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Adjusting for Inter-Row Competition in a Jack Pine Provenance Trial

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Summary

Results from field trials in forest genetics can be severely biased if trees of different genetic identity are allowed to compete with each other following crown closure. Two methods of reducing such bias by adjusting observed values to expected values in large genotypically homogenous stands are given in this paper. One method uses empirical regression models of tree growth and its dependence on competition to calculate adjustments to observations. The second method derives the influence of size of neighbour trees on the size of a subject tree by solving a linear first-order auto-normal scheme of a two-dimensional Markov process. Both a maximum likelihood solution and an iterative solution of ordinary least-squares estimates are presented. The two estimates were identical. The effects of tree mortality on competition and tree growth were addressed for each method. Data of tree height and diameter collected at age 12 and 20 years in a range-wide *Pinus banksiana* (LAMB.) provenance trial in Ontario with 10-tree single-row plots showed that inter-row competition significantly affected provenance mean tree diameters at both ages. Tree heights were little affected by differential competition in the five provenances analyzed. A local Petawawa provenance which ranked among the best in tree height was exposed to substantially less competition than would otherwise be the case in a single provenance stand without mortality. Diameters in this provenance were adjusted downwards by 8% at age 12 years and 11% at age 20. Growth rates of diameters per unit stem size were not significantly affected by competition.

Key words: *Pinus banksiana*, Provenance, Intraspecific Competition Modeling, Growth.

Zusammenfassung

Wenn verschiedene Genotypen miteinander konkurrieren, können die Ergebnisse forstgenetischer Freilandversuche mit schwerwiegenden systematischen Fehlern behaftet sein. Die vorliegende Arbeit stellt zwei Methoden dar, solche systematischen Fehler durch Angleichung der beobachteten Werte an die in großen, genotypisch homogenen Beständen zu erwartenden Werte zu reduzieren. Empirische Regressionsmodelle des Zuwachs in Abhängigkeit von Konkurrenz werden in der ersten Methode verwendet, um die Angleichung der beobachteten Werte zu berechnen. In der zweiten Methode wird der Einfluß der Nachbarstämme auf die Größe des Versuchsstammes durch das Lösen eines linearen „autonormalen“ Schemas erster Ordnung der zwei-dimensionalen Markov-Gleichung hergeleitet. Sowohl eine „maximum likelihood“-Lösung als auch eine iterative Lösung

mit Schätzungen der kleinsten Quadrate werden vorgestellt. Mittels der zwei geschilderten Methoden wird der Einfluß des Stammausfalls auf Konkurrenz und Wachstum angesprochen. Die im Alter von 12 und 20 Jahren erhobenen Höhen- und Durchmesserwerte eines das Verbreitungsgebiet von *Pinus banksiana* (LAMB.) umfassenden Provenienzversuches in Ontario, dessen Parzellen in Einzelreihen von jeweils 10 Stämmen angelegt wurden, wiesen in beiden Altersgruppen einen signifikanten Einfluß von Konkurrenz zwischen Reihen auf die Mitteldurchmesser der Provenienzen auf. Die Baumhöhe wurde in den 5 untersuchten Provenienzen von Konkurrenz nur wenig beeinflusst. Eine örtliche Provenienz, Petawawa, die eine der besten Höhenwuchsleistungen aufwies, wurde in diesem Versuch weitaus weniger Konkurrenz ausgesetzt, als sonst in einem Bestand aus nur einer Provenienz. Der Durchmesser dieser Provenienz wurde für das Alter 12 Jahre um 8% und für das Alter 20 Jahre um 11% nach unten korrigiert. Das Durchmesserzuwachsprozent wurde nicht signifikant durch Konkurrenz beeinflusst.

Introduction

The use of small plot units in forest genetic field trials has increased the effect of competition on tree growth. Methods to assess and adjust for competition are required to obtain accurate estimates of genetic parameters. Only few attempts have been made to introduce competition correction measures in forest genetics. A range-wide jack pine (*Pinus banksiana* LAMB.) provenance (seed source) trial arranged in single row plots offered an opportunity to quantify the effect of inter-row competition and to develop procedures of adjustment. Two methods of quantification and adjustment are introduced. One method (Approach I) relates tree growth to competitive status which enables the calculation of adjusted periodic growth. The second method (Approach II) uses size of neighbouring trees (both within plots and in neighbouring plots) as covariates in a linear analysis of provenance tree heights and diameters. In the latter case we introduce a simple solution to the iterative process of estimating competition effects from a least-squares approximation. Tree mortality is taken into account in both methods.

Review of literature

Separation of genetic and non-genetic variation is the primary objective of quantitative genetic studies (FALCONER, 1981). Hence, minimizing or stratifying environmental variation is a priority in the choice of experimental design. Environmental heterogeneity in forest genetic experiments is unavoidable. Trees are larger than most agricultural crops, and occupy considerable space on variable forest sites. In addition, genetics trials are conducted for many years to several decades. Much attention has therefore been

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focused on ways to reduce, or account for, this heterogeneity and thereby increase the statistical efficiency of genetic experiments with forest trees (LIBBY and COCKERHAM, 1980).

Today genetic trials in forestry often use plots containing only 10 or fewer trees (CORRELL and ANDERSON, 1983; LAMBETH and GLADSTONE, 1983; LIBBY and COCKERHAM, 1980), or far less than the 30–50 trees recommended earlier in order to obtain conditions comparable to those in homogenous forest stands of common genetic identity (EDWARDS, 1956; STERN, 1968). A common argument for using few trees per plot is the statistical efficiency of such designs: i.e. reduction of number of trees and associated plot size (minimizes size of experimental unit and hence within-block environmental variance (LAMBETH and GLADSTONE, 1983)). Reducing plot size also reduces establishment and maintenance costs. However, an important shortcoming of smaller plots is the increased effect of interactions between neighbouring plots. Justification for employing single- or few tree-plots rests ultimately on the purpose and expected duration of the trial. For example, direct estimation of growth and yield of different genetic entries requires a large plot size to achieve a genetically balanced competitive environment within plots (BARTLETT, 1978; EDWARDS, 1956).

It has long been recognized that trees in adjacent plots without wide border separations compete with each other, and that this competition can modify plot values (GÄRTNER, 1982; HÜHN, 1976; STERN, 1968). Competition may seriously distort genetic parameters in trials with small plots (HÜHN, 1976; KEMPTON, 1982). This will be particularly evident where there is a wide range in growth response among the genetic entries as in a range-wide provenance trial. Phenotypic variance caused by competition is a component of the environmental influence (SAKAI and MUKAIDE, 1966; STERN, 1965). If it can be isolated, more accurate estimates of genetic parameters can be obtained (CORRELL and ANDERSON, 1983; COX, 1958; FREEMAN 1979; KEMPTON, 1982; KEMPTON and HOWES, 1981; MATHER, 1961).

In small plots, the yield of one entry may be depressed or enhanced by, respectively, more or less aggressive neighbours capturing or yielding a disproportionate share of available resources. Once even a small superiority has been established, it accelerates quickly, the less vigorous entries performing more poorly than under normal conditions, while the more vigorous entries develop exceptionally well owing to the absence of equal competition (EDWARDS, 1956; HÜHN, 1974).

Competition as used here is defined as an intraspecific density-induced local scarcity of a necessary factor for plant growth (ASSMAN, 1970; BIRCH, 1957; WALTHER, 1960). When the immediate supply of a single essential factor falls below the combined demands of the individual plant's, competition begins (FORD, 1975). Prior to this, growth of individual trees is primarily a consequence of genetic potential and site. The density-induced competition is frequently considered to be a balancing interaction where one plant's loss is potentially a neighbouring plant's gain (DE WITT, 1960; DRAPER and GUTTMAN, 1980; HÜHN, 1973; MATHER, 1961; STERN, 1969).

The issue of density-induced competition and its effects on forest growth and yield have been studied intensively in numerous spacing and thinning experiments planted in monocultures (e.g., ASSMAN, 1970; EVERT, 1984 (for references); HAMILTON, 1969; KIRA *et al.*, 1953; STERBA, 1975; STIELL, 1974). Published accounts on the effect of competition and stand density on various genetically defined forest mate-

rials are, however, still few (FRIES, 1984; FRANKLIN, 1979; MATHESON and RAYMOND, 1983; WILUSZ and GIERTYCH, 1974).

A common element among many individual-tree-based growth models is the inclusion of an index designed to quantify the degree of competitive pressure on single individuals in a stand (HEGYI, 1974; LORIMER, 1983; SMITH and SCOTT, 1983; MOORE *et al.*, 1973; MARTIN and EK, 1984). Competition indices estimate the total competition from surrounding trees that are assumed to be affecting the growth of a subject tree. Such indices usually take into account, directly or indirectly, the number of competitors, the size of the subject tree and its distance to each competitor, and often the size of competing trees (ALEMDAG, 1978; HATCH *et al.*, 1975; DANIELS, 1976).

For agricultural variety trials, where the main objective is genetic inference from yields per unit ground area, the method of nearest neighbour analysis has been applied successfully in adjusting plot values (BARTLETT, 1978; BESAG, 1974; CLIFF and ORD, 1981; DRAPER and GUTTMAN, 1980; FREEMAN, 1979; KEMPTON, 1982; KEMPTON and HOWES, 1981). The analyses rely on the assumption that plot yields are correlated to the yield obtained in adjacent plots due to a common microsite environment or because of local environmental gradients created by the neighbouring crops. A variant of these methods called the 'moving average method' (WRIGHT, 1978) has been successfully applied in forest genetics trials with a large amount of within-block variation. Commonly a one- or two-dimensional first order auto-normal scheme (i.e. a stationary Markov process) is the preferred model to describe neighbour effects (BESAG, 1974; BARTLETT, 1978; DRAPER and GUTTMAN, 1980; KEMPTON and HOWES, 1981; MEAD, 1967; WILLIAMS, 1952).

Material and Methods

Measurements of tree diameter 1.3 m above ground level and height were gathered in April 1985 for an all-range, jack pine provenance trial growing at the Petawawa National Forestry Institute, Chalk River, Ontario (Canada). The experiment was planted in the spring of 1966 with nine replications (blocks) of 99 provenances arranged in 10-tree single-row plots at a spacing of 1.8 × 1.8 m. Provenance plots within replicates were completely randomized. The site is flat to slightly undulating and was cleared of jack pine-aspen forest cover before planting. The soil is a deep aeolian sand with a low water table and moderate fertility. Further details of this trial are given by HOLST (1967).

Trees of five principal provenances, and all adjacent provenance row-plots over the nine replications, were included in the analyses (Table 1). Four principal provenances were selected about the median in height ranking of all 99 provenances when measured in 1978 at 15 years of age from sowing (data on file). For provenances of intermediate rank, one might expect competition from neighbouring trees to balance out on the average, i.e. both positive and

Table 1. — Geographic origin of provenances.

Provenance	Origin	Lat. (N)	Long. (W)	Elevation (m)	Height ranking 1978
Turtle Creek	New Brunswick	45°58'	64°57'	75	47
Downs Lake	Quebec	48°00'	74°15'	500	44
Petawawa Plains	Ontario	45°47'	77°23'	180	9
Lone Rock	Wisconsin	43°35'	90°10'	250	40
Cowan	Manitoba	52°03'	100°23'	365	51

negative competitive effects are expected to influence trees within these seed sources. The one-sided competition situations which prevail in the fast and slow growing provenance plots are not suitable for developing models of competition effects. The fifth provenance is local and ranked among the tallest provenances in the experiment.

The number of provenances included in our analyses is a minimum for developing and testing competition models but sufficient to demonstrate the applied computational methods. None of the 45 principal provenance plots analyzed were edge plots at the perimeter of the test plantation.

Heights were recorded to the nearest even centimetre with a graduated pole, and diameters at breast height (1.3 m) were taken to nearest millimetre with a diameter tape.

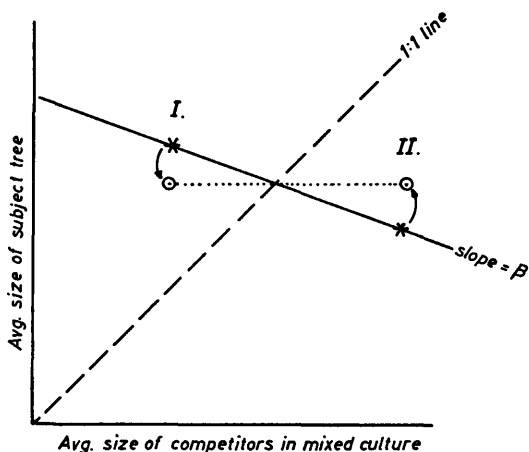
A relative growth rate for height and for diameter was calculated by dividing the average annual increment between 1978 and 1985 by tree size in 1978 (height or diameter).

Multiple comparisons of mean values were performed with the 'Bonferroni-t' method (DOUGLAS *et al.*, 1981). Statistical significance of results are indicated in the text with '*' (0.01 < α ≤ 0.05), '**' (0.001 < α ≤ 0.01), or '***' (α ≤ 0.001). Non-significant results are indicated by 'NS'.

The effects of competition on growth in height and diameter growth are illustrated by empirically derived regression models. The independent variables used are: heights and diameters in 1978, HEGY's competition index (HEGY, 1974), the squared values of these three variables, their logarithms, and reciprocals. Variables included in each of the equations presented constitute the best subset (criterion: maximum coefficient of determination, R^2), with $\alpha = 0.10$ significance level of inclusions.

Analytical objectives

The objective of the analyses was to reduce the error and possible bias in estimates of provenance growth caused by an experimental design in which faster and slower growing provenances occur next to each other in a random fashion. Figure 1 shows the geometric principle of adjustments on a homogenous site. The solid line describes the general relationship between tree size of a subject tree and that of its competitors. With increasing size of competitors the



β = competition coefficient
 * = observed yield in mixed stands
 o = adjusted expected yield in monoculture

Fig. 1. — Geometric principle of adjustment of expected yield from mixed to monoculture conditions.

size of the subject tree decreases at a rate that depends on species, site factors, age, and spacing. In a stand composed of trees of a single provenance, the expected size of a subject tree equals, on the average, that of its competitors. However, in a provenance trial with single-row plots, trees in adjacent rows will differ in average vigor and hence size, due mainly to genetic differences of adaptation (microsite, insects, and disease may have a role too). Figure 1 illustrates two situations (I and II) that leads to opposing adjustments. In I the subject tree (see asterisk, Fig. 1) has grown under less competition than in a single-provenance stand (monoculture) and the observed value is adjusted downwards as illustrated. In situation II, where a tree has been exposed to more competition than in a monoculture, the adjustment is positive.

Approach I

Competition index

The competitive stress at age 15 (1978) of a tree was expressed by HEGY's competition index (HEGY, 1974):

$$(1): CI_i = \frac{1}{N} \sum_{j=1}^N (DBH_j / DBH_i) / DIST_{ij}$$

where CI_i = competition index of subject tree i ;
 DBH_i = diameter (cm) of subject tree i ;
 DBH_j = diameter (cm) of competitor j ;
 $DIST_{ij}$ = distance (m) between tree i and j ;
 N = number of competitors. Here $N = 8$.

An index value was calculated for each tree except the first and last in a row. Only eight trees growing nearest to a subject tree were included in the index (i.e. three in each of the two neighbouring rows and two in the row of the subject tree). Missing competitors were assigned a DBH-value of zero. The zero value of missing competitors underestimate competition by a very small amount because more than 90% of all missing trees died during the first five years of the experiment, i.e. before any competition could be expected to occur. In a large stand without mortality the mean value of DBH_j / DBH_i calculated for each individual tree will depend in a complex manner on the diameter distribution of the population (KENDAL *et al.*, 1983). In order to obtain a reference level of competition we assume here for simplicity, that the ratio will average one. Given this

assumption the competition index is reduced to $\sum_{j=1}^8 1/DIST_{ij} = 3.79$ in a 1.8 m × 1.8 m spaced plantation. This competition index value will be used as a basis for adjustment.

A second competition index based upon potentially available growing space (ALEMDAG, 1978) was also calculated. However, results obtained with this index were similar to those obtained with HEGY's index, and are therefore not shown.

Approach II

Competition coefficients and adjustments

The static model used in the estimation of provenance and competition effects on the dependent variable Y (i.e. height and diameter) was:

$$(2): Y_{ijk} = \mu + \alpha_i + \delta_j + \tau_{ij} + \beta_1 [0.5(Y_{ijk-1} + Y_{ijk+1}) - \mu] + \beta_2 (\bar{Y}_N(ijk) - \mu) + \epsilon_{ijk}$$

where Y_{ijk} denotes the value of the k th tree in the j th replicate of provenance i ; μ is the overall mean; α_i denotes provenance effects ($i = 1 \dots 5$); δ_j stands for replicate (block) effects ($j = 1 \dots 9$), and τ_{ij} is a provenance × block

interaction term; $\bar{Y}_{N(ijk)}$ is the average observation of Y_{ijk} 's two competitors in identical row positions in adjoining rows; ϵ_{ijk} is an error term (assumed independent and normally distributed with variance σ^2). The two terms $\beta_1[0.5(Y_{ijk-1} + Y_{ijk+1}) - \mu]$ and $\beta_2(\bar{Y}_{N(ijk)} - \mu)$ represent the effects of within (β_1) and between row (β_2) competition. The first and last tree in each row of the five selected provenances were not used in the analyses of competition effects (i.e. $k = 2 \dots 9$).

Formulated this way, it is assumed that competitive interaction is primarily related to tree size of the four immediate neighbours in a regular spaced plantation. Only four competitors were included in model (2) as opposed to the eight in model (1) for the sake of simplicity. Including eight competitors would have left too few observations for an adequate analysis because only subject trees with a full set of competitors were included in the analyses. Model (2) is a first-order auto-normal scheme of a two-dimensional Markov process (BARTLETT, 1978; BESAG, 1974; KEMPTON, 1982; MEAD, 1967) if the experimental design is regarded as, (a) a regular lattice of point sites with continuous variables having a multivariate normal distribution, and (b) we assume stability in both time and space.

A first biased estimate of the parameters in (2) was obtained by analysis of covariance using ordinary least-squares techniques (BARTLETT, 1978; BESAG, 1974; KEMPTON, 1982; MEAD, 1967). Averaging over blocks we obtain the expected value of $Y_i (= E(Y_i))$ for provenance i :

$$(3): E(Y_i) = \bar{Y}_i + b_1 \bar{Y}_i + b_2 \bar{Y}_{N(i)}$$

where \bar{Y}_i is the arithmetic average for provenance i and $\bar{Y}_{N(i)}$ is the mean of trees in rows adjacent to provenance i . b_1 and b_2 are the least squares estimations of the within (β_1) and between row (β_2) competition coefficients respectively.

In a single-provenance stand the expected value of $\bar{Y}_{N(i)}$ is equal to \bar{Y}_i . Hence, in order to obtain $E(Y_i)$ as in a "monoculture" the observed average \bar{Y}_i must be adjusted by:

$$(4): \Delta \bar{Y}_i = b_1(\bar{Y}_i - b_2/b_1 \bar{Y}_{N(i)})$$

Equation (4) leads to a convergent iterative process in which adjustments $\Delta Y_i^{(n)}$ and adjusted $Y_i^{(n)}$ values are calculated concurrently. The final adjustment $\Delta Y_i^{(n)}$ is:

$$(5): \lim_{n \rightarrow \infty} \Delta Y_i^{(n)} = (\bar{Y}_i - b_2/b_1 \bar{Y}_{N(i)}) \frac{b_1}{1-b_1}$$

with $|b_1|, |b_2| < 1.0$ we have:

$$\lim_{n \rightarrow \infty} \Delta Y_i^{(n)} = (\bar{Y}_i - b_2/b_1 \bar{Y}_{N(i)}) b_1 / (1-b_1)$$

Expression (4) is only appropriate in the absence of mortality. Any mortality in a regular lattice structure will lower competition at the associated localities. With a total ratio of m_i missing trees in provenance i and a total ratio m_N in the rows adjacent to this provenance, the effective competitive value of a provenance is assumed to be reduced to $(1-m_i)Y_i$ and that of its competitors to $(1-m_N)Y_{N(i)}$. Inserting these values on the right side of (5) and rearranging, we obtain the expectation of Y_i in a single-provenance stand without mortality as:

$$(6): E(Y_i | \text{"monoculture"}) = (\bar{Y}_i + b[(1-m_i)\bar{Y}_i - (1-m_N)\bar{Y}_{N(i)}])(1+bm_i)$$

where $b = b_1/(1-b_1)$, and b_2/b_1 is assumed to be one. In expression (6), the terms enclosed in square brackets adjust for the combined effect of difference in mortality and, in the variable Y , between a provenance i and its neighbours. The last term (i.e. $(1+bm_i)$) accounts for provenance within row mortality after adjustments due to competition effects have been dealt with.

An alternative to the estimation of the competition coefficient β_1 given in (2) is obtained by the maximum likelihood approach in which the solution is found by minimizing (with respect to β_1):

$$(7): L(Y_{ijk} | \text{model (2) with } \beta_1 = \beta_2) = -2 \log | I - B | + n \log \prod_{i=1}^n \text{RSS}(\beta_1) + \text{constant},$$

where RSS is the residual sum of squares in model (2) as a function of β_1 and n is the total number of observations ($= 241$). In this particular case I is an 675×675 identity matrix and B is a complex matrix composed of nine (i.e. one for each replicate) 75×75 competition matrices (C) along the diagonal and zeros in remaining positions. The elements of the 75×75 competition matrix C are β_1 for $i = j \pm 1$ or $j = i \pm 1$ and 0 otherwise. The dimension of C is determined by the number of observations in each replicate (here approximated by: 5 (provenance) \times 3 (rows) \times 5 (average number of trees per row) = 75). Further amplification and details about the maximum likelihood estimation procedures are given by, for example, CLIFF and ORD (1981), DRAPER and GUTTMAN (1980), KEMPTON (1982) and MEAD (1967).

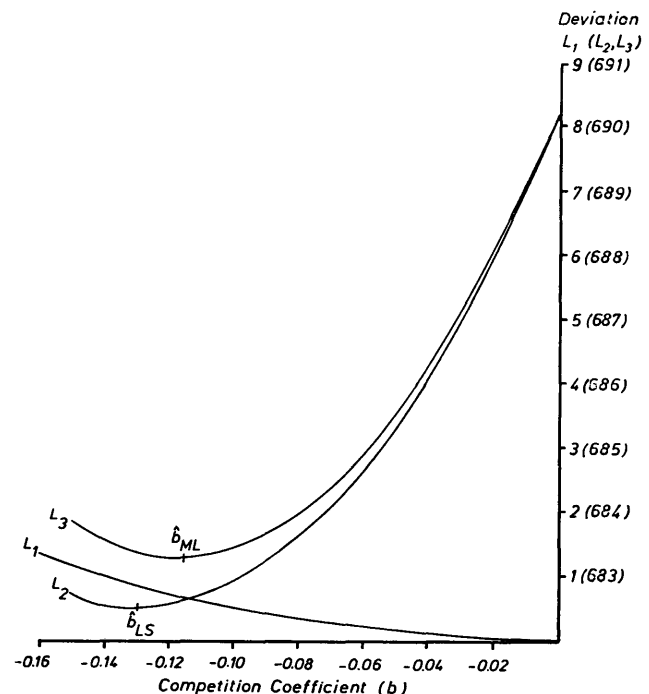


Fig. 2. — Deviance of the nearest neighbour autoregressive model for different values of the competition coefficient β . Dependent variable: DBH 1985 (cm). Explanation of L_1, L_2 and L_3 is given in text. ML = Maximum likelihood solution; LS = least squares solution.

Table 2. — Tree size, tree growth 1978–1985, and competition indices. Approach I. Mean values followed by a common letter do not differ significantly on the 95% probability level (Bonferroni-t test of multiple comparisons). Adj. Diam. = Expected increment at a competition index of 3.79.

Provenance	No. of observations		---Height---		--Diameter--		Survivor -Increment 1978-1985-- Adj.			Relative Growth Rates		Competition index 1978 (Hegy1)	
	1978	1985	1978 m	1985 m	1978 cm	1985 cm	Height m	Diam. cm	Diam. cm	Height	Diam.	Mean	Min.-Max
Turtle Creek	62	59	6.5b	9.9b	8.4b	12.0b	3.3a	3.3ab	3.1	0.40a	0.32a	3.36a	0.55-13
Downs Lake	46	45	6.6b	9.7b	7.9b	10.8bc	3.0ab	2.8b	2.5	0.37ab	0.30ab	3.10a	0.53-12
Petawawa Plains	45	44	7.2a	10.8a	9.8a	13.9a	3.6a	3.9a	3.3	0.40a	0.33a	2.22b	0.44- 4
Lone Rock	33	30	6.6b	9.5b	8.8b	12.2b	2.6b	2.8b	2.4	0.32b	0.26b	2.68ab	0.35-12
Cowan	55	53	6.6b	9.3b	7.9b	10.5c	2.7b	2.8b	2.6	0.33b	0.26b	3.21a	1.16- 8

Table 3. — Correlation between tree growth (increment 1978–1985), tree size and Hegyi's inter-tree competition index. n = 136.

Competition Index (Hegy1)	Tree Size			
	Diam. 1978	Height 1978	Diam. 1985	Height 1985
	-0.71 ***	-0.55 ***	-0.49 ***	-0.26 ***
Competition Index (Hegy1)	---Increment---		Relative Growth Rates	
	Diam.	Height	Diam.	Height
	-0.49 ***	-0.49 ***	-0.03 NS	0.11 NS
Diameter 1978	0.47 ***	0.50 ***	-0.17 *	-0.15 NS
Height 1978	0.52 ***	0.48 ***	0.12 NS	-0.12 NS

The determinant | I-B | was found by the methods outlined by ORD (1975). Minimum deviation of L (= L₃) in (7) was found by graphical interpolation (Figure 2). The significance of competition was assessed from the likelihood ratio which under the null hypothesis is approximately distributed as χ^2 with 1 degree of freedom.

Results

At the age of 20 years, average tree height of the five provenances was 8.8 m with an arithmetic mean stem diameter of 12 cm. Average height and diameter growth of survivors between 1978 and 1985 was from 2.6–3.6 m and 2.8–3.9 cm respectively. Additional results on provenance tree size and growth are given in Table 2.

Approach I

The average competitive stress as expressed by Hegyi's competition index (CI) varied significantly among provenances (Table 2). Trees of four provenances experienced both light (CI < 1.0) and heavy (CI > 8) competition between 1978–85, whereas trees from the Petawawa prove-

Table 5. — Approach II. Observed and adjusted diameters in 1978 and 1985. Neighbours = trees occupying the adjacent rows to the left and to the right of a provenance.

Provenance	---Mortality---		-----Diameter-----			
	Provenance %	Avg. of Neighbours %	Provenance cm	Avg. of Neighbours cm	Prov. Adjusted cm	Adjustment %
1978						
Turtle Creek	14 (3) ¹	26	8.4b	7.3	8.1	-3.6
Downs Lake	36	53	7.9b	8.0	7.2	-8.9
Petawawa Pl.	38	63	9.8a	7.5	9.0	-8.2
Lone Rock	54 (48) ¹	65	8.8b	8.0	8.2	-6.8
Cowan	24	41	7.9b	8.4	7.6	-3.8
1985						
Turtle Creek	18 (6) ¹	29	12.0b	10.1	11.4	-5.0
Downs Lake	38	56	10.8bc	11.1	10.1	-6.5
Petawawa Pl.	39	64	13.9a	10.0	12.4	-10.8
Lone Rock	58 (52) ¹	65	12.2b	10.6	11.2	-8.2
Cowan	26	44	10.5c	11.4	10.0	-5.0

¹) () = mortality, exclusive of provenances rows with 100% mortality. Bracketed numbers are used in adjustments.

nance only were exposed to light or medium strong competition ($0.4 \leq CI \leq 4.5$, Table 2). Table 3 illustrates the average correlation among tree size, tree growth (increment 1978–1985), and competition index variables. Provenance tree growth was, as expected, negatively correlated with competition and positively correlated with tree size. When adjusted for tree size (height or diameter), the correlation between tree growth and competition was weaker but still highly significant (partial correlation coefficients with $136-3 = 133$ degrees of freedom averaged -0.24^{**}). Relative growth rates were, on the other hand, not significantly influenced by competition and were only loosely correlated with tree size. Table 3 clearly indicates that the relative growth rates reflect provenance growth with little or no

Table 4. — Approach II. Analysis of variance of tree height and diameter 1978 and 1985. MS = Mean square.

Source of variation	Degrees of freedom	Form of F-test	Height 1978		Height 1985		Diameter 1978		Diameter 1985	
			MS	F-ratio	MS	F-ratio	MS	F-ratio	MS	F-ratio
Blocks (B)	8	MS _B /MS _{PXB}	1.04	0.40NS	0.59	0.30NS	7.74	1.09NS	3.65	0.60NS
Provenances (P)	4	MS _P /MS _{PXB}	3.54	1.35NS	15.17	7.70***	32.56	4.61**	80.88	13.32***
B x P	30	MS _{BXP} /MS _W	2.62	3.44***	1.97	1.33NS	7.07	2.36***	6.07	1.38NS
Competition (C) ¹	1	MS _C /MS _W	0.41	0.54NS	0.18	0.12NS	32.74	10.91*	63.39	14.37*
Within plots (W)	197 ² 187 ³		0.76		1.48		3.00		4.41	

¹) Competition coefficient set equal to maximum likelihood solution.

²) 1978.

³) 1985.

influence of either competition or tree size (a measure of dominance and thus exerted competition itself). Identical results were obtained in each provenance when analyzed separately (not shown).

Results of the regression analyses of height (HI) and diameter (DI) growth 1978–1985 are shown in (8) and (9). Only those variables found significant at the 0.10 risk level are included in (8) and (9). Equation terms are listed in order of their importance.

$$(8): HI = -7.09 + 2.356(H_{1978}) - 0.1752(H_{1985})^2 + 0.408(DBH_{1978}) - 0.0151(DBH_{1985})^2; (R^2=0.415^{***}, SE=0.63 \text{ m}, n=136)$$

$$(9): DI = 0.64 + 0.502(H_{1978}) - 0.653(CI) + 0.0449(CI)^2; (R^2 = 0.349^{**}, SE = 1.26 \text{ cm}, n = 136)$$

Height growth between 1978 and 1985 depended significantly and foremost on tree height and stem diameter in 1978 (cf. equation 8). The effect of competition was non-significant different from zero after the tree size variables were entered in the regression model. Predictions of height growth are therefore possible from tree size variables alone. This result is not unexpected as it is generally accepted that height growth is unaffected by competition except at extremes not yet reached in this experiment. In contrast, diameter growth shows a strong influence from inter-tree competition, with two of its 3 included terms being CI terms. However, the CI terms contributes less to diameter increment than does the 1978 height. Equations (8) and (9) clearly demonstrate that unaccounted variables are responsible for more variation in observed growth than variables related to height, diameter, and spacing alone ($R^2 < 0.5$). Due to mortality of competitors or above average tree size in 1978 the five principal provenances were exposed to less competition than the chosen reference level of 3.79. The expected diameter growth of the five provenances at a competition index of 3.79 is shown in Table 2 (cf. "Adj. Diam." column). The adjustments of diameter-growth have been calculated as the difference between estimated growth with a competition index of 3.79 and that with the observed index in 1978. Calculated this way, diameter growth would have been 6 to 15% less (0.2–0.6 cm) in a single-provenance stand without mortality than found in our single-row plot trial. Petawawa and Lone Rock received the largest downward adjustments. The adjusted growth figures in Table 2 correlate somewhat better than the observed values with the relative growth rates ($r_0 = 0.81$, $r_{adj} = 0.86$). The adjusted values of diameter increment in Table 2 can in turn be used to obtain improved estimates of single-provenance stand diameters in 1985 simply by adding them to the DBH averages from 1978 (the latter were influenced very little by competition).

Approach II

Inter-tree competition (β) as defined in (2) was a significant covariant in the ANOVA-analysis of actual tree diameter in 1978 and 1985 but was not significant in the analysis of heights (Table 4). Competition explained 6.4% of the phenotypic variation in the 1985 diameters and 3.5% of the variation in the 1978 diameters. In comparison the entire model (2) accounted for 42% of the observed total variation in diameters in 1985 and 58% in 1978. Table 4 depicts additional ANOVA-results.

By the ordinary least-squares (LS) technique we obtained a competition coefficient (b_{LS}) of -0.124 in the analysis

of 1978 diameters and of -0.129 in the analysis of the 1985 diameters. Using the iterative solution in (5) the competition coefficients are reduced to -0.110 and -0.114 respectively. Figure 2 illustrates the estimation procedure of the competition coefficient by the maximum likelihood approach. The maximum likelihood estimate of the competition coefficient was taken as the minimum value of L_3 . In the figure, L_1 and L_2 represent the first two terms of the right side in (7) and L_3 their sum. Minimum of L_2 is the least squares estimate of the competition coefficient. The autoregression term, L_1 , increases exponentially with increasing competition, and the minimum of $L_3 = L_1 + L_2$ can be found by interpolation. KEMPSON (1982) has shown this minimum to lie between the least squares solution and half this value. Estimates obtained were -0.110^* for diameters in 1978 and -0.116^* for diameters in 1985. For any practical purposes the results of the two demonstrated estimation procedures (i.e. least-squares + iteration and maximum-likelihood) are considered identical. Minor discrepancies between estimates are most likely due to rounding and interpolation errors.

Applying the correction formula (6) to diameter averages from 1978 and 1985, adjusted values as shown in Table 5 were obtained. All adjustments were negative with an average of -6% on the 1978 values and -7% on the 1985 values. Without considering mortality, the adjustments would have averaged only -3% to -1% (< 0.5 cm), and diameters of Cowan and Downs Lake would have been adjusted upwards. The necessity to consider mortality in the adjustment process manifests itself in the distinct and highly significant differences in mortality rates among provenances and in the rows growing next to the provenances (Table 5; Chi-square tests of equal mortality in the five provenances and in their neighbours resulted in χ^2 -values greater than 30, $P(\chi^2 > 30, df = 4) < 0.001$). To take an example the provenance Turtle Creek grew under heavier competition than, for instance, Cowan (Table 2), a difference caused by higher mortality rates in the latter provenance and, surprisingly also in its neighbours. Judged by the average size of neighbouring trees alone, the opposite conclusion would have been reached. By including mortality, the adjustments become compatible to the procedures applied to the diameter growth. A strong correlation between the 1985 diameter adjustment percentages in Table 5 and the competition indices in Table 2 confirms this ($r = 0.9892^{**}$). Also, a significant negative correlation between the number of trees in a row in 1985 and the average within-row diameter ($r = -0.213^*$, 90 D.F., based on 9×15 within provenance correlations), indicates that mortality cannot be dispensed with in the adjustment to the expected monoculture yield. Also noteworthy is the increased difference in diameters between the five principal provenances and the provenances in adjacent rows between 1978 and 1985. In 1978 the average difference was 1 cm; by 1985 it had increased to 1.7 cm (Table 5). This phenomenon is believed to be a direct consequence of competition, which will tend to exaggerate differences among rows once a hierarchy has been established.

Provenance rankings of diameters have only been changed slightly by the adjustments. However, as seen in Table 5, the difference between the fastest and the slowest growing provenance in terms of 1985 diameters has been narrowed from 24% to 19% (3.4 to 2.4 cm). Unbalanced competition has thus led to an overestimation of provenance effects on diameters in 1985. Adjustments of the 1978 diameters

have had only negligible influence on the provenance effects.

Discussion

Analysis of tree size, height, and diameter growth in a 20-year-old jack pine provenance trial with 10-tree single-row plots showed that relative growth rates and tree height provided estimates of provenance effects that were little affected by competition. Inferences about provenance diameters and diameter growth were significantly biased owing to planned (i.e. random) but unbalanced inter-row and intra-row competition, the latter due to different levels of mortality.

Approach I

Although inter-tree competition markedly influences individual tree growth in plantations (for example, ALEMDAG, 1978; FORD, 1975; HAMILTON, 1969; MARTIN and EK, 1984; STERBA, 1975), the ability to predict future growth from a tree's competitive status is generally rather poor, (ALEMDAG, 1978; HAMILTON, 1969; HATCH *et al.*, 1975; LORIMER, 1983; MARTIN and EK, 1984), as confirmed also in our study. Often tree diameter, being itself a measure of dominance, is found to be the best tree attribute for growth predictions. Attempts to express inter-tree competition with physiologically more meaningful indices have resulted in only minor advantages (ALEMDAG, 1978; HAMILTON, 1969; HATCH *et al.*, 1975; HEGYI, 1974; MARTIN and EK, 1984; MOORE *et al.*, 1983; SMITH and SCOTT, 1983) and the formulation of a model is still largely a question of personal preference. One reason for the unsatisfactory performance of many competition indices lies in the fact that while above-ground competition is concentrated within the areas occupied by individual crowns, root competition is diffuse and its origin unpredictable for a given tree (STIELL, 1970). It has also been shown that the actual spatial distribution of trees in plantations of a given density (stems per hectare) is a recognizable factor for stem diameter growth (STIELL, 1982).

Currently the greatest limitation on the use of competition indices in growth studies lies in the difficulties of interpretation with regard to changes over time (BESAG, 1974; FORD, 1975; LORIMER, 1983; MEAD, 1967; STERN, 1965). The estimates developed here were satisfactory for the situation and moment of measurement and but a sample of more complex relationships that develop in time. An analysis of a spatial-temporal scheme would be more appropriate but also extremely difficult to perform (BESAG, 1974).

Approach II

The inter-tree competition coefficients calculated here of -0.110 in 1978 and -0.116 in 1985 lie well within the reported range of inter-plant competition reported previously (CORRELL and ANDERSON, 1983; GÄRTNER, 1982; KEMPTON, 1982; MEAD, 1967; STERN, 1968). An increase in the numeric value of the competition coefficient, as in 1978—1985, is commonly observed as tree size increases at a constant spacing (GÄRTNER, 1982; HÜHN, 1974; KIRT *et al.*, 1953; STERN, 1968). In practical terms the competition coefficients reflect the prevalent negative effect of decreased available space on tree diameter growth (for references, see EVERT, 1984). Using the relationship derived between diameter increment and competition index in equation (9), we can estimate that diameters would have been 11% greater if between-row spacing had been 3.6 m instead of 1.8 m. Comparable results were obtained from a jack pine spacing trial in Manitoba

at age 15 years after planting (BELLA and FRANCESCHI, 1974 and 1980).

Inter-tree competition has been known to mask and complicate the estimation of genetic parameters in field trials. HÜHN (1974) reports on an 13-year-old Norway spruce trial in W. Germany where the inclusion of two guard rows (in neighbouring 6-x-6 tree plots) in the statistical analysis increased the relative amount of variance attributed to families by 2%—13% and deflated the standard error of contrast by as much as 28%. Hühn also reasoned that the temporal decline in the relative amount of genetic variance frequently encountered in field trials can be regarded as a natural outcome of increased inter-tree competition. Similar observations have been made by GÄRTNER (1982). A comprehensive study of inter-tree competition by STERN (1968) illustrated how the within-plot intraclass diameter correlation coefficient in Norway spruce and Scots pine changed with plot size, tree size (age), and spacing. The assessed intra-plot correlation coefficient can be related directly to the competition coefficients discussed herein (BARTLETT, 1978; KENDALL *et al.*, 1983). CORRELL and ANDERSON (1983) demonstrated that provenance effects in a 13-year-old *Pinus radiata* trial with 10-tree single-row plots (spacing 2.1×2.1 m) were exaggerated by a factor 1.8 owing to inter-row competition. In that study, inter-row competition was calculated from row means, which makes a direct comparison between their results and ours ambiguous. However, our results imply an approximate biasing competition factor of 1.2 on provenance effects if mortality rates were ignored.

It is interesting to note that, although significant effects of competition have been reported, it seems that ranking of provenances or progeny mean values have been little affected (CORRELL and ANDERSON, 1983; GÄRTNER, 1982; HÜHN, 1974). In the present study, the reduction achieved in the standard deviation of differences between two provenance mean values by accounting for competition was insufficient to increase the number of significant differences among provenances. This also reflects the deliberate choice of four provenances of median rank and one markedly better in growth. In general, an increase in number of significant differences is not to be expected because the reduction in the standard deviation is countered by a reduction in the range of provenance effects (CORRELL and ANDERSON, 1983; HÜHN, 1974).

Formulation of an exact model is of major importance in the analysis of competition effects. Ideally, the model accounts for all spatial heterogeneity arising from competition and microsite commodities (CORRELL and ANDERSON, 1983; KEMPTON, 1982). When the latter is more important than the former it results in positive competition coefficients, because trees growing together will tend to be more alike than trees growing further apart.

The solution proposed here to the iterative process of estimating the competition coefficient and suggested adjustment procedures differs from earlier attempts to allow for competition effect (CORRELL and ANDERSON, 1983; DRAPER and GUTTMAN, 1980; KEMPTON, 1982; KEMPTON and HOWES, 1981) in that it is based on single tree observations and not plot mean values. The plot value approach is more sensitive to the particular randomization of provenances (BESAG, 1974; KEMPTON and HOWES, 1981; MEAD, 1967) and does not adjust for spatial irregularities in competition caused by tree mortality. Further, the use of single tree observations allows and facilitates partial trial analysis and eliminates the problem of setting up an appropriate matrix configuration

and calculating the determinants of bulky matrices (DRAPER and GUTTMAN, 1980; KEMPTON and HOWES, 1981; ORD 1975).

Our assumption of an equal within- and between-row competition coefficient simplifies calculations and adjustment procedures. Separate estimates of the two coefficients consistently reveal that the within-row competition coefficients have negative values that are slightly closer to zero than the between-row competition coefficient owing to positive intra-row diameter correlation coefficients of 0.10 (NS) —0.14 (NS). Within-row height correlation was much stronger (0.24*—0.37*), which in part explains the limited effects of competition on height. Under the present objective of obtaining the expected mean values in single provenance stands, it appears justifiable to forfeit this difference, which otherwise leads to asymmetrical adjustments depending on whether the trees in the center row are bigger than their neighbours or not. Such adjustments are hard to comprehend intuitively, but spatial-directional competition effects are known to exist where gradients of soil moisture, shading, nutrient supply, or even management practices coincide spatially with the experimental design (KEMPTON, 1982; KEMPTON and HOWES, 1981).

By considering only the immediate neighbours in our estimate of the competition coefficient we have implicitly assumed that competition for light is more important than, for example, competition for moisture and nutrients. Although trees beyond the immediate neighbours exert an influence on a subject tree, the effect with respect to light is generally negligible in even-aged plantations (ALEMDAG, 1978; ASSMANN, 1970; DANIELS, 1976; HATCH *et al.*, 1975; KRAMER, 1979; NEWNHAM and MUCHA, 1971; STERN, 1965). The emphasis on light competition does not imply that competition for other factors can be ignored. However, in situations where no growth factors approach the minimum for growth, regulation of light or growing space appears to be most decisive factor for tree growth. This is because it imposes concomitant changes in, for example, moisture regimes and nutrient availability (HEINZE and FIEDLER, 1978; MAGNUSSEN, 1983; MITSCHERLICH, 1975). In a preliminary study we examined the effect of including all eight competitors surrounding a subject tree instead of only four. The net effect was to reduce the number of available observations from 241 to 98 without any substantial increase in amount of variation in tree size that could be accounted for. Furthermore, estimates of competition coefficients from the lesser sample were less precise (larger standard error) than were coefficients from the four competitor models.

It has been assumed throughout this paper that a single common competition coefficient applies, regardless of the provenances involved. A test of this assumption showed that there was no significant interaction between competition and provenances; a similar result was obtained from the regression analysis including HEGYI's competition index. A lack of a "genotype" by "genotype" interaction with competition is more likely in broadly buffered provenances containing several families (number of mother trees exceeded 10 in the provenances studied) than in a mixture of a few competing clones. Differences in competitive ability among provenances would imply genetic variation in provenance requirements of light, growing space, moisture, and nutrients. In a future analysis of all 99 provenances it must be anticipated that statistical differences among provenances will prevail because some extreme provenances will strongly dominate or be severely suppressed by their neighbours. However, the interpretation of such differences will only be meaningful in a serial

balanced experiment designed specifically to estimate genotypic differences in competitive ability (COX, 1958; FREEMAN, 1979; HELGASON and CHEIB, 1961; KEMPTON, 1982; KENDALL *et al.*, 1983; WILLIAMS, 1952). Published records on genotypic variation in the response to density-induced competition are scarce. KIRA *et al.* (1953) and STERN (1969) have reported genotypic variation in self-thinning rates due to density induced competition among provenances, whereas FRIES (1984) found no genotype \times spacing interaction in a Swedish trial of Scots pine clones.

General Aspects

It follows that it is only possible to estimate competitive effects when they can be defined in an analytical model based on an existing situation. FORD (1975), HÜHN (1973), and MATHER (1961) discussed the possible consequences of intraspecific competition on population structures, and SAKAI and MUKAIDE (1967) offer an intriguing solution on separating competition variance from phenotypic variance in large plots. However, the present provenance trial was ill suited for this kind of analysis.

We believe that the methods and adjustment schemes outlined in this study improve the efficiency of small-plot provenance trials by providing, on the average, better estimates of tree size and yield of a provenance monoculture than possible from unadjusted results. At present, the models exemplified here may be considered a necessary initial step towards formulating improved models. Use of competition coefficients is a sound theoretical practice and results have been shown to be consistent (KEMPTON, 1982). Their use is therefore recommended in situations in which unbalanced competition is manifested in genetic forest tree trials, and where traditional covariates are inadequate (BALLARD and MAJID, 1985). Analysis of single-tree plots (EDWARDS, 1956; LAMBETH and GLADSTONE, 1983; LEE, 1983; LIBBY and COCKERHAM, 1980), partial plot measurements (KUNG, 1977; LEE, 1983), assessment of the impact of thinning on genetic parameters (MATHESON and RAYMOND, 1983; WILUSZ and GIERTYCH, 1974), studies of juvenile-mature correlation of traits (FRANKLIN, 1979), and environmental genotypic stability (OWINO, 1977; TAI, 1971) are but few examples of potential applications. Recently, TUSKAN and MCKINLEY (1984) have emphasized and argued for the use of competition indices in phenotypic selection of a "crop ideotype".

Conclusion

The methods proposed here of reducing the bias in observations from genetic field trials in which an unbalanced competition and mortality exist among genotypes, have a potentially wide range of application in forest research. Both methods are feasible on large data sets and their use can be a routine part of the statistical analysis. However, it also became clear that adjustments cannot be expected to compensate fully for competition bias. Large plot experiments with sufficient buffering between plots are therefore still needed in long term yield trials with forest trees.

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