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Alternative Analyses of Parent-Offspring Correlations for Stem Straightness in Jack Pine

By S. Magnussen[1])

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Summary

Parental phenotypes of stem form in jack pine (*Pinus banksiana* Lamb.) explained a highly significant proportion (0.11, P = 0.01) of the variability in stem straightness among their offspring. Overall, the narrow-sense heritability of stem straightness scores was comparatively high (about 0.3) in progenies from 43 assortative matings (mainly positive) of parents with contrasting phenotypic scores. Three statistical procedures (parent-offspring regression, maximum likelihood, and tetrachoric correlations) for calculating parent-offspring correlations in the presence of nonrandom mating, unequal family sizes, and a limited range of straightness scores are compared and discussed. Problems related to using parent-offspring regression for traits with only a few subjective scoring categories dissuade its use. As an alternative, estimating tetrachoric correlations is recommended owing to the computational ease and less restrictive assumptions associated with the procedure.

Key words: stem straightness, heritability, parent-offspring correlation, assortative mating, *Pinus banksiana.*

Introduction

The economic value of a softwood bole for sawn construction-grade products depends foremost on size, straightness, wood density, and the amount and distribution of knots (Brown and Miller, 1975; Persson, 1975; Wilkes, 1987). Attempts to isolate the economic value of stem straightness have confirmed a significant relationship between visually assigned scores and the product value (Brown and Miller, 1975; Bridgwater and Stonecypher, 1979; Grant *et al.*, 1984; Chollet and Roman-Amat, 1987). With an economic impetus to improve stem straightness in trees, many tree improvement programs require that candidate trees for breeding must be of superior stem form (Morgenstern *et al.*, 1975; Shelbourne and Low, 1980; Zobel and Talbert, 1984; Bastien and Roman-Amat, 1987; Cotterill *et al.*, 1987). Genetic improvement of stem straightness can be expected to progress fairly rapidly without compromissing progress in quantitative traits owing to a combination (Shelbourne and Stonecypher, 1971; Wilcox *et al.*, 1975 Burdon, 1977; Bridgwater and Stonecypher, 1979; Cotterill and Zed, 1980; Shelbourne and Low, 1980; Ledig and Whitmore, 1981; Dean *et al.*, 1986) of comparatively high heritability and a favorable — or at least neutral — genetic correlation with growth traits. Density management of forest stands offers additional and immediate tangible ways to improve stem form (Rudolf, 1951; Reukema, 1970; Frömsdorf and Magnussen, 1980; Carter *et al.*, 1986).

Heritability estimates of stem straightness are needed to gauge the potential of genetic gains and to evaluate various breeding strategies (Zobel and Talbert, 1984). This study presents and compares three statistical methods of obtaining this heritability from parent offspring correlations of stem form in 43 jack pine (*Pinus banksiana* Lamb.) parents and their full-sib offspring. The three methods (parent-offspring regression, maximum likelihood, and tetrachoric correlations) are based on different assumptions and derive their estimates from different levels of data aggregation (family, individual, and form category). Problems related to imbalanced mating design, few subjective scoring categories, and unequal family sizes are addressed.

Material and Methods

Stem straightness at age 23 years was assessed in 43 full-sib families of jack pine growing in a randomized complete block design at Sturgeon Lake (Chalk River, Ontario). The full-sib families originated from assortative matings (38 positive and 5 negative) among 48 unrelated trees of contrasting stem form. Parent trees were selected in a local 40-year-old natural jack pine stand. Selected parents were separated by a distance of at least 100 m, which was deemed sufficient to ensure that the trees were unrelated. Matings were completed in 1964, whereas the resulting seed was sown in the spring of 1966. Two-year-old seedlings were outplanted in the spring of 1968 on a former jack pine site of windblown material on alluvial sand. The field design entailed six replicates with five-tree row-plots. Espacement was 1.8 m × 1.8 m. Two surround rows of a local stock were planted along the outside borders. A thinning operation in 1987 removed every third row and all dead, dying, and porcupine damaged trees in the intervening rows. After thinning, the remaining number of trees per family varied from 4 to 22. Tree height at age 23 years averaged 10.7 m, with a diameter of 10.1 cm at 1.3 m above ground level

Assessment of Stem Straightness

A four-point scoring system of stem straightness was used by a single observer to rate the parent trees in 1964. Stems with only minor departures from complete straightness (the amplitude of any deviation being less than 2 cm) were assigned a score of 1 ("Good"), whereas

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[1]) Research Scientist, Forestry Canada, Petawawa National Forestry Institute, P. O. Box 2000, Chalk River, Ontario, KOJ 1JO, Canada.

trees with sinuosity or repeated departures from the vertical (kinks) were assigned a score of 4 ("Very poor") if the largest amplitude of deviation exceeded the diameter at breast height. Trees belonging to neither of these categories were assigned scores of 2 ("Average") if they were scored closer to "Good" than "Very poor" and 3 if they resembled "Very poor" rather than "Good". In 1988, the offspring were rated independently for straightness by three observers.

Exploratory Analyses

The statistical significance of the influence of replicates, observers, and categories of parental crosses on the frequency distribution of progeny form scores was inferred from three independent chi-square tests (SNEDECOR and COCHRAN, 1971). Inferences about the effects of parental scores on the scores of their offspring came from log-linear analyses (BISHOP *et al.*, 1975) of the three-way (female score, male score, progeny score) contingency table of observed progeny scores. The proportion of observations in the cell defined by the female score i (i = 1,2,3,4), male score j (j = 1,2,3,4), and progeny score k (k = 1,2,3,4) is denoted f_{ijk} and the corresdonding proportion predicted by a given log-linear model is denoted F_{ijk}. A chi-square test was used to evaluate the fit of F_{ijk} to the observed f_{ijk} values. Improvement in the goodness-of-fit attributable to a single effect in a long-linear model was estimated by dropping the effect from the model and recalculating the chi-square. The decrease in chi-square caused by excluding a single effect was then tested for significance by comparisons with standard tables of the chi-square distribution. The degrees of freedom for the computed chi-square difference equaled those of the effect in question (see below). All 64 (4 × 4 × 4) observed cell proportions (f_{ijk}) could be fitted exactly by the following saturated log-linear model:

$$[1]\quad \log_e(f) = \log_e(F) = \lambda + \lambda^{f} + \lambda^{m} + \lambda^{fm} + \lambda^{o} + \lambda^{fo} + \lambda^{mo} + \lambda^{fmo}$$

where f = matrix (4 × 4 × 4) of observed proportions
F = matrix (4 × 4 × 4) of predicted proportions
λ = the average log-transformed proportion (df = 1)
λ^{f} = the additive female score effect (df = 4 — 1)
λ^{m} = the additive male score effect (df = 4 — 1)
λ^{fm} = the female × male score effect (df = (4 — 1) × (4 — 1))
λ^{o} = the additive progeny score effect (df = 4 — 1)
λ^{fo} = the female-offspring interaction (df = (4 — 1) × (4 — 1))
λ^{mo} = the male-offspring interaction (df = (4 — 1) × (4 — 1))
λ^{fmo} = the parent-offspring three-way interaction (df = (4 — 1) × (4 — 1) × (4 — 1))

The linear effects (lambdas) in [1] are matrices with sum-to-zero restrictions. The degrees of freedom (df), or rank of each effect, are indicated above. Log-linear models are hierarchical, i.e., each effect is estimated after the effects of all preceding model terms have been accounted for. In the absence of any parent-offspring associations of stem scores the first five terms in [1] (i.e., λ, λ^{f}, λ^{m}, λ^{fm}, and λ^{o}, would suffice to produce a statistically close fit of the expected proportions (F) to the observed proportions (f). The degree to which the remaining terms in [1] can improve the fit will determine their statistical significance. The current tests took the following form (ordered effects included in model goodness-of-fit chi-square statistics appear in parentheses following χ^2):

Hypothesis	Test statistics	df
$\lambda^{fo} = 0$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}) - \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo})$	3
$\lambda^{mo} = 0$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}) - \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{mo})$	3
$\lambda^{fmo} = 0$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo} \lambda^{mo})$	3
	$- \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo}, \lambda^{mo}, \lambda^{fmo})$	3
$\lambda^{fo} = 0 \mid \lambda^{mo}$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{mo}) - \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{mo}, \lambda^{fo})$	3
$\lambda^{mo} = 0 \mid \lambda^{fo}$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo})$	
	$- \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{mo}, \lambda^{fo})$	3
$\lambda^{fmo} = 0 \mid \lambda^{fo}, \lambda^{mo}$	$\chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo}, \lambda^{mo})$	
	$- \chi^2(\lambda, \lambda^{f}, \lambda^{m}, \lambda^{fm}, \lambda^{o}, \lambda^{fo}, \lambda^{mo}, \lambda^{fmo})$	27

The last three tests are conditional on the effects separated by the vertical bar in the test hypothesis (e.g., the hypothesis $\lambda^{fo} = 0 \mid \lambda^{mo}$ tests whether the effect of the female score on the progeny scores is zero after accounting for the effect of the male score).

Parent-Offspring Correlation and Heritability of Stem Straightness

Estimates of parent-offspring correlations, narrow-sense individual-tree heritability of stem straightness, and other genetic parameters were determined using three analytical procedures that shall be described only briefly, the referenced literature details the procedures.

Regression of offspring on midparent

Assuming identical environmental variance structures, and the absence of epistasis and environmental correlations between parents and their offspring, the regression of offspring values on midparent values gives a direct estimate of heritability (NANSON, 1974; BULMER, 1985). The statistical model is

$$[2]\quad \bar{Y}_s = \mu + \beta \cdot X_s$$

where $\bar{Y}_s$ stands for the progeny mean in family s (s = 1,2,...,43) with the mean parental score of x_s. μ and β denote the intercept and slope, respectively. Given the above assumptions, it is assumed that the estimated β is equal to the narrow-sense individual-tree heritability of stem straightness (h^2). With more than one progeny per family and unequal family sizes, a weighted regression with weights (W_s) proportional to the number of offspring (n_s) in a family (s) ensured that more accurate family means were given more weight than less accurate family means (BULMER, 1985). In sum, the following estimator of the slope was used:

$$[3] \quad \hat{\beta} = \sum_s w_s \cdot (x_s - \bar{x}.) \cdot (\bar{Y}_s - \bar{Y}.) \cdot \left(\sum_s w_s \cdot (x_s - \bar{x}.)^2\right)^{-1} \text{ with}$$

$$\operatorname{var}(\hat{\beta}) = MSE_{regr.} \cdot \left(\sum_s w_s \cdot (x_s - \bar{x}.)^2\right)^{-1}$$

where $MSE_{regr.}$ stands for the mean square error of the regression (DRAPER and SMITH, 1981). A lack of linear fit and curvilinear trends (quadratic and cubic) in the parent-offspring relationship were tested for statistical significance in the usual way (SNEDECOR and COCHRAN, 1971, p. 349; DRAPER and SMITH, 1981, p. 37). BARTLETT's chi-square statistics were used to test for variance homogeneity in progeny scores (SNEDECOR and COCHRAN, 1971).

Maximum likelihood

Three types of correlations of stem scores are potentially present in the data: between parents (p_{pp}) in a family, between one parent (male or female) and its offspring (p_{op}), and, finally, among full-sibs (p_{oo}). According to genetic theory, the following estimate was made of narrow-sense individual-tree heritability (h^2) of stem straightness scores:

$$[4] \quad h^2 = 2 \cdot p_{op}/(1 + p_{pp}) = V_A/V_P \quad \text{(FALCONER, 1981, Table 10.6)}$$

where V_A and V_P stand for the additive genetic variance and the phenotypic variance of stem scores respectively. Approximated standard errors of the heritability estimate were obtained using Taylor series expansion (BULMER, 1985, p. 83). Conversely, the correlation of full-sib scores was taken as an estimate of:

$$[5] \quad p_{oo} = (1/2 \cdot V_A + 1/4 \cdot V_D)/V_P \cdot (1 + h^2 \cdot p_{pp}) \quad \text{(FALCONER, 1981, p. 613)}$$

where V_D is the nonadditive genetic variance. From [4] and [5], the ratio of nonadditive to additive genetic variance becomes:

$$[6] \quad V_D/V_A = 2 \cdot (p_{oo} \cdot (1 + p_{pp})/[(1 + h^2 \cdot p_{pp}) \cdot p_{op}] - 1)$$

The three correlations (p_{pp}, P_{op}, and P_{oo}) were estimated by maximizing the following log-likelihood (WETTE *et al.*, 1988) expression (assuming unrelated parents and a multivariate normal distribution of stem scores):

$$[7] \quad \text{log-likelihood (LL)} = 0.5 \cdot \sum_{s=1}^{43} \left(\log_e |R_s| + Z'_s \cdot R_s^{-1} \cdot Z_s\right) + \text{Const.}$$

where s = family indicator variable ($s = 1,2,3,\ldots,43$)
where Rs = correlation matrix of scores in family s (parents included)
where $|R|$ = determinant of R
where Z_s = row vector of standardized scores in family s (parents included)
where Z'_s = transpose of Z_s

The dimension of the square correlation matrix R_s is equal to the number of offspring in family s plus two (parents). A correlation p_{ij} in row i and column j of R_s would be

$$p_{ij} = \begin{cases} 1 & \text{if } i = j \text{ (diagonal elements)} \\ p_{pp} & \text{if observations } i \text{ and } j \text{ are made on the parents} \\ p_{op} & \text{if observation } i \text{ is on a progeny and observation } j \text{ is on a parent (} i \text{ and } j \text{ are interchangeable)} \\ p_{oo} & \text{if observations } i \text{ and } j \text{ are made on full-sibs} \end{cases}$$

It is assumed that the correlations p_{pp}, p_{op}, and p_{oo} are identical across families, i. e., only average estimates for all families are estimated. Each standardized vector Z_s is obtained from the observed scores (averaged over observers) in family s by first subtracting the overall mean score of females, males, and offspring (ignoring block differences) from the corresponding within-family scores and then dividing this difference by the appropriate estimate of the standard deviation of stem scores. Means and variances for the standardization procedures were obtained from an analysis of variance.

Optimization of the log-likelihood in [5] was carried out in three steps. First, the likelihood was computed for 432 triples of correlation values ($0 < p_{pp} < 0.9$; $0 < p_{op} < 0.6$; $0 < p_{oo} < 0.2$) assumed to bracket the optimum solution. Second, from these 432 computed values of the log-likelihood the best (sensu mean quadratic error) quadratic response surface model was sought (KHURI and CORNELL, 1987), with the log-likelihood as the dependent and the „known“ correlation triples as the independent variables. Third, the optimum value of the estimated log-likelihood values of the regression was determined using standard differential calculus procedures. The response surface model reads:

$$[8] \quad LL = a_0 + (p_{pp}, p_{op}, p_{oo}) \cdot A \cdot (p_{pp}, p_{op}, p_{oo})'$$

where a_0 is the intercept and A is a 3 × 3 symmetric matrix of regression coefficients to be estimated. The element-wise inverse of $-2 \cdot A$ was taken as the variance-covariance matrix of the desired correlation triple (ANDERSON, 1984).

Tetrachoric correlations

With this method, the average correlation beetwen parents and offspring is estimated from a two-way contingency table, as outlined by KENDALL *et al.* (1983, chapter 26, p. 325). Let the rows of this table classify the progeny straightness score l (l = 1,2,3,4) and the columns all female parents with score k (k = 1,2,3,4). Each cell in the two-way table contains the number of progenies (n_{kl}) belonging to the specific (k, l) parent-offspring category. The total number of offspring is denoted by N. It is assumed that the proportion (p_{kl}) of the N observations in the cell (k, l) represents the outcome of sampling from a bivariate normal distribution of straightness scores. Ideally therefore, cumulative proportions (P_{ij}) of observations in the table can be equated to double probability integrals of the underlying distribution in the following way:

$$[9] \quad \hat{P}_{ij} = \frac{\sum\limits_{k=i}^{4} \sum\limits_{l=j}^{4} n_{kl}}{N} = \int\limits_{z_1 = \Phi^{-1}(p_i)}^{\infty} \int\limits_{z_2 = \Phi^{-1}(p_j)}^{\infty} f(z)dz$$

for i = j = 1,2,3,4

where P_{ij} is equal to the proportion of all offspring having a minimum maternal score of i combined with a stem straightness of at least j. The term p_i denotes the proportion of all females (males) with a straightness score greater than or equal to i. Similarly, pj is the proportion of all offspring with a score above or equal to j. Φ symbolizes the cumulative density function of a normal distribution and Φ^{-1} its inverse. z is a vector (z_1,z_2) of standardized (mean = 0, variance = 1) normal variates with a joint density distribution f(z) equal to

$$[10] \quad f(z) = (2 \cdot \pi)^{-1} \cdot |R|^{-0.5} \cdot e^{-0.5 \cdot z' \cdot R^{-1} \cdot z}$$

where R is a 2 × 2 correlation matrix of z with off-diagonal elements of p_{op} and diagonal elements of 1. Equation [9] was used repeatedly for i = j = 2,3,4 to generate three equations with p_{op} as the parameter to be estimated. A weighted least-square estimate of p_{op} served as the “best” solution to the equations (weight = P_{ij}). The above procedure for estimating the correlation between a parent and its offspring was completed for both parents. A simple average of the two correlation estimates was used to obtain an estimate of the narrow-sense individual-tree heritability of stem straightness (via [4]). An approximate variance of the estimated correlation was obtained by first applying the “delta technique” (BULMER, 1985, p. 83) to [9] for each of the three P_{ij} values and then adding the pooled variance (weight: P_{ij}) to the regression error variance (lack of fit in [9]). The needed variance estimate of P_{ij} came from the following expression for the variance of multinomial distribution cell frequencies (n_{kl}):

$$[11] \quad \hat{P}_{ij} = \sum_{k=i}^{4} \sum_{l=j}^{4} p_{kl}$$

where $p_{kl} = n_{kl}/N$. This leads to

$$\mathrm{var}(\hat{P}_{ij}) = \sum_{k=i}^{4} \sum_{l=j}^{4} \sum_{k'=i}^{4} \sum_{l'=j}^{4} \mathrm{Cov}(p_{kl}, p_{k'l'})$$

$$\text{where } \mathrm{Cov}(p_{kl}, p_{k'l'}) = \begin{cases} p_{kl} \cdot (1 - p_{kl}) & \text{for } (k,l) = (k',l') \\ -p_{kl} \cdot p_{k'l'} & \text{for } (k,l) \# (k',l') \end{cases}$$

Results and Discussion

Stem Score Frequencies

Of the 483 trees scored for stem straightness, 58% were classified as “average“ 32% as “poor”, and the remaining 10% were about equally split between “good” and “very poor” (Table 1). Blocks (replicates) did not exert any great influence on the stem straightness distributions (*Table 1*). Apart from a manifestly aberrant lack of „very poor“ scores in one block, the remaining contributions to the overall chi-square statistics were all deemed to be due to chance events. All further results disregard the influence of blocks on the straightness scores. Observers, in contrast, disagreed in a statistically significant way in their scoring (*Table 2*). Although their overall average score (2.3) and familiy rankings of mean straightness scores were almost identical (coefficient of rank concordance was 0.91), discrepancies emerged at the top and at the bottom rank scores. For example, the most lenient observer had 14% of the trees listed as “good” as opposed to only 6% with the most demanding observer; at the other end of the scale, the equivalent numbers were 3% and 5%, respectively. The results confirmed the need to remove personal bias in subjectively assigned scores (BANNISTER, 1979); repeated scoring by two or more observers

Table 1. — Relative distribution of stem straightness scores in progenies from assortative matings.

Parents	No. of crosses	Parent offspring				Total offspring
		Good	Average	Poor	Very poor	
Good x good	10	11	70	17	2	106
Good x poor	5	5	66	29	0	41
Average x good	3	14	64	22	0	42
Average x average	12	3	57	38	2	131
Poor x average	3	0	54	41	5	41
Poor x poor	7	0	39	45	16	74
Very poor x very poor	3	8	59	29	4	48
Total/average	43	6	58	32	4	483

Table 2. — Chi-square statistics of straightness score distributions.

Source of variation	df	$\hat{\chi}^2$	$P(\chi^2_{df} \geq \hat{\chi}^2 \mid H_0)$
Replicates	15	23.7	0.07
Replicates[1]	14	19.6	0.14
Observers (A,B,C)	6	47.3	0.00
(A,B)	3	16.6	0.00
(A,C)	3	19.0	0.00
(B,C)	3	19.0	0.00
Cross categories (7)	18	73.7	0.00
Female score	9	43.9	0.00
Male score	9	43.1	0.00
Female score |male score	9	15.4	0.08
Male score |female score	9	14.6	0.10
Female x male |female, male (score combinations)	27	21.8	0.75

[1]) Excluding the "very poor" category in block 4.

Notes:

df = degrees of freedom = (score classes — 1) × (score categories — 1).

χ^2 = computed chi-square statistics

χ^2_{df} = tabulated chi-square distribution.

H_0 = null hypothesis of zero effects.

| = separator of model terms. Terms to the left are conditioned on the terms to the right.

of all trees is one way to counter this problem. Only the average score of the three observers has been used in the analyses. BANNISTER (1979) showed how the average score, apart from giving greater precision, also reduced departures from normality in the data.

The relative frequency distributions of stem straightness scores differend significantly among the seven parental combinations of stem form (*Table 2*). There is a rather weak tendency for progeny scores to cluster around their parental values; the contingency coefficient (SIEGEL, 1956) C of 0.36** ($0 \leq C \leq 1$), which measures the degree of uniqueness or association between parent and offspring scores in the seven frequency distributions, is but one measure thereof. Each parent had a significant impact on the frequency distribution of progeny stem straightness scores (*Table 2*), but the influence decreased to a nonsignificant level once the effect of the other parent had been taken into account. The absence of a significant

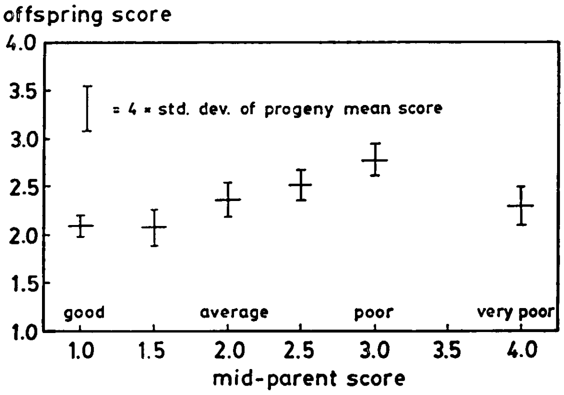

Figure 1. — Mean straightness scores of offspring versus mid-parent scores.

specific parental interaction term (female × male in *Table 2*) supported the contention that additive genetic effects are the main source of the resemblance between parents and their offspring.

Parent-Offspring Regression

Figure 1 illustrates the overall relationship between the midparent stem straightness score and the mean score of their offspring. A trend indicating that the quality of the offspring reflects the quality of the parental average is quite clear in the central part of the range of midparent straightness scores. At the extremes (i.e., "good" × "good" and "very poor" × "very poor"), a breakdown of this trend is evident. Offspring from "good" × "good" proved worse than expected and vice versa for the "very poor" × "very poor" progenies. Although this problem seems to be inherent in practically all studies of offspring-parent relationships (Galton, 1885; Gimelfarb, 1986), one-sided classification errors of the parents in the categories "good" and "very poor" were considered to be the most obvious cause of these aberrant results. For example, misclassification of some "very poor" parents due to purely environmental effects, such as hidden mechanical or overgrown insect damage, may explain the better performance of their offspring. A parental classification scheme with only a few nominal ranks and a single observer is prone to this kind of deterioration of linear trends towards the endpoints (Draper and Smith, 1981). In a purley binary trait, the relationship between midparent values and offspring means will be nonlinear regardless of the magnitude of nonadditive genetic effects (Im and Gianola, 1988). Statistical tests confirmed both the lack of fit to a linear relationship ($F_{4,477} = 10.11^{***}$) and the significance of curvilinear trends (quadratic and cubic, $F_{1,480} > 100$, $P < 0.001$). When the parental combinations of "good" × "good" and "very poor" × "very poor" were dropped, the relationship became almost perfectly linear (computed $F_{4,324}$ ratio for lack of fit was 0.026 n.s.), with a slope almost twice that of the regression based on all data (*Table 3*). Variances of individual progeny scores were homogeneous across parental score combinations (chi-square = 3.70, degrees of freedom = 6, $P > 0.5$).

Table 3. — Estimated correlations (p), regression slope (b), and narrow-sense individual-tree heritability of stem straightness scores.

Statistical method	Parameter	Estimate	
		All data	reduced[1]
Midparent-offspring regression (weighted least squares)	$b = h^2$	0.23 (0.03)	0.43 (0.04)
Maximum likelihood	ρ_{pp}	0.55 (0.03)	0.21 (0.01)
	ρ_{op}	0.24 (0.02)	0.31 (0.02)
	ρ_{oo}	0.19 (0.02)	0.29 (0.03)
	h^2	0.31 (0.04)	0.50 (0.04)
Tetrachoric	ρ_{op}	0.25 (0.05)	0.26 (0.05)
Pearson product moment	ρ_{pp}	0.72 (0.16)	0.12 (0.19)
	h^2	0.28 (0.07)	0.45 (0.10)

[1]) Excluding "good" × "good" and "very poor" × "very poor".

Notes:

Standard errors of estimates are given in parentheses.

h^2 = heritability adjusted for parental correlation of straightness scores (equation [4]).

Correlation subscripts: pp, parents within family; op, one parent offspring; oo, among full-sibs.

Heritability Estimates

Some important assumptions are implicit in the interpretations of parent-offspring correlations (NANSON, 1974; FALCONER, 1981): (1) the environmental variance structure is equal in the two generations, (2) the narrow-sense individual-tree heritability of stem straightness is unchanged from the parent to the offspring generation, and (3) the age and development of parent and offspring are identical. For growth-related metric traits in trees, these expectations are quite unrealistic (NANSON, 1974), but they appear to be reasonable under the present circumstances where scale problems are absent and the observations are subjective scorings in two forest stands with little or no perceived difference in phenotypic expressions of stem form.

Estimates of the narrow-sense heritability (h^2) of stem straightness scores varied from 0.23 to 0.31 depending on the method of derivation (*Table 3*). The lowest estimate came from the weighted least-squares regression of progeny means on midparent values and the highest from the maximum-likelihood procedure. For all practical purposes, and considering the standard errors associated with each of the estimates. the heritabilities are identical. Heritabilities about twice as high were obtained when the results from the parent combinations "good" × "good" and "very poor" × "very poor" were excluded. These latter heritabilities reflect more truly the genetic transmittance of stem straightness from parents to offspring. For gain calculations, however, the lower values should be used whenever selections include offspring from "good" parents where one-sided classification errors exert downward pressure on the heritability. Heritability estimates based on the female-offspring correlations were within 1% of those based on the male-offspring correlations.

It was implied from the exploratory log-linear analyses that additive genetic effects dominate the parent-offspring relationship of stem straightness scores (*Table 2*). The correlation estimates presented in *Table 3* provide a clearer picture of the relative importance of additive and nonadditive genetic variances. Using [6], the ratio of nonadditive to additive genetic variance was estimated to be 0.10 or 0.05 if the parent combinations "good" × "good" and "very poor" × "very poor" were excluded. Nonadditive genetic variances amounted to no more than 5% of the total phenotypic variance when all data were used, and only 2% in the reduced data set.

A relatively strong heritability of stem straightness in jack pine agrees well with the generally favorable results published for other conifers (EHRENBERG, 1963; BRIDGWATER and STONECYPHER, 1970; COTTERILL and ZED, 1980; SHELBOURNE and LOW, 1980 ZOBEL and TALBERT, 1984; DEAN *et al.*, 1986), although exceptions are known (e.g., COTTERILL *et al.*, 1987). The results of this study demonstrated the usefulness of assortative matings to obtain information about genetic inheritance (POLK, 1972; FOSTER, 1987) and they also demonstrated the negative consequences of allowing trees with poor stem form into a breeding population. From these results, it is inferred that collecting seed only from parents with good stem form would, in one generation, improve the average stem form from a score of 2.3 (mean of all progenies) to 2.1 (expected progeny mean of parents with a stem score of one). Further improvement is, of course, possible through assortative matings of trees with superior stem straightness due to the positive effect on additive variances and heritabilities (POLK, 1971; FALCONER, 1981; FOSTER, 1987). Despite the favorable heritability, the offspring of parents selected for superior stem form would still contain considerable phenotypic variation. In fact, the variation is only expected to decrease by about 9% per generation (JACQUARD, 1983).

Comparison of Methods

A single data set cannot produce a representative evaluation of three methods used in this study. Instead, the important features in each method are highlighted here. All three methods are considered as alternatives to the more traditional, but less efficient (only progeny data would be used), analysis of variance.

In the parent-offspring regression, all estimates were derived from means of parent and offspring scores. By using averages, the method treats the trait as a metric and ignores the actual distribution of progeny scores as a source of additional information. Given the aforementioned inherent problems associated with linear regression on data with a very narrow range of rankings, it is not surprising to find that this method yielded the lowest heritability estimates. Despite the attractive theoretical properties of the weighted-regression technique (BULMER, 1985) and its robustness against the influence of nonadditive effects (GIMELFARB, 1986), the method had too many drawbacks to be widely recommendable.

The maximum-likelihood method is theoretically attractive because it offers simultaneously the best fit of the data to a multivariate model that uses single observations as the basis for estimating genetic parameters (O'NEILL *et al.*, 1987; WETTE *et al.*, 1988). Efficient use of all information, irrespective of imbalance in family sizes and irregular mating designs, is thereby possible. WETTE *et al.*, (1988) confirmed in simulation studies these desirable maximum-likelihood properties in the presence of large inequalities of family sizes. However, this method also suffers from the questionable assumption of equal correlations across the range of straightness scores within the parental material and among the offspring. In the maximum-likelihood approach, the parents are considered to be a random sample from an under-lying bivariate (normal) distribution instead of being "fixed" by the actual mating design. Without any specific intentions behind the observed mating frequencies other than technical constraints on personnel and available parental material, this may not be an unreasonable assumption. A consequence of this assumption can be seen in a considerable discrepancy between the maximum-likelihood correlation of parental stem scores (0.55) and the ordinary Pearsonian product-moment correlation (0.72). The difference between the heritability estimate derived from the maximum-likelihood method and the tetrachoric method is traceable to this discrepancy.

Estimates of the parent-offspring correlation, p_{op}, via a stepwise tetrachoric procedure are derived from a simple two-way table of scores pooled across parents and progenies, respectively. Thus, it is far less intensive in terms of the computations required than the maximum likelihood approach. Another attractive property is the low influence of extreme parent combinations on the final correlation estimate. Hence, the tail problems inherent in the parent-offspring regression are less serious with this approach. Also, because the pooled proportions of the four scores observed in parents and progenies are fitted directly to those of a bivariate normal distribution, the method is not (per se) burdened by the assumption of a normal distribution. In addition, by pooling all families with identical parental scores, it circumvents the potential bias in the estimated parent-offspring correlation that can arise from unequal family sizes (Rosner *et al.*, 1977; Ponzoni and James, 1978; O'Neill *et al.*, 1987; Donner and Eliasziw, 1988). However, according to calculations based on the formulae provided in the references cited, bias can be safely ignored in the present study (negative bias was less than 0.6% of any correlation estimate). The tetrachoric method resembles, in many ways, the so-called ensemble method (observations are averaged over categories) advocated by, for example, Donner and Eliasziw (1988) and O'Neill *et al.* (1987). A corollary to this is that, with 43 families and an average family size of 11, the differences in bias between alternative correlation methods ought to be negligible.

Conclusions

A strong genetic control of stem straightness in jack pine confirmed the importance of this trait as selection criteria in a tree improvement program. Inherent problems with the offspring-midparent regression technique for heritability estimations of traits with a limited range of rank scores call for an alternative. The tetrachoric method offers computational ease and has fewer critical assumptions than the maximum-likelihood method; as such, it is well suited for estimating familial correlations.

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