared in the literature previously or have been modified only slightly. All the indices evaluated appear in Table 2. The dots within the figures represent trees from an aerial perspective with varying diameters, the central dot represents the subject tree and the remaining dots represent the 8 nearest competitors.

Holmes and Reed (1991) divided competition indices into 3 categories; influence zone overlap, size ratio, and growing space. We selected indices from each category to get a broad representation and included indices that were both conceptually simple and required only diameter and height for their calculation. Of the 8 indices that we evaluated, only one index ('percent overlap') falls in the first category of 'influence zone overlap' and is positively correlated with level of compe-

Table 2. Competition indices evaluated

Competition Index Name	Definition/Description	Representation
DBH Ratio	$CI_i = \frac{DBH_i}{\overline{DBH}}$	n/a
BA Ratio	$CI_i = \frac{BA_i}{\overline{BA}}$	n/a
Sum DBH Ratio	$CI_i = \frac{\sum_{j=1}^n DBH_j}{DBH_i}$	n/a
Sum BA Ratio	$CI_i = \frac{\sum_{j=1}^n BA_j}{BA_i}$	n/a
Sum Line Length	$CI_i = \sum_{j=1}^n \frac{DBH_i}{DBH_i + DBH_j} \times Dist_{ij}$	
Area	Area delineated by endpoints of lines defined by the CI 'Sum Line Length'	
Percent Overlap	$CI_i = \frac{\sum_{j=1}^n O_j}{I_i}$	
Area Potentially Available (APA)	Each tree is considered to have a circular influence area equal to that used in calculation of the CI 'percent overlap'. A distance proportional to the diameter ratio of 2 adjacent trees is then calculated in much the same way that 'line length' was calculated, and a straight line is drawn perpendicular to that distance vector, limiting the original influence area.	
Where DBH=diameter at 1.3 m, BA=basal area, $CI_i$ =competition index of subject tree $i$ , $\overline{DBH}$ = mean DBH of competitors, $DBH_i$ = DBH of subject tree $i$ , $\overline{BA}$ = mean BA of competitors, and $BA_i$ = basal area of subject tree $i$ . $DBH_j$ = diameter of competitor tree $j$ ; $DIST_{ij}$ = distance between trees $i$ and $j$ ; $n$ = total number of competitors $O_j$ = portion of the influence area of competitor $j$ (radius=0.25 x height $_j$ ) that overlaps influence of subject tree (radius=0.25 x height $i$ ), and $I_i$ = influence area of subject tree $i$ .		

tion. The seven remaining indices either calculate a size ratio between the subject tree and trees assumed to be competitors or use a size ratio coupled with spacing information to infer an estimate of growing space; these indices are negatively correlated with level of competition. In our study, only trees in the nearest 8 positions in the square planting layout were considered as competitors. If a 'competitor' was dead, it was assigned diameter and height values of 0 in calculations.

The indices 'DBH ratio' and 'BA ratio' are clearly defined in Table 2. 'Sum DBH ratio' is the inverse of a simple index proposed by Lorimer (1983) who tested many

variations on Hegyi (1974) competition index

$$CI_i = \frac{DBH_i}{\sum_{j=1}^n \frac{DBH_j}{Dist_{ij}}} \quad (1)$$

Lorimer's variations mostly involved eliminating or modifying the distance term to determine the most effective search radius and inclusion or exclusion of various crown classes as competitors. He concluded that in nearly all cases, excluding the distance term resulted in  $R^2$  (coefficient of determination) values nearly as high or higher than more complex indices that included distance as a factor. Our study evaluated the reciprocal of this simple CI (without distance), which we call 'sum DBH ratio'. We used the reciprocal because its relationship with diameter and height growth was linear and provided slightly higher  $R^2$  values and lower MSE values in the model. 'Sum BA ratio' was included as a variation on the same relationship.

The next 2 indices defined in Table 2, 'sum line length' and 'area', are similar, but 'area' accommodates the differences in distribution of line lengths by going one step further to calculate the area enclosed by joining the endpoints of adjacent lines. For example, suppose there are 4 each of only 2 sizes of competitors—one the same size as the subject tree and one twice as large. If the larger competitors are all on the same side of the subject tree, then the competition index 'area' is 19% larger than if the two sizes of competitor alternate around the subject tree. The value of 'sum line length' would be the same in both cases.

Percentage overlap was modified from (Gerrard's (1969)) calculation of competition quotient and area potentially available (APA) was calculated by using the computer program developed by Nance and Grissom (1987), described in Land and Nance (1987) and based on concepts developed by Daniels (1976). Each tree is considered to have an circular influence area based on either a function of the subject tree's DBH, height, or various crown attributes. In this case, we defined the influence area by the same function used for the CI 'percent overlap'. The APA index was included here for comparison with the simpler indices.

### *Analysis*

Once the indices for subject trees were calculated, they were used as covariates in an analysis of variance model via the General Linear Models Procedure of SAS (SAS Institute, Inc. 1987). The model for diameter and height growth was:

$$y = \mu + \text{Block} + \text{Clone} + \text{Diam} + \text{CI} + (\text{Clone} * \text{CI}) + e \quad (2)$$

where Diam = DBH at end of the first growing season and CI = competition index.

Each combination of mixed or pure clonal plots and spacing was run as a separate analysis because prior analyses revealed that spacing and clonal mixing had highly

significant effects ( $p < 0.01$ ) on growth (DeBell and Harrington 1997) and we did not want differences associated with spacing or effects of clonal mixing to diminish opportunities to detect and understand differences among the performances of the various competition indices. We compared mean square error (MSE) values of models with and without the individual competition indices and calculated a percent change in MSE associated with each competition index. Coefficients of determination ( $R^2$ ) also were calculated. These measures (MSE, % change in MSE, and  $R^2$ ) provided the basis to judge the efficacy of each index.

To judge an index's performance across all spacings and plot types, each was ranked within a plot type (pure vs mixed) and spacing group by the extent the addition of the index to the model decreased MSE. The higher the rank number, the greater the decrease in MSE. Those indices with equal amount of change were given equal rank. The rankings were then totaled so that the greatest number would represent the index that most consistently ranked highest.

In order to evaluate clonal differences in response to intra-genotypic and inter-genotypic competition, 2-year diameter growth was regressed over one of the best competition indices for each spacing and plot type (pure vs. mixed) and results were displayed graphically.

Finally, we examined the use of a competition index to 'adjust' the growth performance of clones that had been subjected to differential competition in a mixed clonal plot. To do so, we calculated and compared least squares mean diameter growth for three clones (11–11, 47–174, and 49–177) under three conditions: (1) mixed clonal plots of 0.5-m spacing adjusted for block and initial DBH (DBH after 1 growing season) alone; (2) pure clonal plots of 0.5-m spacing adjusted for block and initial DBH alone; and (3) mixed clonal plots of 0.5-m spacing adjusted for block, initial DBH, competition index and the interaction between clone and competition index.

## **Results and discussion**

### *Index performance*

Effects of competition indices on analytical models of height growth and diameter growth are displayed in Tables 3 and 4, respectively. In each case, block and initial DBH were included as variables. In the case of mixed plots, clone was always included as a variable as well. Where no index was included, it is designated as 'none' and used as the baseline to evaluate reductions in mean squared error. Within each plot type and spacing, the indices have been listed in order of decreasing MSE. Inclusion of the competition indices in height and diameter growth models decreased mean square error (MSE) substantially in all plot types (mixed vs. pure) and spacings. Coefficients of determination ( $R^2$ ) were generally increased, with the greatest changes occurring in pure plots. The most effective indices reduced MSE for growth in 0.5-m spacing plots by 0–14% in both mixed and pure plots. Reduc-

Table 3. Inclusion of the competition indices in height growth models affected MSE and R<sup>2</sup>

Spacing	Mixed Clonal Plots				Pure Clonal Plots			
	Index	MSE	ΔMSE %	R <sup>2</sup>	Index	MSE	Δ MSE %	R <sup>2</sup>
0.5	None	0.48		0.85	None	0.82		0.64
0.5	Sum BA Ratio	0.47	-2	0.86	APA	0.81	-1	0.64
0.5	Sum DBH Ratio	0.46	-4.0	0.86	Sum BA Ratio	0.77	-6	0.66
0.5	APA	0.45	-6.0	0.86	Sum Line	0.77	-6	0.66
0.5	% Overlap	0.45	-6.0	0.86	Sum DBH Ratio	0.76	-7	0.67
0.5	DBH Ratio	0.43	-10.0	0.87	% Overlap	0.74	-10	0.68
0.5	BA Ratio	0.43	-10.0	0.87	Area	0.74	-10	0.67
0.5	Area	0.43	-10.0	0.87	DBH Ratio	0.73	-11	0.68
0.5	Sum Line	0.42	-13.0	0.87	BA Ratio	0.71	-13	0.69
1	None	0.57		0.81	None	0.6		0.55
1	Sum BA Ratio	0.56	-3.0	0.82	Sum BA Ratio	0.52	-13	0.61
1	% Overlap	0.56	-3.0	0.82	BA Ratio	0.49	-13	0.64
1	Sum DBH Ratio	0.55	-7.0	0.82	Sum DBH Ratio	0.48	-20	0.65
1	Sum Line	0.54	-10.0	0.82	APA	0.48	-20	0.65
1	DBH Ratio	0.54	-10.0	0.82	% Overlap	0.47	-22	0.65
1	APA	0.54	-10.0	0.82	Sum Line	0.46	-23	0.66
1	BA Ratio	0.54	-10.0	0.82	DBH Ratio	0.46	-23	0.66
1	Area	0.54	-10.0	0.82	Area	0.45	-25	0.67
1.5	None	0.44		0.56	None	0.44		0.26
1.5	% Overlap	0.4	-9.0	0.61	DBH Ratio	0.44	0	0.27
1.5	Sum BA Ratio	0.39	-11.0	0.62	Sum BA Ratio	0.44	0	0.26
1.5	APA	0.38	-14.0	0.63	Sum DBH Ratio	0.44	0	0.27
1.5	BA Ratio	0.38	-14.0	0.63	BA Ratio	0.43	-1	0.27
1.5	Sum DBH Ratio	0.35	-20.0	0.65	Sum Line	0.43	-2	0.28
1.5	DBH Ratio	0.34	-23.0	0.66	Area	0.43	-2	0.27
1.5	Area	0.34	-23.0	0.67	APA	0.41	-7	0.31
1.5	Sum Line	0.33	-25.0	0.68	% Overlap	0.41	-7	0.31

tion of MSE in the 1.0-m spacing plots differed somewhat by plot type; the best CI's reduced MSE by 10% in mixed clonal plots and by 26–32% in the pure clonal plots. Reductions of MSE in the 1.5-m plots were higher in the mixed plots than they were in the pure plots, especially for height growth (9–25% and 0–7%, respectively).

Coefficients of determination (R<sup>2</sup>) were low (0.26 to 0.64) in pure clonal plots when the CIs were not included in the model, but R<sup>2</sup> increased by as much as 0.16 in the 1.0-m spacings when the top-performing CI was added. In mixed clonal plots, R<sup>2</sup> values were generally higher (0.56 to 0.85) without CIs and increased by 0.12 with the top-performing CI in the 1.5-m spacing for height growth. Such differences between plot types are due to the fact that clonal differences were much greater in mixed than pure plots (Table 1).

Table 4. Inclusion of the competition indices in diameter growth models affected MSE and R<sup>2</sup>

Spacing	Index	Mixed Clonal Plots			Index	Pure Clonal Plots		
		MSE	Δ MSE %	R <sup>2</sup>		MSE	Δ MSE %	R <sup>2</sup>
0.5	None	0.22		0.81	None	0.32		0.55
0.5	% Overlap	0.21	-5	0.82	APA	0.32	0	0.55
0.5	APA	0.2	-9	0.83	Sum Line	0.31	-3	0.56
0.5	Sum BA Ratio	0.2	-9	0.84	Sum DBH Ratio	0.31	-3	0.57
0.5	DBH Ratio	0.19	-14	0.84	BA Ratio	0.29	-4	0.6
0.5	BA Ratio	0.19	-14	0.84	DBH Ratio	0.3	-6	0.58
0.5	Sum Line	0.19	-14	0.84	Sum BA Ratio	0.3	-6	0.57
0.5	Area	0.19	-14	0.84	Area	0.3	-6	0.57
0.5	Sum DBH Ratio	0.19	-14	0.84	% Overlap	0.28	-12	0.6
1	None	0.29		0.82	None	0.38		0.48
1	% Overlap	0.29	0	0.82	BA Ratio	0.26	-15	0.64
1	Sum Line	0.27	-7	0.84	% Overlap	0.31	-18	0.58
1	Sum BA Ratio	0.27	-7	0.84	Sum BA Ratio	0.3	-21	0.59
1	APA	0.27	-7	0.84	APA	0.29	-24	0.61
1	DBH Ratio	0.26	-10	0.84	Sum Line	0.28	-26	0.62
1	BA Ratio	0.26	-10	0.84	Sum DBH Ratio	0.27	-29	0.63
1	Area	0.26	-10	0.84	DBH Ratio	0.26	-32	0.65
1	Sum DBH Ratio	0.26	-10	0.84	Area	0.26	-32	0.64
1.5	None	0.56		0.74	None	0.49		0.35
1.5	APA	0.54	-4	0.76	Sum BA Ratio	0.48	-2	0.37
1.5	% Overlap	0.54	-4	0.76	BA Ratio	0.47	-3	0.37
1.5	BA Ratio	0.53	-5	0.76	Sum DBH Ratio	0.47	-4	0.38
1.5	DBH Ratio	0.52	-7	0.76	APA	0.47	-4	0.38
1.5	Sum Line	0.52	-7	0.77	% Overlap	0.46	-6	0.4
1.5	Area	0.52	-7	0.77	DBH Ratio	0.46	-6	0.39
1.5	Sum BA Ratio	0.52	-7	0.77	Sum Line	0.45	-8	0.4
1.5	Sum DBH Ratio	0.51	-9	0.77	Area	0.45	-8	0.4

Ranking the indices for overall effect on MSE reduction indicated that 'area' was the highest performing index for prediction of both height and DBH growth (Table 5). In most individual cases (Table 4), as well as in the combined ranking (Table 5), MSE values of the simpler indices compared very favorably to the more complex indices (i.e., APA and percentage overlap).

#### *Clonal response to competition*

An earlier report on the poplar trial (DeBell and Harrington 1997) indicated tree size differed significantly ( $p < 0.01$ ) by clone, spacing, culture or plot type (pure and mixed) and their interactions. The current analysis revealed that response of each clone to an increase in competition, as reflected by diameter or height growth,



Table 5. 'Total rank points' when competition indices are scored in relation to each other

Height Growth		DBH Growth	
Index	Total rank points	Index	Total rank points
Sum of BA ratio	7	APA	11
Sum DBH ratio	13	% Overlap	12
% Overlap	15	BA ratio	12
APA	15	Sum BA ratio	13
BA ratio	18	Sum line length	18
DBH ratio	21	Sum DBH ratio	19
Sum line length	22	DBH ratio	22
Area	23	Area	23

differed by spacing and whether the clone was grown in a mixed clonal plot (thus, competition was inter-genotypic) or one that contained a single clone (intra-genotypic competition). Figure 1 shows the relationship of diameter growth to the 'area' competition index. Competition was greatest within the 0.5-m plots as is apparent from the low 'area' values (which can be visualized as space available to the individual tree). Within this lower range, competition was intense and the response to an increase in 'area' (i.e., denoting a decrease in competition) was more marked than in the 1.0 and 1.5-m plots as exhibited by the steeper slope of the regression lines. As spacing increased, the slope of the lines decreased (lesser degree of response to a decrease in competition) and a wider range of values for this competition index (area) was exhibited.

The differences between clones and their growth response to intraclonal competition (pure plots) and interclonal competition (mixed plots) in the three spacings were significant ( $p < 0.05$ ) and are exhibited clearly in Figure 1. Generally, the mixed plots were characterized by marked differences in the response of particular clones to competition as well as in mean performance. That is, the slopes of the regression lines at all spacings differed more among clones in the mixed plots than they did in the pure plots; also such differences among clones in mixed plots tended to increase with spacing. This is more difficult to see in the 0.5-m spacings where the narrow spacing did not provide as much variation in individual growing space, but can be observed in the insets on Figures 1a and 1b. Diameter growth rates of clone CL were extremely low within the 0.5-m mixed plots and they appear to increase slightly at higher levels of competition (Figure 1a, inset). This relationship is illogical and no doubt an artifact due to a very low sample size: CL was the only clone that was not a hybrid and it grew more poorly than other clones at all levels of competition and thus was readily overtopped in mixed plots leading to even poorer growth and ultimately mortality (survival in the 0.5-m plots was only 44% after 3 years). Genotypic differences in growth rates were also significant ( $p < 0.05$ ) among other clones at 1.0-m and 1.5-m spacings in mixed clonal plots. The initial differentiation was caused by inherent differences in early growth rates, perhaps followed by differences in the response of each of the clones to increases in com-

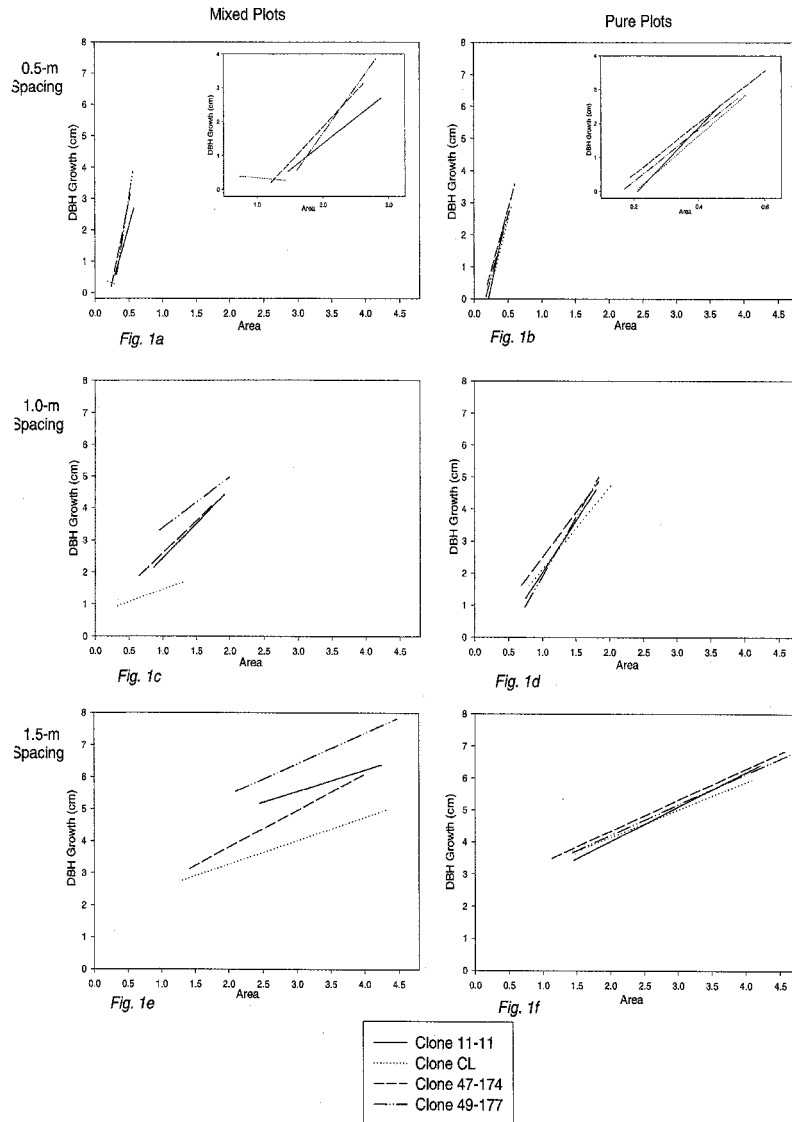


Figure 1. Differences between clones, intraclonal competition in the pure plots, and interclonal competition in the mixed plots can be seen in the relationship between DBH growth and the 'area' competition index.

petition. Once a clone or individual tree gained a competitive advantage, the difference in growth was maintained or increased as the stand grew and developed over the measurement period.

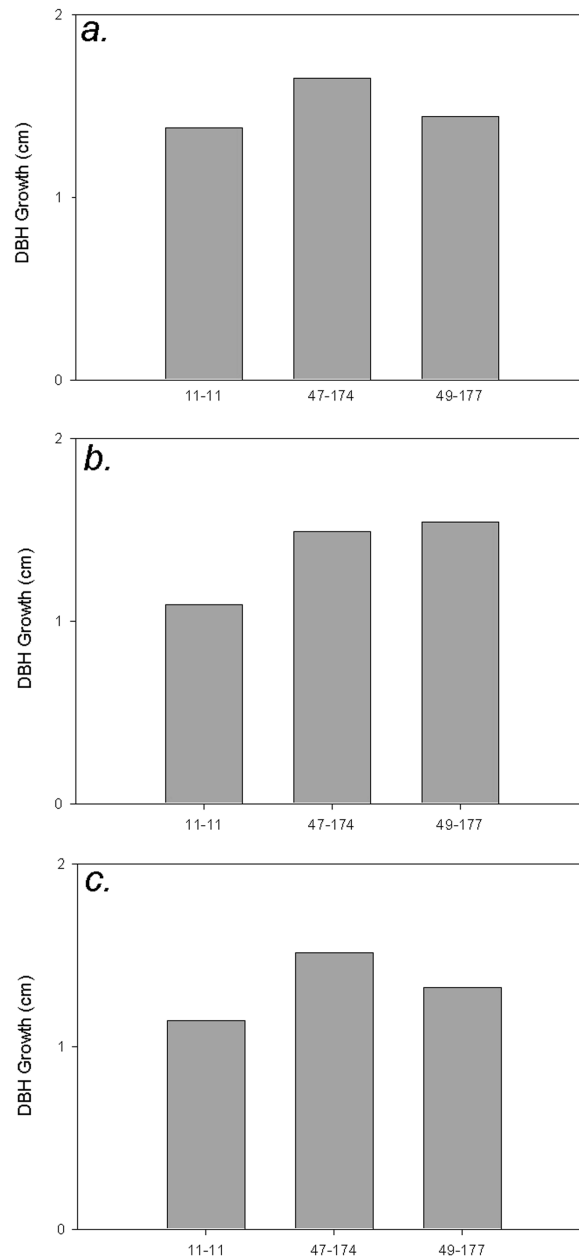
The clonal differentiation exhibited in mixed plots was associated with changes in individual tree (and genotype) performance as competition develops over time. Such changes and their implications in the assessment of genetic traits have been

reported by Franklin (1979) and Tuskan and van Buijtenen (1986), Hühn and Langer (1995). Moreover, such effects probably reflect the continuum of competition processes – from resource depletion to resource preemption – as characterized by Weiner and Thomas (1986) and illustrated for a density-stressed stand of black spruce by Newton and Jolliffe (1998). Resource depletion occurs at low levels of competitive stress at the establishment phase of a stand prior to stand differentiation. Early on in our study, resource depletion would have dominated the competition process in all plots, but at age 3, the depletion process was probably approximated most closely by the pure 1.5-m spacing. During this stage, an individual tree's use of resources can be conceptualized as being directly proportional to the tree's size. As the stand matures and differentiates, competition can be increasingly characterized as or dominated by a resource preemption process where an individual tree's use of above-ground resources is not simply proportional to its size, but is partially influenced by the fact that large competitors passively prevent solar radiation from reaching the smaller competitors and thus disparities are maintained and increased over time. Resource preemption probably dominated the competition process in the 0.5-m mixed plots at age 3.

*Insights gained through use of an index*

Resource depletion and preemption processes have ramifications for selecting clones based on information gathered from single tree or small plots where competition has affected growth performance, particularly if the clones are later to be planted in pure plantations Tuskan and McKinley (1984). Clone 47–174, for example, showed only average performance in the 1.0 or 1.5-m mixed plots (seen as one of the middle lines in Figures 1c and 1e), and thus it might not have been selected if growth in these mixed plots was the basis for clonal selection. It was a top performing clone, however, when planted in pure plots at high levels of intraclonal competition (seen as the highest line in Figures 1b, 1d, and 1f) and had substantially better overall survival than clone 49–177 in pure plots (Table 1). By using a competition index to calculate least square means, however, such confounding effects associated with differences in interclonal competition can be partially 'removed' to aid understanding and refine interpretation.

Consider, for example, the relative performance of the three hybrid clones in the 0.5-m mixed clonal plots as reflected in Table 1 and in Figures 1a. (note: clone CL was excluded from these subsequent comparisons because surviving trees provided an inadequate sample; moreover, the CL clone would have been eliminated from selection because both survival and growth were markedly poorer than other clones; Table 1, Figure 1). The least squares mean DBH growth for clones 11–11, 47–174 and 49–177 in the 0.5-m pure clonal plot was calculated by adjusting only for block and initial DBH effects and is shown in Figure 2a. The same was done for the 0.5-m mixed plots (conditions that might exist in a single-tree progeny trial and to a lesser degree in a single row progeny trial) and is shown in Figure 2b. The marked differentiation between the two conditions due to inter-clonal vs. intra-clonal competition is apparent. Least squared means for the 0.5-m mixed clonal plot data were



*Figure 2.* By using a competition index, interclonal competition can be partially compensated for. a) Mean DBH in the 0.5-m pure clonal plot adjusted for block and initial DBH alone. b) Mean DBH in the 0.5-m mixed clonal plot adjusted for block and initial DBH alone. c) Mean DBH in the 0.5-m mixed clonal plot adjusted for block, initial DBH, interclonal competition and the interaction between clone and interclonal competition as characterized by the competition index 'area'.

therefore calculated with the CI 'area' and the interaction between clone and 'area' as well as block and initial DBH covariates: Figure 2c is based on the same data exhibited in 2b but adjusted for inter-clonal competition. In all 3 cases, the clonal differences in DBH growth were significant ( $p < 0.01$ ). By using the competition index, the clonal differentiation that characterizes the mixed plots is moderated and the trends in clonal means are more similar to those in the pure plot where a homogeneous environment exists. The index has reduced the confounding or exaggerating growth differences associated with differential competition within these mixed clonal plots (caused by early growth differences or variable mortality) and has essentially re-ranked the clones accordingly.

The simple indices examined in this study were useful not only in explaining variation in growth rates of short-rotation *Populus* plantings, but for Douglas-fir and a tolerant species, western hemlock, as well (Brodie and DeBell, unpublished data). The results provide additional evidence that competition indices can enhance the interpretation of growth data from provenance or progeny trials as suggested by Tuskan and McKinley (1984) and Magnussen and Yeatman (1987), Land and Nance (1987), Mäkinen (1997) as well as other types of research plots where individuals are evaluated in non-homogenous competitive environments. Furthermore, our results show that competition indices need not be complex to be effective, particularly when spacing between trees is relatively uniform. Often the information needed to calculate them is readily at hand from routine plantation or study measurements. If used appropriately, indices can help clarify treatment effects and 're-rank' treatments associated with genotype or cultural practices (e.g., fertilization or weed control) in tests that involve single tree or other small plots where different levels of competition may confound observed results.

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### References

- Biging G.S. and Dobbertin M. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41: 360–377.
- Corona P. and Ferrara A. 1989. Competition indices for conifer plantations. *Agric. Ecosystems Environ.* 27: 429–437.

- Daniels R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *For. Sci.* 22: 454–456.
- Daniels R.F., Burkhart H.E. and Clason T.R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. *Can. J. For. Res.* 16: 1230–1237.
- DeBell D.S. and Harrington C.A. 1997. Productivity of *Populus* in monoclonal and polyclonal blocks at three spacings. *Can. J. For. Res.* 27: 978–985.
- Franklin E.C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genetica* 28: 207–212.
- Gerrard D.J. 1969. Competition quotient: a new measure of the competition affecting individual forest trees. *Mich. State Univ. Agr. Exp. Sta. Res. Bull.* 20, 32 p.
- Hegyí F. 1974. A simulation model for managing jack pine stands. In: Fries J. (ed.), *Growth models for stand and tree simulation*. Royal College of Forestry, Stockholm, Sweden, pp. 74–90.
- Holmes M.J. and Reed D.D. 1991. Competition indices for mixed species northern hardwoods. *For. Sci.* 37: 1338–1349.
- Hühn M. and Langner W. 1995. Investigations on the correlation pattern in even-aged stands of larch. II. Dynamic descriptions of phenotypic correlations between neighboring observations. *Silvae Genetica* 44: 325–334.
- Land S.B. Jr. and Nance W.L. 1987. APA: A useful tool for analyses of progeny tests. In: *Proceedings 19<sup>th</sup> southern forest tree improvement conference*; 1987 June 16–18: College Station, TX. Southern Forest Tree Improvement Committee. pp. 300–311.
- Lorimer C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manage.* 6: 343–360.
- Magnussen S. and Yeatman C.W. 1987. Adjusting for inter-row competition in a jack pine provenance trial. *Silvae Genetica* 36: 206–214.
- Mäkinen H. 1997. Possibilities of competition indices to describe competitive differences between Scots pine families. *Silva Fennica* 31: 43–52.
- Martin G.L. and Ek A.R. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For. Sci.* 30: 731–743.
- Mugasha A.G. 1989. Evaluation of simple competition indices for the prediction of volume increment of young jack pine and trembling aspen trees. *For. Ecol. Manage.* 26: 227–235.
- Nance W.L. and Grissom J.E. Unpublished Office U.S. Report For. Serv., Southern Forest Experiment Station 1987. A.P.A. user's guide: a computer program for computing area potentially available by constrained tree polygons.
- Newton P.F. and Jolliffe P.A. 1998. Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. *Can. J. For. Res.* 28: 259–275.
- SAS Institute, Inc. 1987. *SAS/STAT guide for personal computers*. 6th edn. SAS Institute, Inc., Cary, NC, USA.
- Tuskan G.A. and McKinley C.R. 1984. The use of competition indices in advanced-generation selection. *Silvae Genetica* 33: 209–215.
- Tuskan G.A. and van Buijtenen J.P. 1986. Inherent differences in family response to inter-family competition in loblolly pine. *Silvae Genetica* 35: 112–118.
- Weiner J. and Thomas S.C. 1986. Size variability and competition in plant monocultures. *Oikos* 47: 211–222.
- Wimberly M.C. and Bare B.B. 1996. Distance-dependent and distance-independent models of douglas-fir and western hemlock basal area growth following silvicultural treatment. *For. Ecol. Manage.* 89: 1–11.