

Higher frequencies of offspring resulting from self-fertilization may typify artificial Douglas-fir stands in other parts of Europe as well. In 2 of the 3 stands investigated by PRAT and ARNAL (pers. comm.), S was estimated to be 0.15 or greater. Because higher levels of selfed progeny lower the genetic quality of seed crops (MUONA, 1989; SORENSEN and MILES, 1982), special precautions should be taken in the collection and use of seed from these artificial stands. In order to minimize selfed offspring, seed collections should be limited to years with especially good flower crops. In addition, seedlings should be strongly culled in the nursery to help remove inbred individuals (SORENSEN and MILES, 1974). Tight spacing in plantations may also be employed to favor non-inbred individuals by encouraging competition (SORENSEN and MILES, 1982).

The results of this study illustrate a number of useful applications of isozymes in practical forestry. Isozymes may be employed to test the affinity of artificial stands from unknown seed sources, and, at least crudely, to identify their provenance of origin. In addition, isozyme analyses can help in evaluating the genetic quality and diversity of seed crops, and, subsequently, can help foresters make decisions regarding regeneration.

Acknowledgements

We thank the cone collectors from the Bernese Forest Service and from the Swiss Federal Research Institute, Birmensdorf, for providing us with seed from individual trees. VALERIE HIPKINS, PETER ROTACH, CHARLES SPRIGGS, and DIANNE REESE helped with the laboratory analyses. Financial support from the Forest Service of the Canton of Berne and from the Swiss Foundation for Forest and Wood Research is gratefully acknowledged.

Literature Cited

- ADAMS, W. T. and BIRKES, D. S.: Estimating mating patterns in forest tree populations. In: *Biochemical Markers in the Population Genetics of Forest Trees*. (S. FINESCHI, M. E. MALVOLTI, F. CANNATA and H. H. HATTEMER [eds.]). SPB Academic Publishing bv, The Hague, The Netherlands, pp. 157–172 (1991). — ADAMS, W. T. and JOLY, R. J.: Genetics of allozyme variants in loblolly pine. *J. Hered.* **71**: 33–40 (1980). — ADAMS, W. T., NEALE, D. B., DOERKSEN, A. H. and SMITH, D. B.: Inheritance and linkage of isozyme variants from seed and vegetative bud tissues in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [MIRB.] FRANCO). *Silvae Genet.* **39**: 153–167 (1990). — BERNEY, J. L.: Studies on probable origin of some European Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) plantations. Univ. of British Columbia, Vancouver, B. C., 99 pp. (1972). — BRUNK, H. D.: *An Introduction to Mathematical Statistics*. Third edition. Xerox College Publishers, Lexington, MA, 457 pp. (1975). — DIEZ, C. and BUERGI, A.: Wuchsleistung und Qualität von Douglasie (*Pseudotsuga menziesii* [Mirb.] Franco), Riesen-Lebensbaum (*Thuja plicata* DONN) and Roteiche (*Quercus rubra* L.) in der Schweiz. Bericht 329 WSL. 46 pp. (1991). — FARRIS, M. A. and MITTON, J. B.: Population density, outcrossing rate, and heterozygote superiority in ponderosa pine. *Evolution* **38**: 1151–1154 (1984). — KLEINSCHMIT, J.: Neuere Ergebnisse der Douglasien-Provenienzforschung und -Züchtung in der Bundesrepublik Deutschland. Schweiz. Z. Forstwes. **135**: 655–669 (1984). — KLEINSCHMIT, J., RACZ, J., WEISGERBER, H., DIETZE, W. and DIMPFLEMEIER, R.: Ergebnisse aus dem internationalen Douglasien-Herkunftsversuch von 1970 in der BRD. II. Ergebnisse der Feldversuche im Alter 6. *Silvae Genet.* **28**: 226–244 (1974). — LI, P. and ADAMS, W. T.: Range-wide patterns of allozyme variation in Douglas-fir (*Pseudotsuga menziesii*). *Can. J. For. Res.* **19**: 149–161 (1989). — MARCET, E.: Bemerkungen und Beobachtungen über den Augusttrieb (mit besonderer Berücksichtigung der Douglasie). Schweiz. Z. Forstwes. **126**: 214–237 (1975). — MORAN, G. F. and ADAMS, W. T.: Microgeographical patterns of allozyme differentiation in Douglas-fir from southwest Oregon. *Sci.* **35**: 3–15 (1989). — MUONA, O.: Population genetics in forest tree improvement. In: *Plant-Population Genetics, Breeding, and Genetic Resources*. (A. H. D. BROWN, M. T. CLEGG, A. L. KAHLER and B. S. WEIR, [eds.]) Sinauer Assocs. Inc., Sunderland, MA, pp. 282–298 (1989). — NEALE, D. B.: Genetic implications of shelterwood regeneration of Douglas-fir in southwest Oregon. *For. Sci.* **31**: 995–1005 (1985). — NEALE, D. B. and ADAMS, W. T.: The mating system in natural and shelterwood stands of Douglas-fir. *Theor. Appl. Genet.* **71**: 201–207 (1985). — NEI, M.: Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**: 583–590 (1978). — SHAW, D. V. and ALLARD, R. W.: Estimation of outcrossing rates in Douglas-fir using isozyme markers. *Theor. Appl. Genet.* **62**: 113–120 (1982). — SHEA, K. L.: Effects of population structure and cone production on outcrossing rates in Engelmann spruce and subalpine fir. *Evolution* **41**: 124–136 (1987). — SMITH, C. C., HAMRICK, J. L. and KRAMER, C. L.: The effects of stand density on frequency of filled seeds and fecundity in lodgepole pine (*Pinus contorta* DOUGL.). *Can. J. For. Res.* **18**: 453–460 (1988). — SNEATH, P. H. and SOKAL, R. R.: *Numerical Taxonomy*. W. H. Freeman, San Francisco. 573 pp. (1973). — SORENSEN, F. C. and MILES, R. S.: Self-pollination effects on Douglas-fir and ponderosa pine seeds and seedlings. *Silvae Genet.* **23**: 135–138 (1974). — SORENSEN, F. C., MILES, R. S.: Inbreeding depression in height, height growth, and survival of Douglas-fir, ponderosa pine, and noble fir to 10 years of age. *For. Sci.* **28**: 283–292 (1982). — STEINHOFF, R. J., JOYCE, D. G. and FINS, L.: Isozyme variation in *Pinus monticola*. *Can. J. For. Res.* **13**: 112–1132 (1983). — SWOFFORD, D. L. and SELANDER, R. B.: BIOSYS-1: A computer program for the analysis of allelic variation in population genetics and biochemical systematics (Release 1.7). Center for Biodiversity, Illinois Natur. Hist. Surv., Champaign, IL, 43 pp. (1989). — YEH, F. C. and MORGAN, K.: Mating system and multilocus associations in a natural population of *Pseudotsuga menziesii* (MIRB.) FRANCO. *Theor. Appl. Genet.* **73**: 799–808 (1987).

Growth Differentiation in White Spruce Crop Tree Progenies

By ST. MAGNUSSEN¹

(Received 10th March 1993)

1. Abstract

Stem analysis of 288 36-year-old dominant and codominant 'crop' trees in 18 white spruce open-pollinated families revealed a strong genetic control of height growth (heritabilities of 0.3 to 0.6). Heritability estimates for volume growth peaked around age 20 when they reached a level of 0.3 only to decline rapidly thereafter. Rank

stability and the coefficient of genetic prediction between age 36 family means and means obtained at earlier ages were not sufficiently strong to warrant early selection for either height or volume. Height-age and volume-age relationships were successfully modelled with a quadratic log-linear model with three interpretable parameters. Heritabilities of the growth curve parameters varied from 0.14 to 0.72. The opportunity to improve the growth curves by 20% for all ages was explored by using a restricted selection index of the growth curve parameters. An improve-

¹ Forestry Canada, Petawawa National Forestry Institute, Chalk River, Ontario, K0J 1J0, Canada

ment of 6% to 12% in both height and volume per breeding cycle and unit selection intensity is realistic. Growth curve analysis is recommended for the analysis of longitudinal growth series.

Key words: variance components, heritability, coefficient of genetic prediction, rank stability, growth curves, volume.

2. Introduction

White spruce (*Picea glauca* (MOENCH) Voss) is one of the most planted species in eastern Canada (KUHNKE, 1989; RAUSCHER, 1987) and efforts to improve the growth and fitness of this economically important species are occurring on a large scale (BEAULIEU and CORRIVEAU, 1985; CARTER and SIMPSON, 1985; FOWLER, 1986; NIENSTAEDT and KANG, 1987; RAUTER and YING, 1979). A high potential for genetic improvement of this highly variable species (NIENSTAEDT and TEICH, 1972) has been supported by numerous findings of a strong population and within-population differentiation of growth in replicated experiments (for example, CORRIVEAU et al., 1987; KING and RUDOLF, 1969; MURRAY, 1984; NIENSTAEDT and RIEMENSCHNEIDER, 1985; TEICH, 1973; TEICH et al., 1975). Most of the available information on the potential for tree improvement through selection and breeding stems from provenance trials. Information on the performance of white spruce progenies is still scarce and has mainly been concerned with the performance during the first 20 or so years from seed (for example, KHALIL, 1985; NIENSTAEDT, 1984; MERRILL and MOHN, 1984; NIENSTAEDT and RIEMENSCHNEIDER, 1985). The present study presents growth curves (height and stem volume) and genetic parameters of 36-years-old potential crop trees in 18 white spruce families growing in eastern Ontario. Both conventional and growth curve analyses will be shown. Growth curve analysis offers the advantage of a more succinct and parsimonious presentation of the growth results than the univariate approach to results from different ages (MAGNUSSEN and KREMER, 1992, in press; MAGNUSSEN and PARK, 1991). The present report also updates and extends 2 earlier evaluations (ages 8, 11, and 22) of this experiment (HOLST and TEICH, 1969; YING and MORGENSTERN, 1979).

3. Material and Methods

Wind-pollinated families (progenies) from 18 mature white spruce trees were tested in a replicated experiment on a glacial till site in the Research Forest of the Petawawa National Forestry Institute, Chalk River, Ontario. The parent trees were selected among the dominant and codominant trees in 5 stands within the Ottawa Valley. Visited stands were (number of selections given in parentheses): Maple Leaf (2), Sundridge (2), Carnavorn (2), Sandy Lake (4), and Algonquin Park (8). Seed from the selected parents were sown in 1954 and outplanted as 2+2 seedlings in the experiment in the spring of 1958 at a 1.8m square spacing. The experimental design was randomized complete block design with 50 tree plots (5 rows of 10 trees each) and 4 replications (blocks).

Data for this study were gathered in the spring of 1990 (age 36) from a stem analysis performed on a sample of 16 felled 'crop' trees per family (4 per replicate and family to a total of 288 trees). Trees selected for stem analysis were random samples of the 'best' onethird of the innermost 24 trees in each plot. These 'best' individuals were dominant and codominant trees of good form, having a healthy crown, and without any visible sign of damage. On a per area basis the selected 'crop' trees re-

present the final crop of approximately 700 trees per hectare at an age of about 70 years (RAUSCHER, 1987). Survival at age 36 was 67%, with individual families ranging from 54% to 78% (a difference of 8% in survival is significant at the 5% level of significance). Diameter at breast height averaged 13.7cm in all trees and 17.8cm (+30%) in the 288 trees felled for stem analysis. Tree heights averaged 11.2m in the experiment and 12.5m (+12%) in the selected 'crop' trees.

A total of 7 cross sectional disks were removed from each felled tree, one at breast height (1.3m) and 6 taken at equal distances along the remainder of the stem. Location (height) of the disks was recorded in the field to the nearest 0.5 cm. Disks were sanded and 2 orthogonal radii of disturbance-free growth were identified and penciled on the disk, and their length (center to inside bark) measured to the nearest 0.5mm with a ruler. Boundaries of annual growth rings were determined manually via an image analysis system (which displayed the 1 to 8 times magnified image on a black and white monitor) and a cross-hair target device (with automatic data capture) on the displayed image. Errors associated with the determination of ring boundaries were held below 0.1mm at all times. Height-age and diameter-age relationships were determined from the algorithm suggested by CARMEAN (1972) and recommended as the most appropriate in a comparative study of 6 alternative methods (DYER and BAILEY, 1987). Diameters were taken as the area weighted average of the two radial measurements. Stem-volume (inside bark) calculations of the 8 stem segments were done using SMALIAN'S formula for a frustum of a cone (AVERY and BURKHART, 1983).

Individual estimates of height and stem volume at various ages underwent an analysis of variance according to the following model:

$$Y_{ijk} = \mu + \tau_i + \zeta_j + \delta_{ij} + \epsilon_{ijk} \quad (\text{EQ 1})$$

where Y_{ijk} is the trait (height or volume) value of the k 'th tree ($k=1,2,3,4$) in the j 'th replicate ($j=1,2,3,4$) in family i ($i=1,2,\dots,18$), μ is the overall experimental mean value, τ_i denotes the effect attributed to the i th family ($\sum \tau_i = 0$), ζ_j is the effect associated with block j ($\sum \zeta_j = 0$), δ_{ij} stands for the interaction of families with replicates (the 'plot' effect, $\sum \sum \delta_{ij} = 0$), and ϵ_{ijk} is the residual of

Y_{ijk} not accounted for by any of the preceding terms ($\sum \sum \sum \epsilon_{ijk} = 0$). All effects except for the overall mean in

EQ 1 are considered to be random effects with variances σ_{fam}^2 , σ_{rep}^2 , σ_{plot}^2 , and σ_w^2 (w for within plot), respectively. No allowance was made to include stand effects in EQ 1 on the grounds of the sparse sampling scheme which would, at best, only generate unreliable stand estimates. In the selection of parent trees one half (9) was characterized as having a 'slender' crown and the other half as having a 'broad' crown. However, no effect of crown type has been demonstrated in any of the height or volume analyses and no consideration has been given to this stratification (see also HOLST and TEICH, 1969; YING and MORGENSTERN, 1979).

The form of the analysis of variance (ANOVA) is outlined in table 1. At age 11 all trees had heights exceeding the breast height (1.3m). Between age 8 and age 11 the number of trees exceeding the 1.3 mark increased from

Table 1. — Form of the ANOVA (age 11 to 36).

Source of variation	degrees of freedom	Expected Mean squares
Replicates	3	$\sigma_w^2 + 4\sigma_{plot}^2 + 72\sigma_{rep}^2$
Families	17	$\sigma_w^2 + 4\sigma_{plot}^2 + 16\sigma_{fam}^2$
Fam. x Repl.	51	$\sigma_w^2 + 4\sigma_{plot}^2$
Within plot	216	σ_w^2
Total	288	

117 to 288. The correct form of the Expected Mean Squares in table 1 were adjusted accordingly for these ages. Variance components were estimated by equating the observed mean squares to the expected ones and solving the ensuing equations. Variances of the estimated variance components were calculated from standard formulae as given by, for example, BECKER (1984). Statistical significance of family effects were assessed with the observed F-ratio of the mean squares (MS) $MS_{fam.}/MS_{fam. \times rep.}$ by comparing it to tabulated values of the F distribution with 17 and 51 degrees of freedom. F-ratios exceeding the 5% probability level of a type I error were declared significant.

It was assumed that the families were made up of true half sibs and, therefore, that the family variance component estimated one quarter of the additive genetic variance (FALCONER, 1981). This interpretation ignores the fact that both full sibs and selfs are likely to occur in the progenies of a single parent (COLES and FOWLER, 1976; FOWLER and PARK, 1983; KING et al., 1987). Although the estimated additive genetic variance will be overestimated by this assumption, the absence of a verified correction factor justifies the given interpretation.

The degree of additive (exploitable through selection and breeding) genetic control over height and volume growth was calculated in the form of individual narrow sense heritability (h_i^2) and family mean repeatability (h_{fam}^2). Equations 2 and 3 give the computational formulae. Implicit in both expression is the assumption of no stand effect and similar allele frequencies in these stands. In a survey of isozyme variation of white spruce in the Ottawa Valley CHELIAK et al. (1988) found no significant stand differentiation in allele frequencies (only 0.7% of the genic variance was attributable to 'stands'). The made assumptions seems, therefore, reasonable. Standard errors of the heritability estimates were obtained via the 'delta' method (a TAYLOR series expansion) as outlined by GORDON et al. (1972).

$$h_i^2 = \frac{4 \times \sigma_{fam}^2}{\sigma_{fam}^2 + \sigma_{rep}^2 + \sigma_{plot}^2 + \sigma_w^2} \quad (EQ 2)$$

(EQ 3)

$$h_{fam}^2 = \frac{\sigma_{fam}^2}{\sigma_{fam}^2 + \sigma_{rep}^2/4 + \sigma_{plot}^2/4 + \sigma_w^2/16}$$

The value of juvenile (age < 36) height or volume as a predictor of age 36 genetic worth (additive genetic value)

was assessed via the 'coefficient of genetic prediction' or CGP (BARADAT, 1976) which is the standardized regression of the genetic value of one trait (the 'juvenile' expression) on the phenotypic (observable) value of the same trait at age 36. In other words CGP predicts the standardized change in genetic worth at age 36 obtained by a change of one standardized unit in the phenotypic expression of the juvenile trait (realized by selection of superior phenotypes). BARADAT (1976) provides the computational details. Phenotypic rank stability of family means over age was gauged by the SPEARMAN rank correlation coefficient (SNEDECOR and COCHRAN, 1971).

Both the height-age and the volume-age relationship of single trees (Y_{ijk}) could be described by a simple linear model (on a natural log-log scale):

(EQ 4)

$$Y_{ijk} = \exp(\alpha_{ijk} + \beta_{ijk} \times \log(\text{age}) + \gamma_{ijk} \times \log^2(\text{age})) + \epsilon_{ijk}$$

where α_{ijk} , β_{ijk} , and γ_{ijk} are the intercept of the log transformed trait value at age one, the slope of the linear relationship between the log transformed trait value and the log of age, and the curvature of this relationship, respectively. β is essentially the initial relative growth rate (growth per unit size and unit time) and γ is half the rate at which the relative growth rate declines with age.

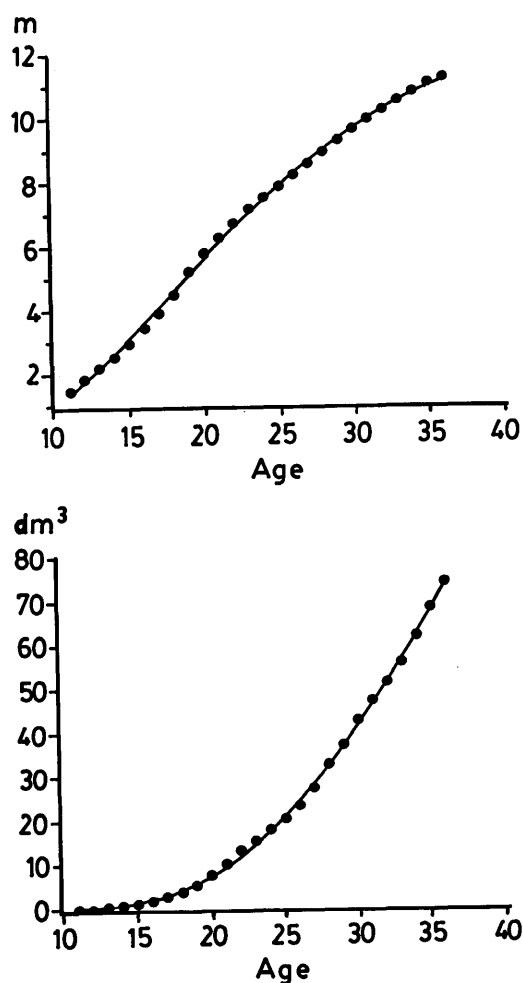


Figure 1. — Height (top) and stem volume (bottom) over age for a single tree. Circles represent the observed values and the full line the fitted regression model (cf. EQ 4).

The error term (ϵ_{ijk}) accounts for the lack of fit between the model expectations and the observed trait values. Further aspects of the coefficients have been demonstrated by MAGNUSSEN and PARK (1991) and MAGNUSSEN and KREMER (1993, in press). The regression coefficients of individual trees were determined by non-linear regressions using the GAUSS-NEWTON method of estimation (GALLANT, 1987). Figure 1 illustrates a typical example of the goodness of fit. A multivariate analysis (MANOVA) of the three regression coefficients was performed using the same model expansion as in the univariate case of single tree heights and volume (cf. EQ 1). Variances, covariances, and heritability estimates of the 3 regression parameters were obtained in a similar way as outlined for height and volume. Estimation errors of α , β , and γ were ignored in these computations. The excellent fit and small standard deviations on the estimates (<7%) justified this omission. WILK's likelihood ratio criterion (MORRISON, 1976) was used in the multivariate analysis of the significance of family effects on the regression coefficients α , β , and γ . The form of the multivariate analysis of variance followed in principle the above outline for the univariate traits (height and volume).

With the breeding objective of improving the height and volume growth curve by 20% for any given age by recurrent selection and breeding of superior genotypes, a selection index was constructed that would achieve this objective in the shortest possible time frame (by maximizing the correlation between the index and the genetic worth of the selection candidates, (BAKER, 1986; HAZEL, 1943)). According to the model in EQ 4 an increase in α will provide a 'lift' of the entire growth curve. With the inherent correlations among the growth curve parameters an unrestricted selection for α will lead to changes in beta and gamma coefficients that will tend to counteract the 'lift'. From EQ 4 we can derive that an improvement of the α by 0.183 ($\exp(0.183)=1.20$) while restricting the 2 remaining coefficients (β and γ) to 0 change would accomplish the breeding goal. Using the formulae for a selection index with restriction (LIN, 1985), index weights were calculated and the rate of genetic progress per unit selection intensity and generation were determined. Errors

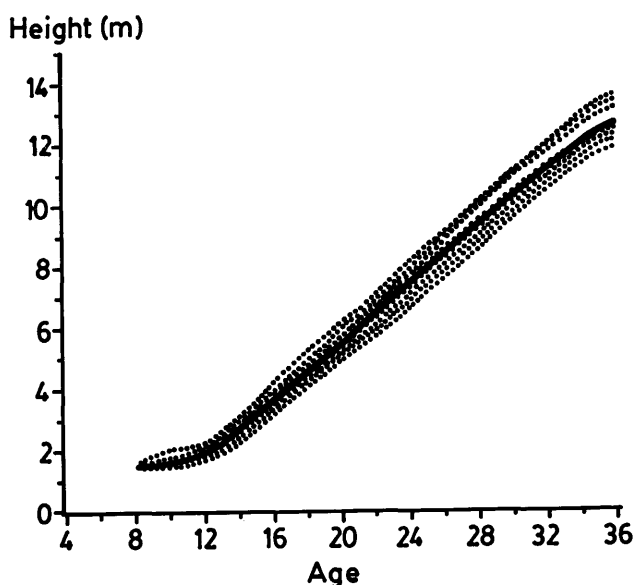


Figure 2. — Trend in average (fat solid line) and family mean height (dashed lines) over age.

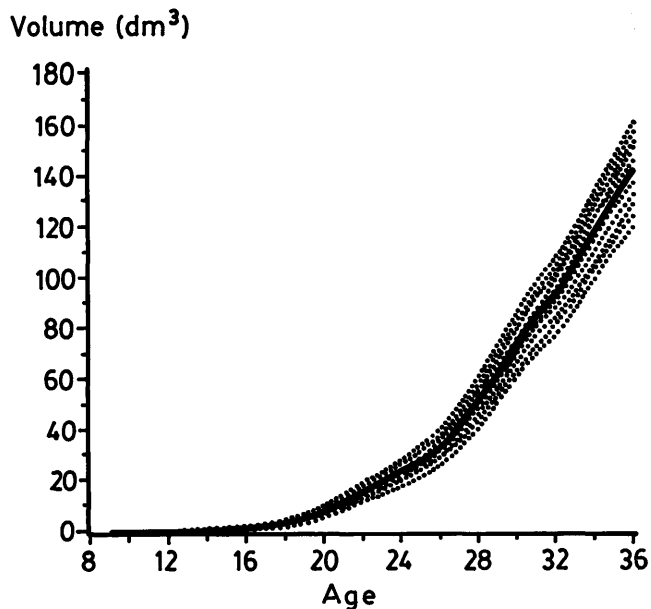


Figure 3. — Trend in average (fat solid line) and family mean stem volume (dashed lines) over age.

of the selection index coefficients due to sampling were determined via the formulae given by TALLIS (1968).

4. Results and Discussion

Between ages 10 years and 36 years the average tree height increased from 1.6m to 12.5m. The age-trend in average height and in the means of individual families is illustrated in figure 2. Family differences increased from approximately 0.5m at age 10 to 1.8m at age 36. Relative to the mean of all families these differences amounted to 28% and 15%, respectively. Tree heights followed, by and large, a normal distribution with notable differences only at age 30 and 31 (test: SHAPIRO and WILK's W-test on within plot residual heights, SHAPIRO and WILK, 1965). Statistically significant family differences were found at all but one age (age 12); the F-ratio for families fluctuated between 2.04 ($P=0.03$) and 3.11 ($P<0.01$) with a maximum around age 16. It was, however, not possible to locate these significant difference in trees 21 years or older (test: BONFERRONI, significance level 5%, MILLER, 1981). In younger trees the statistical separation of the means was weak, with only 2 broadly overlapping (70% or more) groups identifiable as statistically different from each other. Until age 12 the height growth rate was very low, probably as a result of the typical planting 'check' in this species (BALL, 1990; BELL and EK, 1988; RAUSCHER, 1987). A period from age 14 to age 32 is characterized by an almost constant annual 0.5m increase in height. Generally the height growth depicted in figure 2 compared favorably with results published for eastern Canada and the Great Lakes region (KING and RUDOLF, 1969; MERRILL and MOHN, 1984; MURRAY, 1984; NIENSTAEDE and RIEMENSCHNEIDER, 1985). The mean height of the selected 'crop' trees are about 15% above the age 11 and age 22 results published earlier for the entire trial (HOLST and TEICH, 1969; YING and MORGENSTERN, 1979).

Total stem volume (inside bark) showed an exponential increase over age (Fig. 3), from 4dm³ per tree at age 12 to 132dm³ per tree at age 36. Family differences increased in absolute terms with age (range 0.01dm³ to 0.06dm³ at age 12 versus 111dm³ to 149dm³ at age 36) but decreased on a

relative scale from a sixfold difference at age 12 to a 28% difference (on the mean) at age 36. The analysis of variance revealed a quadratic trend in the F-ratio for families, starting at 1.1 around age 12 and increasing to approximately 2 around age 20 only to decrease again to 1.1 around age 36. Only family mean volumes between ages 16 to 23 differed significantly ($P < 0.05$); nevertheless, the simultaneous inference about the family means with the BONFERRONI test failed to separate any homogenous subgroups (MILLER, 1981). The average stem volume of 24dm^3 at age 25 is at the lower range of average stem volumes reported for a 25-year-old provenance study in Quebec (BEAULIEU and CORRIVEAU, 1985). On a per hectare basis the 36-year results correspond to a volume of 92m^3 (with 700 crop trees per hectare).

Throughout the ages covered the families continued to change ranks for both height and volume. Figure 4 depicts the SPEARMAN rank correlation of the family ranking at age 36 with the ranking held at younger ages. Family ranking from age 14 and onwards were significantly ($P < 0.01$) correlated with ranking at age 36. On the average, the rank correlation of family mean height between any 2 ages dropped at an annual rate of 0.03. There was no sign that the annual change in the rank correlation would decrease in trees older than 15 years. Hence, the correlation of family ranking of heights would vanish in about 30 years. This makes any attempt at juvenile selection (age < 40) a very risky proposition. At age 22 the rank correlation between the family means of all trees and family means of 'crop' trees was 0.88 ($P < 0.01$), as opposed to only 0.32 ($P > 0.10$) at age 11. In other words 'crop' tree selection (for height) at age 11 is not possible in white spruce.

Rank correlations of family means of stem volume (Fig. 4) showed an even faster rate of change than found for height. The average annual drop in the family mean rank correlation of stem volume was 0.04 per year between ages 13 and 36. There was no manifest tendency for the changes in family mean ranking to slow with age. After

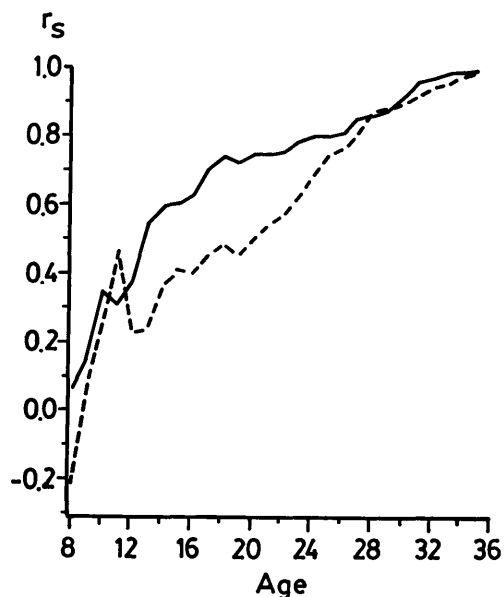


Figure 4. — Spearman rank correlation (r_s) between age 36 family means and means at younger ages. Rank correlations for family mean height are indicated by the solid line and those of stem volume by the dashed line. Critical values at the 5% level of significance = 0.468, and 0.590 for the 1% level of significance.

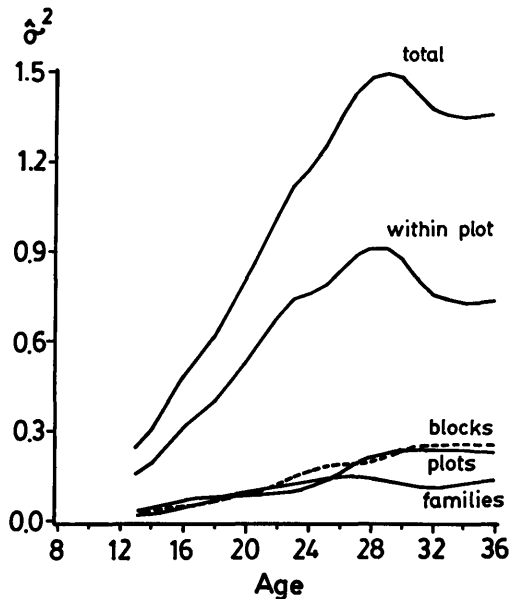


Figure 5. — Age trends in variance components for height.

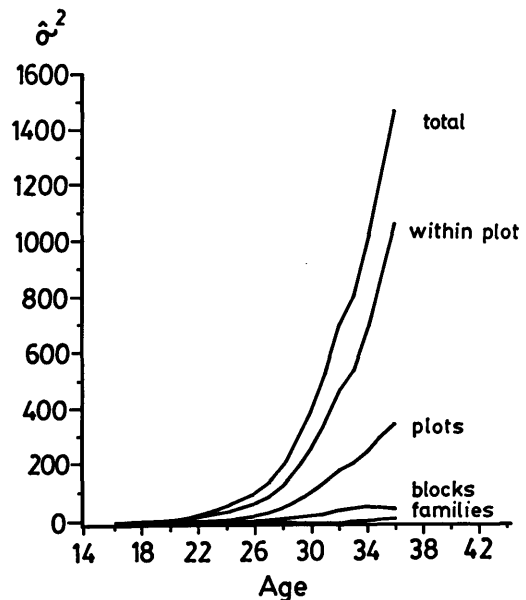


Figure 6. — Age trends in variance components for stem volume.

25 years, then, the rank correlation of family volume means would vanish. Only ranks obtained after age 19 were statistically significant correlated with age 36 ranks. A trial selection for volume of the top 5 families at age 12 would only include one family among the top 5 at age 36; the average rank of the top 5 families at age 12 would drop from 3 to 10 during the 24 years. These results points to considerable risk or outright loss of genetic gain that a breeder might incur by embracing juvenile selection based on a few significant correlations of juvenile traits (KHALIL, 1985; YING and MORGENSTERN, 1979).

Age trends in the variance components of height and volume are provided in figures 5 and 6. A linear increase in the variance of heights with age was evident until around age 28, when a slight dip occurred. Most of the total height variance was due to the within-plot tree to tree variation (54% to 66%) which is a typical result in most forest genetic trials (FINNS et al., 1992). Families, blocks, and plots contributed comparable amounts of var-

iance (10% to 15%) to the total. The stem volume variances due to within-plot differences and plots increased exponentially with age whereas the block and family variances only increased linearly. Over 2/3 of the total variance was due to the among-tree variation in a plot, and about 20% was due to variations among plots. Families contributed a relative variance of 6% to 8% between ages 16 and 22 years but only about 1% after age 26. The age trend in both height and volume are typical for most forest genetic trials with conifers (FINNS et al., 1992).

Heritability of height remained fairly strong (0.34 to 0.59) throughout the experiment but with a declining trend starting around age 14 (Figure 7). Family mean repeatability followed the trends in the individual tree heritabilities but at a slightly (~ 0.05) higher level. Previously reported individual tree heritabilities for height in this experiment have been considerably lower (HOLST and TEICH, 1979; YING and MORGENSTERN, 1979). The elimination of the strong influence of non-crop trees (which are smaller and often suppressed) from the within-plot variances is the main cause for this difference in level of heritabilities (see also MATHESON and RAYMOND, 1984). A focus on crop trees gives, everything else being equal, the most realistic view of the potential for improvement in traits of economic value. At age 36 the genetic gain in height growth would be approximately 4% per unit selection intensity in a simple mass selection on phenotypic values. Heritability estimates reported by NIENSTAEDT and RIEMENSCHNEIDER (1985), and NIENSTAEDT (1984) for white spruce progenies in the Lake States are quite similar to the values reported herein. For height, the coefficient of genetic prediction remained fairly constant around 0.4, indicating that the loss in genetic gain in height growth at age 36 by selecting of the best families between age 12 and 20 instead of at age 36 would be between 25% and 42% (as measured by the difference to the family mean repeatability). Again, the time advantage compared to the loss of absolute gain per breeding cycle appears insufficient to support an endorsement of early family selection. Due to the relatively small family sample sizes the standard errors of the

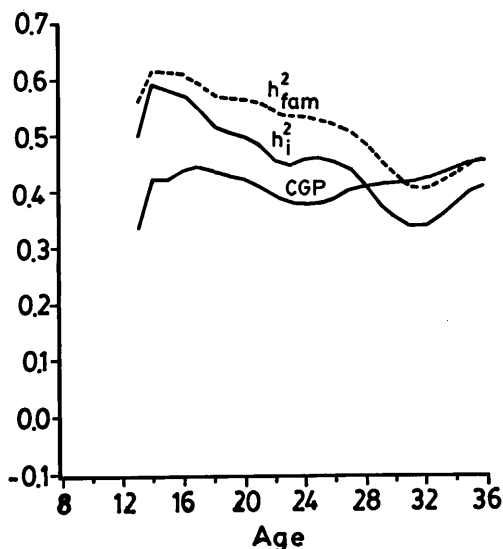


Figure 7. — Age trends in individual narrow sense heritability (h^2_i) of tree height, family mean repeatability (h^2_{fam}) of tree height, and the coefficient of genetic prediction (CGP) between family mean height at age 36 and the family mean height at younger ages.

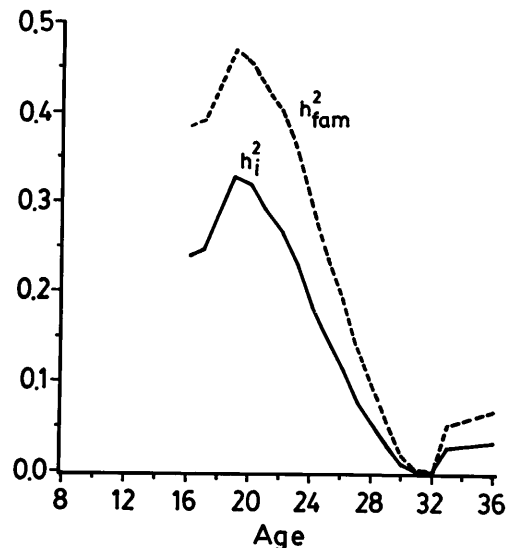


Figure 8. — Age trends in individual narrow sense heritability (h^2_i) of stem volume and the family mean repeatability (h^2_{fam}) of stem volume.

heritabilities and CGP were large ($\sim 50\%$) compared to the estimates themselves.

Volume individual tree heritabilities peaked around age 20 at values of approximately 0.30 and then declined sharply to near zero values at age 30 (Figure 8). Family mean repeatability were generally 50% to 100% higher and with the same trends as in the individual tree heritabilities. It is conjectured that the peak in volume heritability coincides with the peak in inter-tree competition as hypothesized by others (for example, NAMKOONG et al., 1972; FRANKLIN, 1979). The low heritabilities at age 36 means that genetic gains in volume at that age will be modest. In this example a gain of about 1% per unit selection intensity is to be expected albeit with a standard error of similar magnitude. Low or 0 genetic control over diameter growth is main cause for the trend in volume heritabilities (FOSTER 1986; MERRILL and MOHN, 1984; YING and MORGENSTERN, 1979). The coefficient of genetic prediction (CGP) for volume at age 36 remained low (< 0.10 non significant) throughout the experiment (not shown).

Summary statistics of the growth curve analyses are provided in table 2. Family effects on both height and volume growth curve parameters (α , β , and γ) were statistically highly significant ($F_{fam}(51,147) = 2.24$ ($P < 0.01$) for height and $F_{fam}(51,147) = 1.65$ for volume ($P = 0.01$)). Individually and combined the MANOVA residuals of the three growth curve parameters appeared ($P > 0.44$) to be normally distributed (CAMPBELL, 1980). Note the strong negative correlation between the β and the γ coefficients, indicating that trees with a high initial growth rate also have a faster decline of the relative growth rate over time. Similar correlation patterns have been reported for larch provenances (MAGNUSSEN and PARK, 1991) and for a progeny trial with maritime pine (MAGNUSSEN and KREMER, 1993, in press). In other words, time will tend to equalize or outright reverse the juvenile ranking based on relative growth rates. The decline in heritability after a short-lived juvenile peak is partly due to this negative correlation between initial growth rate and its subsequent rate of decline. Structural changes in the trees as they age, shifts in allocation pattern over time, and aging per se are believed to be factors that lowers the (relative) growth

Table 2. — Average regression coefficients for the growth curves of height and stem volume (cf. EQ 4); the total phenotypic standard deviation of the regression coefficients and the correlation (r , PEARSON product moment) amongst the coefficients. All correlations are highly significant ($P < 0.001$).

Trait	Coeff.	mean	Std. dev.	$r(\alpha, \beta)$	$r(\alpha, \gamma)$	$r(\beta, \gamma)$
height	α	-9.51	3.06	-0.99	0.97	-0.99
	β	5.66	1.93			
	γ	-0.64	0.32			
volume	α	-51.22	17.63	-0.99	0.99	-0.99
	β	28.19	9.16			
	γ	-3.49	1.30			

rate and thus cause alpha and gamma to be negatively correlated. The strong correlation amongst all 3 growth curve parameters indicate that a transformation into a growth curve dependent on only one parameter would be feasible. However, this simplification would actually complicate the interpretation because the single parameter would then influence the intercept, the slope, and the curvature of the growth trajectory.

Genetic control (as expressed in the heritability estimates) of the growth curve parameters was quite strong for the volume growth curves (Table 3) but only moderate for the height growth curve. With an appreciable phenotypic variance both at the individual tree level and at the family level the opportunities to improve by selection and breeding each of the 3 parameters must be considered as very favorable (improvements would range from 16% to 46% per unit of selection intensity). Given the high standard errors of the heritability estimates (35% to 56%) the confidence interval of the gain predictions will be wide. It is of special interest to note the strong genetic control of the coefficient associated with aging and structural change (γ) because the full impact of the decline in relative growth rates with age may not be felt until the second half of the rotation. In light of the negative correlation (the genetic correlations were similar to the phenotypic correlations listed in table 2) between β and γ , a

juvenile selection for maximum tree size would be an indirect selection for a high β -value but at the same time a strong (negative) γ -value leading to a selection for trees with a faster aging process. For short rotation crops this may hardly be a reason for concern but, with an estimated rotation age between 60 and 80 for white spruce, the cumulative effect of the negative correlation may become quite serious. Selection for improved growth must, therefore, take the particular correlation structure of the growth parameters into consideration before the desired long term benefits can be expected to materialize (MAGNUSSEN and KREMER, 1993, in press). Selection for 'correlation breakers' is feasible inasmuch as some individuals seem to combine a high initial growth rate with a moderate rate of decline over time. Nonlinear selection indices (MAGNUSSEN, 1991), which are selection indices constructed to achieve maximum simultaneous gain in all index variables, and selection indices for the optimum growth curve (TALLIS, 1968; MAGNUSSEN and KREMER, 1993, in press) facilitates this task. Growth curve analysis appears well suited for this type of optimization in comparison with the more traditional evaluation based on achieved size at specific ages.

Selection on an index constrained to yield a specified growth curve response would satisfy the long term breeding objectives in a consistent manner (LIN, 1985; TALLIS, 1968). Here a 20% improvement of height and volume

Table 3. — Variance components and heritabilities of growth curve parameters.

Trait	Coeff.	σ^2_{ph}	$\sigma^2_{ph.fam}$	σ^2_{fam}	h^2_i	h^2_{fam}
height	α	9.13	1.07	0.31	0.14	0.29
	β	3.55	0.51	0.22	0.25	0.43
	γ	0.09	0.02	0.01	0.44	0.53
volume	α	310.71	80.43	51.82	0.67	0.64
	β	83.80	20.66	15.01	0.72	0.73
	γ	1.69	0.40	0.28	0.66	0.70

σ^2_{ph} = total phenotypic variance
 $\sigma^2_{ph.fam}$ = family phenotypic variance
 σ^2_{fam} = family variance
 h^2_i = individual narrow sense heritability
 h^2_{fam} = family mean repeatability

Table 4. — Index coefficients and summary statistics for the restricted selection indices for improved height and volume growth curves. Objective: 20% improvement by achieving an 0.1823 improvement in α while maintaining β , and γ at their current levels.

$$\text{Index (I)} = \delta_a \cdot \alpha + \delta_b \cdot \beta + \delta_c \cdot \gamma$$

Trait	Type of selection	Index variable	Index coeff. (δ)	s.e.(δ)	$\sigma^2_{\text{Index}}^a$	corr (index, genetic merit)	Generations needed for 20% improvement ^b
height	mass	α	0.211	0.768	4.83	0.36	2.2
		β	0.041	0.067			
		γ	-0.240	0.237			
	family	α	0.843	3.071	8.94	0.54	3.0
		β	0.164	0.270			
		γ	-0.959	0.950			
volume	mass	α	0.071	0.026	0.281	0.23	0.5
		β	0.245	0.108			
		γ	0.844	0.614			
	family	α	0.282	0.102	2.122	0.15	1.5
		β	0.978	0.432			
		γ	3.374	2.455			

a) Includes error variance due to estimation from sample data (TALLIS, 1968).

b) Errors of index has been accounted for (TALLIS, 1968)

regardless of age was chosen as the long term breeding objective. It is easy to see a gain in the α coefficient by 0.1823 (because $\exp(0.1823)=1.200$) with no change in the other 2 growth curve coefficients would accomplish this improvement. Accordingly, a selection index with restrictions (LIN, 1985) was computed for both a simple mass selection and a family selection. MAGNUSSEN and KREMER (1993) have shown that this way of achieving a desired (optimal) growth curve is fairly efficient compared to a more efficient, but also much more complex, calculations of an index based on either a simultaneous selection on all 3 parameters or on the selection for the desired 'curve' per se under the outlined global objectives of a 20% improvement.

Selection index coefficients and summary statistics for the various selection scenarios (height, volume, mass, family) are listed in table 4. It is apparent that selection on growth curve parameters promise to achieve the set goal in a shorter time span than possible with selection on a single trait value (either directly or indirectly by juvenile selection) due to an integration of the entire growth history into a few variance components. Despite concerns about (a) the modest correlation between the estimated index and the true genetic merit of the index, (b) some negative eigenvalues of matrices used in the index calculations, and (c) large standard errors of the index coefficients (BAKER, 1986), an improvement of 6% to 10% per breeding cycle and per unit selection intensity seems plausible when the improved material is deployed to site and climatic conditions comparable to those experienced during the testing period.

5. Acknowledgements

The more than 20,000 tree-ring measurements were meticulously done by JOY LAVEREAU. Her excellent work is greatly appreciated. Felling, extraction disks, and field measurements were done by STAN KRANZ and BILL SELKIRK, their contributions are equally appreciated. I would also like to thank Dr. K. JOHNSEN and 2 anonymous reviewers for helpful comments and suggestions on an earlier version of this article.

6. Literature

AVERY, T. E. and BURKHART, H. E.: Forest Measurements. McGraw-Hill, New York, NY (1983). — BAKER, R. J.: Selection indices in plant breeding. CRC Press, Boca Raton, FL (1986). — BALL, W. J.: Site preparation affects white spruce seedling performance after 20 years. For. Mgmt. Note 47. Forestry Canada, N.-W. Region, Edmonton, Alberta (1990). — BARADAT, P.: Use of juvenile-mature relationships and information from relatives in combined multi-trait selection. Pages 121-138. In: Proc. IUFRO, Joint Meeting on Advanced Generation Breeding, Bordeaux, France, June 1976. (1976). — BEAULIEU, J. and CORRIVEAU, A.: Variabilité de la densité du bois et de la production des provenances d'épinette blanche, 20 ans après plantation. Can. J. For. Res. 15: 833-838 (1985). — BECKER, W. A.: Manual of quantitative genetics. 4th Edition. Academic Enterprises, Pullman, WA (1984). — BELL, K. L. and EK, A. R.: Growth and survival modeling for planted conifers in the Great Lakes region. For. Sci. 34: 458-473 (1988). — CAMPBELL, N. A.: Robust procedures in multivariate analysis. I. Robust covariance estimation. Appl. Statist. 29: 231-237 (1980). — CARTER, K. K. and SIMPSON, J. D.: Status and outlook for tree improvement programs in the northeast. North. J. Appl. Forestry 2: 127-131 (1985). — CHELIAK, W. M., MURRAY, G. and PITEL, J. A.: Genetic effects of phenotypic selection in white spruce. For. Ecol. and Mgmt. 24: 139-149 (1988). — COLES, J. F. and FOWLER, D. P.: Inbreeding in neighboring trees in two white spruce populations. Silvae Genet. 25: 29-34 (1976). — CORRIVEAU, A., BEAULIEU, J. and MOTKE, F.: Wood density of natural white spruce populations in Quebec. Can. J. For. Res. 17: 675-682 (1987). — DYER, M.

- E. and BAILEY, R. L.: A test of six methods for estimating true heights from stem analysis data. *For. Sci.* 33: 3–13 (1987). — FINNS, L., FRIEDMAN, S. T. and BROTSCHOL, J. V.: Handbook of Quantitative Forest Genetics. Kluwer Academic Publishers, Dordrecht, The Netherlands (1992). — FOSTER, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *For. Sci.* 32: 944–959 (1986). — FOWLER, D. P.: Strategies for the genetic improvement of important tree species in the Maritimes. *For. Can. Inf. Rep. M-X-156* (1986). — FOWLER, D. P. and PARK, Y. S.: Population studies of white spruce. I. Effects of self pollination. *Can. J. For. Res.* 13: 1133–1138 (1983). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genet.* 28: 207–212 (1979). — GALLANT, R. A.: Nonlinear statistical models. John Wiley and Sons, New York, NY (1987). — GORDON, I. L., BLYTH, D. E. and BALAAM, L. N.: Variance of heritability ratios estimated from phenotypic variance components. *Biometrics* 28: 401–415 (1972). — HAZEL, L. N.: The genetic basis for constructing selection indices. *Genetics* 28: 476–490 (1943). — HOLST, M. J. and TEICH, A. H.: Heritability estimates in Ontario white spruce. *Silvae Genet.* 18: 23–27 (1969). — KHALIL, M. A. K.: Heritability of juvenile characters of white spruce (*Picea glauca* (MOENCH) Voss) in central Newfoundland, Canada. *Theor. Appl. Genet.* 69: 247–251 (1985). — KING, J. N., DANCIG, D. P. and DHIR, N. K.: Genetic structure and mating system of white spruce (*Picea glauca*) in a seed production area. *Can. J. For. Res.* 14: 639–643 (1984). — KING, J. P. and RUDOLF, P. O.: Development of white spruce and Norway spruce trees from several seed sources 29 years after planting. *USDA For. Serv. Res. Note NC-70* (1969). — KUHNKE, P. H.: Silviculture statistics for Canada. *Forestry Canada Inf. Rep. NOR-X-301* (1989). — LIN, C. Y.: A simple stepwise procedure for deriving selection index with restrictions. *Theor. Appl. Genet.* 70: 147–150 (1985). — MAGNUSSEN, S.: Selection index: economic weights for maximum simultaneous genetic gain. *Theor. Appl. Genet.* 79: 289–293 (1990). — MAGNUSSEN, S.: Index selection with nonlinear profit function as a tool to achieve simultaneous genetic gain. *Theor. Appl. Genet.* 82: 305–312 (1991). — MAGNUSSEN, S., and KREMER, A.: Selection for an optimum tree growth curve. *Silvae Genetica*, in press (1993). — MAGNUSSEN, S. and PARK, Y. S.: Growth-curve differentiation among Japanese larch provenances. *Can. J. For. Res.* 21: 504–513 (1991). — MATHESON, A. C. and
- RAYMOND, C. A.: Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*. *Silvae Genet.* 33: 125–128 (1984). — MERRILL, R. E. and MOHN, C. A.: Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. *Can. J. For. Res.* 15: 494–497 (1985). — MILLER, R. G., JR.: Simultaneous statistical inference. Springer-Verlag, New York (1981). — MORRISON, D. F.: Multivariate statistical methods. McGraw-Hill, New York (1976). — MURRAY, G.: Variation in height of white spruce provenances after 10 and 20 years in five field tests. Pages 82–89. In: *Proc. 29th Northeastern Forest Tree Improv. Conf.*, Morgantown, WV (1984). — NAMKOONG, G., USANIS, R. A. and SILPN, R. R.: Age-related variation in genetic control of height growth in Douglas-fir. *Theor. App. Genet.* 42: 151–159 (1972). — NIENSTAEDT, H.: Inheritance and correlation of frost injury, growth, flowering, and cone characteristics in white spruce, *Picea glauca* (MOENCH) Voss. *Can. J. For. Res.* 15: 498–504 (1984). — NIENSTAEDT, H. and KANG, H.: Establishing a *Picea glauca* (MOENCH) Voss base breeding population for the Lake States region of the United States. *Silvae Genet.* 36: 21–30 (1987). — NIENSTAEDT, H. and RIEMENSCHNEIDER, D. E.: Changes in heritability estimates with age and site in white spruce, *Picea glauca* (MOENCH) Voss. *Silvae Genet.* 34: 34–44 (1985). — NIENSTAEDT, H. and TEICH, A. H.: Genetics of white spruce. *USDA For. Serv. Res. Paper WO-15* (1972). — RAUSCHER, H. M.: White spruce plantations in the upper Great Lakes region: Status and problem solving needs. *North. J. Appl. For.* 4: 146–149 (1987). — RAUTER, R. M. and YING, C. C.: Genetic improvement of white spruce. In: *Tree Impr. Symposia. Ont. Min. Nat. Resources and The Great Lakes Forest Research Centre. Toronto, Ont. 19–21 Sept. 1978.* (1979). — SHAPIRO, S. S. and WILK, M. B.: An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611 (1965). — SNEDECOR, G. W. and COCHRAN, W. G.: *Statistical Methods*. 6th Edition. Iowa State University Press, Ames, Iowa (1971). — TALLIS, G. M.: Selection for optimum growth curve. *Biometrics* 24: 169–177 (1968). — TEICH, A. H.: White spruce provenances in Canada. *Env. Canada, Forestry Serv. Inf. Rep. PS-X-40* (1973). — TEICH, A. H., SKEATES, D. A. and MORGENSTERN, E. K.: Performance of white spruce provenances in Ontario. *Can. For. Serv. Petawawa Forest Exp. Station and Ont. Min. of Nat. Res., For. Res. Branch Special Joint Report no 1* (1975). — YING, C. C. and MORGENSTERN, E. K.: Correlations of height growth and heritabilities at different ages in white spruce. *Silvae Genet.* 28: 181–185 (1979).

Genetic Variation in Second-Year Slash Pine Shoot Traits and Their Relationship to 5- and 15-Year Volume in the Field

By C. K. SMITH, T. L. WHITE and G. R. HODGE

Department of Forestry, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611, USA

(Received 15th March 1993)

Summary

Seedlings of 64 open-pollinated slash pine (*Pinus elliottii* ENGELM. var. *elliottii*) families were grown from seed to 18 months of age in raised outdoor boxes under 2 nitrogen (N) treatments (5 ppm and 50 ppm). Twenty-one shoot characteristics were measured and analyzed, of which the most promising twelve were evaluated for use in multi-trait selection indices to predict parental breeding values of 5- and 15-year field volume. Genetic parameters were estimated for each seedling trait and individual-tree heritabilities ranged from 0.15 to 0.70. There was a moderate to high degree of genetic commonality for all traits across both N treatments (type B genetic correlations = 0.56 to 0.97). Caliper, green weight, and total height at 18 months were genetically correlated within each treatment (type A genetic correlations = 0.72 to 0.97) and bud burst was not correlated with any trait in either treatment. Family means for height at 13 months (low N treatment),

the difference in heights between 9 months and 13 months (low N), bud burst (high N), and total numbers of branches (high N) were the traits most positively correlated with 15-year breeding values for field volume growth ($r_{j-m} = 0.24$ to 0.37). All possible 2- and 3-trait indices were formed and correlations between predicted genetic values and true breeding values ($\text{Corr}(g,\hat{g})$) were calculated to assess indices with the best predictive ability. Total numbers of branches (high N), total numbers of cycles (high N), and the difference in height from 9 to 13 months (low N) formed the most precise index for predicting 15-year volume ($\text{Corr}(g,\hat{g}) = 0.51$). This 3-trait index was not effective at identifying the best 10% of the families used in the experiment.

Key words: Heritability, genetic correlation, type B genetic correlation, juvenile-mature correlations, selection indices, genetic gain efficiency.