

A Method for Using Random Parameters in Analyzing Permanent Sample Plots

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The use of random parameter models in forestry has been proposed as one method of incorporating different levels of information into prediction equations. By explicitly considering the variance-covariance structure of observations and considering some model parameters as random rather than fixed, one can incorporate more complex error structures in analyzing data.

Competition indices and variance component techniques were applied to 92 Scots pine (*Pinus sylvestris* L.)-dominated permanent sample plots on drained peatlands in northern Finland. By quantifying stand, plot, and tree level variation, it was possible to identify the level (stand, plot, or tree) at which the explanatory variables contributed to the model. The replication of plots within stands revealed little variation among plots within a single stand but significant variation occurred at stand and tree levels. Positive and negative effects of inter-tree competition are identified by examining simple correlation statistics and the random parameter model.

Keywords competition, drained peatland, *Pinus sylvestris*, random parameters.

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1 Introduction

1.1 Random Parameters

Random parameters are parameters that vary randomly from unit to unit. For example, Lappi and Bailey (1988) used a site index formulation where the height curve for a given stand was predicted using the population curve and random stand effects. Biging (1985) found good results when using a random parameter formulation to account for between-tree differences in height development. Lappi (1986) used random parameters to localize a stem form equation. Palmer et al. (1991) demonstrated the use of nonlinear models with random coefficients to estimate population growth curves as well as variability in individual growth. In applications to growth curves, Jenrich and Schluchter (1986) emphasize unbalanced designs while Laird and Ware (1982) emphasize serial correlation between observations. Random coefficients are also described in the experimental design literature, most often termed random effects. Models for experiments involving both random and fixed effects are termed mixed models. In the present discussion, random parameters and random effects are not differentiated.

The application of random parameter models to nested error structures is discussed below. An example demonstrates their use in analyzing individual tree growth measured on permanent sample plots.

1.2 Peatland Growth and Yield

Peatlands (sites with peat soil and/or dominated by mire vegetation) cover 9 million ha in Finland and account for approximately 25 % of the productive forest land. Peatland drained for forestry purposes covers approximately 5.6 million ha. Research into growth of stands on drained peatland has focused mainly on developing operational drainage and fertilization guidelines (e.g., Heikurainen 1982, Paavilainen and Päivänen 1995) and investigating growth disorders caused by hydrological and nutritional imbalances (Paarlahti et al. 1971, Kolar 1983). As well, site classification of drained and undrained peatlands has received considerable attention

(Heikurainen and Pakarinen 1982, Laine 1989, Laine and Vasander 1990).

A few studies have been concerned with the growth and yield of trees on drained peatlands, particularly with reference to inter-tree competition. Using spatial growth models, Miina (1994) and Miina et al. (1991) predicted that stands with trees in clusters would have a 5–20 % reduction in volume growth over stands with more even spacing. Thinning stands following drainage resulted in improved nutrient status of the foliage and an increase or no change in volume and basal area growth (Hökkä 1993).

The objective of our investigation was to estimate the relative importance of inter-tree competition on individual tree growth on pine peatland stands.

2 Method

2.1 Model

The general form of a random parameter model is:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\alpha} + \mathbf{Z}\boldsymbol{\beta} + \boldsymbol{\varepsilon} \quad (1)$$

where \mathbf{y} is a vector of n observations, \mathbf{X} a $n \times p$ matrix of independent fixed variables, \mathbf{Z} a $n \times q$ design matrix, $\boldsymbol{\varepsilon}$ a vector of n errors, $\boldsymbol{\alpha}$ a vector of p unknown population parameters, and $\boldsymbol{\beta}$ a vector of q unknown random parameters. In the following discussion, \mathbf{y} , $\boldsymbol{\beta}$, and $\boldsymbol{\varepsilon}$ are assumed to follow independent multivariate normal distributions. That is,

$$\begin{aligned} \mathbf{y} &\sim NID(\mathbf{X}\boldsymbol{\alpha}, \sigma_{\varepsilon}^2\mathbf{I} + \mathbf{Z}\mathbf{D}\mathbf{Z}') \\ \boldsymbol{\beta} &\sim NID(0, \mathbf{D}) \\ \boldsymbol{\varepsilon} &\sim NID(0, \sigma_{\varepsilon}^2\mathbf{I}) \end{aligned} \quad (2)$$

where $NID(\boldsymbol{\mu}, \boldsymbol{\Sigma})$ refers to a normally and independently distributed random variable with mean vector $\boldsymbol{\mu}$ and variance-covariance matrix $\boldsymbol{\Sigma}$. The normality assumption is required for computing valid probabilities for the statistical tests described later.

2.2 Estimating the Model Components

Several methods for estimating the components of the random effects model have been developed. For balanced models (equal numbers of observations for each combination of independent variables), these generally yield the same results. For unbalanced models, these various methods do not necessarily yield the same estimates. In this study, the restricted maximum likelihood (REML) estimates were used. Maximum likelihood estimates (ML) are functions of sufficient statistics and have the desirable property of being consistent and asymptotically normal and efficient (Harville 1977). The ML estimates, however, do not account for the loss in degrees of freedom used in estimating the population effects. This was overcome by first placing all the random effects in the error vector and fitting the population effects using generalized least squares. The variance components were then estimated from the residuals. This approach is called REML (Searle et al. 1992). The ML estimates are based on the assumption of an underlying distribution for the data, most often the normal or multivariate normal (Harville 1977). We used here the MIXED procedure in SAS (Wolfinger et al. 1992, SAS... 1992) and the REML estimates based on the assumptions of an underlying normal distribution. Let $\mathbf{V} = \sigma_{\varepsilon}^2\mathbf{I} + \mathbf{Z}\mathbf{D}\mathbf{Z}'$, the covariance matrix of \mathbf{y} . Then, the REML estimates minimize the log likelihood

$$\begin{aligned} L(\bar{\boldsymbol{\alpha}}, \mathbf{V}; \mathbf{y}) &= -\frac{1}{2} \cdot \log(\det(\mathbf{V})) \\ &\quad -\frac{1}{2} \cdot \log(\det(\mathbf{X}^* \mathbf{V} \mathbf{X}^*)) \\ &\quad -\frac{1}{2} (\mathbf{y} - \mathbf{X}\bar{\boldsymbol{\alpha}})' \mathbf{V}^{-1} (\mathbf{y} - \mathbf{X}\bar{\boldsymbol{\alpha}}) \end{aligned} \quad (3)$$

\mathbf{X}^* is a $n \times p^*$ matrix whose columns are any p^* linearly independent columns of \mathbf{X} . The coefficients were estimated as the generalized least squares estimate

$$\bar{\boldsymbol{\alpha}} = (\mathbf{X}^* \hat{\mathbf{V}}^{-1} \mathbf{X})^{-1} \mathbf{X}^* \hat{\mathbf{V}}^{-1} \mathbf{y} \quad (4)$$

The estimated variance-covariance matrix of $\bar{\boldsymbol{\alpha}}$ is $(\mathbf{X}^* \hat{\mathbf{V}}^{-1} \mathbf{X})^{-1}$ and $\hat{\mathbf{V}}$ is the matrix of REML estimates of the variances of the random effects.

To test the hypothesis $H_0 \mathbf{c}'\boldsymbol{\alpha} = k$, the following large sample property is used. Under H_0 , the test statistic $z(\bar{\boldsymbol{\alpha}})$ is asymptotically distributed as a standard normal random variable:

$$\frac{\mathbf{c}'\bar{\boldsymbol{\alpha}} - k}{\sqrt{\mathbf{c}'(\mathbf{X}^* \hat{\mathbf{V}}^{-1} \mathbf{X})\mathbf{c}}} = z(\bar{\boldsymbol{\alpha}}) \sim N(0, 1) \quad (5)$$

For smaller sample sizes, a conservative approximation is to replace the standard normal distribution in equation 5 with the Student's t distribution with ν degrees of freedom where ν is the minimum degrees of freedom associated with any of the sums of squares used to estimate the variance components.

2.3 Interpreting the Model

One of the strengths of estimating variance components is that they help in interpreting the contributions of the independent variables to the model. This will be demonstrated in the example to follow. Briefly, as independent variables are added to the model, they help decrease the residual variation if they are associated with the dependent variable. Depending on which variance components are affected by the addition of an independent variable, the influence of the variable in the model may be speculated. For example, if the addition of a variable measured on individuals results chiefly in a reduction of the random error (σ_{ε}^2) term, then the variable is probably providing information at the individual observation level. If, however, the addition of a variable measured at the individual level reduced one of the other variance components, say σ_{β}^2 , then the variable is probably providing information at the class 1 level. In addition, the individual-level variable could potentially be replaced by a class 1 level variable.

3 Application to Tree Growth Analysis

3.1 Data

The data were collected from a series of permanent sample plots (PSPs) established in 1984–1988 to monitor the growth of forests on drained peatland in middle and northern Finland (the SINKA dataset described in detail by Penttilä and Honkanen 1986 and summarized by Mielikäinen and Gustavsen 1993). Approximately 300 Scots pine dominated stands representing the range from oligotrophic to meso-eutrophic sites were selected from the Finnish National Forest Inventory records. Denser, higher stocked stands were more likely to be selected than sparser stands.

Three circular plots per stand were established, the size of the plot being adjusted according to stand density so that the three plots combined contained approximately 100 trees (the lower diameter at breast height (dbh) limit was 4.5 cm if the stand was past the pole stage, 2.5 cm otherwise). The plot centre was permanently marked and various site and stand attributes, including drainage information, were recorded. The trees were mapped, marked at 1.3 m above the ground, and the species and dbh recorded. A smaller subplot was superimposed on the main plot and trees on these subplots were referred to as "sample" trees. At the time of plot establishment the sample trees were cored at breast height and past (under bark) 5-year dbh growth recorded, as well as breast height age in some cases. Total height was measured and past 5-year height growth measured for the sample trees. Diameter at 6 m above ground was recorded for the sample trees taller than 9 m and signs of external damage (abiotic and biotic) were also noted. The tree measurements were repeated after five growing seasons.

Those stands with less than 75 % Scots pine by basal area and those with any sort of cuttings, drainage work, or fertilization treatments within the monitoring period or in the last 10 years before plot establishment were deleted from the data. A total of 92 stands were selected for further analysis (see Table 1).

Table 1. A summary of the 92 stands used in this investigation.

Attribute	Mean (minimum–maximum)
North coordinate (km N)	7295 (7106–7504)
East coordinate (km E)	479 (376–633)
Elevation (m)	143 (30–300)
Degree days (>5 °C)	919 (735–1060)
Peat depth (cm)	ranges from 25 to >100
Depth to groundwater (cm)	ranges from 1 to >100
Last year of drainage	1973 (1959–1979)
Mean stand dbh (cm)	8.3 (4.3–15.1)
Mean stand height (m)	7.7 (3.5–15.0)
Stand basal area (m ² ha ⁻¹)	12.9 (0.9–35.2)
Density (stems ha ⁻¹)	1586 (274–4646)

3.2 Factors Affecting Growth

The main factors affecting tree growth on peatland sites are essentially the same as those on mineral soils, namely, climate (macro and micro), hydrology, nutrition, and genotype (biotic damaging agents are ignored in this discussion). These factors are all part of the forest ecosystem and interact to influence tree growth. Consideration of the interaction of, and correlation between, these factors as well as their manipulation by human intervention is particularly important on drained peatlands.

Finding measures to describe the factors affecting growth is not always straightforward. Variables usually must be summed or averaged over both time and space. The average yearly growing degree days (dd = sum of the average daily temperature for those days above 5 °C) was available for all stands and was used as a summary of the length of the growing season.

Drainage is the one of the major factors affecting hydrology on peatland stands. Tree growth following drainage may be dramatically different from pre-drainage growth. One difficulty with traditional site classification schemes (e.g., vegetation types, site index, productivity index) is that they implicitly assume that the site quality remains constant through the life of the stand. Particularly during the first rotation following drainage, considerable changes occur in the site

productivity as reflected in the understory vegetation and tree growth. Several site classification schemes for drained peatlands have been proposed (Heikurainen and Pakarinen 1982, Hänell 1988). They are based primarily on ground vegetation and reflect, to some extent, the productivity of the site. In this study, the nutrient status of the stands examined was assumed to be balanced (i.e., no chronic deficiencies) and no recently fertilized stands were considered. The tree itself was felt to be the best indicator of the suitability and potential of the site for tree growth. The tree, in effect, is the product of all the factors, including genotype, which affect tree growth. Dominant and codominant trees, in particular, are least affected by neighbouring trees and perhaps best summarize a site's productivity with respect to tree growth.

The trees within a stand may compete with each other and several inter-tree competition indices have been developed to describe this process (e.g., Tomé and Burkhart 1989) and competition has been used in model construction to modify potential tree growth (e.g., Magnussen and Brand 1989). For this example, the angle sum and centre of competition following Pukkala (1989) were used to describe competition. The angle sum is calculated for a target tree as the summation of the horizontal angles (α) formed between the target tree centre and the sides of each of the neighbouring trees at breast height (1.3 m), weighted by relative basal area (ba). That is, for tree i

$$\text{angle sum} = \sum_{j \neq i} \alpha_j \cdot \left(\frac{ba_j}{ba_i} \right)^{1.6} \quad (6)$$

where j include all trees within a 4 m radius. The exponent 1.6 is an empirical parameter taken from Pukkala (1989). The centre of competition indicates the symmetry or balance of the basal area of the surrounding trees and is calculated by assuming the tree of interest has coordinates (0,0) and by calculating the average coordinates of the neighbouring trees, weighted by basal area. The distance of the tree of interest to the weighted centre of the neighbours was termed the centre of competition.

$$\text{centre}_i = \sqrt{\bar{x}_i^2 + \bar{y}_i^2} \quad (7)$$

where

$$\bar{x}_i = \left(\sum_j w_j x_j \right) / \left(\sum_j w_j \right)$$

$$\bar{y}_i = \left(\sum_j w_j y_j \right) / \left(\sum_j w_j \right)$$

$$w_j = ba_j / (ba_i)$$

A large centre of competition indicates that more and/or larger trees are predominantly to one side of the tree than the other. A centre of competition of 0 indicates the basal area of the neighbouring trees is balanced around the tree of interest.

The other measure of competition investigated follows Pukkala's (1989) adaptation of Wu et al.'s work on ecological field theory which deals with the share of resources that individual trees exploit relative to neighbouring trees (Wu et al. 1985, Pukkala 1989). The resources available to the tree depend on the tree's need for resources, the neighbouring trees' demand for resources, and the total resources available. Following the notation of Pukkala (1989) the effect of tree j on available resources at distance s from tree j can be represented as

$$\Phi_j(s) = \Phi_j(0) \exp(-b_j s^2) \quad (8)$$

Symbols used in equations 8 through 11:

- $\Phi_j(s)$ = the proportion of resources used by tree j at distance s from tree j . $0 < \Phi_j(s) \leq 1$ for all $j=1, \dots, N$
- s = distance of the calculation point from tree j in meters
- $\Phi_j(0)$ = proportion of resources used by tree j at the tree location = $dbh_j / 30$
- b_j = $2 / dbh_j$
- $I_j(x,y)$ = resources remaining at the point (x,y) after the effects of trees 1 through j have been removed
- $I_0(x,y)$ = 1 and $0 \leq I_j(x,y) \leq 1$ for $j=1, \dots, N$
- $\Phi_j(x,y)$ = proportion of the resources used by tree j at (x,y)

- N = the total number of trees within 5 m of the point (x,y) .
- $R_j(x,y)$ = resources remaining at (x,y) after the effect of all trees but j is computed
- $I(x,y)$ = $I_N(x,y)$ = resources remaining at (x,y) after the effect of all trees is computed.
- CI_j = competition index for tree j
- $R_j(x_j,y_j)$ = residual surface at the nearest coordinate point to tree j
- $\Phi_j(x_j,y_j)$ = proportion of resources taken by tree j at its nearest calculation point
- c = 1.6 (taken from Pukkala 1989)

Since height measurements were not available for all trees, dbh was substituted for height in the calculation of $\Phi_j(0)$. The resources remaining at any point (x,y) after the resource use of all trees has been removed can be represented as

$$I_j(x,y) = \{1 - \Phi_j(x,y)\} I_{j-1}(x,y) \quad j = 1, \dots, N \quad (9)$$

This index of remaining resources was calculated at the intersections of a 1 m grid superimposed on the PSP and forms the interference surface. The residual surface (the interference surface after removing tree j) can be represented as

$$R_j(x,y) = \{1 - I(x,y)\} / \{1 - \Phi_j(x,y)\} \quad (10)$$

The competition index for tree j is equal to the weighted average of the residual surface around the tree, multiplied by the tree's resource demand relative to its neighbours, i.e.,

$$CI_j = \left[\frac{\{1 - R_j(x_j, y_j)\} / \{\Phi_j(x_j, y_j)\}}{\left(\sum \{ (1 - R_j(x, y)) \Phi_j(x, y) \} \right) / \left(\sum \Phi_j(x, y) \right)} \right] \cdot \left[\frac{\text{resources used by others}}{\text{resource needs}} \right] \cdot \left[\text{total resources used weighted by demand} \right] \quad (11)$$

This competition index reflects the proportion of

resources available to tree j under the assumption that a tree's resource use is proportional to its size (in this case, dbh). This competition index is referred to here as the field competition index or field.

3.3 Variables to Summarize Growth

To investigate the possible effects of inter-tree competition on tree growth, individual tree basal area growth including bark was selected as the variable of interest. This is partly due to practicality (dbh was measured on all trees) and also because the effects of competition are expected to become evident in dbh growth before height growth. Basal area was used instead of dbh as it lends itself to summation on an area basis more readily than dbh, although the correspondence between the two measures is obvious. The effect of inter-tree competition was expected to be manifested as a slowing of the basal area growth. That is, the coefficient of angle sum was expected to be negative as was the coefficient for the field competition index. A positive coefficient for the centre of competition would indicate a tree grows faster when the competition is arranged unevenly around the tree rather than being balanced around the tree. A non-significant coefficient would indicate that there is no detectable effect of spatial asymmetry of the basal area of neighbouring trees.

The average annual relative growth rate of basal area (bargr)

$$\text{bargr} = \frac{(ba_2 - ba_1) / (ba_1)}{t_2 - t_1} \quad (12)$$

was selected as the measure to be predicted rather than the absolute growth. The relative growth rate has the advantage of removing, to some extent, the effect of tree size and also eliminates the measurement scale from the units of measurement.

3.4 Model

The following model was proposed as a description of the relationship between competition (ei-

ther angle sum and centre of competition or the field competition index), basal area (ba), growing degree days (dd), plot basal area ($\text{plot } ba$) and bargr :

$$\text{bargr} = \text{fixed}(BA, DD, PLOTBA, COMPETITION) + \text{random}(\text{stand}, \text{plot}(\text{stand}) + \epsilon) \quad (13)$$

$$\begin{aligned} \text{bargr}_{ijk} = & a_0 + a_1 \cdot BA_{ijk} + a_{dd} \cdot DD_{jk} \\ & + a_{\text{plot}ba} \cdot PLOTBA_{jk} \\ & + a_{\text{competition}} \cdot COMPETITION_{ijk} \\ & + b_k + b_{k(j)} + \epsilon \end{aligned} \quad (14)$$

where

$$\epsilon = \epsilon_{\text{tree}} + \epsilon_{\text{error}}$$

where bargr_{ijk} is the bargr of tree i within plot j of stand k , b_j is the random effect of stand k , and $b_{k(j)}$ is the random effect of plot j within stand k . Written in matrix form, (Eq. 14) becomes

$$\text{bargr} = [I \ BA \ DD \ PLOTBA \ COMPETITION] \cdot a + Z_{st} + b_{st} + Z_{p(st)} \cdot b_{p(st)} + \epsilon \quad (15)$$

where the st subscript represents stands, the p represents plots within stands, and the ϵ refers to random error. The Z_{st} matrix has a 1 in cell ik if observation i is in stand k and a zero otherwise. The $Z_{p(st)}$ matrix has a 1 in cell ij if observation i is in plot j (where each plot is given a unique number) and a zero otherwise.

3.5 Fitting the Model

Only trees on the inner subplot were used in fitting the model. Trees on the outer, larger plot were used in the calculation of competition indices for the trees on the inner plot. Thus, all trees in the analysis had a full complement of neighbours. The relative basal area growth rates for the trees were estimated from the period with two subsequent measurements, i.e. the estimates reconstructed from cores were not used.

Tree basal area was added to the model first to remove the effect of tree size. Subsequent terms were added to the model by selecting the fixed effect which minimized the random error components and was statistically significant in the model.

4 Results and Discussion

The full results are given in Table 2: both stand level and plot level variance components are significantly different from the error variance in all models. The statistical significance of variation at the plot within stand level indicates that the replication of plots within stands was required for this study. The magnitude of the estimated plot variation (a coefficient of variation of approximately 23%) is lower than the other sources of variation (coefficient of variation of 44% at the stand level and 70% at the tree level for model 4 in Table 2) and may be of less practical importance relative to the other sources of variation. The low variation between plots and between stands may be an artifact of the initial screening to select denser, well-growing stands.

Had only one plot per stand been established, the between-plot variation would have been confounded with the between-stand variation. This would have resulted in both slightly larger estimates of stand level variation and less sensitive tests for the coefficients. The variation within a stand is particularly important on drained peatlands, where minor changes in topography and proximity to drainage ditches can have a measurable nonlinear effect on tree growth.

The estimates of the coefficients for fixed effects and the variance components are given in Table 2. The coefficient for tree basal area was negative, as expected. Generally, as trees grow larger, their relative growth rate slows down. The coefficient for degree days was not statistically different from zero, possibly indicating that degree days is not one of the more important factors in determining tree growth on these sites or that the range in degree days was not great enough to be important in the model.

4.1 Inter-tree Competition

The coefficient associated with plot basal area is significant and negative indicating plot basal area has a negative effect on bargr , likely acting as a broad measure of site occupancy and competition. As the plot basal area increases, each tree has a smaller share of the total resources leading to slower growth. This is borne out by the reduc-

Table 2. Results of the model building with bargr as the dependent variable.

Coefficients ^a							
Model	Independent variables	Tree basal area	Degree days	Plot basal area	Angle sum	Centre of competition	Field
1	1						
2	ba	-0.00032681**					
3	ba + dd	-0.00032672**	-0.00004541				
4	ba + field	-0.00028529**					0.00399483**
5	ba + plotba	-0.00032179**		-0.00303572**			
6	ba + angle + centre	-0.00017957**			0.00002056	0.00415163**	
7	ba + field + plotba	-0.00028129**		-0.00301441**			0.00388892**

Variance components ^b				
Model	Independent variables	Stand	Plot (stand)	Error
1	1	0.00204450**	0.00042496**	0.00455862
2	ba	0.00161538**	0.00044718**	0.00414018
3	ba + dd	0.00161947**	0.00044614**	0.00414087
4	ba + field	0.00164049**	0.00043045**	0.00412214
5	ba + plotba	0.00113448**	0.00044105**	0.00412724
6	ba + angle + centre	0.00145679**	0.00057757**	0.00383269
7	ba + field + plotba	0.00116670**	0.00042258**	0.00410949

^a a double asterisk beside the estimated coefficient indicates rejection of the hypothesis H_0 : coefficient = 0 at the 1 % level of significance.

^b a double asterisk beside the estimated variance component indicates rejection of the hypothesis H_0 : variance component $\neq \sigma^2$ at the 1 % level of significance.

tion in variance components at the stand levels when plot basal area is added to the model (compare the variance estimates for model 5 vs. 2 in Table 2).

The individual tree measure of competition, field, is positively correlated with relative growth rate ($r = 0.21$, $p < 0.01$, $n = 1629$) and has a positive coefficient in the model when tree basal area is included. The positive correlation is worth noting. On drained peatlands, neighbouring trees can have the beneficial effect of lowering the water table through evapotranspiration. Thus, if excess moisture is still limiting growth, the field measure of competition may be correlated with evapotranspiration and thus be positively correlated with growth. Again, once plot basal area is in the model and the negative effects of neighbouring larger trees are accounted for, competition has a positive effect on a tree's relative basal area growth (model 7).

The angle sum measure of competition is also positively correlated with bargr ($r = 0.10$, $p < 0.01$, $n = 1629$) but the coefficient in the model is not significant once basal area and centre are in the model. The centre of competition is significant in predicting growth even within the limited range in values (mean = 4 cm, ranging from <1 to 60 cm). As the asymmetry of the location and size of the neighbouring trees increases, so does the magnitude of the bargr.

There was no discernible trend between the residuals (ϵ of Eq. 14) and individual tree basal areas, indicating the model fit all sizes of trees equally well. This implies that competition affects all of the trees, regardless of size, given that the effects of tree basal area are accounted for. This is in agreement with Hökkä (1993) who found an increase in nutrient status of all trees following thinning, implying all had been negatively affected by competition for nutrients prior to thinning.

Thus, neighbouring trees appear to have two effects on basal area growth: a dominant positive effect probably due to increased transpiration associated with more trees, and a smaller negative effect probably associated with sharing of limited resources among individuals. The positive effect can be captured by the individual tree basal areas, leaving the competition indices to explain the negative effects in the model.

4.2 Implications

Our results have implications both for revising sampling designs and for model-building. The smaller magnitude of the plot level variation compared to the stand level indicates that, for future data collection for similar purposes, less emphasis is required at the plot level. The between-plot variability may be reduced with larger plot sizes but the sampling cost would increase, indicating that there is a trade-off between precision and cost. In order to study competition, then, more stands and more trees within each plot should be sampled at the expense of replicating plots within a stand.

For model building, it is important to separate the positive and negative effects of competition. The positive effects of competition may be summarized by other measures (such as individual tree basal area), leaving competition measures to represent the negative effects. All trees appear to be affected by competition implying that all trees may respond to thinning or any other action that affects competition. This hypothesis requires additional research.

5 Conclusions

The use of random components in analyzing forestry data can provide estimates of the magnitude and sources of variation. Particularly when observations are nested within a hierarchical arrangement, each level with its own sources of variation, analysis of the variance components can improve the sensitivity of the analysis. In this case, the trees are nested within plots within stands; explicitly incorporating this nesting into

the model to describe growth leads to a correct allocation of the random variance to each level – tree, plot, and stand. The analysis also leads to recommendations to improve the sampling design based on the magnitudes of the different sources of variation.

In the application examined, inter-tree competition appeared to be reducing individual tree growth rates on the peatland sites examined but the negative effect of competition decreased with increasing asymmetry of the size and location of the neighbouring trees. As well, competition had the positive effect of improving growth, probably through improved transpiration and fewer drainage problems. The implication for management is that thinning treatments on drained peatlands should be undertaken only when measures are taken to ensure that drainage does not deteriorate as a result of decreased transpiration. The applicability of the model to all sizes of trees implies that all will respond to decreases in competition, but further studies are required.

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