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## Age-related Trends in Genetic Parameters for Jack Pine and Their Implications for Early Selection

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### Abstract

Trends in genetic parameters for height growth of jack pine (*Pinus banksiana* Lamb.) were examined over three series of family tests throughout New Brunswick. Data were analyzed for each site and across sites within each series. Although individual narrow sense heritability estimates from single-site analyses varied substantially

from site to site and showed no consistent age-related pattern, the estimates from across-site analyses showed an increasing trend to age 20. Similar as individual narrow sense heritability, the coefficient of additive genetic variance estimated from single site showed more variation than those estimated from across site analyses. Age-age (type-a) genetic correlations for height were high and could be well predicted by a  $LAR^2$  model, where  $LAR$  is the natural logarithm of the ratio between two ages at assessment. Type-b genetic correlations were high and of similar magnitude at different ages. Genetic correlations between height at different ages and volume at one-half rotation age were generally high. Taking the volume at one-half rotation age as the target trait, the selection for target trait from early selection at

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ages 5~7 could be more efficient per year than direct selection.

*Key words:* early selection, heritability, coefficient of additive genetic variance, genetic correlations, *Pinus banksiana*, selection efficiency.

## Introduction

Jack pine (*Pinus banksiana* Lamb.) is the most widely distributed pine species in Canada, and is an important source of pulpwood, lumber, and timber. The wide genetic variation found in this species (MAGNUSSEN and YEATMAN, 1989b; PARKER and VAN NIEJENHUIS, 1996; VAN NIEJENHUIS and PARKER, 1996) suggests that jack pine is a prime candidate for genetic improvement to increase its productivity and quality. Operational breeding programs for jack pine started in New Brunswick in the late 1970s as a part of the New Brunswick Tree Improvement Council (NBTIC) program, and generally followed a strategy that included selection of superior families from open-pollinated progeny tests for seed orchard roguing and mass selection for next-generation breeding (FOWLER, 1986).

The Maritimes Region of Canada, consisting of 3 provinces, New Brunswick, Nova Scotia, and Prince Edward Island, has been divided into eco-geographic seed zones based on forest classification, climate, and phenology (FOWLER and MACGILLIVRAY 1967), which were initially used to control the movement of tree seeds and seedlings in the region. However, current information from provenance, stand, and family tests suggests that New Brunswick can be treated as a single breeding zone for jack pine (FOWLER, 1986).

Direct selection on traits at rotation age can maximize gain, but results in an extremely long generation time. The lower limit of rotation age is about 40 years for jack pine in New Brunswick. Waiting for even one-half rotation age for final evaluation would be inefficient in terms of genetic gain per unit time, suggesting that selection at an early age is highly desirable for jack pine improvement programs in New Brunswick.

Age-related trends for genetic parameters are crucial for developing tree breeding strategy and early selection. A number of studies have documented temporal trends in these parameters for Scots pine (*P. sylvestris* L.) (HAAPANEN, 2001; JANSSON et al., 2003), loblolly pine (*P. taeda* L.) (BALOCCHI et al., 1993; GWAZE et al., 1998; SVENSSON et al., 1999; GWAZE et al., 2000; LAMBETH and DILL, 2001; GWAZE and BRIDGWATER, 2002), maritime pine (*P. pinaster* Ait.) (KUSNANDAR et al., 1998), slash pine (*P. elliottii*) (HODGE and WHITE, 1992), and lodgepole pine (*P. contorta* Dougl. var. *contorta*) (XIE and YING, 1996). However, very little data have been published regarding time trends in genetic parameters for jack pine. RIEMENSCHNEIDER (1988) found that heritability for height was highest at age 1 year, lowest at age 2, and intermediate thereafter up to age 7. He also found that the LAMBETH (1980) model generally fit genetic age-age correlations well, but may underestimate the corresponding genetic correlations. Consequently, RIEMENSCHNEIDER (1988) concluded that selection as early as age 1 would be an efficient strategy for improving jack

pine growth. In open-pollinated jack pine progeny tests in Ontario, MAGNUSSEN and YEATMAN (1989a) found that individual heritability for height increased slightly from 6 to 14 years. CARTER et al. (1990) reported the potential of using greenhouse tests in early family selection for jack pine. However, their findings were based on data at an earlier age (less than age 7), a single site, or a few families. Large amounts of data are needed to obtain reliable and stable genetic parameter estimates and their temporal trends.

The objectives of the study were, on the basis of three series of jack pine progeny tests that included 321 families, (1) to estimate genetic parameters, (2) to examine temporal trends of the parameters, and (3) to evaluate early selection efficiency for jack pine in New Brunswick.

## Materials and Methods

### Materials

Three series of open-pollinated family field tests were established by the NBTIC in 1979, 1982, and 1983 as part of a jack pine breeding program. Overall, 12 sites were used for this study (*Tables 1-3*). All sites were well prepared before planting. The families included in the series originated from open-pollinated seed collected from jack pine plus trees selected from across New Brunswick. These plus trees were phenotypically superior individuals that exhibited desirable attributes, such as rapid growth, good crown form, and stem straightness. A total of 321 half-sib families were included in this study, namely 150, 77, and 94 open-pollinated families for the 1979, 1982, and 1983 series, respectively. A common set of families was planted in the sites for each series. Seedlots from a few natural stands were also included in the tests as checklots, but data from these sources were excluded in the analyses. All the sites and the selected plus trees are located within the same breeding zone.

A randomized complete block design with ten blocks of four-tree row plots was planted in all series. The seedlings were grown in the greenhouse for 5 months in paperpots and were outplanted at 2 x 2 m spacing. Height (HT) was measured at varying ages after planting (*Table 1*). Tree diameter at breast height (dbh) was also measured at age 20 in the 1979 series, age 18 in the 1982 series, and age 19 in the 1983 series. Individual tree volume was calculated following HONER et al. (1983). The traits analyzed in the study are referred to as  $HT_n$  and  $Vol_n$ , where n represents years after planting.

### Statistical models and analysis

After removing runt trees or trees with significant damage (< 1% of the total trees), analyses of variance of  $HT_n$  and  $Vol_n$  were first conducted for each site within series. Then, to remove scale effects, individual tree observations were standardized by dividing each observation by the square root of the random error variance estimated from that test. Using standardized data, pooled analysis for each series was carried out using the model:

$$Y_{ijkl} = \mu + S_i + B_{j(i)} + f_k + sf_{ik} + bf_{kj(i)} + e_{ijkl} \quad [1]$$

where  $Y_{ijkl}$  is the observed HT<sub>n</sub> or Vol<sub>n</sub> observation of the l<sup>th</sup> tree in the k<sup>th</sup> family grown in the j<sup>th</sup> block within the i<sup>th</sup> site,  $\mu$  is the overall mean,  $S_i$  is the fixed effect of i<sup>th</sup> site,  $B_{j(i)}$  is the fixed effect of the j<sup>th</sup> block within the i<sup>th</sup> site,  $f_k$  is the random effect of the k<sup>th</sup> family,  $sf_{ik}$  is the random interaction between the i<sup>th</sup> site and the k<sup>th</sup> family,  $bf_{kj(i)}$  represents the random effects of plot, and  $e_{ijkl}$  is the random error due to the l<sup>th</sup> tree in the k<sup>th</sup> family growing in the j<sup>th</sup> block within the i<sup>th</sup> site. Single-site analyses were carried out using the same model, but the terms for site and its interaction with family were dropped. Variance components were estimated using the REML option of SAS Proc Mixed procedure (LITTELL et al., 1996).

Assuming that open-pollinated families account for one-quarter of the total additive genetic variation ( $\sigma_A^2$ ), individual narrow sense heritability ( $h_i^2$ ) and additive genetic coefficient of variation ( $CV_A(\%)$ ) were calculated as follows:

$$\text{Single-site } h_i^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^2 + \sigma_e^2) \quad [2]$$

$$\text{Across-site } h_i^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^3 + \sigma_{sf}^2 + \sigma_e^2) \quad [3]$$

$$CV_A = 100 * \sigma_A / \bar{x} \quad [4]$$

where  $\sigma_f^2$  is the estimated family variance,  $\sigma_{sf}^2$  the estimated variance of site-by-family interaction,  $\sigma_{sf}^3$  the estimated plot variance,  $\sigma_e^2$  the estimated random error variance, and  $\bar{x}$  is the trait average in the trial.

The approximate variances of heritability estimates were calculated using the formula [5] (DIETERS et al., 1995):

$$\text{Var}(aX_1 / X_2) = a^2 \text{var}(X_1) / X_2^2 \quad [5]$$

where  $a$  is a constant,  $X_1$  and  $X_2$  are two random variables for heritability estimation: e.g.,  $a$  equals to 4,  $\text{var}(X_1)$  is the variance of the estimated variance component due to family ( $\sigma_f^2$ ) obtained from REML estimates of Mixed procedure, and  $X_2^2$  is the phenotypic variance.

Additive genetic correlation of two traits (same traits at different ages were treated as different traits) in the same individual were estimated for each site and across sites within each series using formula [6]:

$$r_A = \sigma_{ij} / \sqrt{\sigma_i^2 \sigma_j^2} \quad [6]$$

where  $\sigma_{ij}$  is the family covariance component between traits  $i$  and  $j$ , and  $\sigma_i^2$  and  $\sigma_j^2$  are family variance components for traits  $i$  and  $j$ , respectively, estimated from the previous variance components analysis using model [1].  $\sigma_{ij}$  was calculated as  $0.5(\sigma_{(i+j)}^2 - \sigma_i^2 - \sigma_j^2)$ , where  $\sigma_{(i+j)}^2$  is the variance component for the sum of the traits (STONECYPHER, 1992). The corresponding standard errors were calculated following FALCONER and MACKAY (1996).

Type-b genetic correlation, which is essentially a measure of G x E interaction (BURDON, 1977), was calculated as [7]:

$$r_B = \sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^2) \quad [7]$$

where  $\sigma_f^2$  and  $\sigma_{sf}^2$  are family and family-by-site variance components estimated from paired-site analysis by model [1], respectively. Each pair-wise combination within each series was first examined; an average type-b genetic correlation at each measurement age for each series was then obtained. Because data were standardized,  $r_B$  is not influenced by scale effects. Therefore,  $r_B$  can be interpreted as family-by-site interaction caused by parental rank changes across test sites within series. Standard errors for type-b genetic correlations were not calculated, as sampling errors are large and difficult to specify (FALCONER and MACKAY, 1996).

Simple regression analysis was used to fit age-related trends for height heritabilities and type-b genetic correlations. The model developed by LAMBETH (1980) was used to predict age-age genetic correlations of height [8] for each site and each series, respectively:

$$\hat{r}_{A(T_1, T_2)} = a + b(LAR) \quad [8]$$

where  $\hat{r}_{A(T_1, T_2)}$  is the estimated additive genetic correlation between times  $T_1$  (early) and  $T_2$  (late),  $a$  is the intercept,  $b$  the regression coefficient, and  $LAR = \ln(T_1/T_2)$ . Regression equations were also fitted with  $LAR^2$  as LAMBETH and DILL (2001) demonstrated that  $LAR^2$  was a better independent variable for predicting age-age genetic correlations than  $LAR$  alone. No model related to volume was developed, because volume data were only available at one age for each series.

Efficiency of early forward selection was examined by taking volume at one-half rotation age (Vol20 for the 1979, Vol18 for the 1982, and Vol19 for the 1983 series, respectively) as the target trait to be improved. Assuming equal intensity of selection at target and young ages, the selection efficiency ( $Q$ ), expressed as the ratio of correlated response in volume at age  $T_2$  from a height selection at age  $T_1$  per year, was calculated as in [9] (FALCONER and MACKAY, 1996)

$$Q = r_A h_{i1} T_2 / h_{i2} T_1 \quad [9]$$

where  $T_1$  and  $T_2$  are the ages for juvenile height and target volume selection (age = 18~20), respectively,  $r_A$  is the calculated genetic correlation between the height at  $T_1$  and volume at  $T_2$ , and  $h_{i1}$  and  $h_{i2}$  are the square roots of individual narrow sense heritabilities for height at  $T_1$  and volume at  $T_2$ , respectively. A time lag of 5 years for breeding phase was usually assumed for jack pine in New Brunswick area.

The relative accuracy of backward parental selection was also evaluated by group rank classification (CARTER et al., 1990). Using standardized data, parental breeding values (PBV) for each family at each age within a series were predicted first by best linear unbiased prediction (BLUP) using statistical package MTDFReML (BOLDMAN et al., 1995) following model [1]. The ranking of families by height PBVs at  $T_1$  was compared with the ranking of PBVs by the target trait for each series (Vol20, Vol18 and Vol19 for the 1979, 1982 and 1983 series, respectively). Correct classification occurs when both early and target trait placed the family in the same group, e.g., top 25%. The percentages of correct classification at  $T_1$  were calculated under different selection

scenarios: top 25% and top 50%. The high percentage represents a high efficiency of early selection.

## Results

### Mean height

The average HT at various ages and volume around one-half rotation age for each site and overall of each series are summarized in *Tables 1-3*. The mean HT exhibited large variation among sites within series at each age, and this is especially obvious at the early age. For example, site mean for HT7 ranged from 237 to 314 cm for 1979 series, from 207 to 281 cm for the 1982 series, and from 187 to 325 cm for the 1983 series. Sites within ecoregion zone 5 in New Brunswick, such as the GPC site, always outperformed sites within other ecoregion zones because of Zone 5's high number of growing degree days and suitable rainfall in summer. Despite the substantial site-to-site variation, the series mean HT was comparable among series at each age, e.g., ranging from 242 to 273 cm for HT7. These heights were

similar to jack pine family tests growing in the Ottawa Valley in Ontario (MAGNUSSEN and KEITH, 1990; MAGNUSSEN and YEATMAN, 1989a), but shorter than those growing in Wisconsin (Riemenschneider, 1988). Similar to height growth, volume varied from site to site within each series. The overall mean volume was 68 (at age 20), 58 (at age 18), and 63 dm<sup>3</sup> (at age 19) for the 1979, 1982, and 1983 series, respectively.

### Age-related trends of genetic parameters

Single-site individual heritabilities ( $h_i^2$ ) estimated for HT varied substantially from site to site within series (*Tables 1, 2, 3*), e.g., for HT7, 0.16-0.36 for 1979; 0.24-0.42 for 1982; and 0.12-0.43 for 1983. The corresponding standard errors were low, around 0.05. No consistent patterns between single-site  $h_i^2$  estimate and height growth were found, although 6 of the 12 sites showed an increasing trend of single-site  $h_i^2$  with height (*Tables 1-3*).

The temporal pattern for single-site  $h_i^2$  estimates for HT varied from series to series. Although an increasing

*Table 1.* – Estimates of mean HT (cm) and Vol (dm<sup>3</sup>), individual narrow-sense heritability ( $h_i^2$ ), and additive genetic coefficient of variation ( $CV_A$ (%)) at various ages at each site and across sites in 1979 jack pine family testing series.

Trait	DNR			GPC			JDI			Across-site		
	Mean	$h_i^2$	$CV_A$	Mean	$h_i^2$	$CV_A$	Mean	$h_i^2$	$CV_A$	Mean	$h_i^2$	$CV_A$
HT5	131	0.12	11.4	180	0.24	13.9	155	0.14	6.6	156	0.11	7.6
HT7	237	0.16	6.3	314	0.36	8.0	262	0.20	6.2	273	0.22	6.2
HT10	392	0.19	6.4	503	0.37	6.7	414	0.31	6.7	437	0.26	6.4
HT14	659	0.35	6.2	766	0.40	6.1	638	0.48	7.1	695	0.36	6.1
HT20	989	0.58	6.2	1103	0.49	5.8	834	0.34	5.1	975	0.40	5.8
Vol20	69	0.36	17.7	74	0.45	20.5	60	0.24	16.0	68	0.30	17.4

*Table 2.* – Estimates of mean HT (cm) and Vol (dm<sup>3</sup>), and individual narrow-sense heritability ( $h_i^2$ ), and additive genetic coefficient of variation ( $CV_A$ (%)) at various ages at each site and across sites in 1982 jack pine family testing series.

Trait	AFT			BCC			GPC			JDI			NBI			Across-site		
	Mean	$h_i^2$	$CV_A$	Mean	$h_i^2$	$CV_A$												
HT7	207	0.28	11.8	247	0.42	12.7	281	0.42	10.8	241	0.37	10.8	224	0.24	11.0	242	0.25	10.3
HT12	411	0.21	8.4	538	0.47	9.5	596	0.44	7.4	468	0.40	7.6	528	0.46	8.2	509	0.32	7.4
HT18	689	0.24	7.7	811	0.38	6.6	847	0.44	6.6	714	0.48	6.9	896	0.45	5.9	791	0.37	6.3
Vol18	39	0.14	13.2	53	0.30	18.3	68	0.31	22.7	57	0.41	18.1	72	0.35	25.4	58	0.25	16.9

trend with age was clear within the 1979 series (*Table 1*), the single-site  $h_i^2$  estimates within the 1982 and 1983 series showed mixed patterns (*Tables 2, 3*). Some sites within the 1982 and 1983 series showed an upward trend with age, and others showed an increase followed by a plateau, or an increase followed by a decrease.

The across-site  $h_i^2$  estimates for HT were comparable from series to series, around 0.25 at age 7 and 0.40 at half-rotation age (18–20 years) (*Tables 1–3*). Although it was not synchronous between series, the increase in across-site  $h_i^2$  with age was a general trend observed in this study. The standard errors for these estimates were

*Table 3.* – Estimates of mean HT (cm) and Vol (dm<sup>3</sup>), individual narrow-sense heritability ( $h_i^2$ ), and additive genetic coefficient of variation ( $CV_A(\%)$ ) at various ages at each site and across sites in 1983 jack pine family testing series.

Trait	BCC			GPC			JDI			NBI			Across-site		
	Mean	$h_i^2$	$CV_A$	Mean	$h_i^2$	$CV_A$									
HT7	187	0.12	7.7	325	0.43	7.6	259	0.24	7.1	269	0.26	7.1	260	0.26	7.9
HT12	457	0.29	8.7	617	0.46	6.1	541	0.39	6.6	525	0.25	5.2	533	0.34	6.6
HT19	814	0.48	7.3	910	0.56	5.4	816	0.30	5.6	838	0.33	4.9	843	0.43	6.1
Vol19	57	0.30	17.3	72	0.42	19.8	66	0.41	19.5	57	0.22	14.3	63	0.27	16.8

*Table 4.* – Average type-b (on diagonal and in bold) and age-age genetic correlations estimated from across sites within each series analyses for 1979, 1982, and 1983 jack pine family tests.

1979 series						
Var	HT5	HT7	HT10	HT14	HT20	Vol20
HT5	<b>0.78</b>	0.93	0.93	0.86	0.82	0.76
HT7		<b>0.74</b>	1.00	0.97	0.96	0.83
HT10			<b>0.91</b>	0.97	0.95	0.83
HT14				<b>0.90</b>	0.98	0.84
HT20					<b>0.88</b>	0.84
Vol20						<b>0.85</b>
1982 series						
Var	HT7	HT12	HT18	Vol18		
HT7	<b>0.80</b>	0.97	0.91	0.83		
HT12		<b>0.82</b>	0.99	0.86		
HT18			<b>0.83</b>	0.87		
Vol18				<b>0.80</b>		
1983 series						
Var	HT7	HT12	HT19	Vol19		
HT7	<b>0.94</b>	1.00	0.97	0.74		
HT12		<b>0.89</b>	0.98	0.78		
HT19			<b>0.95</b>	0.86		
Vol19				<b>0.88</b>		

low, approximately 0.04. When data for all the series were pooled, a significant regression relationship ( $p < 0.002$ ) between across-site  $h_i^2$  and age was detected [10].

$$h_i^2 = 0.104 + 0.012(\text{age}) \quad (r^2 = 0.74) \quad [10]$$

Single-site  $h_i^2$  estimates for volume at one-half rotation age varied from site to site within each series (Tables 1~3), however the across-site  $h_i^2$  estimates, ranging from 0.25 to 0.30, were very stable from series to series. With a few exceptions,  $h_i^2$  estimates for volume were generally comparable with those of height at the same age but slightly lower in magnitude.

Different from single-site  $h_i^2$ , the single-site  $CV_A$  at age 7 were relatively stable within series but varied from series to series (Tables 1~3). At all ages, the single-site  $CV_A$  were slightly higher for the 1982 series than the other two series, especially at age 7. Correspondingly, the across-site  $CV_A$  was higher for the 1982 series than the other two series at age 7, but after that, the across-site  $CV_A$  were comparable across series. The  $CV_A$  for volume, around 17~20%, at one-half rotation age was almost 2~3 times higher as that for height at the same age. A decreasing trend with age for height was found for single-site  $CV_A$  in all sites except site DNR and JDI in the 1979 series, and BCC in the 1983 series, and for across-site  $CV_A$  in all three series (Tables 1~3). The average function for all series was  $CV_A = 8.876 - 0.164 \cdot \text{age}$  ( $r^2 = 0.41$ ).

All single-site genetic correlations between heights at various ages (data not shown) were impressively high and comparable from site to site within series except those between HT5 and HT14 ( $r_A = 0.43$ ) or HT20 ( $r_A = 0.31$ ) for the DNR site in the 1979 series. Consequently, age-age correlations for height from across-site analyses were strong and similar in value among series, all above 0.91 except between HT5 and HT14 ( $r_A = 0.86$ ) or HT20 ( $r_A = 0.82$ ) in the 1979 series (Table 4). Standard errors were low to moderate, ranging from 0.04 to 0.13, however, correlations involving HT5 or HT7 showed relatively large standard errors. As expected, as time between measurements increased, the genetic correlations between ages decreased.

Single-site genetic correlations between height at different ages and volume at one-half rotation age were all positive but varied from site to site within series (Figure 1). For example, in the 1983 series, while the genetic correlations were all over 0.9 in the BCC site, much lower correlations were found at NBI site. No obvious temporal pattern for single-site correlation stood out. Across-site genetic correlations, however, were comparable among series and generally increased with later height measurement (Table 4, Figure 1).

Details of the results of fitting age-age genetic correlation models for height are summarized in Table 5. The regression of HT single-site, age-age genetic correlations on  $LAR$  or  $LAR^2$  varied considerably from site to site both for intercept and slope. The BCC site in the 1983 series and the JDI site in the 1982 series showed an especially poor regression models. Site BCC in the 1983 series had genetic correlations near 1 for all ages, and

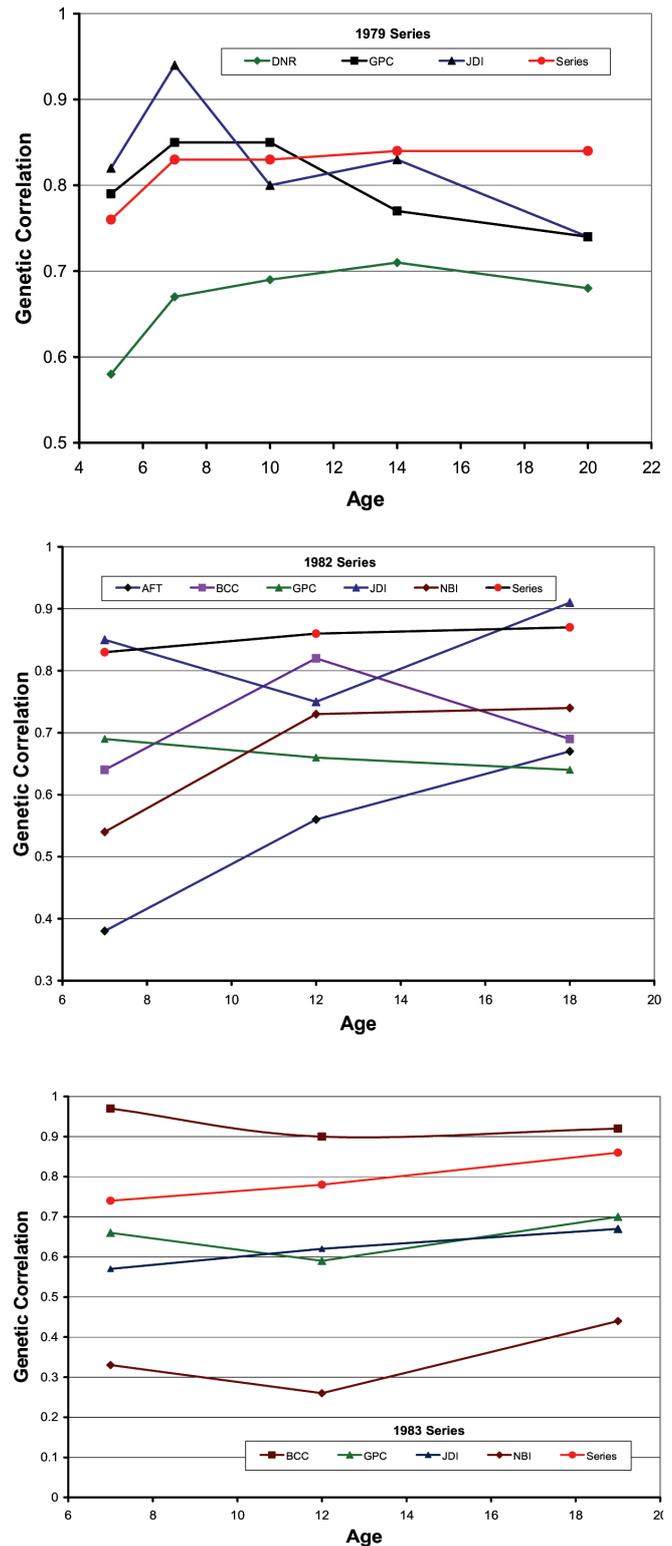


Figure 1. – Genetic correlations between height at different ages and volume at one-half rotation age (1979 series --- 20 years, 1982 series --- 18 years, and 1983 series --- 19 years) by site and across sites within series.

the JDI site in the 1982 series had a marginally higher correlation between HT7 and HT18 ( $r_A = 0.85$ ) than between HT12 and HT18 ( $r_A = 0.83$ ). Regression of age-age genetic correlation from across-site analysis on  $LAR$  or  $LAR^2$  model resulted in similar intercepts and slopes among series except for the 1983 series, which showed a

Table 5. – Parameter estimates for regression equations for fitting *LAR* and *LAR*<sup>2</sup> model for height for each site, across sites within series and across series for 1979, 1982, and 1983 jack pine family tests.

Series	Site	LAR model			LAR <sup>2</sup> model		
		a	b	r <sup>2</sup>	a	b	r <sup>2</sup>
1979	DNR	1.18	0.54	0.79	0.94	-0.34	0.80
	GPC	1.08	0.21	0.69	1.02	-0.14	0.81
	JDI	1.00	0.08	0.47	0.97	-0.04	0.36
	Across-sites	1.03	0.14	0.63	0.99	-0.09	0.67
1982	AFP	1.00	0.13	0.47	0.96	-0.11	0.55
	BCC	1.15	0.33	0.99	1.05	-0.24	0.99
	GPC	1.10	0.30	0.94	1.01	-0.22	0.97
	JDI	0.88	0.01	0.01	0.88	-0.02	0.02
	NBI	1.07	0.28	0.57	0.98	-0.19	0.50
	Across-sites	1.05	0.15	1.00	1.01	-0.10	0.99
1983	BCC	0.96	-0.06	0.12	0.98	0.04	0.09
	GPC	1.05	0.17	0.58	0.99	-0.12	0.63
	JDI	1.03	0.17	0.56	0.97	-0.11	0.51
	NBI	1.14	0.37	0.73	1.02	-0.26	0.77
	Across-sites	1.01	0.04	0.44	1.00	-0.07	0.49
Across-series	1.04	0.13	0.57	1.00	-0.09	0.63	

lower slope in the *LAR* model than the other series (Table 5). When all series were pooled, the time trend for age-age genetic correlations could be predicted by a simple regression equation using either *LAR* or *LAR*<sup>2</sup> as the only independent variable (Table 5).

The *LAR*<sup>2</sup> model generally gave a better fit than the *LAR* model, especially for all across-site within each series and series-combined models. Due to the substantial variability for single-site models and close correspondence between across-site results, together with the slightly better fit for *LAR*<sup>2</sup>, we chose to use model [11] as the standard for jack pine populations in New Brunswick:

$$\hat{r}_A = 0.998 - 0.09(LAR^2) \quad (r^2=0.63) \quad [11]$$

The average type-b genetic correlations for HT were strong for all series (Table 4), 0.74–0.91 for 1979, 0.80–0.83 for 1982, and 0.88–0.95 for 1983, indicating little genotype-by-environment interactions. The type-b genetic correlations were generally constant at different ages in all series. Type-b genetic correlations for volume were always comparable with those for height at the same age (Table 4).

#### Selection efficiency

The selection efficiency in volume at one-half rotation age, through early selection on height, was shown in Table 6. Although the magnitudes of selection efficiency varied with time and site, analyses on single site data

indicated that selection made at the first measurement year for all sites except AFT in the 1982 series would be more efficient than direct volume selection at one-half rotation age. Similar conclusions were also obtained through across-site analyses.

Table 7 lists the percentage of families correctly classified at different ages compared with the target traits (Vol20, Vol18 and Vol19 for the 1979, 1982, 1983 series, respectively). Under the upper quarter scenario (selecting the top 25% of the families), over 70% of the families which were grouped into the top 25% by target trait could be correctly identified by the 5-year height in the 1979 series. The percentages were increased to over 74% and over 86% if the objective is to select the top 25% or 50% of the families by the 7-year height in all series.

#### Discussion

In tree improvement, precise and stable estimates of the genetic parameters that apply to the population of interest are very important for tree breeding programs. Although genetic parameters estimated from single-site data were widely reported and applied in tree improvement, heritabilities and correlations estimated for a particular site may be unreliable (COTTERILL and DEAN, 1990), overestimated (WHITE and HODGE, 1989), and not so informative for making early selection if reported without sufficient reference to the specific site conditions. These single-site genetic parameters are helpful

*Table 6.* – Selection efficiency, expressed as the ratio of correlated response in volume around one-half rotation age from a selection on height at different ages for the 1979, 1982, and 1983 jack pine series.

1979 series	Target trait: Vol20				
	HT5	HT7	HT10	HT14	HT20
DNR	2.51	2.09	1.81	0.95	0.54
GPC	2.70	1.93	1.84	1.08	0.71
JDI	2.23	2.12	1.17	0.76	0.68
Across-sites	2.93	2.15	1.51	1.02	0.74

1982 series	Target trait: Vol18		
	HT7	HT12	HT18
AFT	0.52	0.62	0.53
BCC	1.04	0.89	0.61
GPC	1.14	0.75	0.54
JDI	1.72	1.03	0.84
NBI	1.25	0.86	0.65
Across-sites	1.43	0.97	0.72

1983 series	Target trait: Vol19		
	HT7	HT12	HT19
BCC	4.85	1.31	0.58
GPC	1.29	0.76	0.53
JDI	1.95	0.92	0.92
NBI	0.56	0.32	0.29
Across-sites	1.54	0.88	0.54

in adjusting breeding value prediction because they may represent the environmental heterogeneity among sites (WHITE and HODGE, 1989). Large site-to-site variability in genetic parameters has been reported for other tree

*Table 7.* – Percentage of families correctly classified in upper quarter and half, based on parental breeding values, when selection is made based on early height to improve target trait (i.e., Vol20, Vol18 and Vol19 for the 1979, 1982, 1983 series, respectively).

Var.	Series	Upper Quarter			Upper Half		
		1979	1982	1983	1979	1982	1983
HT5		70%			82%		
HT7		75%	74%	80%	86%	87%	92%
HT10		83%			87%		
HT12			84%	88%		92%	96%
HT14		85%			92%		

species (JOHNSON et al., 1997; GWAZE et al., 2000; LAMBETH and DILL, 2001; JANSSON et al., 2003). Genetic parameters estimated from across-site analyses, which were referred to as “standard parameter estimates” by COTTERILL and DEAN (1990), were more reliable with low standard error. The results in this study support the above-mentioned inferences. Although large site-to-site variation in genetic parameter estimates was obvious, especially for  $h_i^2$ , the estimated genetic parameters from across-site analyses were relatively stable and generally of similar magnitude between the three test series. A  $h_i^2$  around 0.40 for height or 0.27 for volume at half rotation ages estimated from across-site analyses obtained in this study can be used as “standard heritabilities” for jack pine in New Brunswick. The  $h_i^2$  estimates in this study agree well with results for jack pine published elsewhere (RIEMENSCHNEIDER, 1988; MAGNUSSEN and YEATMAN, 1989a; KLEIN, 1995) and other jack pine progeny test series in New Brunswick (NBTIC Establishment Reports).

While no consistent time trend for single-site  $h_i^2$  was found, an increasing trend with age was true for across-site  $h_i^2$  for each series. The increasing trend may be an effect of competition or of increasing mortality with increasing age. FOSTER (1989) concluded that competition affects both variances and heritability. A general

increase with age of individual narrow sense heritability for height in other conifers has been reported (COTTERILL and DEAN, 1988; MCKEAND, 1988; HODGE and WHITE, 1992; BALOCCHI et al., 1993; JANSSON et al., 2003), and others have noted a non-linear, age-related trend (GWAZE and BRIDGEWATER, 2002) or that it is fairly constant with age (XIE and YING, 1996; SVENSSON et al., 1999; HAAPANEN, 2001). Information on age-related trends for jack pine is scarce. RIEMENSCHNEIDER (1988) found that individual narrow sense heritability estimates for jack pine were fairly constant, around 0.2, from age 3 up to age 7. MAGNUSSEN and YEATMAN (1989a) found a slight increase in jack pine individual narrow sense heritability for height from 0.13 at age 6 to 0.18 at age 14.

The time trends for  $CV_A$  in this study are in agreement with observations in other pine species, e.g. Scot pine (JANSSON, 1998; HAAPANEN, 2001; JANSSON et al., 2003), maritime pine (COSTA and DUREL, 1996), ponderosa pine (NAMKOONG and CONCLE, 1976), and loblolly pine (FOSTER, 1986).

In this study, age-age genetic correlations for height were impressively high, and this is not surprising because all the sites and plus trees were within the same breeding zone. The results, especially the high correlations between tree height at early and late ages, suggest that the genes involved in early age height growth appear to be similar to those affecting growth at half-rotational age and show the potential for selecting jack pine at a young age in New Brunswick. The age-age genetic correlations in this study were in close agreement with estimates for jack pine reported by RIEMENSCHNEIDER (1988), but higher than those reported by MAGNUSSEN and YEATMAN (1989a).

A model that can predict the genetic age-age correlations involving ages not assessed is necessary for early selection. The most common model used to predict age-age correlations is the model developed by Lambeth (1980), in which age-age phenotypic correlations predicted by the age ratio ( $LAR$ ) were used as an approximation of genetic age-age correlations. Later study suggests that  $LAR^2$  was a better prediction variable than  $LAR$  for genetic age-age correlations for loblolly pine (LAMBETH and DILL, 2001). Results in this study agree with their findings. Using  $LAR^2$  yielded a somewhat better fit in most of the combinations, especially when the models were developed from across-site or series-combined analyses (Table 5). However, such superiority of  $LAR^2$  over  $LAR$  has not been found in other conifers (GWAZE and BRIDGEWATER, 2002; XIE and YANCHUK, 2002). Compared with the LAMBETH and DILL (2001)  $LAR^2$  equation ( $r_g = 1.02 - 0.098(LAR_2)$ ,  $r^2 = 0.47$ ), model [11] in this study had slightly lower values for both intercept and slope. In other words, for given age-to-age combinations, jack pine has a very similar juvenile-mature genetic correlation as predicted by the LAMBETH and DILL (2001) equation.

It is interesting to note the effects of site on model parameters. The estimated regression intercept in both  $LAR$  and  $LAR^2$  models was similar in size from site to site and from series to series, suggesting site has low

effects on coefficient 'a'. The regression slope varied greatly in size in both single-site  $LAR$  and  $LAR^2$  models, although the variation was low for the latter. Some sites showed a slight decrease and others showed a sharp decrease for genetic correlation with increasing age interval. However, with one exception, models developed from across sites within each series and across series showed very similar and stable intercept and slope, and this is especially true for  $LAR^2$  models. These results indicate that models developed from single-site data may be unreliable and applicable only for specific site conditions. Some of  $LAR$  models from single-site data analysis in this study (Table 5) agree very well with the RIEMENSCHNEIDER (1988) model ( $r_A = 1.07 + 0.177(LAR)$ ,  $r^2 = 0.93$ ) for jack pine, but others, especially those based on across-site analyses, had a slightly lower slope (Table 5). This is not surprising because the Riemenschneider (1988) model was developed on the basis of only up to 7-year-old tree data from one site.

Besides age-related heritability and age-age genetic correlation, information on genotype-by-environment interaction should be considered when deciding the optimum age for selection (LOPEZ-UPTON et al., 1999). When genotype-by-environment interaction variance is large, earlier selected families may perform differently from site to site, so testing or breeding strategies should be modified to address this. This study indicated that the average type-b genetic correlations were high and at a constant level at different ages for each series, suggesting early selection may be appropriate for a wide range of environments in New Brunswick. Others have found an increasing trend in type-b correlations over age, with older ages yielding higher type-b correlations (DIETERS et al., 1995; JOHNSON et al., 1997) or a relatively constant level (HODGE and WHITE, 1992).

In this study we have used volume at one-half rotation ages as the selection criterion. Results in this study indicate that both backward and forward early selection for jack pine in New Brunswick could be effective. High genetic correlations between height growth at early age (e.g., at age 5 or 7) and volume around one-half rotation age (Table 4 and Figure 1) should explain this observation. Although the highest selection efficiency was achieved at the first measurement year, i.e., age 5 or 7, the true optimal age could potentially be even earlier. Thus, the current practice in New Brunswick of making parental selection at 7 years seems to be conservative. No information regarding early selection for jack pine has been reported except by RIEMENSCHNEIDER (1988), who suggested that selection as early as age 1 would be an efficient strategy for improving jack pine rotation-age growth.

In conclusion, single-site genetic parameters for height varied from site to site, but across-site ones were relatively stable across series. Age-age genetic correlations for height were well described by the linear model using  $LAR^2$  as the independent variable. Using volume at one-half rotation ages as the target trait, early selection at 5~7 years with a time lag of 5 years for the breeding phase could obtain higher selection efficiency than those from direct selection.

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## Book-Review

**Flora der Gehölze. Bestimmung, Eigenschaften, Verwendung.** Von A. ROLOFF und A. BÄRTELS. 2006. Verlag Eugen Ulmer, Stuttgart, ISBN 3-8001-4832-3. 844 Seiten mit 2350 Zeichnungen. Gebunden. 29,90 EUR (D); 30,80 EUR (A); 52,20 SFr.

The second edition of this flora identifies about 4000 species and varieties of woody plants, both conifers and broadleaves, and bamboo species grown in forest parks and gardens in Central Europe.

The first chapter describes how to use this guide. The remaining introductory sections provide further information on woody plants. Nomenclature and classification explains how plants are classified and the use of both scientific and popular names. This section is followed by a glossary of botanical terms. The use of woody plants is explained and endangered species are listed. Finally, there are keys to help you to identify any genus before turning to the descriptions of the species. The expertly written descriptions provide full details of structure,

distinguishing features such as leaves, flowers and fruit, and information on distribution and winter hardiness. About 2350 of the species are illustrated by a precise line drawing showing the leaf. Specific characters are additionally pointed out. In some cases the nomenclature is not common (for example *Quercus robur* ssp. *sessiflora*) – the co-author A. BÄRTELS is using *Q. petraea* in all of his books.

New in this edition is the key to identify deciduous plants in the winter. An index of the German plant names and the corresponding scientific names is given at the end of the book.

The handy book is fascinating by the comprehensive descriptions – a separate recommendation is unnecessary.

*Title: „Flora of woody plants. Identification, attributes, use“.*

M. LIESEBACH (Waldsiedersdorf)