Application and comparison of spatial models in analyzing tree-genetics field trials

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Tree height of jack pine full-sib families, originating from all possible combinations of three parental provenances and growing on three sites, was analyzed with 1 classical model and 11 nearest-neighbour spatial process models. Extension of the classical linear model with spatial interaction terms was deemed necessary in light of significant neighbourhood correlations among effect-free observations (residuals) on two of the three sites. The strength and extent of spatial and temporal correlations are demonstrated in both visual and tabular form. Only 4 of the 11 spatial models provided a substantial reduction (5–20%) in the significant difference between two estimates of full-sib family tree height. Spatial adjustments averaged 1–3% at the family level, with few families adjusted by more than 10%. The cumulative (temporal) effect of spatial covariance was demonstrated in rank correlations between adjusted and observed family means. No simple trends were obtained when adjusted variance components and heritabilities were compared with their unadjusted counterparts, but most models tended to deflate genetic effects and reduce heritabilities. It is concluded that although spatial analyses provide an attractive tool for the experimenter, the lack of a cause and effect hypothesis in forest genetic trials necessitates model searching without the guarantee of true treatment effects. Spatial analysis provides good indicators of the need to collect additional site information for more powerful analyses. Careful planning and intensive site preparation may greatly reduce spatial covariances and the need for spatial analyses.

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La hauteur des familles bi-parentales de Pin gris originant de toutes les combinaisons possibles de trois provenances parentales et croissant sur trois sites ont été analysées avec 1 modèle classique et 11 modèles spatiaux de plus proche voisin. L'extension du modèle classique linéaire avec les termes de l'interaction spatiale a été jugée nécessaire à la lumière des corrélations significatives de voisinage entre les observations sans effets sur deux des trois sites. La force et l'étendue des corrélations spatiales et temporelles sont démontrées sous forme visuelle et en tableaux. Seulement 4 des 11 modèles spatiaux conduisaient à une réduction substantielle (5–20%) de la différence significative entre deux estimations des familles de hauteur. Les ajustements spatiaux exprimaient en moyenne 1–3% du niveau de la famille avec quelques familles ajustées par plus de 10%. L'effet cumulatif temporel de la covariance spatiale a été démontrée dans les corrélations de rang entre les moyennes de famille ajustées et observées. Aucune tendance linéaire n'a été obtenue lorsque les composantes ajustées de la variance et les facteurs héréditaires ont été comparés avec leurs contreparties non ajustées mais la plupart des modèles tendent à diminuer les effets génétiques et réduire les facteurs héréditaires. Nous concluons que même si les analyses spatiales procurent un outil attrayant pour le chercheur, le manque de cause et d'effets hypothétiques dans les essais en génétique forestière nécessitent des modèles de recherche sans garantie de vrais effets de traitements. L'analyse spatiale fournit de bons indicateurs de la nécessité d'obtenir de l'information additionnelle sur les sites pour une analyse plus puissante. La préparation intensive de sites et une planification soignée peuvent réduire de beaucoup les covariances spatiales et le besoin d'analyses spatiales.

[Traduit par la revue]

Introduction

Environmental gradients (physical factors, topography, etc.) within replicated blocks and competition among neighbouring treatment units pose a serious impediment to reliable (precise) estimations of treatment effects in most field trials (Binns 1987; Correll and Cellier 1987; Hühn 1973; Loo-Dinkins and Tauer 1987; Love 1936; Smith 1938; Stern 1968). One of the most effective countermeasures to ameliorate such effects has been the use of incomplete block designs (Cochran and Cox 1957), or a reduction in plot size and hence, block sizes (Cochran and Cox 1957; Cotterill and James 1984; Lambeth and Gladstone 1983; Libby and Cockerham 1980; Loo-Dinkins and Tauer 1987; Wright and Freeland 1960). Reduction of plot sizes, however, leads inevitably to increased interaction among plants receiving different treatments and in the case of interplant competition, to the less efficient designs (Cochran and Cox 1957; Hühn 1974; Magnussen 1989*a*). Genetics trials with forest trees are especially faced with problems of this nature. Patchy microsite patterns in forest soils and large numbers of genetic entries have complicated experimental designs.

Although various lattice and incomplete block designs (Yates 1937) have greatly improved the situation, persistent problems remain owing to strong temporal modifications of spatial processes in forest stands with pronounced environmental gradients over short distances (Correll and Cellier 1987; Leps and Kindlmann 1987; Loo-Dinkins and Tauer 1987; Modjeska and Rawlings 1983; Stern 1965; Reed and Burkhart 1985).

Uniformity trials (Love 1936; Modjeska and Rawlings 1983; Smith 1938; Stern 1968) have often demonstrated that observations taken on neighbouring plots are more similar than observations taken at random, an indication of positive spatial covariances. The presence of positive, or for that matter negative, spatial covariances may cause a serious violation of the assumption of independent observation, a cornerstone in the analysis of variance (Searle 1987). To apply ordinary least-squares techniques to a data set in the presence of significant spatial covariances, or autocorrelations as they are usually referred (Cliff and Ord 1981), may introduce a serious loss of precision in estimates of effects and variance components (Besag and Kempton 1986). Inter-
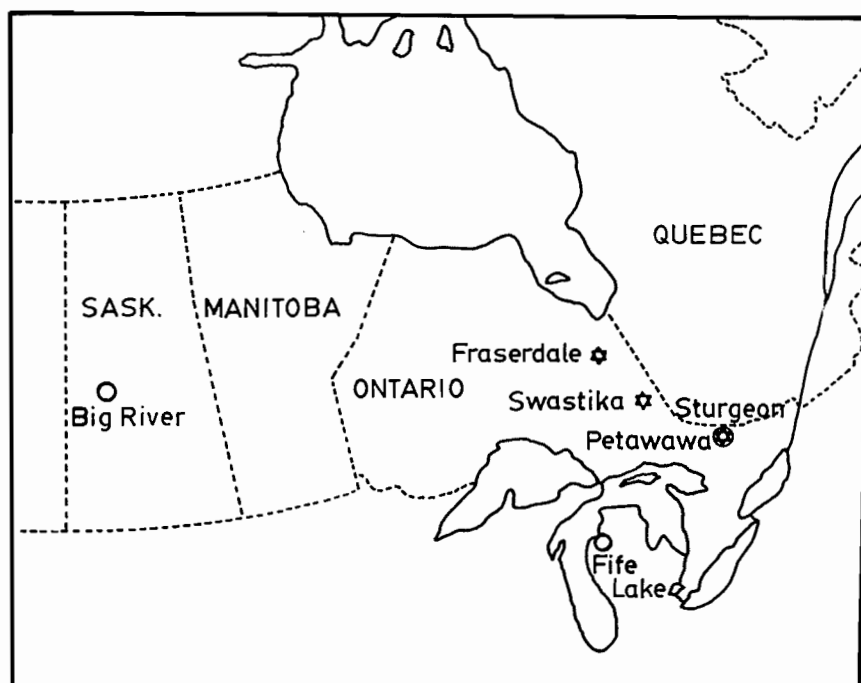
FIG. 1. Geographic location of test sites and parental jack pine provenances. Open circles, provenances; stars, test sites.

est is strong, therefore, in analytical methods that can reduce the loss of precision due to spatial correlations of observed values (i.e., observations are not indepenent) (Magnussen 1989a). Fortunately, rapid developments have been made over the last 2 decades in our capablity to model and statistically analyze environmental variation in space (Bartlett 1978; Besag 1974; Besag and Kempton 1986; Cliff and Ord 1981; Draper and Guttmann 1980; Green et al. 1985; Kempton and Howes 1981; Wilkinson et al. 1983).

The present study illustrates how, by proper model choice, nearest-neighbour (NN) analyses may reduce the effects of spatial autocorrelation in data from three forest-genetics trials in Ontario (Canada). A total of 11 spatial models are analyzed in this study and compared with classical two-way analysis of variance. The chosen models represent all the various types of spatial models that may prove useful in forestry trials. The purpose of presenting several models is twofold: first, to heighten the awareness of field experimenters about potentially powerful models, many of which are still not widely accepted, and second, to demonstrate that model choice is important. Model choice is especially difficult in forest-genetics trials where there is no clear distinction between effects and treatment and where genetic effects cannot be estimated without errors. These unique problems tend to blur the distinction between model types. An apparent uncritical testing of various model types is therefore warranted in forest-genetics trials. A detailed or thorough statistical description of the models is beyond the scope of this study. Effects of analytical model choice on estimates of genetic variances and heritabilities are demonstrated.

Height growth data, genetic identifiers (labels), and spatial locations (plot, rows, and column numbers) were the only sources of information available for spatial analyses. Evaluation of the merits of each spatial model was therefore limited to the magnitude of error variances, effects on genetic variances, and the significance of treatment dif-ferences. Other worthwhile criteria such as fit to biological reality, mapping of soil variation, and interpretable biological parameters could not be part of the evaluation owing to the lack of appropriate data.

Material and study area

Tree height of 49[1] jack pine (*Pinus banksiana* Lamb.) full-sib families was studied at Sturgeon Lake, Fraserdale, and Swastika, Ontario, Canada (cf. Fig. 1). A randomized block design with 3×3 square plots (1.5×1.5 m tree spacing) and four replications was implemented on each site. Double surround rows planted with a local provenance served to eliminate possible edge effects along outside block borders. All sites were typical jack pine sites of low fertility (flat to undulating sandy soils) with a history of natural jack pine cover. The full-sib progenies originated from controlled pollinations within and between representative trees from three jack pine provenances (Big Rivers, Petawawa, Fife Lake) (Fig. 1). Parental trees were random selections from a provenance trial at the Petawawa National Forestry Institute (Holst 1967). An average of five full-sib families from each of the nine possible provenance combinations were outplanted for field testing on the three sites. Tree height and survival were assessed at ages 6, 7, and 8 years from seed. Plot means were used as entries in the statistical analysis and spatial models, and a pooled estimate of the within-plot variance was used in the heritability estimates. All experiments were balanced at the plot mean level. A detailed description of height results and survival is given by Magnussen and Yeatman (1988).

Family heritability was derived separately for each provenance combination (i.e., based on an average of only five full-sib families) as

$$h_f^2 = \sigma_f^2/(\sigma_f^2 + \sigma_p^2/4 + \sigma_w^2/4n_H)$$

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[1]On a third site (Sturgeon) 50 families were tested.

where σ_f^2, σ_p^2, and σ_w^2 are the maximum likelihood estimates of family, plot, and within-plot variances, respectively, and n_H is the harmonic mean of trees per plot ($2 < n_H < 9$).

Spatial correlation analysis

The experimental design and field layout on all three sites aimed at minimizing the site variation within blocks. Any within-block variation due to environmental gradients tends to make observations from neighbouring plots more similar than observations from more distant plots (Bartlett 1978; Smith 1938; Wright and Freeland 1960). This prevailing tendency of neighbouring plot observations to be more similar than observations drawn at random from within the block can be so strong that the assumption of independent observations within the block is violated. A measure of the spatial similarity is obtained through correlation analyses of effect-free growth data. Correlation coefficients (ρ) are computed in the usual manner for neighbouring observations and compared with values expected under the assumptions of random association of values (Cliff and Ord 1981). Coefficients exceeding expected values (under the null hypothesis) by a significant margin supports the contention of significant spatial association or spatial autocorrelation among neighbouring values. A directional breakdown of correlations may help identify the source of the autocorrelation. In an attempt to assess the extent of autocorrelations, it is customary to compute correlation coefficients for first-, second-, and third-order neighbours. (The order of the relationship refers to the spatial closeness of the observations. First-order neighbours share common borders, second-order neighbours have common first-order neighbours, etc. Diagonal plots are in the present context not considered as neighbours.) However, higher order autocorrelations suffer from the confounding effects of spatially intermediate observations (Besag 1974; Cliff and Ord 1981); it is therefore desirable to express higher order correlations conditional on the intermediate results. The partial autocorrelation coefficients (ϕ) are such conditional estimates. For example, a second-order partial coefficient estimates the correlation between two second-order neighbours after the effect of their common first-order neighbour has been removed (Anderson 1976).

Interpretation of the autocorrelations helps determine whether a classical analysis that assumes independent observations is appropriate. If it is decided that the pattern of spatial autocorrelation is significant, then the aforementioned assumption of independent observation is invalid, and an improved model that incorporates this spatial dependency must be formulated. Spatial and partial autocorrelations may prove helpful in the search for an appropriate spatial model (Anderson 1976).

In the present study, effect-free observations were residuals from an analysis of variance of tree height, with blocks and families (here assumed fixed) as explanatory effects.

Analytical models

General

The basic linear models for analyzing tree heights reads

[1] $Y_{ijp} = \mu + \delta_i + \tau_j + e_{ijp} + \mathrm{SI}_{ijp}$

where Y_{ijp} is the mean tree height of family j growing in the pth plot in replicate (block) i, μ is the grand mean, δ_i is the additive effect of block i ($\sum_i \delta = 0$), and τ_j denotes the additive effect of family j ($\sum_j \tau_j = 0$). The term e_{ijp} is a random residual (innovation term) assumed independent and normally distributed with mean zero and variance σ_e^2. Finally, SI_{ijp} stands for a model-dependent spatial interaction term that is used to describe the assumed spatial relationship of the observations. Replicates and families in [1] are treated as fixed effects.

The preceding analysis of spatial autocorrelations indicated that the spatial interaction term in [1] would be significant in Sturgeon and in Fraserdale, but not in Swastika. Examples of various applied spatial interaction terms are provided in Table 1 (subscripts referring to blocks and families have been dropped to simplify the notation). In theory, at least, an inspection of the spatial correlations and the partial autocorrelation coefficients ought to aid the selection of an appropriate spatial interaction extension of [1] (Anderson 1976; Fomby et al. 1980). However in this data set, little support was evident for a specific model. Rather, an array of plausible models suggested themselves. A brief description of these models appears in the following section on spatial models. Basically, the spatial interaction terms in the models of Table 2 allow estimation of a dispersion (variance–covariance) matrix V of the observations (Y). V, in turn, is used to weight the observations (Searle 1987) before the family and block effects (parameters τ and δ) are estimated. Once V is determined, the solutions are in most cases derived by weighted least squares, i.e.

[2] $\left[\begin{smallmatrix}\hat{\tau}\\\hat{\delta}\end{smallmatrix}\right] = (X^T V - X)^{-1} \cdot (X^T V - Y)$

where X symbolizes the design matrix (incidence matrix of families and blocks) of the experiment (the superscript T denotes a transposed matrix, whereas $-$ denotes the Moore–Penrose generalized inverse of a matrix).

Generalized least-squares estimates (Searle 1987) of family means ($Y_{j..}$) were obtained via [2] as

[3] $\hat{Y}_{j..} = \hat{\mu} + \hat{\tau}_j$

For each of the nine provenance combinations a provenance-cross estimate was obtained as the grand mean ($\hat{\mu}$) plus the average effect ($\hat{\tau}_j$) of the families belonging to the particular provenance combination. The variance among full-sib families within a specific provenance combination was computed as the variance of the family estimates ($\hat{Y}_{j.}$). It is assumed that this variance estimates one-half of the additive variance plus one-quarter of the nonadditive (dominance) variance (Falconer 1981).

Spatial models

All spatial models aspire to eliminate or at least reduce the observed spatial autocorrelations in a data set by superimposing a hypothetical relationship between observations of known spatial positions. Generally, the classical two-way model (blocks and treatments) is extended to allow interactions among immediate neighbours (plant or plots) in the experiments. Spatial correlations of observations can occur due to either overlap of treatment effects, microsite effects, or a combination thereof. A priori knowledge of cause and effect will of course assist in the choice of an appropriate model.

Spatial interaction models are usually categorized into three groups: (i) There is no competition between plots; but the fact that neighbouring plots are side by side means that

TABLE 1. Spatial models used in the analysis of plot means from three replicated randomized block trials (subscripts referring to blocks and families (see example) have been omitted to improve clarity)

Model	Reference	Description
(0) $Y_p = \mu + \delta_{b(p)} + \tau_{k(p)} + \varepsilon_p$	Snedecor and Cochran 1971	Generalized least squares
(1) $Y_p = \mu + \tau_{k(p)} + \lambda_{col} \sum_{col(p)} \tau_{k'}$ $+ \lambda_{row} \sum_{row(p)} \tau_{k''} + \varepsilon_p$	Draper and Guttman 1980	Effect overlap
(2) $Y_p = \mu + \delta_{b(p)} + \tau_{k(p)} + \lambda_{col(p)} \sum_{col(p)} \tau_{k'}$ $+ \lambda_{row} \sum_{row(p)} \tau_{k''} + \varepsilon_p$	Besag and Kempton 1986	Effect overlap
(3) $Y_p - Y_{p-1} = \tau_{k(p)} - \tau_{k(p-1)} + \varepsilon_p - \varepsilon_{p-1}$	Besag and Kempton 1986	First difference
(4) $Y_p - Y_{p-1} = \tau_{k(p)} - \tau_{k(p-1)} + (\varepsilon_p - \varepsilon_{p-1}) + \gamma_{y(p)}(\lambda)$	Besag and Kempton 1986	First difference with errors-in-variables
(5) $Y_p = \delta_{b(p)} + \tau_{k(p)} + \lambda_{col} \sum_{col(p)} Y_{p'}$ $+ \lambda_{row} \sum_{row(p)} Y_{p''} + \varepsilon_p$	Besag and Kempton 1986	Yield interference
(6) $Y_p = \mu + \tau_{k(p)} - N_{col(p)}^{-1} (\sum_{col(p)} Y_{p'} - \mu^0 - \tau_{k'}^0)$ $- N_{row(p)}^{-1} (\sum_{row(p)} Y_{p''} - \mu^0 - \tau_{k''}^0) + \varepsilon_p$	Wright 1978	Moving plot averages (Papadakis)
(7) $Y_p^0 = \mu + \tau_{k(p)} + \lambda_{col} N_{col(p)}^{-1} (\sum_{col(p)} \varepsilon_p^0)$ $+ \lambda_{row} N_{row(p)}^{-1} (\sum_{row(p)} \varepsilon_p^0) + \varepsilon_p$ where $Y_p^0 = Y_p - \lambda_{col}^0 \sum_{col(p)} \tau_{k'}^0 - \lambda_{row}^0 \sum_{row(p)} \tau_{k''}^0$ and $\varepsilon_p^0 = Y_p - \mu^0 - \tau_k^0 - \lambda_{col}^0 \sum_{col(p)} \tau_{k'}$ $- \lambda_{row}^0 \sum_{row(p)} \tau_{k''}$	Correll and Anderson 1983	Effect overlap and yield interference
(8) $Y_p = \mu + \tau_{k(p)} + \lambda_{col} \varepsilon_{p-1} + u_p$ $Y_p = \mu + \tau_{k(p)} + \lambda_{row} \varepsilon_{p-1} + u_p$	Fomby et al. 1980	First-order autoregressive scheme
(9) $Y_p = \mu + \tau_{k(p)} + \lambda_{col} \varepsilon_{p-1} + \lambda_{col}^s \varepsilon_{p-2} + u_p$ $Y_p = \mu + \tau_{k(p)} + \lambda_{row} \varepsilon_{p-1} + \lambda_{row}^s \varepsilon_{p-2} + u_p$	Fomby et al. 1980	Second-order autoregressive scheme
(10) $Y_p = \mu + \tau_{k(p)} + \varepsilon_p + \lambda_{col} \varepsilon_{p-1}$ $Y_p = \mu + \tau_{k(p)} + \varepsilon_p + \lambda_{row} \varepsilon_{p-1}$	Fomby et al. 1980	Moving average scheme (first order)
(11) $Y_p = \tau_{k(p)} + \xi_p(\lambda) + \varepsilon_p$	Green et al. 1985	Least squares smoothing (two dimensional)

Definitions

Main effects
μ is the grand mean
Y_p is the observed mean in plot p
$Y_{p'}$ is the observed mean in neighbouring column plot
$Y_{p''}$ is the observed mean in neighbouring row plot
$\delta_{b(p)}$ is the block effect associated with plot p
$\tau_{k(p)}$ is the treatment effect (full-sib family) associated with plot p
$\tau_{k'}$ is the treatment effect associated with plot in neighbouring column
$\tau_{k''}$ is the treatment effect associated with plot in neighbouring row
Notation
$\Sigma_{row(p)}$ is the summation over p's row neighbours; $\Sigma_{col(p)}$ = summation over p's column neighbours
N is the number of neighbouring plots surrounding plot p (interior plots have a total of four first-order neighbours)
0 as a superscript denotes initial generalized least squares solutions to a reduced model
s as a superscript denotes effects associated with second-order neighbours
p is plot number. Plots are arranged row-wise (or column-wise) as a continuous sequence of spatially contiguous plots (i.e., plot p and $p - 1$ are first-order neighbours and p and $p - 2$ are second-order neighbours)
Spatial effects and residuals
λ is the coefficient of plot interference ($-1/N < \lambda < 1/N$). Directional interference terms are indicated by subscripts
ε_p is the difference between expected and observed plot means (random error). The residuals ε_p may be spatially correlated
γ is the error associated with observations (y) in plot p
u_p is the independent plot error or term (these terms have zero spatial autocorrelation)
ξ_p is the environmental value of plot p

the yields will be similar. (*ii*) There is competition; the treatment on a neighbouring plot affects the plot yield. (*iii*) There is competition; the plant(s) on a neighbouring plot affects the plot yield. Of course, all three types of neighbour effects are possible simultaneously, but one is likely to be predominant. In genetics trials, *ii* and *iii* would be inseparable. It may be impossible to distinguish in practice when more than one effect is present, however complicated and sophisticated the model may be. The neighbour effect may operate in one or two dimensions, but this is not mathematically important; the models are similar.

A common feature of most spatial models is the use of one or two constants (λ_{row} and λ_{col} in Table 1) to describe the average spatial relationship among neighbouring units (Magnussen 1989*a*). This rigid structure is a necessary simplification to ensure a solution to the problem. In reality, the spatial process can be far more complex. In an attempt to relax rigid spatial assumptions, so-called errors-in-variables models (model 4 in Table 1) have been introduced. In most forest-genetics applications, however, the source of spatial interaction in unknown and the choice of a spatial model may, as a result, be somewhat arbitrary. Experience in agriculture seems to indicate that a more orderly model choice is possible and that models of a certain type tend to yield comparable estimates of spatial terms (Kempton 1984).

Spatial relationships (λ) will within the current model context operate on (*i*) plot means (Y_p), (*ii*) genetic effects (τ_k), or (*iii*) residuals (phenotypic) (ε). Spatially, these relationships will extend in one or two directions (columns and rows) and include one or two neighbouring plots in each direction (diagonals excluded).

Eleven different spatial models and 1 reference model (model 0) were chosen to analyze the three field experiments. All models of potential use in forestry have been included. Model 0 is the classical linear model for a two-way analysis of variance that ignores any spatial autocorrelation of residuals. Results from all other models are compared with this model. Models 1 and 2 postulate that spatial covariances arise through effect overlap among neighbouring plots, i.e., not only will the genetic value of a seed lot that happens to be growing on above-average plots be overestimated, but also the effects of seed lots growing in adjacent plots (and vice versa). Competition effects are another example of effect overlap, where the effects of suppressors are overestimated and those of the suppressed plots are underestimated (Magnussen and Yeatman 1987; Magnussen 1989*b*). The likelihood of significant effect overlap will, of course, decrease rapidly with the number of randomized replicates. Solutions to models 1 and 2 are found by different techniques; whereas model 1 uses a direct search, a simultaneous solution to both the treatment and interference coefficient (λ) is employed in model 2.

Model 3 describes all spatial covariances (phenotypic) as being explainable by the shared microsite of two neighbouring plots. Independent residuals are thus obtained by a simple difference scheme (Besag and Kempton 1986). A relaxation of this scheme is provided in model 4 by adding a new error term. Model 5 limits the spatial interactions to a fraction, $-1/N < \lambda < 1/N$, of the observed field values (N = number of considered neighbouring plots). The fraction λ is found by analysis of covariance (iterated) or maxi-

mum likelihood estimation. Model 6 (Papadakis; Bartlett 1978) assumes that residuals from a classical two way analysis of variance provides reliable estimates of microsite fertility. When used subsequently as a covariate, these residuals may remove bias and environmental covariances from the treatment estimates. Model 7 combines effect overlap with spatial correlations (phenotypic) arising from a shared microsite. First, effects overlap are estimated and in a second pass, the effects of spatial correlations are estimated. Models 8 to 10 limit the spatial associations to residuals (ε). They differ in the extent of spatial correlation and in whether a truly independent error term (u) exists or not. Model 11 assigns an environmental value to each plot, under the assumption that the environment changes gradually and in a smooth fashion among neighbouring plots (i.e., the response surface is almost linear within an area covered by a plot and its four neighbours). Environmental values are found by simultaneously minimizing the squared deviations from a smoothed response surface of estimated environmental values (the smoothing depends on a tuning constant λ) and the estimated error sum of squares (see Green et al. 1985).

Parameter estimation for all models followed procedures outlined in the cited references. Where applicable, the minimum standard deviation of a treatment difference served as a stopping criterion for direct search (enumeration) algorithms. Step size in any search algorithm was kept sufficiently small to allow estimation of a minimum error variance within 0.5% of its global minimum (*ex post facto*). Included models have, whenever possible, been expanded to accommodate spatial interactions along two major axes of the field trials. Programming software has been written in SAS® Interactive Matrix Language.

Results

Observed spatial autocorrelations

Residuals in a two-way (families, replicates) analysis of variance of plot means revealed a positive and significant correlation among values obtained from neighbouring plots on two sites. Positive correlations indicated that competition was minimal at all ages in agreement with the average height of the trees (age 8: 3.0 m at Sturgeon, 2.1 m at Swastika, and 1.6 m at Fraserdale). When residuals of 8-year-old height were subdivided into three classes of equal width (1.3 SD) and plotted as moving four-plot averages, the configurations shown in Fig. 2 emerged.

High and low residual values were clearly concentrated in patches on the Sturgeon and the Fraserdale sites. Residuals in the Swastika site indicated a far less contiguous distribution of microsite residuals. A quantitative impression of the average correlations among the actual plot residuals is provided by the spatial autocorrelations in Table 2. An increase in the spatial correlations over time mirrors the cumulative effect of good sites on tree growth. Second- and third-order correlations were, as expected, far less important than first-order correlations. The nonsignificance of virtually all second- and higher order partial autocorrelations suggests that the spatial process can be adequately described by considering only the first-order correlations (Anderson 1976).

Plot residuals of total height were strongly correlated over time. Residuals 1 year apart were correlated with a product-
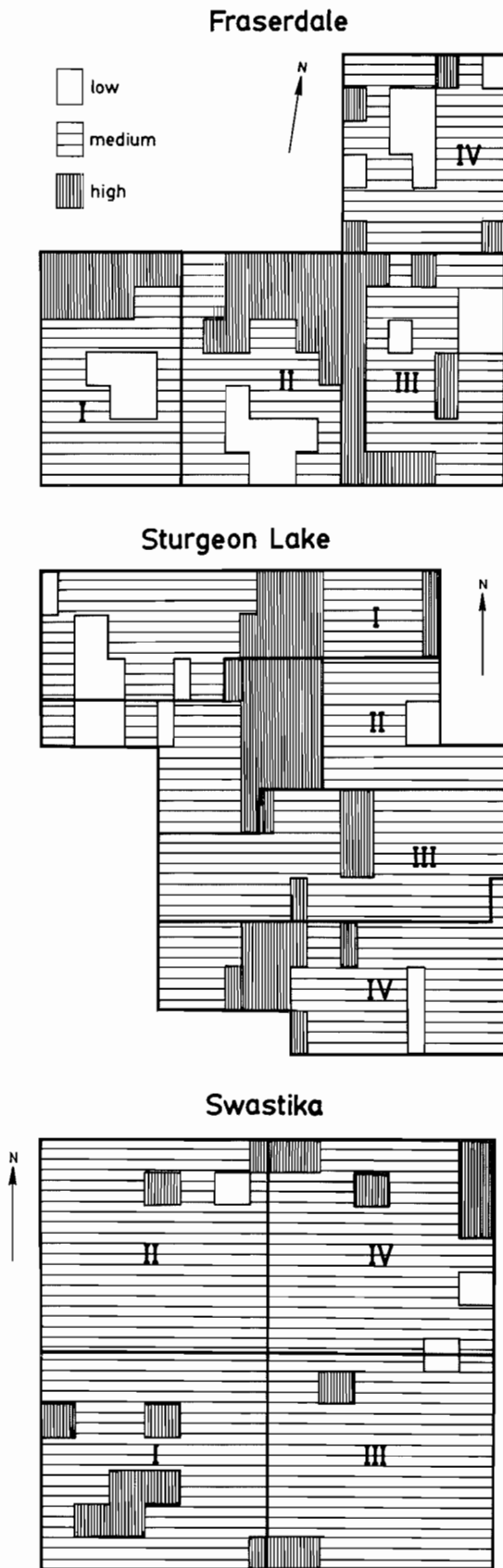
FIG. 2. Contour maps of moving four-plot averages of plot tree height residuals (age 8) on three sites. The residual classes high, medium, and low each represent an interval of a width equal to 1.3 times the site-specific standard deviation of the residuals.

moment correlation coefficient of 0.95 (significant at $P < 0.05$). Two years apart, the correlation among residuals dropped to 0.86.

Evaluations of spatial models

Evaluations of the various spatial models are based on their reduction of the standard error of a difference (SED) between two treatments (i.e., full-sib families) when compared with the SED derived from a classic two-way analysis of variance (e.g., using [1] without the spatial interaction term). It must be emphasized, however, that the calculation of SED is not without problems inasmuch as the exact degrees of freedom in many models are unknown. Only intuitively appealing approximations are available (Besag and Kempton 1986). Comparison of the effectiveness of the various spatial models with reduced observed spatial correlations of ordinary least-squares residuals (not shown) indicated that only models that substantially reduced SED were successful correlation breakers. Basically, the reduction in spatial correlations followed the trend in SED. Hence, only SED is taken as an indicator of model performance.

Seven of the 11 spatial models reduced the average SED between the mean tree height of two full-sib families by 5–20%, compared with the error estimated from the classical analysis of variance of a randomized block design (Table 3). The models that failed to produce any marked error reduction were the effect-interference models (1 and 2), the first-difference model (3), and the least-squares smoothing model (11).

Random allocation of full-sib families to plots within blocks effectively prevented the emergence of any significant spatial covariance among family effects obtained from neighbouring plots. The absence of strong interplot competition, as indicated by the positive autocorrelations of ordinary least-squares residuals (Table 2), acted in a similar fashion. The failure of the first difference method, on the other hand, rests with its rigid and rather unrealistic assumption of a perfect linear relationship between residuals from adjacent plots within a single row. Its extension with errors-in-variables, however, proved much more successful (model 4).

Least-squares smoothing proved unsuccessful because too many degrees of freedom were used to fit the microsite quality response surface (ξ in model 11). Microsite quality patterns as complex as those illustrated in Fig. 2 can best be described mathematically by higher order polynominals or Fourier transforms. Even when more than 100 df were used to determine trends in plot fertilities by higher order polynomials ($\lambda < 0.1$), the fertility estimates correlated poorly ($0.03 < r < 0.28$) with the original residuals from the two-way analysis of variance.

Greatest benefits (in terms of SED) from applying spatial models arose in the analysis of plot means from Sturgeon and Fraserdale, as expected (see Table 2). In Swastika, blocks accounted for 25–29% of the total variation, and blocking efficiency (BE) (i.e., the reduction factor of the residual mean square due to blocking; Snedecor and Cochran 1971) was much higher (BE = 11.5) than on the two other sites (BE < 1.12). By ignoring blocks in Swastika, most spatial models performed (in terms of SED) less well than the randomized block model.

TABLE 2. Spatial (ρ) and partial spatial (ϕ) autocorrelation of tree height plot residuals from a two-way analysis of variance

	Age (years)	Sturgeon					Swastika					Fraserdale				
		ρ_1	ρ_2	ρ_3	ϕ_2	ϕ_3	ρ_1	ρ_2	ρ_3	ϕ_2	ϕ_3	ρ_1	ρ_2	ρ_3	ϕ_2	ϕ_3
North–south	6	0.26*	0.10	0.09	0.04	0.06	0.18*	−0.05	0.11	0.09	0.09	0.27*	0.15	0.04	0.08	−0.02
	7	0.33*	0.19*	0.12	0.09	0.04	0.19*	−0.09	−0.14	−0.13	−0.10	0.29*	0.17*	0.06	0.09	−0.01
	8	0.36*	0.23*	0.20*	0.12	0.10	0.21*	−0.11	−0.02	−0.16*	0.04	0.39*	0.20*	0.04	0.10	−0.06
East–west	6	0.22*	0.12	0.03	0.08	−0.12	0.01	−0.00	0.03	0.00	0.03	0.24*	−0.11	−0.04	−0.18	0.04
	7	0.30*	0.18*	0.06	0.10	−0.02	0.01	0.04	0.06	0.04	0.06	0.19*	−0.10	−0.09	−0.14	−0.04
	8	0.40*	0.22*	0.07	0.07	−0.05	−0.01	−0.06	0.12	−0.06	0.12	0.27*	−0.11	−0.07	−0.19	−0.02
Total	6	0.24*	0.11	0.05	0.06	0.01	0.10	−0.03	−0.04	−0.04	−0.03	0.25*	0.03	0.01	−0.04	0.01
	7	0.31*	0.19*	0.08	0.10	−0.01	0.10	−0.02	−0.04	−0.01	0.06	0.24*	0.04	−0.01	−0.02	−0.02
	8	0.38*	0.22*	0.13	0.09	0.02	0.10	−0.09	0.05	−0.10	0.07	0.30*	0.05	−0.01	−0.04	−0.01

NOTE: Computation and significance ($p = 0.05$) testing of ρ and ϕ followed formulae given by, for example, Anderson 1976, Cliff and Ord 1981. Order (lag) of correlations is indicated by subscripts.
*Significant at the 5% risk level (or lower).

Four models (first difference extended with errors-in-variable (4), yield interference model (5), moving block average or Papadakis (6), and the first-order autoregression model (8)) provided attractive reductions of SED at Sturgeon and Fraserdale. Henceforth, only these four models applied to the analysis of Sturgeon and Fraserdale plot means will be dealt with. The modified Papadakis model (7), the second-order autoregression model (9), and the moving-average model (10) have proven their effectiveness in other trials, but the patchy character of microsites in the present study rendered them less efficient.

Adjustments of spatial effects led to estimates of family means different from those arising from an ordinary least-squares analysis of a randomized block design (model 0). A quantification of these differences is provided in Table 4. Analysis with models 4, 6, or 8 leads to an average 2.3% adjustment of family means in Sturgeon and 3.7% in Fraserdale. The yield interference model (5) resulted in about one-half of these adjustments. From the underlying similarities of the models, one could have expected the yield interference model to conform with models 4, 6, and 8.

In Sturgeon, all adjustments were below 10%, whereas up to 16% of the families received an adjustment of more than 10% in Fraserdale. The majority of families were only marginally adjusted (<3%). Compared with an average standard error of a family mean difference of approximately 9% in Sturgeon and 11% in Fraserdale, most adjustments should be considered trivial. Significant differences (t-test at the 5% risk level) among families increased as a result of spatial adjustments (Table 4). Compared with the number of significant differences claimed with ordinary randomized block design analysis, 30–40% more were claimed following a spatial analysis, with the first difference extended with the errors-in-variables model. A more modest increase of 4–20% followed from application of model 5 (yield interference), 6 (moving average), or 8 (autoregressive scheme). Spatially adjusted and nonadjusted family means of total tree height were strongly correlated (Table 5), but the correlation decreased with age. Similar results were obtained with height increments. This decrease reflects the cumulative nature of tree growth, and hence a buildup of bias due to environmental covariances.

When family means were averaged by provenance cross, the influence of spatial adjustments almost disappeared (adjustments of cross means < 1%). Robustness at this level was due to the effective sampling of microsites within each replicate (4–6 plots per cross).

Family variances and estimated family heritabilities were model dependent (Table 6). The first difference extended with errors-in-variables method increased the variance and heritability estimates, in most cases, by more than 10%; results with models 5–7 generally deflated both family variances and heritabilities. A single model (model 8, for example) could produce estimates that (depending on site and year) were either above or below estimates from a randomized block design. Without the nested design structure (families in crosses), the effect of spatial adjustments on genetic (family) variance components would have been a predictable increase, inasmuch as the treatment mean squares generally increased at the expense of the error mean squares. Normally, this would also translate into a slightly higher family repeatability.

Discussion

The applications and comparisons of spatial models presented were limited to the common situation in which there has been no mapping of soil properties, surface vegetation, or topography (contours). Such auxiliary data would have permitted formulation of biologically realistic models of the spatial processes, for example, by using response surfaces of physical attributes as covariates (Khuri and Cornell 1987). Alternatively, a systematic dispersion of check plots across the field test area would also generate a simple basis for adjusting for within-block site heterogeneities (Lin and Poushinsky 1983; Yates 1937).

Results obtained with various spatial models and trees averaging 3 m or less indicated that competition effects in the three experiments were negligible (effect-interference models performed poorly) and that local trends in environmental gradients outweighed large-scale patterns in both the Sturgeon and Fraserdale data. The failure of least-squares smoothing to fit a simple response surface supports this contention.

The benefits of a 20% reduction in error mean squares and of an increase in the number of significant treatment differences achieved by using spatial methods seem to justify, once more, the additional analytical work (Wright 1978). Advances in matrix orientated software packages and

TABLE 3. Average standard error of a difference (SED) between two full-sib families in percent of the randomized block design analysis (model 0)

Model	Age (years)	Sturgeon					Swastika					Fraserdale				
		% SED	Rows λ	Rows λ″	Columns λ	Columns λ″	% SED	Rows λ	Rows λ″	Columns λ	Columns λ″	% SED	Rows λ	Rows λ″	Columns λ	Columns λ″
0	6	100(26.3 cm)					100(17.3 cm)					100(21.6 cm)				
	7	100(33.0 cm)					100(22.5 cm)					100(29.6 cm)				
	8	100(45.4 cm)					100(28.5 cm)					100(37.9 cm)				
1	6	99	0.02		0.28		126	0.22		0.06		101	0.36		0.30	
	7	102	0.08		0.28		131	0.04		0.02		102	0.36		0.40	
	8	99	0.12		0.50		132	0.01		0.02		99	0.36		0.62	
2	6	98	0.26		—		97	0.03		—		98	0.33		—	
	7	99	0.25		—		98	0.02		—		97	0.44		—	
	8	99	0.10		—		99	0.03		—		98	0.33		—	
3	6	107	—		—		112	—		—		104	—		—	
	7	106	—		—		115	—		—		107	—		—	
	8	109	—		—		113	—		—		108	—		—	
4	6	87	3.6		—		94	5.4		—		84	2.8		—	
	7	87	3.2		—		93	5.6		—		82	2.6		—	
	8	86	3.6		—		96	4.4		—		81	2.4		—	
5	6	92	0.62		0.02		113	0.46		0.54		97	0.62			
	7	90	0.76		0.02		111	0.40		0.64		97	0.68			
	8	93	0.68		0.00		112	0.32		0.62		97	0.64			
6	6	98	(1.0)		(1.0)		98	(1.0)		(1.0)		84	(1.0)		(1.0)	
	7	97	(1.0)		(1.0)		97	(1.0)		(1.0)		86	(1.0)		(1.0)	
	8	92	(1.0)		(1.0)		96	(1.0)		(1.0)		80	(1.0)		(1.0)	
7	6	94	0.28	-0.70	0.02	-0.07	108	0.22	-1.19	0.06	-1.19	99	0.36	-0.57	0.30	-0.57
	7	96	0.28	-0.74	0.08	-0.74	109	0.04	-1.21	0.02	-1.21	97	0.36	-0.65	0.40	-0.65
	8	98	0.30	-0.63	0.12	-0.63	110	0.00	-1.16	0.04	-1.16	99	0.36	-0.56	0.62	-0.56
8	6	96	0.38	0.14			113	0.50	0.29			92	0.58	0.12		
	7	96	0.48	0.14			112	0.56	0.31			92	0.58	0.14		
	8	96	0.42	0.11			112	0.58	0.24			90	0.60	0.15		
9	6	95	0.19				113	0.28				94	0.32			
	7	96	0.25				114	0.31				94	0.34			
	8	96	0.24				118	0.34				92	0.35			
10	6	98	0.23				188	0.49				95	0.43			
	7	99	0.32				119	0.61				96	0.49			
	8	97	0.29				115	0.63				94	0.53			
11	6	100	>100				100	>100				100	>100			
	7	100	>100				100	>100				100	>100			
	8	100	>100				100	>100				100	>100			

NOTE: λ = first-order spatial interaction parameter, λ″ = second-order spatial interaction parameter (model 9) or coefficient of local fertility trend (model 7). λ-Values in parentheses are ones that are fixed in the modelling.

TABLE 4. Relative frequency adjustments (sign ignored) of family means by various spatial models relative to estimates from a randomized block analysis

Age (years)	Adjustment (rounded to nearest 2%)																		Avg. (%)		Significance ratio[a]	
	0%		2%		4%		6%		8%		10%		12%		14%		16%					
Sturgeon																						
6	21	69	53	31	22	0	2	0	2	0									2.3	1.0	1.2	1.0
	19	28	52	52	24	14	5	6	0	0									2.4	2.2	1.0	1.0
7	21	62	47	35	28	3	3	0	1	0									2.4	1.1	1.2	1.0
	19	22	52	47	21	26	8	3	0	2									2.5	2.4	1.0	1.0
8	28	64	40	33	28	3	2	0	2	0									2.3	1.1	1.2	1.1
	26	28	45	47	19	19	10	5	0	1									2.4	2.2	1.0	1.1
Fraserdale																						
6	21	53	45	41	12	6	8	0	8	0	6	0	0	0	0	0	0	0	3.2	1.3	1.4	1.1
	16	22	39	29	23	21	14	12	2	10	4	4	2	2	0	0	0	0	3.4	3.7	1.0	1.2
7	25	47	29	41	22	12	2	0	8	0	10	0	2	0	2	0	0	0	3.9	1.5	1.3	1.1
	10	27	43	22	16	21	23	10	2	10	4	6	2	2	0	2	0	0	3.7	3.9	1.0	1.1
8	22	35	29	53	27	10	6	2	8	0	2	0	6	0	0	0	0	0	3.7	1.8	1.3	1.2
	18	14	29	27	27	33	18	12	2	4	4	4	2	2	0	2	0	2	3.6	4.2	1.0	1.0

NOTE: Each cell displays the results from four models (4 and 5, top line, and 6 and 8, bottom line).
[a]Ratio of the number of significant family differences in models 4, 5, 6, and 8 to that of the randomized block design analysis.

TABLE 5. Spearman's rank correlation between ordinary least-squares estimates of family means and spatially adjusted estimates

Age (years)	Model 4	Model 5	Model 6	Model 8
Sturgeon				
6	0.91	0.99	0.92	0.93
7	0.88	0.98	0.88	0.88
8	0.86	0.98	0.87	0.88
Fraserdale				
6	0.92	0.99	0.92	0.90
7	0.88	0.99	0.88	0.87
8	0.84	0.97	0.86	0.83

NOTE: No. of families = 50 in Sturgeon and 49 in Fraserdale. All coefficients are highly significant (risk level 1% or lower).

the power of today's computers have drastically reduced the cost and time involved in spatial analyses. A point may soon be reached where spatial analyses of balanced data will barely be more demanding than the generalized least-squares methods. However, severe limitations are expected to persist in the case of unbalanced data (Green et al. 1985).

Results from the three sites confirmed that spatial adjustments of treatment effects in many cases amount to no more than a few percentage points (Besag and Kempton 1986; Correll and Anderson 1983; Wright 1978). It was also shown that the impact of adjustments on the ranking of effects, although modest at first, tends to increase over time. Our nested design with four to six full-sib families per provenance cross were enough to sharply reduce the effects of within-replicate heterogeneity. All conclusions reached in a previous paper (Magnussen and Yeatman 1988) about the performance of provenance hybrids are, therefore, unaffected by spatial adjustments.

Variance components and heritability estimates in the nested design revealed no consistent effect of spatial adjustments. Further evidence is of course needed, but the implication may well be that classical estimation procedures of variance components and heritabilities in nested designs are fairly robust against the influence of spatial heterogeneity. It is not possible to reconcile the different trends in family variances and heritabilities with the underlying assumptions of the respective models. Without a justified model preference, we are not able to conclude whether these estimates have been deflated by environmental interactions.

A direct comparison of the various analytical models described in this paper is difficult, inasmuch as they proceed from many different statistical principles with explicit assumptions about associated covariance structures (Cliff and Ord 1981). Model preferences may (but ought not to) change from trial to trial and may even, as already discussed, change between growth phases (pre- and post-canopy closure). In trials with simple environmental trends, the least-squares smoothing appears very promising by giving maximum separation on trends and treatment effects (if the model is valid) (Green et al. 1985). Justification of a particular model for general application appears impossible. Unless some spatial methods are clearly superior, there is no reason to lightly discard classical methods. Results from the Swastika site stressed this point.

Future analyses of tree heights on the same three sites may very well show that both competition and local fertility trends have become important factors. Hence, an extension of Besag's yield interference model (5) to incude competition (Besag and Kempton 1986) or the extended Papadakis method (7) may prove more efficient than current models.

All models and effect estimates have been based on plot means because the trials focus on family means within various provenance combinations (Magnussen and Yeatman 1988). Often, however, unbiased estimates are also needed at the single tree level to calculate individual tree heritabilities and variance components. Unfortunately, the computer resources needed to estimate the parameters in a spatial model increase with the cube of the number of trees in the experiments. With, say, more than 1000 trees per experiment, which is common in forestry, the work-space requirements exceed easily what is available in all but the largest mainframes. Cumbersome matrix inversion algorithms are

TABLE 6. Average within-cross family variance components (σ_f^2) and family heritability (h_f^2) of tree height (cm)

Age (years)	Model 0[a]		Model 4		Model 5		Model 6		Model 8	
	σ_f^2	h_f^2	σ_f^2	h_f^2	σ_f^2	h_f^2	σ_f^2	h_f^2	σ_f^2	h_f^2
Sturgeon										
6	100 (70)	100 (0.53)	137	121	89	94	93	96	107	104
7	100 (136)	100 (0.58)	108	109	76	93	76	90	93	98
8	100 (241)	100 (0.56)	110	111	70	88	72	89	81	93
Fraserdale										
6	100 (47)	100 (0.51)	119	118	66	80	81	98	109	108
7	100 (70)	100 (0.45)	100	100	106	113	59	82	111	133
8	100 (77)	100 (0.35)	113	126	43	57	51	74	73	89

[a]Numbers in parentheses represent ordinary least-squares estimates that have been equated to 100. Estimates from models 4, 5, 6, and 8 are relative to 100.

required to circumvent the problem and to obtain the model parameter solutions. (Kendall et al. 1983). In such situations, the moving-average technique originally suggested by Papadakis in 1937 (see Papadakis 1984 for further details and references) and promoted by Wright (1978) becomes very attractive because it applies equally well at the plot level and at the individual tree level without extensive computational requirements. However, if adjustments of spatial covariances reduce the genetic effect to the same degree as they reduce environmental variance, little is gained by this additional analytical effort. Simulation studies (Magnussen 1989a; Ripley 1987) are clearly needed to improve our analysis of spatial processes.

Conclusions

Strong spatial covariances among neighbouring observations in forest field trials are quite common. Hence, special efforts are needed to reduce the loss in precision of estimated treatment effects that such covariances introduce. Carefully planned and laid out experiments, with emphasis on homogeneous blocks and intensive site preparation, may greatly reduce the problems of spatial covariances. Although analysis with spatial process models may reduce the significant differences among treatment means by a substantial amount, the lack of a cause and effect hypothesis necessitates model searching and does not guarantee true estimates. To choose a correct model, it must be known whether spatial patterns arise from physical realities and whether the nature of the observed process is stochastic (random), deterministic, or a mix of both. In trials with forest trees, the experimenter may succumb to the general everything affects everything perception, which makes the problem intractable and the choice of model left to chance. Even the best scientific judgment and scrutiny of assumptions cannot legitimately convert a data-analytical reality into a spatial effect, because we are still dealing with theoretical parameters in theoretical models and not real biological processes.

Model formulation and choice are major problems in forest-genetics trials because of their dichotomy of genetic and environmental values (Falconer 1981) and also because spatial patterns are frequently here and now measures derived from the data itself. A lot depends on how genotypes were allocated, and also on the reliability of the so-called environmental residuals. Instinctive prejudice against spatial adjustments has been promoted by these shortcomings.

Meanwhile, the fact that randomization alone does not prevent the experimenter from obtaining spurious results, and the intuitive appeal of using all relevant information, points towards the use of neighbour analysis as an ancillary explorative tool rather than as a routine.

Spatial neighbour analysis will never assure a complete elimination of spatial covariances, because the pattern of microsite variation is often so arbitrary that it is difficult to adjust for them completely (predicted patterns can be dealt with in the design phase). The Sturgeon and Fraserdale sites are cases in point. It should also be stressed that it is impossible to demonstrate that adjusted treatment effects are closer to their true values, because the relative performance of a treatment cannot be separated from its environment. However, Monte-Carlo simulations based on data from uniformity trials give some indication of the validity of spatial (neighbour) adjustment procedures (Wilkinson et al. 1983).

Spatial correlation of plot yields (adjusted for treatment effects) are poor guides for model choice. For example, if neighbouring plot values were locally negatively correlated due to competition, but because of large-scale spatial heterogeneity, neighbours were still positively correlated over the experiment as a whole, the adjustments would achieve precisely the opposite of what is required. The lack of a randomization theory can be explained as follows: if treatment comparisons are statistically biased by trend effects, then the bias will depend upon the actual positions of the treatments in the field; hence the whole realized design serves, in a model-dependent way, as ancillary information. Spatial analysis without auxiliary physical or biological information may, for the above given reasons, simply conclude that more site data are needed before valid conclusions can be reached from the actual field trial. This alone may fully justify the additional work associated with spatial process analysis.

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