Possibilities of Competition Indices to Describe Competitive Differences between Scots Pine Families

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Possibilities of distance-independent and -dependent competition indices to describe the competition stress of an individual tree was studied in southern Finland. Five half-sib open-pollinated families and one check lot of Scots pine (*Pinus sylvestris* L.) was used as study material in order to analyse competitive interactions of crown form and stand density variation. Almost all competition indices correlated strongly with radial increment. Thus distance-independent indices were adequate to describe competition in young row plantations, where distance effects between trees were implicitly eliminated. Correlations between indices and height increment were not significant. Along with the increase in competition, the width and length of the crown and the diameter increment of the stem of some narrow-crowned families decreased slowly compared to wide-crowned families.

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1 Introduction

Competition is a spatial process in which the performance of any individual tree depends on its ability to acquire essential growth resources. The crown processes and the crown structure are important for both production of dry matter and for the technical quality of stems. Differences in crown structure determine the amount of intercepted light and mechanical abrasion between trees (e.g. Assmann 1970, Cannell 1978, Oker-Blom and Kellomäki 1982, Kuuluvainen 1988).

Crown shape and quantity of the branches are affected by tree genotype (e.g. Cannell et al. 1983, Madgwick 1983, Velling 1988). Conifer breeders (e.g. Kärki 1985, Pulkkinen and Pöykkö 1990, Pulkkinen 1991, Pöykkö 1993) have paid special attention to genetically narrow-crowned trees, because it is assumed for monocultures of these types that the within-stand competition would be less than in stands of trees with wider crown. However, most studies of genotypical effects upon growth of narrow crowned trees have dealt with competition only in theory.

Studies of forest reproduction, growth and mortality have used measures of competition between individual trees (e.g. Glover and Hool 1979, Martin and Ek 1984). Several measures of competition have been developed and incorporated into models based on individual trees for many tree species. Most of these competition measures are competition indices which are based on the size, number, proximity and spatial arrangement of neighboring trees. The general structure of many indices is often similar, but the functional form varies, ranging from simple density values (e.g. Lemmon and Schumacher 1962, Spurr 1962) to detailed estimates of crown geometry (e.g. Gates et al. 1979, Ford and Diggle 1981). The broad issue of these approaches has recently been summarised by Ford and Sorrensen (1992).

Indices can be grouped into categories according to treatment of spatial arrangement. Distance-independent indices do not account for spatial arrangement of trees. They evaluate competition in relation to the mean density of a stand. It is assumed that spacing is equal throughout a stand and that the number, size or biomass of trees in a stand is adequate for describing the competitive stress. On the other hand, distance-dependent indices take into account the spatial distribution of trees. These indices are based on the premise that stand variables are not sufficient expression of the competitive influence of neighbors.

The general goal of this study was to provide insight into the role of competitive differences between Scots pine (*Pinus sylvestris* L.) families in influencing growth. The specific objectives were (1) to determine which properties associated with competition (i.e. size, number, angular dispersion and distance to neighbors) might be important predictors of growth in pine plantations and (2) to quantify how growth reactions depend on crowding level in different pine families.

2 Material and Methods

2.1 Material

Five half-sib open-pollinated families of Scots pine were chosen as study material. The mother trees were plus trees (superior phenotypes in mature stands) from south-central Finland. Families were selected so that they would, based on earlier studies, differ with respect to growth and crown characteristics (Velling, pers. comm.). One check lot (normal stand progeny) was also included for comparison.

The material was collected from two progeny tests in central Finland (Table 1). Each family was replicated in eight complete blocks in progeny test no. 577/1 and two to four blocks in progeny test no. 691/1. Square plots were located randomly within blocks and experiments were surrounded by border rows. The initial spacings were 2.0 × 2.0 (577/1) and 0.75 × 1.5 (691/1) meters in test plantations. Due to mortality caused by competition of ground vegetation after planting, however, the range of density per plot at the time of measurements was from 740 to 8520 stems per hectare (Table 2). Some plots had no undamaged trees left, so sample trees were selected randomly from other blocks. After the early phases of the plantations, mortality had been small. The age of the plantations was 15 and 17 years in 691/1 and 577/1 respectively.

A total of 96 sample trees were measured, 48 in each progeny test. Measurements were taken in the spring of 1993 before the growing period (24 trees in each test) and after the growing period in the autumn (also 24 trees). Sample trees were selected from the center of each plot. Only dominant and codominant trees that were not damaged were accepted as sample trees in order to analyse trees which will form the final stand and have the most economical value. Suppressed trees which will be removed in thinnings were not accepted as sample trees. Diameter at breast height, total height, distance and compass direction to each neighboring tree within a circular plot (radius 3.0 meters) around each sample tree were measured. Trees situated further away were not considered as possible competitors based on previous studies in Scots pine (Pukkala and Kolström 1987). The diameter of the crown (mean

Table 1. General information about the test plantations and extractable nutrient amounts of mineral soil on an air-dry matter basis.

Test no.	577/1	691/1
Time of establishment	5.–10.6.1978	27.–30.5.1980
Location N/E	61°49'/29°41'	61°48'/29°17'
Altitude	87 m	81 m
Forest site type	Old field	Old field
Soil type	Sandy mull	Sandy mull
Site preparation	Ploughing and tilling	Ploughing and tilling
Spacing	2 × 2 m	0.75 × 1.5 m
Blocks	8	2–4
Plot size	8 × 8 m	4.5 × 6.0 m
Seedlings/plot	16	24
Nutrients:		
N_t (g/kg o.m.)	48.54	54.13
Ca (mg/kg)	246.57	370.12
Mg (mg/kg)	26.16	19.27
K (mg/kg)	28.44	49.54
P (mg/kg)	1.74	2.46

of maximal and perpendicular to maximal diameter) and the annual height increment of the sample tree were also measured, and sample discs were taken at breast height. The diameter increments were recorded to the nearest 0.01 mm from the sample discs. The basic properties of the sample tree population are given in Table 2.

Samples of mineral soil were taken from the surface soil (0–10 cm) of the plots; and the concentrations of nitrogen and extractable phosphorus, potassium, calcium and magnesium were determined (Table 1). Differences in nutrient concentration were statistically significant between test plantations (except Mg) but not between families. N, Ca and Mg concentrations had no correlation and K and P concentrations had weak negative correlations with radial increment. Thus, site fertility was thought to have an equal influence on growth between families, and the variables describing nutrient concentration were not included in the final analysis.

2.2 Methods

The competitive stress of a tree was described by 8 different competition indices (Table 3). Some indices were used as proposed by the original authors, but most were modified in order to improve their applicability. Stem diameter and height were used to describe the size difference between the subject tree and its competitors. The first three indices are distance-independent measures from a circular plot (radius 3.0 m). CI_1 is the stem number and CI_2 is the basal area of the plot. The subject tree was not included in the indices. CI_3 is the ratio between the size of the subject tree and the mean size of the trees on the plot.

Three types of distance-dependent indices were evaluated. The first two indices are distance-weighted size ratios. CI_4 determines the competitive stress as the sum of size ratios divided by the distance of the competitors from the subject tree. In CI_5 the size ratio is multiplied by the

Table 2. Properties of the sample tree population and survival of seedlings. Dbh is diameter at breast height, Rank is family ranking in the register of progeny test result (among 577 progenies) according to height growth (Venäläinen et al. 1994). E627–E719d are plus tree families and StMa11 is control (standard stand seed lot).

Family	DBH (cm)			Height (m)			Survival % 577/1			Survival % 691/1			Rank
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	
E627	7.7	9.8	12.9	5.5	6.7	7.7	50.0	65.6	81.8	33.3	53.1	79.2	44
E630	4.9	11.0	16.5	5.1	6.5	7.3	12.5	47.3	75.0	8.3	51.4	91.7	515
E635c	5.5	10.0	14.7	5.7	6.8	7.8	18.8	53.1	68.8	62.5	66.7	70.8	229
E641	6.2	10.5	13.6	5.6	6.6	7.7	12.5	44.5	87.5	20.8	54.5	95.8	338
E719d	6.9	10.6	14.1	4.1	6.6	7.9	50.0	65.5	81.3	16.7	63.5	91.7	492
StMa11	5.8	10.4	15.5	5.8	6.7	7.6	43.8	58.4	81.3	26.1	55.5	79.2	

Table 3. Competition indices.

Index	Expression	Authorship
A. Stand density measures, distance-independent indices		
1.	$CI_1 = n$	
2.	$CI_2 = \sum_{j=1}^{n} BA_j$	Beck (1974)
3.	$CI_3 = \left(S_i / \overline{S}\right)^{EX}$	Glover and Hool (1979)
B. Distance weighted size ratios		
4.	$CI_4 = \sum_{j=1}^{n} \left(S_j / S_i\right)^{EX} / DST_{ij}^{c}$	Hegyi (1974)
5.	$CI_5 = \sum_{j=1}^{n} \left(S_j / S_i\right)^{EX} \times \exp\left(c \times DST_{ij} / \left(CR_i + CR_j\right)\right)$	Monserud and Ek (1977)
C. Size weighted angle summations		
6.	$CI_6 = \sum_{j=1}^{n} \alpha_j \left(S_j / S_i\right)^{EX}$	Pukkala and Kolström (1987)
7.	$CI_7 = \sum_{j=1}^{n} \beta_j \left(S_j / S_i\right)^{EX}$	Pukkala and Kolström (1987)
D. Influence-zone overlap		
8.	$CI_8 = \sum_{j=1}^{n} O_{ij} / A_i \left(S_j / S_i\right)^{EX}$	Gerrard (1969)

i = subject tree, j = competitor, n = total number of competitors, S = size measure (dbh, height), $\overline{S}$ = the arithmetic mean size on the plot, DST = distance between trees, CR = maximum potential crown width, α = horizontal angle from the subject tree to both sides of the stem of its neighbor at a height of 1.3 m, β = vertical angle from the midpoint of the subject tree to the base and to the top of the neighboring tree, O = overlap area, A = influence-zone area, C = distance weighting parameter, EX = size weighting parameter

exponential term that accounts for the distance term and the linear overlap of maximum potential crown widths of the subject tree and competitors.

CI_6 and CI_7 are the sums of the angles from a subject tree to its neighbors. CI_6 is the sum of the horizontal angles from the subject tree to both sides of the stem of its neighbors at a height of 1.3 m multiplied by the size ratio. CI_7 is the sum of the vertical angles from the midpoint of the subject tree to the base and top of neighboring stems multiplied by the size ratio of these trees.

The influence-zone indices are based on a hypothetical circular zone of influence around each tree. This zone is thought to be the expected growing space of open-grown trees. CI_8 is the sum of the area of the neighboring tree's influence zones that overlap the subject tree's zone weighted by the size ratio. The maximum relation observed between crown diameter and stem diameter was used in the determination of the radii of the influence zone.

Exponent C is the weighting factor for distance between the subject tree and its competitors, and EX is the weighting factor for the size relation. As C increases, nearer neighbors are weighted more than remote neighbors. Initially, various combinations of C and EX were tried with large class intervals. It was then possible to 'narrow in' on further iterations of the best parameter values, until the values shown in Table 4 were accepted. These values accounted for the largest correlation between the value of competition index and the sum of radial increments of the years 1990–1992 for all families.

There is some indication that the pattern of directional distribution of competitors in the neighborhood will affect the performance of a particular plant (Mack and Harper 1977, Waller 1981, Weiner 1982). Plants tend to be smaller when surrounded by neighbors than when the neighbors are crowded to one side. A measure of angular dispersion (Pukkala 1989) was used as an index of the grouping of neighbors.

Differences in growth response to competitive stress among families were analyzed by the regression technique with the best competition index (CI_4) based on diameters, grouping index and dummy variables describing families (standard stand lot as the base population). Cross-products between dummy variables and the competition index were also included in regression equations. The stepwise regression procedure was used and independent variables were accepted or rejected according to the 0.10 level of risk.

3 Results

Correlations between radial increment and competition indices showed that indices differed only slightly in their predictive ability despite the substantial difference in design (Table 4). Indices based on diameter relations were, however, a little better than those based on height relations. The best weighting factor for the size relation (EX) was systematically higher in height indices, i.e. height differences had to be weighted more than diameter differences. Values of EX were greater than one, which suggests that the variation in diameter increment associated with competition was not linear, i.e. large neighboring trees were relatively stronger competitors than smaller trees. In the interpretation of exponents it should be noted that all subject trees were dominant or codominant trees, and thus the results cannot be generalized to other crown classes.

Table 4. Correlations between radial increment and competition indices. The explanations of the competition indices are given in Table 3. EX is the size and C is the distance weighting factor. Both diameter (D) and height (H) were tried as size measure. GI is grouping index.

Index	Index	EX	C	r
CI_1	-	-	-	–0.640
CI_2	-	-	-	–0.506
CI_3	D	-	-	–0.219
CI_3	H	-	-	0.035
CI_4	D	1.3	0.4	–0.698
CI_4	H	3.0	0.6	–0.663
CI_5	D	1.2	0.4	–0.697
CI_5	H	2.0	2.2	–0.681
CI_6	D	1.2	-	–0.692
CI_6	H	3.1	-	–0.608
CI_7	D	1.3	-	–0.697
CI_7	H	2.8	-	–0.657
CI_8	D	0.8	-	–0.652
CI_8	H	1.9	-	–0.638
GI	-	-	-	0.239

Grouping index was also significantly correlated coefficient with radial increment (Table 4). However, it did not improve the predictive ability of simple regression models, when the competition index was already in the model (Table 5).

Mean diameter of the crown clearly decreased with the increase in competition index (Fig. 1a). Families E627 and E635c had narrower crowns at low levels of competition, but the rate of decrease in the crown diameter was lower per unit increase in competition index compared to the other families. However, variation in crown diameter within families was high compared to differences between families. Thus, only the dummy variable of family E630 was statistically significant (Table 5).

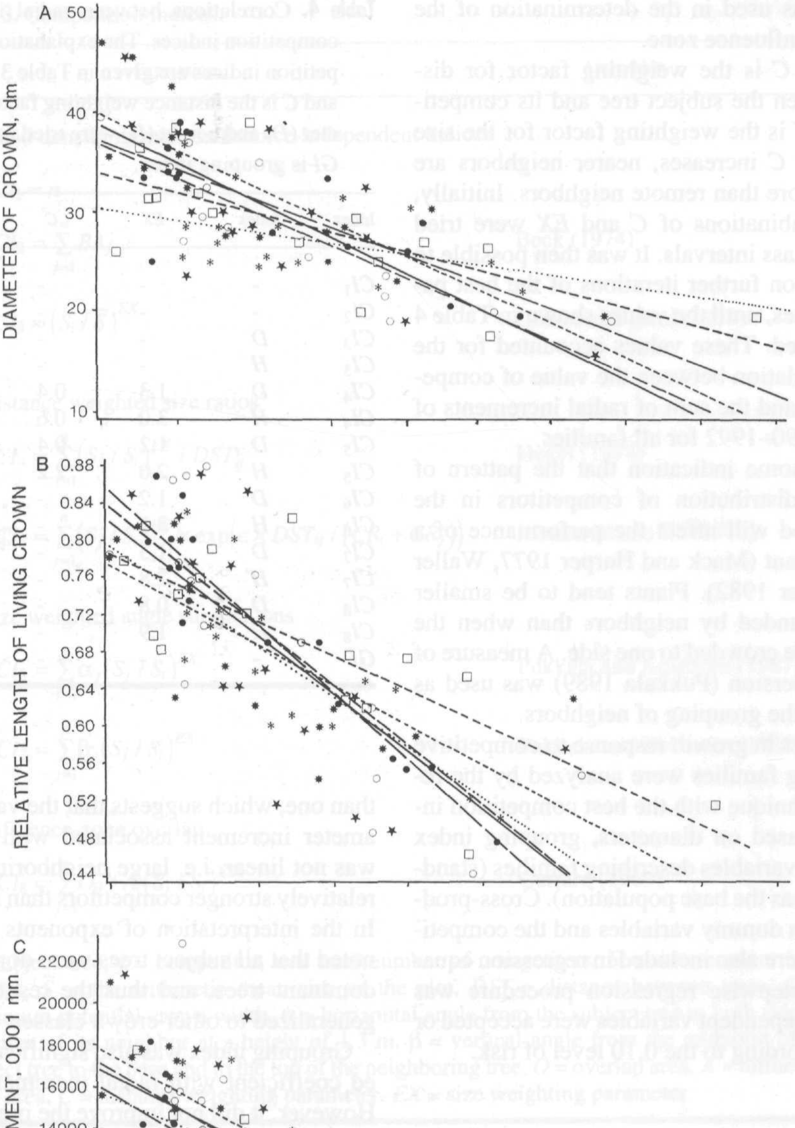

Fig. 1. Diameter of the crown (A), relative length of the living crown (B), and radial increment of the stem (sum of the years 1990–1992) (C) by competition index (*CI*) in plots of different families.

Table 5. Regression coefficients for width and relative length of the living crown and for radial increment (sum of the years 1990–1992). Explanations of the symbols are given in Tables 2 and 3.

X-variable	B	SE B	Beta	t	p >
Width of living crown (dm), $R^2 = 0.57$					
Intercept	35.92	0.83	-	43.17	0.001
CI_4	–2.79	0.27	–0.72	–10.15	0.001
E630	2.27	1.27	0.13	1.80	0.077
Relative length of living crown, $R^2 = 0.75$					
Intercept	0.81	0.01	-	67.09	0.001
CI_4	–0.06	0.01	–0.84	–12.00	0.001
$CI_4 \times$ E635c	0.01	0.01	0.17	2.44	0.017
Radial increment (0.1 mm), $R^2 = 0.54$					
Intercept	171.35	5.47	-	31.32	0.001
CI_4	–19.16	1.90	–0.81	–10.09	0.001
E635c	–47.42	12.17	–0.44	–3.90	0.001
E719d	–15.57	7.59	–0.14	–2.05	0.043
$CI_4 \times$ E635c	11.22	3.66	0.37	3.06	0.003

B = coefficient of regression, SE B = standard deviation of regression coefficient, Beta = standard coefficient of regression, t = value of t-test, p = level of risk.

In addition, the relative length of the living crown was clearly related to the competition index. Families E627, E630 and E635c had shorter crowns at the low level of competition but the rate of decrease in the crown length for families E630 and E635c was low (Fig. 1b).

The same relationship was apparent between the radial increment of a stem and the competition index (Fig. 1c). Families E627, E635c and E719d had smaller diameter increments at low competition levels than the other families did. However, the diameter increment of families E627 and E635c decreased at a slower rate per unit increase in competition index compared to families that had wider crowns at low competition levels (Table 5).

Correlations and regressions between height increment and competition indices were not statistically significant.

4 Discussion

Detailed knowledge of how the growth rate of trees respond to their immediate neighborhood allows comparisons among responses of genotypes to changing stand density. Use of various expressions of competition indices as measures of competition for individual trees is based on the premise that a tree's total competitive ability for all resources can be indicated by a simple expression of amount, size, distance and spatial distribution of neighboring trees. Indices do not explicitly indicate the mechanism of neighbor interference, i.e. competitive stress is experienced only by the degree of crowding.

Another problem in the use of competition indices arises because the current size of neighboring trees is not independent of the size of a subject tree and it is not valid to use them in regression analysis (Weiner and Thomas 1986). However, if the size increase of the neighboring trees over the study period is small compared with their size at the beginning of the study period, the error will also be small. In addition 'double use' of an individual first as a subject tree and then as the competitor for another tree transgresses the requirements of regression analysis. In this study the problem was avoided by selecting only few sample trees per plot.

The use of stand variables to describe growth of individual trees is the main problem of distance-independent indices, i.e. all counted trees contribute equally to the competition estimate, despite size or proximity. Thus, distance-dependent competition indices have been observed to express competitive stress better in natural stands (e.g. Hamilton 1969, Daniels 1976, Ker 1980, Martin and Ek 1984, Mugasha 1989). However, the result of this study, that distance-independent indices were adequate to describe competitive interactions in row plantations, where distance effects between trees were implicitly eliminated, agrees with the findings of Opie (1968), Moore et al. (1973), Alemdag (1978) and Ganzlin and Lorimer (1983). Consequently, in young pine plantations, when the radial growth of a tree is predicted, it is sufficient to consider only stem number or basal area around a subject tree.

The use of distance-dependent indices requires appropriate definition of the radius within which neighbors are actual competitors and to what degree. Thus, definition of a competition index depends on the subjective interpretation of the researcher. According to this study, all distance-dependent indices are adequate for describing the competitive stress in plantation grown Scots pine. When proper weighting factors of size and distance are used, none of the indices is superior to the others.

The growth level of individual trees was related to competition pressure i.e. to the local level of growth resources. However, factors other than the mother tree and competition considerably influenced on the phenotype of an individual tree. High variation in crown diameter and radial increment at low competition index values suggests that competition was not strong enough to influence the phenotype of a tree. On the other hand, individual observations at high values of competition index had a considerable effect upon the parameters of the regression equations, and thus exceptional values may lead to misinterpretations.

The results of this study suggest that the genotype of trees and competition have interactive effects on width and length of the crown and stem diameter increment. In wide spacing families E627 and E635c had narrower crowns than other families, but crown diameter and radial growth of the stem decreased slowly with the increase in competition level. On the other hand, family E719d had a low level of radial growth regardless of competition pressure. Evidently phenotypic plasticity in response to competition is genetically determined and some genotypes are more stable than others (Bradshaw 1965).

It seems that families E627 and E635c were not able to utilize available environmental resources as efficiently as other families in low competition levels. On the other hand, under highly crowded conditions their phenotype and thus their ability to acquire resources for growth was not reduced as much as wider crowned families. Also the high ranking of family E627 and E635c based on height growth in the national progeny test register (Venäläinen et al. 1994) suggests that it may be possible to increase the productivity of the stand per hectare by selecting phenotypically stable, exceptionally narrow-crowned genotypes and planting them in high densities.

The results of this study do not describe the theoretical possibilities of tree improvement to increase timber production, because genetic variation within half-sib families is high compared to that of full-sib families (e.g. Pöykkö 1982). Empirical research on this topic can only partly solve the problem, because no systematic test plantation exists which covers enough genetically different types of stands planted in different densities. However, these results give us a chance to indicate the main effects of silviculture and tree improvement on growth and quality of trees. They emphasize the need to combine silvicultural methods with the genetic manipulation of trees, i.e. in order to produce maximal yield, the genotype of the trees must be suited to the particular environment and to the silvicultural system used.

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