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# Multiple-Trait Combined Selection in Jack Pine Family-Test Plantations Using Best Linear Prediction

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## Summary

Best linear prediction (BLP) was applied to data from a jack pine open-pollinated family test in Manitoba to estimate trait breeding values for selection of parents for advanced generation breeding. The test includes 215 families and 1 control lot planted in 15 replications at 3 locations. Families in the test originated from 76 stands, with 1 to 5 families from each stand. Stands were grouped by proximity into 18 areas. Height and diameter at 20 years on individual trees were adjusted by subtraction of mean within-family deviations of neighboring trees. At 21 years on trees average or better for height growth and past stem quality (stage 2 trees), stem quality was scored, western gall rust galls were counted, and wood density was estimated from Pilodyn penetrations. The observation vector for each tree comprised deviations of its own measurement or score, its family mean, and its area mean from the test mean for all traits except stem quality, which had only tree value and family mean. For each stage 2 tree, the variance of the observation vector (V matrix) and the covariance of the observation vector with trait breeding values (C matrix) were calculated from variance and covariance components and family size values. Derivatives of V and C were used along with the observation vector to calculate BLP breeding values for 5 traits. Various weight vectors were applied to trait breeding values to produce total scores used for selection, until a satisfactory gain relationship among traits was found. Owing to relatively high heritabilities and low imbalance effect of family size differences, results from BLP differed little from results of index selection with these data.

Key words: Pinus banksiana, multiple-trait selection, combined selection, index selection, best linear prediction, sliding block adjustment, heritability, genetic gain, genetic correlation.

FDC: 232.11; 165.62; 165.3; 165.5; 174.7 Pinus banksiana.

## Introduction

Although forest tree breeding programs are primarily concerned with increasing growth of planted trees, breeders often also wish to improve or maintain other traits, such as stem straightness (BROWN and MILLER, 1975; BRIDGWATER and STONECYPHER, 1979; COTTERILL and ZED, 1980; SHELBOURNE and LOW, 1980; DEAN et al., 1983; PARK et al., 1989; ADAMS and MORGENSTERN, 1991), wood quality (DEAN et al., 1983; ERNST et al., 1983; KING et al., 1988; PARK et al., 1989; MAGNUSSEN and KEITH, 1990; CORRIVEAU et al., 1991; YANCHUK and KISS, 1993), and rust resistance (WHITE and HODGE, 1988; HODGE et al., 1989; LAFARGE, 1989; SLUDER, 1994). Index selection is a method of assessing the genetic worth of genetic entities (individuals or families for example) as a linear function of multiple performance attributes (SMITH, 1936). Optimum weights for the attributes are calculated from assigned economic weights and from knowledge of genetic and phenotypic variances and covariances of the attributes (HAZEL, 1943). For improvement of multiple traits, index selection will always be equal or superior in efficiency to independent culling, which is always equal or superior to tandem selection (HAZEL and LUSH, 1942; BAKER, 1986). When trees grown in replicated genetic test plantations are being assessed for selection, genetic gain can be enhanced by combining information from observations on the individual trees being assessed with information from observations on their relatives. Simultaneous use of information from an individual being assessed along with information from the performance of relatives has been termed "combination selection" (LUSH, 1947) or "combined selection" (FALCONER, 1989, p. 236). Combined selection on a linear function of family and individual merit, weighted by within-family and family

heritability, for any single trait must be at least as efficent as the better of individual selection or family selection (LUSH, 1947; FALCONER, 1989). A combined index will also be more efficient than family selection followed by selection within the best families (COTTERILL and DEAN, 1990).

A limitation of index selection is use of the same second moment estimates for all entries. Entries with less information from relatives, owing to mortality for example, are more likely to be selected than entries from families with more trees, owing to a larger error contribution to predicted breeding value for the smaller families (WHITE and HODGE, 1989). The technique of best linear prediction (BLP) accommodates imbalance in a data set, allowing weighting of family information according to its reliability for each assessed entry. Consequently, entries with more information from relatives are more likely to be selected when BLP is used (WHITE and HODGE, 1989). Both methods provide a vector of breeding values for n assessed traits for one entry as the solution to the matrix equation:

$$\hat{g} = C'V^{-1}(y - \alpha)$$

where $\hat{g}$ is the vector of n predicted breeding values, C' is the transposed matrix of covariances between m observations and n breeding values, $V^{-1}$ is the inverse of the m x m matrix of observation variances and covariances, and $(y - \alpha)$ is the m x 1 column vector of deviations of observed values from their expectations (WHITE and HODGE, 1989). BLP accommodates imbalance by changing the models used to estimate elements of C and V, in accordance with differences among entries in the quantity and quality of assessment data.

Predicting breeding values of individual trees in open-pollinated family tests requires an appropriate model for calculating the covariance between observed trait values on individual trees and breeding values of traits on the same trees. Open-pollinated families may include pairs of trees that are full sibs, but if the number of pollen parents is large enough, the genetic correlation among sibs can be assumed to be close to the true half-sib correlation of 1/4 of total additive genetic variance in the seed parents' natural breeding populations (CHELIAK et al., 1985; MAGNUSSEN and YEATMAN, 1990; MAGNUSSEN, 1993).

Another potential source of error in the covariance model, however, is a contribution from genetic variation among populations in different locations to variation among open-pollinated families. Some genetic variation among seed parents of tested families in a breeding program may be associated with variation among the populations which produced the seed parents (CHRISTOPHE and BIROT, 1983; HARVEY and TOWNSEND, 1985; KLEIN, 1989; ERICSSON et al., 1994), although such variation is not always detectable (YEATMAN, 1974; MAGNUSSEN and YEATMAN, 1990; CORRIVEAU et al., 1991). Pollen parents of any one family are likely to be predominantly from the seed parent's vicinity. Consequently, genetic variation among pollen parents is unlikely to include a contribution from variation among populations. Genetic variation among gametes within pollen and seed parents would also not include any population contribution. If genetic variation among pollen parents and among gametes within parents is assumed equal to that among seed parents, and if the variation among seed parents includes a population contribution absent from pollen and gamete genetic variation, then the latter will be over-estimated. Over-estimation of pollen parent and gamete contributions to within-family genetic variation will result in inflated estimates of the covariance of observed tree traits with trait breeding value. Assessment of source-related variation among families, and adaptation of the covariance model to accommodate such varia-

tion, can avoid impairment of accuracy in predicting breeding values.

BLP has been used in tree improvement for family selection for 5-year height with unbalanced data (LAFARGE, 1989) and for family selection for growth and rust resistance (WHITE and HODGE, 1988). No reports have been seen on use of BLP for combined selection. This report describes use of BLP for multiple-trait combined selection of individual trees in an open-pollinated jack pine (*Pinus banksiana* LAMB.) family test. Traits assessed were height and diameter at 20 years from planting, and stem quality, resistance to western gall rust (*Endocronartium harknessii* Y. HIRATSUKA), and wood density at 21 years from planting.

**Materials and Methods**

The family test was planted in 1972 with 209 open-pollinated progenies of wild parent trees selected from 49°N to 51°N latitude and 95°W to 96°30'W longitude in Manitoba, Canada, 6 families from Saskatchewan, Canada, and one control lot of mixed origin in southeastern Manitoba for a total of 216 entries (*Figure 1*). In most stands visited for selection, there was a deliberate attempt to select three parents, separated by not less than 100 m, to allow partitioning of genetic variation within breeding populations from that between populations (KLEIN, 1989). Parent trees were selected by subjective visual assessment for above-average bole quality and average or above-average size. Details of test establishment have been reported previously (KLEIN, 1982). The test comprises four
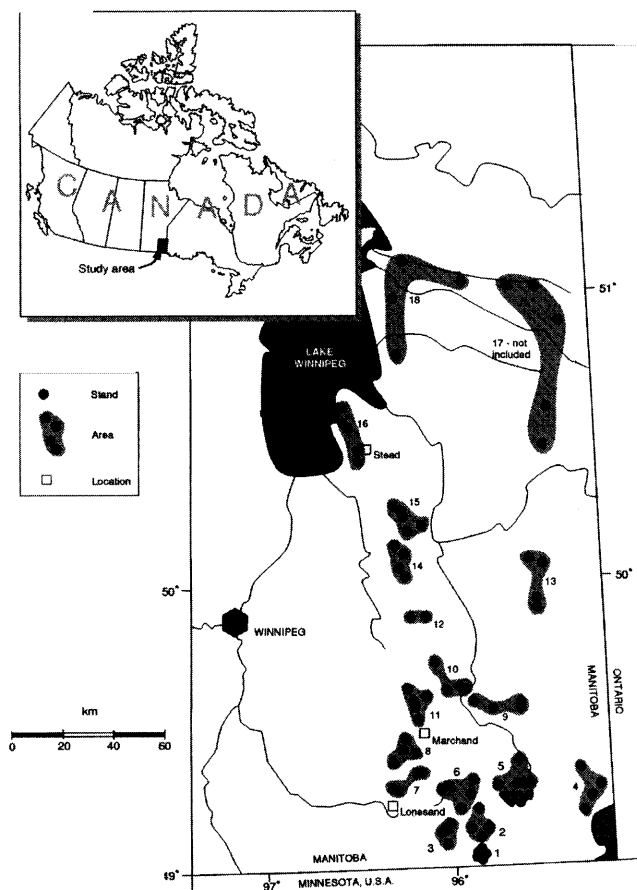


Figure 1. – Stands, areas, and plantation locations of jack pine family test. Note that area shading is used only to indicate grouping of stands into areas, and does not correspond to distribution of jack pine in the study area.

plantations on brunisolic soils developed on excessively drained sand and gravel deposits, at 49°13' N 96°20'W (Lonesand, 2 plantations), 49°28' N, 96°09' W (Marchand), and 50°28' N, 96°25' W (Stead). Climate at the test sites is characterized by mean temperatures for January and July of −19°C to −17°C and 19°C to 20°C, and mean annual precipitation of 500 mm to 530 mm. The design is cubic lattice (COCHRAN and COX, 1957) with 4-tree row plots and 15 replications in total, of which 6 are in 1 plantation (Stead) and 3 each are in the other 3 plantations (*Figure 1*). At 15 years, the test was thinned to leave 2 trees on each plot judged to be the best in terms of size and straightness.

Total height in cm and diameter outside bark at breast height (1.3 m) in mm were measured on all living trees following the 20th growing season after planting. Data from suppressed or severely damaged trees were eliminated from further use.

Scoring of secondary traits was done the following year. Trees were chosen for scoring of secondary traits if they were average or better in height and periodic height growth since year 15, in relation to neighboring trees. Trees close to average in height were chosen for scoring of secondary traits only if they were above-average in stem quality scores at 10 years and 15 years (KLEIN, 1986, 1992). Stem quality was assessed on a scale of 1 to 6 (best) as a single composite trait primarily expressing stem straightness, with extra credit for exceptionally thin and flat branches, or less credit for thick and ascending branches or frequent forks. Assignment of scores was intended to be relative to the general level of stem quality for a subjectively perceived neighborhood (COTTERILL and DEAN, 1990). The total number of western gall rust galls was recorded, whether alive or dead on any part of the crown. For assessment of wood density, 2 penetration measurements were taken through the bark on opposite sides of each tree at about 1 m above ground using a 6 joule "Forest" Model Pilodyn (MICKO et al., 1982; SPRAGUE et al., 1983; VILLENEUVE, 1986; KING et al., 1988; PARK et al., 1989; YANCHUK and KISS, 1993). These measurements were converted to an estimate of wood density using a model developed from 30 inner border row trees in the test plantations;

$$D = 0.6122 - 0.00046 \, dbh - 0.01 \, (Pdn1 + Pdn2)/2$$

where D is wood density in g/cm$^3$, dbh is diameter at breast height outside bark in mm, and Pdn1 and Pdn2 are the 2 Pilodyn determinations in mm.

*Statistical analyses*

Removing site effects from height and diameter values

Adjustment of height for block effects has been proposed to increase the accuracy of breeding value prediction (WHITE and HODGE, 1989; COTTERILL and DEAN, 1990). Partly because effectiveness of the original cubic lattice design has been compromised by mortality and disqualifying damage, a method of spatial neighbor adjustment for site effects (LOO-DINKINS, 1992; MAGNUSSEN, 1990) was developed for this analysis. Height and diameter values for individual trees were adjusted by subtracting from measured values, the estimated local site effects of a sliding block or neighborhood positioned symmetrically around each tree. This procedure was similar to the adjustment procedure described by WRIGHT (1978) in using the within-family deviation of neighbors to estimate site effect at the target tree. It differed in using individual trees rather than linear plots, and in constructing for each tree a neighborhood extending an equal distance in all directions rather than 2 sides. Use of individual trees rather than multiple-tree

contiguous plots should avoid upward bias due to auto-correlation in the genetic parameters calculated from the adjusted values (MAGNUSSEN, 1994).

Family means across locations were used as the base for calculating within-family deviations of individual trees. A SAS data step (SAS Institute Inc., 1990a) identified neighbors of a tree, then accumulated within-family deviations of neighbors and number of neighbors. Maximum distance for a neighbor was defined as;

$$(Row - row')^2 + (Column - column')^2 <= 18.$$

A tree three rows and 3 columns or 4 rows and 1 column from the target tree would be a neighbor, but a tree 4 rows and 2 columns from it would not be a neighbor. The number of planting positions included varied from 19 for a corner tree to 60 for an interior tree. This fixed, and rather large, neighborhood size was not tested for optimality but was intended to be conservative. The means of within-family deviations of neighbors for height and diameter were used as height and diameter adjustments for a target tree. These adjustments were subtracted from measured values to yield adjusted height (AH) and adjusted diameter (AD) for the target tree, and the process repeated for all trees. Adjusted values were used for all subsequent analyses involving height and diameter.

Blocking variables

Three planting locations represented the only blocking variable used initially in the analyses reported here. Replications and cubic lattice blocks within replications were ignored. The Lonesand location combined 2 plantations with relatively high proportions of unusable trees, separated by about 1 km, on the same soil association (KLEIN, 1982). The Marchand and Stead locations were single plantations.

Gall counts and wood density

Gall counts were transformed into proportionate rank scores for all statistical and quantitative genetic analyses, after square root and logarithmic transformations failed to reduce departure from normality. These scores are roughly equivalent to percentile scores. To reduce complexity, infrequent high gall counts were grouped into classes so that there were 10 classes in each location. A tree's proportionate rank for it's number of rust galls is the sum of the proportion of trees in classes with more galls, and half of the proportion of trees in the same class. Trees with no galls have the highest rank. The transformation was done within locations. Rank scores are proportionate ranks multiplied by 10 to avoid an excessive number of leading zeroes in parameter estimates. Hence:

Gall rank score = 10 x (trees with more galls + trees in class/2)/trees in location

True probability levels for test statistics can not be assumed to equal values for a normal distribution. It is hoped that rank scores represent degree of rust resistance more closely than number of galls/tree or presence-absence values.

Location effects for wood density were subtracted from all tree values. The adjusted values were multiplied by 100 to reduce the number of leading zeroes in parameter estimates.

Family source variables

The 209 eastern breeding district families were obtained from 76 stands, with 1 to 5 but usually 3 families from each. Stands were numbered 1 to 76 from south to north, and the numbers became the values of the independent classification variable "stand" in each tree's record. Neighboring stands were then grouped subjectively, while keeping number of families

similar between groups. Groups were numbered 1 to 18 from south to north, becoming values of the classification variable "area" (*Figure 1*). Use of the variables stand and area allowed assessment of the geographic or population contribution to genetic variation among families.

All trees from area 17 were excluded from final analysis based on results of preliminary analysis. Separation of height and diameter means for this area from those of the next poorest area (19 cm and 4 mm) were more than double the next largest differences among area means (9 cm and 1 mm). Removal of area 17 data from analysis of variance reduced height and diameter area mean squares by 36% and 29%. Exclusion of area 17 data from subsequent analyses avoided excessive weighting of area effects in estimation of height and diameter breeding values of the remaining trees, with very little likelihood that any superior trees were lost.

## Analysis of variance

Analyses of variance were performed on 2 data sets. The stage 1 data set had adjusted height in cm (AH) and adjusted diameter in mm (AD) for 4707 valid trees. The stage 2 data set had 2410 average or better trees from stage 1, with observations on stem quality (SQ), rank scores of rust gall counts (RG), and wood density in g/cm$^3$ x 100 estimated from Pilodyn determinations, adjusted for location effect (WD), in addition to AH and AD. The model used initially for analysis of variance for all traits was:

$$Y_{ijklm} = \mu + L_i + A_j + LA_{ij} + S(A)_{jk} + LS(A)_{ijk} + F(AS)_{jkl} + LF(AS)_{ijkl} + e_{ijklm}$$

where $Y_{ijklm}$ is the trait value for tree m of family l from stand k in area j, growing in location i, $\mu$ is the test mean across locations, $L_i$ is the effect of location i, $A_j$ is the effect of area j, $LA_{ij}$ is the interaction effect of location i by area j, $S(A)_{jk}$ is the effect of stand k in area j, $LS(A)_{ijk}$ is the interaction effect of location i and stand k in area j, $F(AS)_{jkl}$ is the effect of family l in stand k and area j, $LF(AS)_{ijkl}$ is the interaction effect of location i and family l in stand k and area j, and $e_{ijklm}$ is error, including within-family genetic variation and all within-family environmental variation within locations, that is, replication, plot, and within-plot effects. All effects except $\mu$ were considered random.

Univariate and multivariate analyses of variance were performed using the SAS General Linear Model procedure (SAS PROC GLM) with type III sums of squares (SAS Institute Inc., 1990b). Method of moments variance components and covariance components were calculated from the sums of squares and sums of cross products, and random model error terms provided by the PROC GLM procedure. In an attempt to avoid negative variance components (MILLIKEN and JOHNSON, 1984) and covariances which gave correlations outside the acceptable range of −1 to +1, this protocol was repeated using models with various effects from the original model removed, if they were non-significant for some traits.

Application of the above criteria supported removal from the model of the locations term and its interactions. Anomalous results were also reduced by removal of either the stands or areas effect. It was decided to retain areas and drop stands, because areas were judged to be more plausible representations of natural breeding populations than stands. Accordingly, the chosen model for stage 1 analysis of AH, AD, and their covariance, and for stage 2 analysis of SQ, RG, WD, and all other trait pair covariances was;

$$Y_{jlm} = \mu + A_j + F(A)_{jl} + e_{jlm}.$$

Standard errors of variance and covariance components were calculated as described by BECKER (1984).

Heritabilities (area, family, within-family, and individual) were calculated using the following formulas;

$$h_a^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_{f(a)}^2/k1 + \sigma_e^2/k2)$$

$$h_{f(a)}^2 = \sigma_{f(a)}^2 / (\sigma_{f(a)}^2 + \sigma_e^2/k3)$$

$$h_w^2 = 3\sigma_{f(a)}^2 / \sigma_e^2$$

$$h_i^2 = (\sigma_a^2 + 4\sigma_{f(a)}^2) / (\sigma_a^2 + \sigma_{f(a)}^2 + \sigma_e^2)$$

where $h_a^2$, $h_{f(a)}^2$ represent area and family in area heritability, $h_w^2$ is within-family heritability, and $h_i^2$ is individual heritability; the heritability of mass selection, $\sigma_a^2$, $\sigma_{f(a)}^2$, and $\sigma_e^2$ are variance components due to corresponding effects in the model, and k1, k2, and k3 are harmonic means of families/area, trees/area, and trees/family. Standard errors of heritability estimates were adapted from FALCONER (1989, p. 182). Genetic correlations between traits and their standard errors were calculated from variance and covariance components as described by FALCONER (1989, p. 317).

### Calculation of breeding values

Calculation of breeding values required performance data in the required form, variance and covariance components from statistical analysis outputs, models for matrix elements, and a calculation procedure in the form of program code.

Performance data values enter the calculation as the difference between random effect observed values and fixed effect expected values. Although site means can be used as expected values (WHITE and HODGE, 1989), observed values in this instance were already adjusted to remove site effects, in different ways for different traits, prior to statistical analysis. Because the test mean was the only fixed effect in the model, it was used as the expected value for all traits. Family means and area means were used as performance data values, along with tree observations, for traits having significant family and area effects. Only SQ area effects failed to show significant differences. The input data file thus included, for each of 2410 stage 2 trees, observed − expected values for trees, family means and area means for AH, AD, RG, and WD, and for trees and family means for SQ. These 14 values constituted the observed − expected vector in the BLP algorithm for each tree (*Table 1*). Family, area, and test means for AH and AD were from the stage 1 data set.

The V matrix is the variance of the observation vector for each tree being evaluated, hence the matrix has a row and a column for each element in the observation vector, in this instance 14 rows and columns. Each element of V is calculated according to a linear model representing the theoretical expectation of the variance of the indicated observation or covariance of the indicated observation pair (*Table 2*). Terms in these models are variance and covariance components, and for elements where the row or column observation is a family or area mean, family size values. The C matrix represents the covariance of the observation vector with a theoretical true genetic value vector having one element for each trait being assessed. Elements in C are covariances between the observations specifying the 14 rows and the trait breeding values specifying the 5 columns. Models for C elements are functions

*Table 1.* – Variables in tree data file used for prediction of breeding values.

| Group | Variable |
|---|---|
| Identity | Area |
| | Family |
| | Replication |
| | Block in replication |
| | Plot in block |
| | Tree in plot |
| | Height year 20, cm |
| | Diameter year 20, mm |
| Observed-expected $(y - \alpha)$ | Tree AH - test AH mean, cm |
| | Family AH mean - test AH mean |
| | Area AH mean - test AH mean |
| | |
| | Tree AD - test AD mean, mm |
| | Family AD mean - test AD mean |
| | Area AD mean - test AD mean |
| | |
| | Tree SQ - test SQ mean, score units |
| | Family SQ mean - test SQ mean |
| | |
| | Tree RG - test RG mean, prop. rank x 10 |
| | Family RG mean - test RG mean |
| | Area RG mean - test RG mean |
| | |
| | Tree WD - test WD mean, g/cm$^3$ x 100 |
| | Family WD mean - test WD mean |
| | Area WD mean - test WD mean |
| Family structure | Trees in family, stage 1, $n1_{jl.}$ |
| | Trees in area, stage 1, $n1_{j..}$ |
| | Families in area, $n_{j.}$ |
| | Trees in family, stage 2, $n2_{jl.}$ |
| | Trees in area, stage 2, $n2_{j..}$ |

of genetic variance and covariance components and family size values (*Table 3*). To calculate new values of matrix elements when required by a change in family size, family size values were included in the data record for each tree, and all matrix element values were calculated for each tree.

Components and family sizes for matrix elements involving only AH and AD are from stage 1 analysis, while elements involving a secondary trait, even in combination with AH or AD, use components and family sizes from stage 2 analysis.

Program code was written in SAS Interactive Matrix Language (SAS/IML) (SAS Institute Inc., 1990c). The program first stored the constant values of 45 variance and covariance components for 3 model effects (areas, families, error) for each of 5 traits and 10 trait pairs. A data record from a tree was read and stored in 3 separate vectors for tree identification, performance observation values (already in observed − expected form), and family size values (*Table 1*). Each element of the V and C matrices was calculated from stored variance and covariance components and the tree's family size values according to the expectation for the specified element, or by setting it equal to a previous element having the same model. One program statement was required for each of the 14 x 14 elements of V and 5 x 14 elements of C. One more statement

caused execution of the BLP algorithm with the newly calculated V and C and the tree's performance observation values, writing 5 trait breeding value estimates to a vector. The tree identification vector was concatenated to the breeding value vector, the result written to an output file, and the next record read.

Covariance of predicted breeding value with true breeding value was calculated for all traits and trait pairs for each tree as:

$$\text{Cov} (\hat{g}, g') = C'V^{-1}C$$

Correlation of predicted breeding value with true breeding value (Corr $(\hat{g}, g)$) was calculated for the diagonal elements of Cov $(\hat{g}, g')$, representing 5 correlations for 5 single trait breeding values, as:

$$\text{Corr} (\hat{g}, g) = \{\text{Cov} (\hat{g}, g)/\text{Var}(g)\}^{1/2}$$

(WHITE and HODGE, 1989) where Cov $(\hat{g}, g)$ is the covariance of predicted breeding value with true breeding value for 1 trait, from 1 of the diagonal elements of Cov $(\hat{g}, g')$, and Var $(g)$ is the total genetic variance for that trait, calculated as $4\sigma_{f(a)}^2 + \sigma_a^2$.

Selection index (SI) breeding value predictions were calculated for stage 2 trees for comparison with BLP values. The algorithm was similar, differing only in that V and C needed to be calculated only once, using harmonic means of the family size values read for each tree for BLP. This algorithm $(\hat{g} = C'V^{-1}(y - \alpha)$, WHITE and HODGE, 1989) differs from the customary SI formula (b = $V^{-1}Ca$ with varying notation) in solving for trait breeding values rather than index weights.

Selection was based on total score, calculated as the sum of assigned trait weights multiplied by each tree's trait breeding values. Trait weights were assigned by an iterative procedure intended to lead ultimately to the combination of trait gains which would maximize net value at harvest of the selected trees. A trial vector of weights was applied, providing total scores for all trees. The best 64 trees were selected based on these scores, with the restriction of 1 selection per family. Mean breeding values of the selected trees, representing gains in the 5 traits, were inspected to identify potentially favorable trade-offs. Weights were then increased for traits in which more gain was desired, while weights for traits to be given less or unchanged gain were reduced or left unchanged. Selection was repeated with the new weights, new gains were calculated, and results inspected again, until a set of gains was produced which appeared likely to offer more favorable value yield at maturity than other sets of gains bracketing the chosen set. Subjectivity was unavoidable in this procedure, because the value of stem quality and rust resistance breeding value units in relation to tree size breeding value units is not known. It was preferred because it is interactive, whereas the restricted selection index approach (LIN, 1985) requires choosing trait gain proportions in advance. Adverse correlations can result in actual amounts of gain being unfavorable when desired proportions are imposed (MAGNUSSEN and KEITH, 1990).

Predicted gain in tree cone volume, approximated by $(AD/2)^2$ x AH, was calculated as the difference between cone volume from AH and AD mean breeding values of the selected trees and that from the stage 1 test means for AH and AD. Predicted gain in tree dry weight was calculated from the product of cone volume and WD for the test mean and the mean of the selected trees.

### Results

For the adjustment of height and diameter, number of valid trees in the defined neighborhood of each measured tree

*Table 2.* – Coefficients of variance and covariance components for calculating elements of matrix of variances and covariances of observations (V matrix) for the best linear prediction of breeding values for AH, AD, SQ, RG, and WD with stage 2 trees. Note that a row of coefficients applies to the observation effect or effects in the same row, and to any of the traits or trait pairs of the same trait stage. A complete model for a matrix element is the sum of area, family, and error variance or covariance components for a trait or trait pair, each multiplied by the effect component coefficient for the effect or effect pair for that element, appropriate to the stage or stages of the trait or traits.

| Trait stage(s) | Variance or covariance component types for trait or traits observed | Observation effect(s)[1] | Effect component coefficient[2] | | |
| --- | --- | --- | --- | --- | --- |
| | | | Area | Family | Error |
| 1 | $\sigma_{AH}^2$ $\sigma_{AD}^2$ $\sigma_{AH,AD}$ | TT | 1 | 1 | 1 |
| | | TF FF | 1 | 1 | $1/n1_{jL.}$ |
| | | TA FA AA | 1 | $1/n_{j.}$ | $1/n1_{j..}$ |
| 2 | $\sigma_{SQ}^2$ $\sigma_{RG}^2$ $\sigma_{WD}^2$ $\sigma_{SQ,RG}$ $\sigma_{SQ,WD}$ $\sigma_{RG,WD}$ | TT | 1 | 1 | 1 |
| | | TF FF | 1 | 1 | $1/n2_{jL.}$ |
| | | TA FA AA | 1 | $1/n_{j.}$ | $1/n2_{j..}$ |
| 1,2 | $\sigma_{AH,SQ}$ $\sigma_{AH,RG}$ $\sigma_{AH,WD}$ $\sigma_{AD,SQ}$ $\sigma_{AD,RG}$ $\sigma_{AD,WD}$ | TT | 1 | 1 | 1 |
| | | TF FF | 1 | 1 | $1/n2_{jL.}$ |
| | | TA FA AA | 1 | $1/n_{j.}$ | $1/n2_{j..}$ |

[1] TT = Variance of a tree observation or covariance of 2 traits of a tree, TF = covariance of a tree observation with a trait mean for the tree's family, FF = variance of a family mean or covariance of family means of 2 traits, TA = covariance of a tree observation with a trait mean for the tree's area, FA = covariance of a family mean with a trait mean for the family's area, AA = variance of an area mean or covariance of area means of 2 traits.

[2] $n1_{jL}$ = stage 1 trees in family, $n1_{j.}$ = stage 1 trees in area, $n_{j.}$ = families in area, $n2_{jL}$ = stage 2 trees in family, $n2_{j..}$ = stage 2 trees in area. Because areas were not signigicant for SQ, the areas component for any element in the V matrix involving SQ is set to 0, with a coefficient of 1.

*Table 3.* – Coefficients of variance and covariance components for calculating elements of matrix of covariances of observations with trait breeding values (C matrix) for best linear prediction of breeding values for AH, AD, SQ, RG, and WD with stage 2 trees. A complete model for a matrix element is the sum of area and family variance or covariance components for a trait or trait pair, each multiplied by the effect component coefficient for the effect for that element, appropriate to the stage or stages of the trait or traits.

| Trait stage(s) | Variance or covariance component types for trait or traits involved in the covariance of an observation with a breeding value | Observation effect | Effect comp. coeff. | |
| --- | --- | --- | --- | --- |
| | | | Area | Family |
| 1 | $\sigma_{AH}^2$ $\sigma_{AD}^2$ $\sigma_{AH,AD}$ | Tree | 1 | 4 |
| | | Family | 1 | $1+3/n1_{jL.}$ |
| | | Area | 1 | $1/n_{j.}+3/n1_{j..}$ |
| 2 | $\sigma_{SQ}^2$ $\sigma_{RG}^2$ $\sigma_{WD}^2$ $\sigma_{SQ,RG}$ $\sigma_{SQ,WD}$ $\sigma_{RG,WD}$ | Tree | 1 | 4 |
| | | Family | 1 | $1+3/n2_{jL.}$ |
| | | Area | 1 | $1/n_{j.}+3/n2_{j..}$ |
| 1,2 | $\sigma_{AH,SQ}$ $\sigma_{AH,RG}$ $\sigma_{AH,WD}$ $\sigma_{AD,SQ}$ $\sigma_{AD,RG}$ $\sigma_{AD,WD}$ | Tree | 1 | 4 |
| | | Family | 1 | $1+3/n2_{jL.}$ |
| | | Area | 1 | $1/n_{j.}+3/n2_{j..}$ |

ranged from a minimum of 1 neighbor for one target tree to a maximum of 35 neighbors. There were 75 trees of the 5114 valid trees that had fewer than 10 neighbors, and the median number of neighbors was 23. Mean within-family deviation of neighbors ranged among the 5114 neighborhoods from −193 cm to 208 cm for height (standard deviation 75 cm) and −20 mm to 28 mm for diameter (standard deviation 6.7 mm).

There were 4707 trees included in the stage 1 data set analyzed for AH and AD, with means of 688 cm and 85 mm, and 2410 trees in the stage 2 data set analyzed for SQ, RG and WD, with means of 3.91, 4.995, and 38.7 g/cm$^3$ x 100. The 17 areas left in the analysis included 191 families. Frequency distributions of gall counts at the 3 locations, and the equivalent proportionate ranks, are in *table 4*. Rank score equivalents of gall count classes were similar across locations, so calcula-

tion of rank scores within locations made little difference to analysis results. More than 75% of the 2410 stage 2 trees were free of western gall rust galls.

The amount of imbalance was not high, but was greater in the stage 2 data set, where the choice of larger trees for inclusion would be expected to reduce family size more in families with relatively poor growth. Coefficients of the variance component for families differ more between the area and families mean square for stage 2 trees. In addition, there is a larger fraction of error mean square in the F-ratio denominator for areas in the stage 2 analysis (*Table 5*).

Probability of a higher F-ratio for areas, with no effect, was less than 0.0001 for AH and AD, less than 0.01 for WD, and less than 0.05 for RG (*Table 6*). The proportion of total variance due to areas ranged from virtually nil for SQ up to 3.3% for

*Table 4.* – Rank scores (proportionate rank x 10) of western gall rust gall counts in Manitoba jack pine family test plantations.

| | Location | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1: Lonesand | | | 2: Marchand | | | 3: Stead | | |
| Class | Galls | Trees | Score | Galls | Trees | Score | Galls | Trees | Score |
| 1 | 0 | 670 | 6.121 | 0 | 432 | 6.134 | 0 | 722 | 6.335 |
| 2 | 1 | 44 | 1.994 | 1 | 29 | 2.018 | 1 | 87 | 2.223 |
| 3 | 2 | 28 | 1.578 | 2 | 21 | 1.571 | 2 | 46 | 1.548 |
| 4 | 3 | 29 | 1.249 | 3 | 23 | 1.179 | 3 | 36 | 1.132 |
| 5 | 4 | 16 | 0.988 | 4 | 10 | 0.884 | 4 | 25 | 0.822 |
| 6 | 5 | 16 | 0.803 | 5 | 13 | 0.679 | 5 | 21 | 0.589 |
| 7 | 6-7 | 20 | 0.595 | 6 | 8 | 0.491 | 6 | 12 | 0.421 |
| 8 | 8-11 | 20 | 0.364 | 7 | 6 | 0.366 | 7-8 | 17 | 0.274 |
| 9 | 12-15 | 11 | 0.185 | 8-9 | 10 | 0.223 | 9-11 | 12 | 0.127 |
| 10 | 16-29 | 11 | 0.058 | 10-13 | 8 | 0.062 | 12-31 | 7 | 0.030 |
| Total | | 865 | | | 560 | | | 985 | |

*Table 5.* – Type III random model mean square expectations and F-ratio denominators.

| Source of variation | | df | Type III mean square expectations[1] | Coefficient of mean squares for F-ratio denominator | |
|---|---|---|---|---|---|
| | | | | F(A) | E |
| *Stage 1 trees* | | | | | |
| Areas | A | 16 | $\sigma_e^2 + 23.577\sigma_{f(a)}^2 + 272.82\sigma_a^2$ | 0.9877 | 0.0123 |
| Families in A | F(A) | 180 | $\sigma_e^2 + 23.87\sigma_{f(a)}^2$ | | 1.000 |
| Trees in F | E | 4116 | $\sigma_e^2$ | | |
| *Stage 2 trees* | | | | | |
| Areas | A | 16 | $\sigma_e^2 + 11.241\sigma_{f(a)}^2 + 130.93\sigma_a^2$ | 0.9239 | 0.0761 |
| Families in A | F(A) | 180 | $\sigma_e^2 + 12.167\sigma_{f(a)}^2$ | | 1.000 |
| Trees in F | E | 2213 | $\sigma_e^2$ | | |

[1] $\sigma_e^2$, $\sigma_{f(a)}^2$, and $\sigma_a^2$ = variance components for trees in families, families in areas, and areas.

*Table 6.* – Analysis of variance results, variance components from type III sums of squares, and heritability for all traits. Values for AH and AD are based on the stage 1 data set.

| Source of Variation | Statistic | Trait | | | | |
|---|---|---|---|---|---|---|
| | | AH | AD | SQ | RG | WD |
| A | Mean square | 36,546 | 1808 | 4.015 | 15.31 | 12.65 |
| | F-ratio | 3.56 | 5.32 | 1.09 | 1.74 | 2.34 |
| | P>F | 0.0001 | 0.0001 | .3631 | 0.0414 | 0.0035 |
| | Var. comp. | 96.380 | 5.382 | 0.003 | 0.050 | 0.055 |
| | (s.e.) | (2.714) | (0.134) | (0.001) | (0.004) | (0.003) |
| | % total | 2.6 | 3.3 | 0.1 | 1.1 | 2.0 |
| F(A) | Mean square | 10,337 | 342 | 3.833 | 9.15 | 5.66 |
| | F-ratio | 3.08 | 2.31 | 2.26 | 2.14 | 2.38 |
| | P>F | 0.0001 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| | Var. comp. | 293.439 | 8.159 | 0.175 | 0.401 | 0.270 |
| | (s.e.) | (9.312) | (0.308) | (0.010) | (0.023) | (0.014) |
| | % total | 7.8 | 5.0 | 9.3 | 8.5 | 10.0 |
| E | Var. comp. | 3357.588 | 147.865 | 1.700 | 4.270 | 2.375 |
| | (s.e.) | (70.690) | (3.113) | (0.051) | (0.128) | (0.071) |
| | % total | 89.6 | 91.6 | 90.5 | 90.4 | 88.0 |
| Area | $h^2_a$ | 0.72 | 0.81 | 0.08 | 0.42 | 0.56 |
| | (s.e.) | (0.01) | (0.01) | (0.02) | (0.02) | (0.02) |
| Family | $h^2_f$ | 0.68 | 0.57 | 0.56 | 0.53 | 0.58 |
| | (s.e.) | (0.01) | (0.01) | (0.02) | (0.02) | (0.02) |
| Individual | $h^2_i$ | 0.34 | 0.24 | 0.37 | 0.35 | 0.42 |
| | (s.e.) | (0.02) | (0.02) | (0.03) | (0.03) | (0.03) |
| Within-family | $h^2_w$ | 0.26 | 0.17 | 0.31 | 0.28 | 0.34 |
| | (s.e.) | (0.02) | (0.02) | (0.03) | (0.03) | (0.03) |

AD. Probability of a higher F-ratio for families in areas with no effect was less than 0.0001 for all traits. The contribution of families in areas varied from a low of 5.0% for AD to 7.8%, 8.5%, 9.3%, and 10% for AH, RG, SQ, and WD. Within-family sampling error was lowest for WD at 88.0% and highest for AD at 91.6%.

Narrow-sense or individual heritability was highest for WD (0.42) and lowest for AD (0.24), while the other 3 traits had similar intermediate values (0.34, 0.35, 0.37 for AH, RG, and SQ) (*Table 6*). Family heritabilities were more than double the individual heritability values for the traits of the stage 1 data set. The stage 2 traits had higher within-family and individual heritabilities than the stage 1 traits, but lower family and area heritabilities, partly owing to smaller family sizes of the stage 2 data set. Area heritability was higher than family heritability for AH and AD, near 0 for SQ, and intermediate between individual and family heritability for RG and WD. Standard errors of variance component and heritability estimates were less than 1/10 the size of the estimates for all significant effects.

Areas covariances that were not set to zero yielded genetic correlations that were larger in amplitude than families covariances for every trait pair. Amplitude of area effect genetic correlations was >1 for AHxAD, and was >0.7 for AHxRG

(0.86), AHxWD (−0.92), ADxWD (−0.84), and RGxWD (−0.76). Note that all 3 area covariances with WD yielded large negative genetic correlations. In the case of AHxRG, ADxRG, and RGxWD, the areas covariance was opposite in sign to the families covariance. The only genetic correlations for families in areas greater than 0.5 in amplitude were AHxAD (0.69) and ADxWD (−0.56). Other trait pairs, including AHxWD and all pairs involving stem quality or rust resistance, had family genetic correlations <0.2 in amplitude (*Table 7*). Variance and covariance components used to calculate elements of the V and C matrices are assembled in *table 8*.

Mean breeding value estimates for AH and AD of 12.3 cm and 1.54 mm are the result of scoring breeding values only on trees judged average or better than average in height and periodic height growth from year 15. Breeding value estimates for SQ, RG, and WD averaged close to the expected value of 0. Distribution of trait breeding values was apparently symmetric except for RG, with a skewness of −1.03. Distribution of RG breeding values was also was bimodal, with peaks at 0.40 and −0.12. These peaks may correspond to trees with no galls and with 1 gall, belonging to families with near-average family mean proportionate ranks (*Figure 2*).

Area mean breeding value predictions for AH and AD, adjusted to sum to zero, were above the test mean for all areas

Table 7. – Trait pair covariances from type III sums of cross-products used for BLP and SI, and genetic correlations ($r_G$). Area covariances with stem quality (SQ) were assigned zero value because area effects were not significant for this trait. Standard errors are in parentheses below estimates.

| Source of Variation | | Trait pair | | | | |
|---|---|---|---|---|---|---|
| | | AHxAD | AHxSQ | AHxRG | AHxWD | ADxSQ |
| A | Cov | 23.117 | 0.000 | 1.302 | -1.460 | 0.000 |
| | | (0.560) | (0.008) | (0.037) | (0.046) | (0.002) |
| | $r_G$ | 1.015 | - | 0.860 | -0.917 | - |
| | | 0 [1] | - | (0.003) | (0.002) | - |
| F(A) | Cov | 33.737 | -0.633 | -0.373 | -0.892 | -0.112 |
| | | (1.066) | (0.006) | (0.016) | (0.038) | (0.004) |
| | $r_G$ | 0.689 | -0.120 | -0.047 | -0.136 | -0.109 |
| | | (0.030) | (0.020) | (0.020) | (0.020) | (0.022) |
| E | Cov | 459.897 | 5.771 | -2.013 | -4.558 | -0.461 |
| | | (9.683) | (0.173) | (0.060) | (0.137) | (0.014) |

| Source of Variation | | Trait pair | | | | |
|---|---|---|---|---|---|---|
| | | ADxRG | ADxWD | SQxRG | SQxWD | RGxWD |
| A | Cov | 0.249 | -0.374 | 0.000 | 0.000 | -0.040 |
| | | (0.007) | (0.014) | (0.000) | (0.000) | (0.001) |
| | $r_G$ | 0.059 | -0.845 | - | - | -0.760 |
| | | (0.007) | (0.003) | - | - | (0.005) |
| F(A) | Cov | -0.045 | -0.717 | 0.024 | 0.006 | 0.034 |
| | | (0.005) | (0.036) | (0.001) | (0.001) | (0.001) |
| | $r_G$ | -0.029 | -0.565 | 0.092 | 0.029 | 0.104 |
| | | (0.022) | (0.015) | (0.020) | (0.020) | (0.020) |
| E | Cov | -1.374 | -5.595 | -0.005 | 0.146 | 0.092 |
| | | (0.041) | (0.168) | (0.000) | (0.004) | (0.003) |

[1])The formula for standard error of a genetic covariance gives a value of 0 for $r_G > = 1$.

southwest of an imaginary line connecting areas 5 and 10, and less than the test mean for all areas on the other side of this line. There is no clear pattern to the variation of the 17 SQ area means, suggesting it might be fortuitous. All 7 areas south of the Marchand test location had positive RG breeding values. Area 8, west of that site, and 7 of the 9 areas further north, had negative mean breeding values for RG. Only 2 areas had mean breeding values for WD that deviated from the test mean by more than 1%. There was some tendency for area mean breeding values of WD to be negatively associated with area mean breeding values of AH, AD, and RG, as expected from the area genetic correlations (Figure 3).

Correlation of predicted and true breeding value varied over a small range among families despite the wide spread among families in number of trees measured. Mean correlations ranged from 0.657 for AD to 0.698 for WD. The range from minimum to maximum correlation for any trait was not more than 5% of the mean correlation (Table 9).

Gains of 5.7%, 6.1%, 10.4%, 10.2%, and −0.5% for AH, AD, SQ, RG, and WD were yielded by selection of the 64 unrelated trees with the best total scores using the chosen weight vector

Table 8. – Variance and covariance components for calculating elements of V matrix and C matrix for prediction of breeding values by BLP and SI.

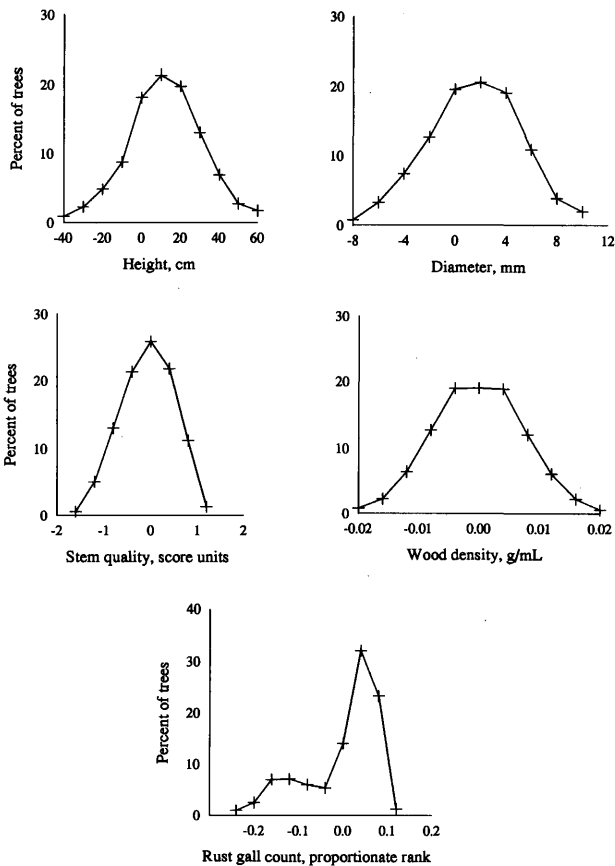| Trait(s) | Effect | | |
|---|---|---|---|
| | Areas | Families | Error |
| AH | 96.380 | 293.439 | 3357.588 |
| AD | 5.382 | 8.159 | 147.865 |
| SQ | 0.000 | 0.175 | 1.700 |
| RG | 0.050 | 0.401 | 4.270 |
| WD | 0.055 | 0.270 | 2.375 |
| AHxAD | 23.117 | 33.737 | 459.897 |
| AHxSQ | 0.000 | -0.633 | 5.771 |
| AHxRG | 1.302 | -0.373 | -2.013 |
| AHxWD | -1.460 | -0.892 | -4.558 |
| ADxSQ | 0.000 | -0.112 | -0.461 |
| ADxRG | 0.249 | -0.045 | -1.374 |
| ADxWD | -0.374 | -0.717 | -5.594 |
| SQxRG | 0.000 | 0.024 | -0.005 |
| SQxWD | 0.000 | 0.006 | 0.146 |
| RGxWD | -0.040 | 0.034 | 0.092 |

*Figure 2.* – Percentage frequency distribution of trait breeding values.

of 0.1, 0.2, 2.8, 1.2, and 0.4 (*Table 10*). None of the selected trees had fewer than 11 neighbors for adjustment of height and diameter. The gains for AH, AD, and WD were equivalent to a cone volume gain of 19.0% and a dry weight gain of 18.4%. The list of 64 trees selected according to the same weight vector, but using trait breeding value estimates calculated by SI, had only one tree not in common with the BLP list. SI gain estimates and BLP gain estimates for the SI list differed only · marginally from the BLP select list (*Table 10*). Setting the economic weight for WD at 0 increased the negative genetic gain in wood density from −0.5 to −1.0, but allowed slight increases in gain for cone volume (0.8%) and dry weight (0.2%). Doubling the WD weight to 0.8 reduced the wood density loss by 0.3% to −0.2%, but resulted in loss of 0.6% in cone volume gain and 0.2% in dry weight gain. There were reductions in RG gain, apparently fortuitous, from both changes in WD weight.

Number of selected trees from each area ranged from 0 to 9. Southwestern areas provided more selections than northern and eastern areas, as well as having generally higher mean breeding values for AH, AD, and RG (*Figure 3*).

## Discussion

Measurements and analyses reported here were done with the primary purpose of selecting recurrent parents in the measured family test plantations for an applied breeding program. Effects of the selection thinning at 15 years, and of adjustment of measurements for site effects, acted on the observed trait values for all assessed trees, as well as on the variance and covariance components and heritability estimates. These parameter estimates should be valid for
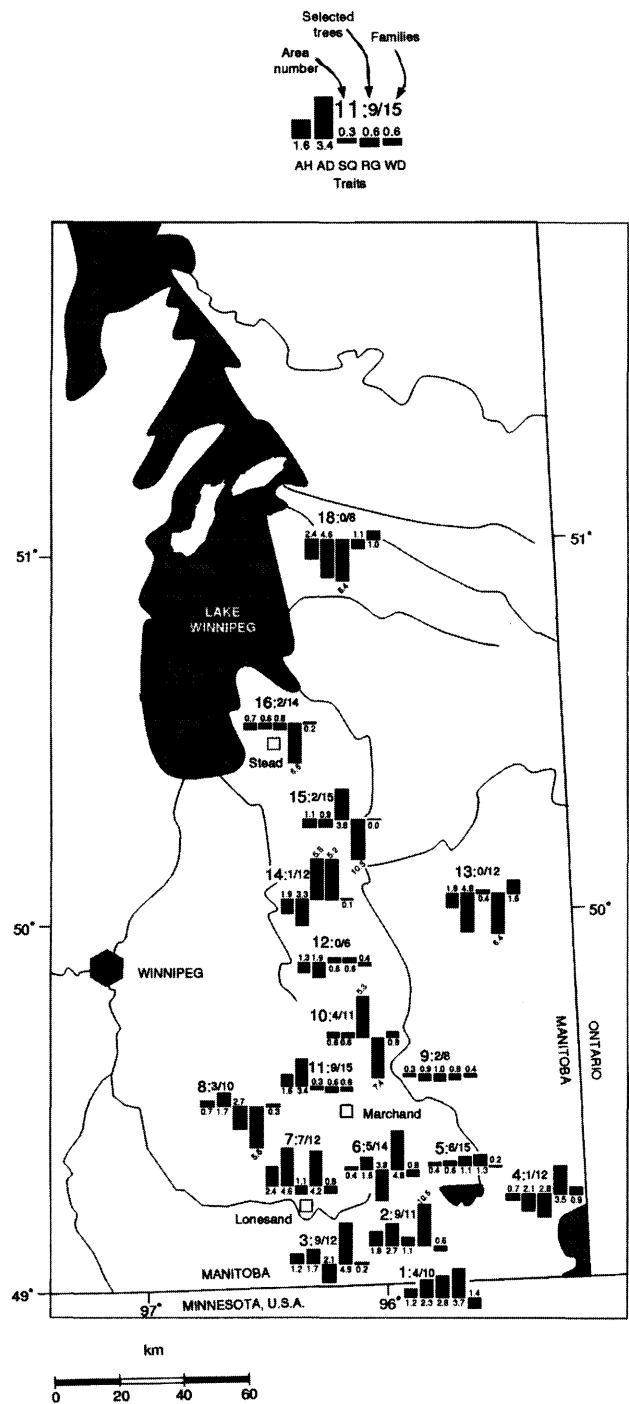


*Figure 3.* – Trait mean breeding values expressed as percentage of test mean, adjusted to sum to zero, number of selected trees, and number of families, by area. Maximum bar length is 5; larger values written diagonally. Values less than 5 written below bar if positive, above bar if negative.

application to selection in the assessed population, but may not apply to jack pine data obtained in different circumstances (MATHESON and RAYMOND, 1984; COTTERILL, 1987; LOO-DINKINS, 1992). Trees designated to be removed in the thinning at 15 years were not measured, so the effect of the thinning on genetic parameter estimates is not known.

Observations for all assessed traits were adjusted in some way to remove effects of site variation, but this adjustment did not suppress expression of genotype x environment interaction.

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Table 9. - Maximum, minimum, and mean family values of correlation (r) between predicted and true trait breeding values.

| Rank | AH r | AH Fam | Stage 1 trees fam | Stage 1 trees area | Area fams | AD r | AD Fam | Stage 1 trees fam | Stage 1 trees area | Area fams |
|------|------|--------|------|------|------|------|--------|------|------|------|
| 1 | 0.6828 | 311 | 30 | 270 | 11 | 0.6645 | 311 | 30 | 270 | 11 |
| 2 | 0.6824 | 156 | 29 | 370 | 15 | 0.6638 | 656 | 29 | 270 | 11 |
| 196 | 0.6718 | 454 | 17 | 147 | 6 | 0.6461 | 454 | 17 | 147 | 6 |
| 197 | 0.6718 | 524 | 17 | 179 | 8 | 0.6445 | 114 | 19 | 350 | 15 |
| mean | 0.6786 | | | | | 0.6570 | | | | |
| SI | 0.6787 | | | | | 0.6574 | | | | |

| Rank | SQ r | SQ Fam | Stage 2 trees fam | Stage 2 trees area | Area fams | RG r | RG Fam | Stage 2 trees fam | Stage 2 trees area | Area fams |
|------|------|--------|------|------|------|------|--------|------|------|------|
| 1 | 0.6759 | 311 | 23 | 147 | 11 | 0.6659 | 311 | 23 | 147 | 11 |
| 2 | 0.6759 | 656 | 23 | 149 | 11 | 0.6659 | .656 | 23 | 149 | 11 |
| 196 | 0.6463 | 361 | 5 | 69 | 8 | 0.6373 | 116 | 5 | 90 | 8 |
| 197 | 0.6420 | 114 | 3 | 166 | 15 | 0.6350 | 361 | 5 | 69 | 8 |
| mean | 0.6627 | | | | | 0.6519 | | | | |
| SI | 0.6635 | | | | | 0.6525 | | | | |

| Rank | WD r | WD Fam | Stage 2 trees fam | Stage 2 trees area | Area fams |
|------|------|--------|------|------|------|
| 1 | 0.7089 | 656 | 23 | 149 | 11 |
| 2 | 0.7089 | 311 | 23 | 147 | 11 |
| 196 | 0.6832 | 361 | 5 | 69 | 8 |
| 197 | 0.6819 | 114 | 3 | 166 | 15 |
| mean | 0.6981 | | | | |
| SI | 0.6987 | | | | |

Use of a one-way model for expression of observed trait values on assessed family-test trees and for estimation of second moments was appropriate because interactions with location as well as the location main effect were negligible when the original model was applied. Adjustment of tree values for site effects left only family effects that included an area contribution, and within-family error, as important sources of variation.

Area effects partitioned from family effects within areas would have otherwise inflated estimates of genetic variation, by 66%, 33%, 20%, and 12% for AD, AH, WD, and RG. Stand effects on 10-year height and diameter in the same family test included close to half of the total families variance (KLEIN, 1989). Stand effects for tree height at 8 to 12 years from seed in lodgepole pine (Pinus contorta DOUGL. ex LOUD. var. latifolia ENGELM.) in Sweden varied from 0.150 to 0.492 of total additive variance (ERICSSON et al., 1994). In contrast, a test of 100 open-pollinated jack pine families from 10 stands in 5 areas in Ontario, Canada, did not detect stand or area effects on height at 6 years from sowing (YEATMAN, 1974) or on height or diameter at 14 years from sowing (MAGNUSSEN and YEATMAN, 1990). Population effects were not significant for ring width or for relative density of total wood or outer wood, but were significant for relative density of inner wood, accounting for 2% of total variance, of white spruce (Picea glauca (MOENCH) VOSS) in Quebec, Canada (CORRIVEAU et al., 1991).

Heritability values are not used in calculating BLP breeding values, but the magnitude of heritability estimates provides an indirect indication of the efficiency of selection. The matrix product $C'V^{-1}$ which is multiplied by a tree's observation vector to calculate the tree's trait breeding value vector uses the same variance components used to calculate heritability.

Magnitude of area heritability for the 5 assessed traits does not show any direct relationship with amplitude of area mean breeding values expressed as a percentage of test mean (Figure 3). Stem quality and rust resistance, with nil and low area heritability, have the proportionately largest area breeding value means. A plausible indirect relationship can be inferred, in that height and diameter, with high area heritability and medium amplitude breeding value means, show a coherent pattern in the geographic distribution of these means, whereas the longer bars for stem quality appear to point up or down at random, and those for rust resistance show a less definite pattern than for height and diameter.

Individual heritability values for height, diameter, and stem quality at 20 years from planting were 0.34, 0.24, and 0.37; above average for comparable reported values. Values from this

study include areas variance in the numerator as in ERICSSON et al. (1994). Mass selection among trees in the family test, the hypothetical operation to which individual heritability applies, would not likely be restricted to application within areas. A few higher values have been reported for individual heritability of height in jack pine (MAGNUSSEN and YEATMAN, 1986), lodgepole pine (ERICSSON et al., 1994), and radiata pine (*Pinus radiata* D. DON) (COTTERILL and ZED, 1980); of diameter in radiata pine (COTTERILL and ZED, 1980; SHELBOURNE and LOW, 1980); of stem straightness in loblolly pine (BRIDGWATER and STONECYPHER, 1979); branch angle in jack pine (ADAMS and MORGENSTERN, 1991); and branch quality in radiata pine (SHELBOURNE and LOW, 1980). Most reported values for heritability of height, diameter, and stem and branch quality traits in pine species are lower, including most of the values in reports which included the higher values (YEATMAN, 1974; BRIDGWATER and STONE-CYPHER, 1979; COTTERILL and ZED, 1980; SHELBOURNE and LOW, 1980; BRIDGWATER et al., 1983; DEAN et al., 1983; ERNST et al., 1983; KLEIN, 1989; PARK et al., 1989; MAGNUSSEN and KEITH, 1990; MAGNUSSEN and YEATMAN, 1990; ADAMS and MORGEN-STERN, 1991; BARNES et al., 1992; ERICSSON et al., 1994).

These relatively high heritability values for height and diameter may be partly due to effectiveness of the sliding block adjustment for local site effects. In addition, measurement age

might have coincided with a favorable stand development stage (FRANKLIN, 1979). An unusually high level of genetic variablity is not a likely factor, judging from the low values for this test at 10 years (0.096 and 0.098) (KLEIN, 1989). Values for diameter were lower than for height in most of the studies cited, as well as in this study. It is difficult to infer causes of differences in heritability estimates of stem and branch quality traits from different programs.

The value of 0.35 for resistance to western gall rust in this study is the only value available for western gall rust on jack pine. Unpublished data from a jack pine family test in Saskatchewan, Canada, with a higher frequency of galls and a higher proportion of galled trees, yielded a value of 0.44.

Wood density, calculated as a joint function of Pilodyn penetration and diameter, had a heritability of 0.42, which agrees well with the value of 0.40 for jack pine wood density from Pilodyn readings reported by PARK et al. (1989). Higher values have been reported for direct measurement of wood density from increment cores of jack pine (0.58, ERNST et al., 1983) and loblolly pine (0.85, BRIDGWATER et al., 1983). Lower values were reported for jack pine (0.31, MAGNUSSEN and KEITH, 1990), and radiata pine (0.33, DEAN et al., 1983). Heritability of Pilodyn penetration measurements not converted to wood density was about half that of specific gravity from increment cores in

*Table 10.* – Comparison of genetic gain estimates using SI and BLP to select best 64 trees, restricted to 1 tree per family.

| Method | Total score | Trait breeding value | | | | | Cone volume dm³ | Dry weight kg |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | AH cm | AD mm | SQ | RG | WD g/m³*100 | | |
| Test mean | | 687.52 | 85.47 | 3.91 | 5.00 | 38.71 | 12.56 | 4.860 |
| *SI score of SI selects, weight vector 1*[1] | | | | | | | | |
| Mean | 6.60 | 39.29 | 5.28 | 0.39 | 0.50 | -0.21 | 14.96 | 5.762 |
| % test mean | | 5.72 | 6.18 | 9.92 | 10.11 | -0.54 | 19.18 | 18.54 |
| *BLP score of SI selects, weight vector 1* | | | | | | | | |
| Mean | 6.63 | 39.47 | 5.30 | 0.39 | 0.50 | -0.21 | 14.98 | 5.766 |
| % test mean | | 5.74 | 6.20 | 10.04 | 10.09 | -0.54 | 19.27 | 18.62 |
| *BLP score of BLP selects, weight vector 1* | | | | | | | | |
| Mean | 6.63 | 39.07 | 5.24 | 0.41 | 0.51 | -0.20 | 14.95 | 5.756 |
| % test mean | | 5.68 | 6.13 | 10.43 | 10.19 | -0.51 | 19.04 | 18.43 |
| *BLP score of BLP selects, weight vector 2*[2] | | | | | | | | |
| Mean | 6.73 | 38.99 | 5.55 | 0.41 | 0.48 | -0.41 | 15.05 | 5.764 |
| % test mean | | 5.67 | 6.50 | 10.49 | 9.51 | -1.05 | 19.85 | 18.60 |
| *BLP score of BLP selects, weight vector 3*[3] | | | | | | | | |
| Mean | 6.57 | 39.11 | 5.01 | 0.41 | 0.50 | -0.09 | 14.87 | 5.743 |
| % test mean | | 5.69 | 5.86 | 10.38 | 9.94 | -0.23 | 18.44 | 18.16 |

[1]) Score = 0.1AH + 0.2 AD + 2.8SQ + 1.2RG + 0.4WD
[2]) Score = 0.1AH + 0.2 AD + 2.8SQ + 1.2RG + 0.0WD
[3]) Score = 0.1AH + 0.2 AD + 2.8SQ + 1.2RG + 0.8WD

interior spruce (*Picea glauca, P. engelmannii* PARRY and their hybrids) (YANCHUK and KISS, 1993).

The adverse genetic correlations within areas between diameter and wood density forced a choice between greater gain in volume and dry weight, or reduced loss in wood density. Correlations of similar magnitude have been found in some instances where diameter and wood density are targets of improvement for conifers (DEAN et al., 1983; KING et al., 1988; PARK et al., 1989; CORRIVEAU et al., 1991). In other instances the correlation between these or equivalent traits has been weak (BRIDGWATER et al., 1983; ERNST et al., 1983; BARNES et al., 1992) or untestable due to lack of diameter variation (MAGNUSSEN and KEITH, 1990; YANCHUK and KISS, 1993). Most jack pine harvested in the area of use of this breeding program is used for pulp outside the province of Manitoba. Wood density of the pulpwood is not a factor in the price received by the province. In the absence of any indication of the value of wood density to users of eastern Manitoba jack pine, it is a matter of conjecture whether to place any economic weight on wood density breeding value.

Absence of other adverse genetic correlations within areas allowed simultaneous improvement of height, diameter, stem quality and rust resistance, that is, 4 of the 5 target traits. In some pine breeding programs, correlations of growth with stem straightness have been favorable or neutral (BRIDGWATER and STONECYPHER, 1979; COTTERILL and JACKSON, 1985; BARNES et al., 1992), while others have encountered adverse correlations (SHELBOURNE and LOW, 1980; PARK et al., 1989; ADAMS and MORGENSTERN, 1991). The lack of a strong negative within-area genetic correlation between wood density and height is in agreement with many reports for conifer species (MAGNUSSEN and KEITH, 1990; CORRIVEAU et al., 1991; YANCHUK and KISS, 1993), but not all (DEAN et al., 1983; PARK et al., 1989).

The occurrence of strong genetic correlations at the area level for trait pairs not strongly correlated at the family level can be interpreted as evidence for linkage disequilibrium. If that is the case, adverse genetic correlations should weaken in advanced generations due to recombination and inter-area matings. It is possible that the persistence of these correlations is associated with an adaptive advantage. Effects of possible linkage disequilibrium on breeding values and adaptability in advanced generations of this program will need to be carefully monitored.

BLP rather than SI was chosen as the method for scoring genetic value because of the varying family size and the absence of usable trees of some families in some locations. Absence of a blocking variable in the model, which was justified by non-significant location interactions in the initial analysis, removed the unbalancing effect of families with no valid trees in some locations. Furthermore the relatively high values of individual heritabilities reduced the importance of information from relatives, and hence the potential influence of family size on accuracy of selection (LUSH, 1947). It is difficult to infer from this outcome, what degree of imbalance in some hypothetical future selection situation, would be sufficient to justify the additional coding and computer time required to obtain predicted breeding values by BLP instead of SI. The extra effort and time in this instance involved incorporating family size variables in the tree observation file, and coding and calculating expressions for the elements of V and C.

## Acknowledgments

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# Buchbesprechungen

**Isozyme Investigations in Norway spruce (Picea abies L.) and silver fir (Abies alba Mill.): A Practical Guide to Separation Methods and Zymogram Evaluation.** Part 1 of a series on isozyme methodology. Edited by the Federal and State Working Group "Conservation of Forest Gene Resources". By M. KONNERT (Ed.). Translated by W. D. MAURER. 1995. Bayerische Landesanstalt für forstliche Saat- und Pflanzenzucht, Teisendorf. 74 pages. DM 20,–.

In the last years biochemical-genetic markers have been employed increasingly for the assessment of the genetic structures of forest tree populations. In particular isozymes (allozymes) have proved to be most powerful tools as gene markers due to (1) their far-reaching independency on environmental factors; (2) their ontogenetic stability; (3) the codominant expression of most alleles at the enzyme gene loci studied, and last but not least (4) the relatively simple and reliable interpretation of the zymograms obtained after separating the isozymes by electrophoretical techniques.

In order to guarantee the comparability of the analysis data obtained in different biochemical-genetic laboratories, in February 1992 the Federal and State Working-Group "Conservation of Forest Gene Resources" called for a Sub-Working Group "Biochemical-genetic analysis". At present active participants of this sub-working group are the scientists working in the isozyme laboratories of the State Forest Research Institutes in Baden-Württemberg, Bavaria, Hesse, Lower Saxony and Schleswig-Holstein, Rhineland-Palatinate, Saxony as well as from the German Federal Research Center for Forestry and Forest Products.

The objective of this group is

– to discuss the state-of-the-art isozyme investigations on forest tree species;

– to exchange data materials in particular with respect to nomenclature issues;

– to clarify methodical uncertainties concering all the steps of isozyme analysis from collecting the sample materials to interpreting the zymograms obtained finally;

– to standardize separation methodology;

– to coordinate isozymatic investigations on the different tree species.

The present publication summarizes the results of isozyme studies on Norway spruce (*Picea abies* (L.) KARST.) and silver fir (*Abies alba* MILL.) available up to spring 1995. It was prepared at the best of the editors' knowledge and belief but does not claim completeness for the data material presented. This manual is intended to be a guide for the applied researchers in forest tree genetics to be able to work independently, to harmonize techniques and to make comparison of data easier for them.

The following topics are covered:

1) Methodical details

– extraction of isozymes from seed, buds, needles;

– separation by starch-gel-electrophoresis, polyacrylamide-electrophoresis, isoelectric focussing (composition of gels, buffer systems, electrophoretic conditions);

– visualization of enzymes (composition of staining solutions).

2) Description and genetic interpretation of the resulting isozyme patterns

– genetic analysis (segregation data, analysis of progenies from controlled pollination);

– designation of loci and alleles, Rf-values;

– for fir linkage data are included;

3) A separate chapter deals with specialities and difficulties in interpreting zymogrammes, particularly when dealing with diploid tissue; possibilities of multiple evaluation are demonstrated graphically.

4) Literature dealing with "inheritance and linkage" for spruce and fir is compiled at the end of the manual.

It is planned to continually actualize this edition when new findings concerning additional gene loci, more alleles etc. will be obtained. Furthermore it is intended to compile step by step similar manuals on isozyme investigations on different tree species for the practical lab work. They will be published in the same form and with the same intention.

The "Norway spruce/white fir" manual (German and English version) can be obtained from

Bayerische Landesanstalt für forstliche
Saat- und Pflanzenzucht,
Forstamtsplatz 1,
D-83317 Teisendorf, Germany
Tel. 0 86 66 / 98 83-0
Fax 0 86 66 / 98 83-30
at the price of DM 20,–.

A. Behm (Teisendorf)

**Praktische Landschaftspflege.** Grundlagen und Maßnahmen. Von E. Jedicke (Hrsg.), W. Frey, M. Hundsdorfer und E. Steinbach. 1993. Verlag Eugen Ulmer, Stuttgart. ISBN 3-8001-4091-8. 280 Seiten mit 103 Abbildungen und 61 Tabellen. Broschiert DM 58,–.

Kulturlandschaften prägen heute unser Landschaftsbild. Sie im Rahmen des „Naturschutzes" zu erhalten, haben sich die Autoren zum Ziel gesetzt. Vor dem Hintergrund eines Wandels im Umweltbewußtsein und aus der Nahrungsmittelproduktion ausscheidender landwirtschaftlicher Flächen zeigen sie Möglichkeiten auf, wie Kompromisse zwischen Landwirtschaft und Naturschutz erreicht und ggf. der Landwirtschaft neue Einkommensquellen geschaffen werden können. Nicht die Ausweisung kleinflächiger Naturschutzgebiete ist das Anliegen der Autoren sondern der Schutz der Kulturlandschaft im Biotopverbund, der zu einer Ausweitung der Pflegearbeiten führt.

Auf den Inhalt, der in 7 Kapitel mit mehreren Unterkapiteln gegliedert ist, kann in einer Rezension nur in Stichworten eingegangen werden: Im 1. Kapitel werden die wichtigsten Begriffe aus der Ökologie allgemein verständlich beschrieben und eine Einführung in ausgewählte Kreisläufe des Ökosystems gegeben. Das folgende Kapitel schildert ausführlich die Entstehung der heutigen Kulturlandschaft und zeigt Konfliktpunkte zwischen Landwirtschaft und Naturschutz auf. So werden unter anderem Auswirkungen auf die Naturgüter Boden und Trinkwasser sowie die Möglichkeiten und Grenzen des integrierten und alternativen Landbaus, von Extensivierungsmaßnahmen sowie der Flurbereinigung aufgezeigt. Mit 80 Seiten bildet das 3. Kapitel einen Schwerpunkt des Buches. Hier beschreibt der Herausgeber 13 Lebensraumtypen mit ihren charakteristischen Eigenschaften und stellt ihre Pflegebedürftigkeit vor. In der Beschreibung zur Gefährdung der Forstbiotope führt der Herausgeber u. a. die „Anpflanzung biotopfremder Baumarten" an. Vergeblich sucht der Leser jedoch beim Lebensraumelement „Hecke und Gebüsche", was bei der Wahl des Pflanzenmaterials zu beachten ist, muß er sich mit dem durchaus fragwürdigen Hinweis „aus nahegelegenen Beständen" begnügen (fragwürdig hinsichtlich der Eigentumsfrage, der Autochthonie · bzw. Angepaßtheit). Aber gerade bei Bäumen und Sträuchern für den Bereich der Flurgehölze ist die Standorteignung und die Identität des Pflanzgutes nicht immer gewährleistet. Im 4. Kapitel werden verschiedene Betriebsformen diskutiert, die für eine Umsetzung eines Maßnahmenkatalogs aktiver Landschaftspflege mit etwa 140 Einzelmaßnahmen in Frage kommen. Praktische Hinweise erhält der Leser auf 50 Seiten im 5. Kapitel über die Eignung von Maschinen und Geräten sowie deren Einsatzmöglichkeiten. Hier werden und das hebt das Buch von anderen ab, sowohl Kosten als auch der Zeitbedarf der unterschiedlichen Arbeitsverfahren dargestellt, die so einen ökologischen und ökonomischen Verfahrensvergleich erlauben. Dem Einsatz von Tieren in der Landschaftspflege, einschließlich Überlegungen zu deren Wirtschaftlichkeit, ist ein eigenes, kleines Kapitel gewidmet. Hinweise zu einschlägigen Rechtsvorschriften und der behördlichen Organisation des Naturschutzes enthält das letzte Kapitel. Ein umfassendes Literaturverzeichnis und ein Sachregister runden das als Handlungsanleitung konzipierte Buch ab. Das Literaturverzeichnis ist etwas gewöhnungsbedürftig, da die Literatur nach dem für das jeweilige Kapitel verantwortlichen Autor sortiert ist. So wird zuerst die Literatur zu den Kapiteln 3 und 6 angeführt, bevor die der vorangegangenen Kapitel folgt.

Auch wenn die 4 Autoren ihr Werk als eine vorläufige Zusammenfassung des aktuellen Wissens im noch jungen Aufgabengebiet der Landschaftspflege sehen, vermißt der Leser eine eindeutige Abgrenzung der Begriffe Naturschutz und Landschaftspflege, die häufig synonym verwandt werden. Auch auf die Frage der Finanzierung einer großflächigen Landschaftspflege wird, wie bei vielen Naturschutzvorhaben, nicht eingegangen. In einer Neuauflage, die die Autoren schon heute in Aussicht stellen, kann die Kritik Berücksichtigung finden.

Trotz der angebrachten Kritikpunkte kann das Wagnis, eine die heutigen Erfahrungen zusammenfassende Anleitung zur Landschaftspflege herauszugeben, als gelungen bezeichnet werden. Das Buch stellt eine wertvolle Handlungsanleitung dar, in der praktische Hinweise zur Planung und Ausführung aktiver Landschaftspflege zusammengestellt sind. Planern und Gutachtern gibt das Buch konkrete Hinweise zur Konzeption von Pflegemaßnahmen in der Landschaft und den Durchführenden (z. B. Land- und Forstwirten, Naturschutzverbänden, Biologen, Geographen) verständliche Informationen über Hintergründe und zur Organisation der Pflegemaßnahmen.

M. Liesebach (Grosshansdorf)

**Sonnen-Strategie.** Politik ohne Alternative. Von H. Scheer. 1993. Verlag Piper, München und Zürich. ISBN 3-492-03599-X. 304 Seiten mit 11 Abbildungen und 18 Tabellen. DM 36,–.

Das Buch stammt aus der Feder eines Politikers, der sich seit Jahren für die Nutzung der Sonnenenergie einsetzt. Klimaänderungen durch Treibhausgase, Ozonloch, Luft- und Gewässerverschmutzung, Tropenwaldzerstörung, Versteppung, nukleare Unfälle, Überbevölkerung stehen in direktem und indirektem Zusammenhang mit der Energienutzung. Der hohe Energieverbrauch der Industrieländer und die Energieknappheit in den Entwicklungsländern sind mit für den Nord-Süd-Konflikt, die Umwelt- und Naturzerstörungen verantwortlich. Der Autor fordert zur Abwehr der gegenwärtigen Umweltgefahren die Ablösung fossiler und nuklearer Energien durch Sonnenenergie – unter Berücksichtigung von Biomassenutzung, Photovoltaik, solarthermischer Kraftwerke, Wasserkraft- und Windkraftwerken. Das Buch soll einen Beitrag dazu leisten, aus der theoretisch möglichen Nutzung der Sonnenenergie für alle zivilen Energiebedürfnisse eine reale Möglichkeit werden zu lassen. Im vorliegenden Buch wird aufgezeigt, daß die Widerstände gegen den Aufbau eines auf Sonnenenergie gestützten Energiesystems vor allem von denen kommen, die das gegenwärtige Energiesystem aufgebaut haben bzw. an ihm verdienen.

Dieses informative Buch ist verständlich geschrieben und jedem zu empfehlen, der sich mit dem verstärkten Einsatz regenerativer Energieträger beschäftigt. Wenn mit dem Umbau des gegenwärtigen Energieversorgungssystems begonnen wird, ist im Holz auch ein wichtiger Energierohstoff der Zukunft zu sehen.

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