Variation, Inheritance and Correlations of Growth Characters and Melampsora Leaf Rust Resistance in Full-Sib Families of Populus

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Abstract

Genetic variation of *Populus* for growth traits and resistance to *Melampsora* leaf rust (MLR) was assessed at ages 1 and 2 in the nursery and 4 in the field. Two females of *Populus deltoides* and 2 males each of *P. deltoides*, *P. nigra*, and *P. maximowiczii* were employed as parents of the controlled crosses. Generally, the *P. deltoides* x *P. maximowiczii* crosses had greater growth and were more resistant to MLR than the *P. deltoides* x *P. nigra* (DxN) and *P. deltoides* x *P. deltoides* crosses. However, 1 DxN family had the highest MLR resistance at all ages and diameter growth at age 4. The variation in growth and in particular, the resistance to MLR, was under fairly strong genetic control. Of the genetic effects, the males were the most prominent. The male and female interaction (dominance) was about one-third that of the male effect. The one exception was the resistance to MLR at age 4 when there was predominance of dominance effect. These results indicate that the genetic effect in this study was mainly additive. The estimates of narrow-sense heritability were moderate (0.48) to high (0.98) for MLR resistance and low (0.17) to moderate (0.62) for growth. With a single exception, the standard errors for heritabilities were smaller than the estimates themselves. The genetic correlations between first-year height and all other nursery traits were negative and high. In contrast, the genetic correlations between second-year height and all other traits were positive and varied between moderate (0.34) to high (0.88). The genetic correlations were also larger than their corresponding phenotypic correlations. These results suggest a significant contribution of the environmental variance to the performance of intra- and inter-specific crosses of *Populus*. The genetic correlations suggest the possibility of simultaneous selection for fast growth and high resistance to MLR. The genetic/phenotypic correlations among MLR resistance at different ages were very strong (0.91 to 1.0), suggesting a feasibility of early selection for this trait.

Key words: Poplars, breeding, intraspecific and interspecific hybrids, quantitative genetics, heritability.

FDC: 165.53; 443; 181.6; 232.1; 172.8 *Melampsora*; 176.1 *Populus*.

Introduction

Populus L. species and hybrids (Salicaceae) are multipurpose trees and are capable of fast growth. *Populus deltoides* BARTR. ex MARSH. (section *Aigeiros* DUBY) and its hybrids, especially those with *P. nigra* L. (section Aigeiros), and *P. maximowiczii* HENRY (section *Tacamahaca* SPACH.), are suitable for short rotation intensive forestry and agroforestry (Anonymous, 1979; DICKMANN and STUART, 1983). *Populus deltoides* and its hybrids with *P. nigra* constitute the majority of the cultivated poplars of the world (Anonymous, 1979). *Populus deltoides* x *P. nigra* hybrids, *P.* x *canadensis* MOENCH syn. *P. x euramericana* (DODE) GUINIER, are considered among the earliest cultivated forest trees (ZSUFFA, 1975). Therefore, *P. deltoides, P. nigra,* and *P. maximowiczii* are important for the breeding of hybrid poplar cultivars and varieties for intensive poplar culture programs, and many breeding programs concentrate on *P. deltoides* crosses with *P. nigra* and *P. maximowiczii* (DICKMANN and STUART, 1983). The geographical natural range of *P. deltoides* is in North America, that of *P. nigra* in Europe and western Asia, and that of *P. maximowiczii* in eastern Asia (Anonymous, 1979).

The main traits of interest for improvement in poplar breeding programs include growth, disease resistance, rooting ability of stem cuttings, and climate tolerance (ZSUFFA, 1975). Leaf rust caused principally by *Melampsora medusae* THUM. in North America, is one of the commonest, most serious, and widely distributed foliage diseases of *P. deltoides*, its hybrids and other poplars (DAVIDSON and PRENTICE, 1968; SCHIPPER, 1976; Anonymous, 1979). This disease can significantly affect the survival and growth of poplar plantations, thus, is an important trait to be incorporated in a *P. deltoides* breeding program (JOKELA and MOHN, 1976).

A thorough understanding of genetic control of the traits is required to facilitate their improvement by breeding. Also, information on genetic correlations among the traits, and relative performance of different intraspecific and interspecific hybrids for the traits of interest is needed to facilitate effective breeding. Variation, inheritance and correlations of several growth, phenological, wood and/or morphological characters had been determined in *P. deltoides* (WILCOX and FARMER, 1967; FARMER and WILCOX, 1968; FARMER, 1970a, and b; MOHN and RANDALL, 1971; NELSON and TAUER, 1987) and *P. nigra* (ZSUFFA, 1974). All of these studies were based on either clonal tests or open-pollinated family tests, in which additive genetic variance could not be separated from non-additive genetic variance. Inheritance of *Melampsora* leaf rust (MLR) resistance had also been determined in *P. deltoides* based on clonal tests (WILCOX and FARMER, 1967; FARMER and WILCOX, 1968), open-pollinated progeny tests (FARMER, 1970b; NELSON and TAUER, 1987) and *in-vitro* screening for infection of leaf disks of full-sib F_1 progeny (PRAKASH and HEATHER, 1986, 1989). MLR resistance was found to be under strong genetic control in this species. Resistance to MLR was also examined in full-sib families of controlled crosses between and within *Populus tremula* L. and *P. tremuloides* MICHX. (GALLO et al., 1985). There is no information on genetic variation, heritability and correlations of traits of interest in controlled interspecific hybrids of *P. deltoides* with *P. nigra* and *P. maximowiczii.*

Although *P. deltoides* x *P. nigra* and *P. deltoides* x *P. maximowiczii* are considered to have improved fast growth and other characteristics, and many breeding programs concentrate on these crosses, there is no information on their relative performance for different traits. In a growth chamber test, *P. deltoides* x *P. nigra* clones showed more vigorous growth than *P. deltoides* and *P. nigra* clones (CAINE and ORMROD, 1983).

The objective of this study was to determine the relative performance of full-sib progeny of intraspecific *P.*

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deltoides and interspecific *P. deltoides* x *P. nigra*, and *P. deltoides* x *P. maximowiczii* controlled crosses and genetic parameters for growth traits and MLR resistance. In this paper, we present results on genetic variation, heritability, and genetic and/or phenotypic correlations of growth traits and MLR resistance of these intraspecific and interspecific hybrids of *Populus* at ages 1 and 2 in the nursery and age 4 in the field.

Materials and Methods

Parents and controlled crosses

Two females of *Populus deltoides* (D17 and D32), and 2 males each of *P. deltoides* (D476 and D477), *P. nigra* (N166 and N167), and *P. maximowiczii* (M10 and M11) were employed as parents of the controlled crosses. These parental trees/clones were selected randomly. Parental trees are registered in these accession codes at the Ontario Forest Research Institute (OFRI), Ontario Ministry of Natural Resources, Maple, Ontario. Three *P. deltoides* parental clones (D17, D476 and D477) were from a natural population at Cherry Beach in Toronto, Ontario, and the fourth (D32) was from Ottawa, Ontario. Both *P. nigra* parents originated in Hungary, and both *P. maximowiczii* parents originated in Japan.

Twelve controlled crosses were made in March to April, 1983 at the OFRI by following a factorial mating design in which 2 females of *P. deltoides* were controlled-pollinated with 2 males each of *P. deltoides, P. nigra*, and *P. maximowiczii.* The pollen of the 6 male parents was collected by using the pollen-forcing technique (Rajora, 1986). The controlled pollination was done on the female flowers of *P. deltoides* on bottle-grafted twigs placed in the greenhouse as described in Rajora (1986). Hybrid seeds were collected, dried and cleaned manually. The cleaned seeds were stored in a desiccator over $CaCl_2$ in a freezer until they were germinated.

Seed germination and seedlings in the greenhouse

The hybrid seeds were germinated at the end of June, 1983 in sterilized silica sand in Petri dishes. The seedlings were then transplanted into Leach tubes (Ray Leach Container Nursery, Canby, OR) filled with "Promix" (a mixture of 60% peat moss, 20% perlite, and 20% vermiculite) and arranged in flats kept in the greenhouse. The seedlings were grown in the greenhouse until the last week of September, when these were transferred to a shade house for overwintering.

Nursery test

The overwintered healthy seedlings of 9 full-sib families were transplanted at the 1 m x 1 m spacing in the nursery test at Maple, Ontario in May, 1984 in a randomized complete block design. These 9 full-sib families included 4 *P. deltoides* x *P. deltoides* (D17 x D476, D32 x D476, D17 x D477, and D32 x D477), 3 *P. deltoides* x *P. nigra* (D17 x N166, D17 x N167, and D32 x N167), and 2 *P. deltoides* x *P. maximowiczii* (D17 x M10, and D17 x M11) families. The remaining 3 full-sib families (D 32 x N166, D32 x M10, and D32 x M11) could not be included in this test because of unavailability of required number of healthy seedlings from these families. The nursery test consisted of 576 F_1 progeny of 9 families in 4 blocks, each block consisting of 4 4-tree plots of each family. The plots were completely randomized within a block. Two border rows of the same plant material were planted. The test site was well prepared. The plantation was regularly watered and mechanically weeded.

The nursery test was conducted for 2 years. Data were recorded on total height of each plant at the end of the growing seasons in 1984 and 1985 at the age of 1, and 2 years, respectively, diameter at the root collar (DRC) at the end of the growing season in 1985, and *Melampsora* leaf rust incidence on a 0 (no spores on leaves) to 10 (all leaves covered with *Melampsora* spores and/or leaves fallen or dead) scale at the time of peak rust incidence in 1984 and 1985. Data were also recorded on internodal lengths in the first year towards the end of the growing season. For this purpose, 2 plants per plot per family were randomly chosen. Three internodes in the middle portion of a plant were measured.

Field test

Healthy F_1 hybrid seedlings of 8 full-sib families (D17 x D476, D17 x D477, D32 x D477, D17 x N166, D17 x N167, D32 x N167, D17 x M10, and D17 x M11) were transplanted from the nursery to a field test at Maple, Ontario in the spring of 1986. D32 x D476 family did not have required number of healthy surviving plants for the field test. The field test was conducted in a randomized complete block design with 4 blocks. Each block consisted of 5 2-tree plots of each family. Two border rows of the same plant material were planted. The plots were completely randomized within a block. The test site was well prepared.

Data were recorded on DRC and *Melampsora* leaf rust incidence (visually on a 0 to 10 scale) at the age of 4 years in 1987.

Data analysis

Melampsora leaf rust (MLR) resistance was calculated as 10 — scored rust incidence for each plant, and the data was tested for normality. Analysis of variance and covariance for a random model tested the hypotheses about the significance of parent and cross-related effects for growth traits and MLR resistance and also for the purpose of estimating variance and covariance components for these effects. The statistical analysis for individual plants was:

$$Y_{ijkl} = \mu + b_i + f_j + m_k + fm_{jk} + e_{ijk} + w_{ijkl}$$

where

Y_{ijkl} = the lth plant of the jk family in the ith block;
μ = the grand mean;
b_i = the ith block (i = 1, ..., 4);
f_j = the jth female (j = 1, 2);
m_k = the kth male (k = 1,..., 6);
fm_{jk} = the jkth family;
e_{ijk} = residual error;
w_{ijkl} = the within-plot error.

Assuming no linkage, inbreeding and epistasis, the components of variance among pollen parents (σ_m^2) or among seed trees (σ_f^2) estimate one-quarter of the additive genetic variance. The component of variance among full-sibs (σ_{fm}^2) estimates one-quarter of the dominance genetic variance. Individual tree heritabilities (h_i^2) were estimated as $h_i^2 = 2(\sigma_m^2 + \sigma_f^2)/(\sigma_w^2 + \sigma_e^2 + \sigma_{fm}^2 + \sigma_m^2 + \sigma_f^2)$, where σ_w^2 and σ_e^2 are the within-plot, and residual variance components, respectively.

ANOVA was also conducted for a random model for growth traits and MLR resistance to estimate variance and covariance components for effects due to blocks, families, families x blocks and error. Family heritabilities (h_f^2) were estimated according to Wright (1976) as $h^2_f = \sigma_F^2/(\sigma_F^2 +$

$\sigma_{Fb}^2/_b + \sigma_e^2/_{Nb}$), where σ_F^2, σ_{Fb}^2, and σ_e^2 are variance due to families, families x blocks, and error, respectively; and b, and N are the number of blocks, and plants of a family in a block, respectively.

Standard errors of individual tree (h_i^2 and family (h_f^2) heritabilities were calculated according to BECKER (1984).

The ranking of the families and the hybrids of *P. deltoides* x *P. deltoides* (DxD), *P. deltoides* x *P. nigra* (DxN), and *P. deltoides* x *P. maximowiczii* (DxM) for each growth trait and *Melampsora* rust resistance was determined by conducting the DUNCAN's Multiple Range Test at $\alpha = 0.05$.

Results

Nursery: first-year

All 4 intraspecific full-sib families of *P. deltoides* (DxD) exhibited significantly better height growth than the interspecific *P. deltoides* x *P. nigra* (DxN) and *P. deltoides* x *P. maximowiczii* (DxM) full-sib families. On average, they grew 25.6%, and 21.3% taller than the average of DxN, and DxM, respectively (*Table 1*). The DxD intraspecific crosses were less resistant to the MLR than all the DxN and DxM interspecific crosses, but intra- and interspecific variation to the MLR resistance was apparent (*Table 1*). On an average, DxM, and DxN had the longest, and shortest internodal length, respectively (*Table 1*). There was, however, great variation in internodal length within the DxD, and DxN crosses.

Nursery: second-year

The rank for height changed significantly in the second-year relative to that at first-year (*Table 1*). On an average, the DxD crosses were at the same height as the DxN crosses but were significantly shorter (23%) than the DxM crosses. The D32xD477 at 195.6 cm, and D17xM10 at 262.1 cm were the shortest, and tallest families, respectively, but great variation in height within the intra- and interspecific crosses was apparent. The variation pattern for DRC was similar to that for the height (*Table 1*). The average of the DxD and DxN crosses was similar. However, the DxD crosses were, on average, 24% less in DRC than the DxM crosses. There was a great variation in DRC within the DxD and DxN crosses. There was a significant decrease in the resistance to MLR at second-year (*Table 1*). Nevertheless, the interspecific crosses were still significantly more resistant than the intraspecific crosses. The most resistant interspecific cross (D17xN166) was 242% better than the least resistant cross (D32xD476).

Field test: fourth-year

On an average, the interspecific crosses exhibited more DRC than the intraspecific crosses (*Table 1*). There was, however, great variation within the DxD and DxN crosses. The pattern for MLR incidence and the ranking of crosses for MLR resistance at age 4 in the field were similar to that of MLR resistance at age 2 in the nursery. On an average, the DxN and DxM crosses were significantly more resistant to MLR than the DxD crosses. Of particular interest was good DRC for D17xN166 and the fact that it maintained its superiority for MLR resistance in the field.

Genetic parameters

The results of the analysis of variance are summarized in *table 2*. For growth traits, the largest percentage of the variance was due to the within-plot effect. It accounted for 64 % (height at second-year) to 91 % (DRC at fourth-year) of the total variance. The within-plot variance for resistance to MLR at 35 % (age 2) to 41 % (age 1) of the total was also one of the most prominent effect. The effect owing to the blocks was significant for height in the first year and for resistance to MLR in the first and fourth years. However, it accounted only for about 3% of the total variance. The residual effect was significant for the internodal length, height at age 2, and first- and second-year resistance to MLR, but it accounted only for 3 % (MLR resistance at first-year) to 11% (MLR resistance at second-year) of the total variance.

Of the genetic effects (*Table 2*), the effect owing to the males was highly significant and the most important, accounting for 9 % (DRC at fourth-year) to 41 % (MLR resistance at second-year) of the total variance. The effect owing to the females was significant only for the internodal length and the first- and second-year resistance to MLR. Its percentage variance varied from 2 (internodal length) to 11 (MLR resistance at first-year) of the total variance. The variance component owing to male and female interaction (dominance) was significant for second-year height, second-year DRC, and first- and fourth-year resistance to MLR. The percentage variance for male-female interaction was about one-third that of the male effect for most traits. The one exception was the fourth-year resistance to MLR, which, at 31%, was greater than the male effect.

The estimates of individual and family heritabilities for the different traits are in *table 2*. The DRC at age 4 had the lowest estimate while the resistance to MLR had the highest estimate of individual heritability. On an average, the resistance to MLR, and DRC were, respectively, the most (0.77) and the least heritable (0.21) of the traits investigated. As expected, the estimates of family heritability were greater than the corresponding estimates of individual heritability. The greatest increase was for the DRC, the trait with the lowest individual heritability. The standard errors for individual heritability varied from about one-half to three-fifth of the size of the estimate. The one exception was the fourth-year resistance to MLR with standard error slightly above that of the estimate of individual heritability. The standard errors for family heritability varied from about one-eighth to one-half the size of the estimate.

The phenotypic and additive genetic correlations, based on individual trees, among the nursery traits are in *table 3*. Phenotypically, the first-year height correlated positively with the second-year height and DRC, but negatively correlated with the resistance to MLR. Genetically, however, the first-year height was negatively correlated with all the other traits. The second-year height showed strong and positive phenotypic and genetic correlations with the DRC. It also exhibited moderate and positive phenotypic and genetic correlations with the resistance to MLR, The first- and second-year resistance to MLR had a perfect genetic correlation and they exhibited positive but low genetic and phenotypic correlations with the DRC. Also, of interest was the greater genetic correlation relative to that of the phenotypic correlation for all the traits. The standard errors of genetic correlations varied among the traits, ranging from 0% to 180% of the estimates and averaging 58%.

At age 4 in the field, the MLR resistance had positive but moderate genetic correlation (0.572±0.356) with the DRC. The phenotypic correlation (0.32) was smaller than the corresponding genetic correlation.

Table 1. — Means a) and (coefficient of variation) for growth characters and *Melampsora* leaf rust resistance of *Populus* families and hybrids. D x D = *P. deltoides* x *P. deltoides*, D x N = *P. deltoides* x *P. nigra*, D x M = *P. deltoides* x *P. maximowiczii*, DRC = diameter at root collar.

Family/Hybrid	Inter-nodal Length (cm)	Height (cm)		Diameter (mm)		*Melampsora* Leaf Rust Resistance (0-10 Scale)		
		First-year	Second-year	Second-year DRC	Fourth-year DRC	First-year	Second-year	Fourth-year
(A) FAMILIES								
D17xD476	2.51 BC (28.6)	64.3 A (15.1)	207.10 CDE (8.8)	26.30 C (12.8)	55.00 C (17.0)	7.70 E (15.8)	2.10 FG (57.2)	1.90 E (38.5)
D32xD476	2.75 A (27.3)	64.20 A (12.0)	197.90 E (14.1)	26.60 C (14.1)		6.70 F (22.2)	1.90 G (66.1)	
D17xD477	2.40 CD (21.8)	63.90 A (15.5)	214.30 CD (14.4)	26.50 C (19.2)	59.50 BC (15.4)	8.20 D (10.8)	3.20 E (43.8)	3.10 D (37.7)
D32xD477	2.73 A (21.6)	60.60 A (16.9)	195.60 E (15.1)	25.90 CD (20.2)	61.90 AB (17.7)	7.90 DE (17.1)	2.50 F (67.6)	1.70 E (53.5)
D17xN166	2.27 D (29.8)	52.10 BC (21.2)	197.60 E (15.8)	27.00 BC (20.9)	66.90 A (18.1)	9.50 A (7.5)	6.50 A (34.5)	6.40 A (38.0)
D17xN167	2.05 E (27.7)	50.20 BC (20.4)	202.30 DE (15.7)	23.90 D (20.4)	59.70 BC (20.9)	9.00 C (6.7)	4.10 D (29.8)	3.40 D (39.4)
D32xN167	2.42 CD (24.9)	48.80 C (24.5)	218.70 C (18.3)	29.00 B (22.1)	65.10 AB (22.5)	9.50 AB (5.7)	5.40 BC (21.2)	4.40 C (49.0)
D17xM10	2.65 AB (25.9)	54.00 B (16.2)	262.10 A (15.4)	33.60 A (24.3)	65.80 AB (19.0)	9.20 BC (9.0)	5.10 C (35.7)	4.90 BC (28.9)
D17xM11	2.83 A (22.9)	50.50 BC (26.8)	238.90 B (23.9)	31.70 A (32.7)	62.50 AB (25.9)	9.30 AB (6.6)	5.70 B (18.6)	5.30 B (25.7)
(B) HYBRIDS								
DxD	2.60 B (25.7)	63.30 A (15.0)	203.80 B (13.7)	26.30 B (16.8)	58.70 B (17.2)	7.60 B (17.8)	2.40 B (61.1)	2.30 B (49.9)
DxN	2.25 C (28.2)	50.40 B (22.1)	206.00 B (17.2)	26.60 B (22.6)	63.90 A (21.0)	9.30 A (7.0)	5.30 A (35.4)	4.70 A (49.8)
DxM	2.74 A (24.5)	52.20 B (21.9)	250.60 A (19.9)	32.70 A (28.6)	64.10 A (22.5)	9.20 A (7.9)	5.40 A (28.1)	5.10 A (27.3)

a) means followed by the same letter in vertical columns are not significantly different at $P<0.05$.

Table 2. — Percent components of variance and heritability estimates for growth characters and *Melampsora* leaf rust (MLR) resistance of poplar families.

Trait	σ^2_b	σ^2_f	σ^2_m	σ^2_{fm}	σ^2_e	σ^2_w	h^2_i	h^2_f
Internodal length	1.4	2.3**	12.6***	0	3.7**	80.0	0.302±0.151	0.811± 0.121
First-year height	3.3**	0	30.1***	0	1.1	65.5	0.621±0.339	0.953±0.266
Second-year height	0.5	3.9	18.6***	6.6*	6.0***	64.4	0.452±0.293	0.911±0.261
Second-year DRC	0	0	12.1***	8.4**	0	79.5	0.241±0.201	0.936±0.177
Fourth-year DRC	0.2	0	8.5**	0	0.7	90.8	0.170±0.103	0.696±0.085
First-year MLR resistance	3.9**	10.7***	30.6***	10.7**	3.4***	40.7	0.861±0.521	0.968±0.464
Second-year MLR resistance	0	8.5***	40.5***	6.0	10.5***	34.5	0.980±0.551	0.980±0.489
Fourth-year MLR resistance	3.2*	0	23.0***	30.6***	3.2	40.0	0.478±0.596	0.996±0.530

Note: *) $P < 0.05 > 0.01$; **) $P < 0.01 > 0.001$; ***) $P < 0.001$; σ^2_b, variance due to blocks; σ^2_f, females variance; σ^2_m, males variance; σ^2_{fm}, females x males variance; σ^2_e, residual (plot error) variance; σ^2_w, within plot varince; h^2_i, individual tree heritability; h^2_f, family heritability; DRC, diameter at root collar.

Table 3. — Genetic (r_A) and phenotypic (r_P) correlation coefficients, based on individual trees, among growth characters and *Melampsora* leaf rust (MLR) resistance of poplar families in the nursery. Note: DRC, diameter at root collar.

		First-year height	Second-year height	Second-year DRC	First-year MLR resistance
Second-year height	r_A	-0.489±0.093			
	r_P	0.298			
Second-year DRC	r_A	-0.560±0.321	0.884±0.111		
	r_P	0.310	0.818		
First-year MLR resistance	r_A	-0.979±0.016	0.434±0.338	0.251±0.456	
	r_P	-0.433	0.130	0.088	
Second-year MLR resistance	r_A	-0.965±0.027	0.343±0.367	0.356±0.423	1.000±0.000
	r_P	-0.332	0.207	0.239	0.521

Since the identities of individual trees within the full-sib families were not retained between the nursery and the field tests, their correlations were based on the family means (*Table 4*). With the exception of the first-year height, all of the traits were positively correlated to each other. One important observation is the strong and positive correlations between the MLR resistance in the field and that at ages 1 and 2 in the nursery.

Discussion

There is potential for genetic improvement of growth and MLR resistance through interspecific breeding of *Populus deltoides* with *P. nigra* and *P. maximowiczii*. This is particularly true for the DxM hybrids that generally exhibited greater growth and more resistance to the MLR than the intraspecific DxD and the interspecific DxN crosses (*Table 1*). However, 1 DxN family (D17xN166) had the highest MLR resistance at all ages (1, 2, and 4), and diameter growth at age 4. Inferior height growth of interspecific DxN and DxM hybrids as compared to the intraspecific DxD hybrids in the first year in nursery suggests that hybrid vigour for this trait was not expressed in the first year but was expressed in the second year and later stages of the growth.

The data suggest that variation in growth and in particular, the resistance to MLR, is under fairly strong genetic control (*Table 2*) and accordingly, should be responsive to selection. The block and residual effects were most likely due to the within-nursery heterogeneity with respect to variability to light, irrigation, and mechanical weeding and their influence on the microenvironment. Of the genetic effects, the males were the most prominent.

Table 4. — Phenotypic correlation coefficients, r_P, based on family means of growth characters and *Melampsora* leaf rust (MLR) resistance in the field with these characters in the nursery. Note: DRC, diameter root collar.

	Fourth-year DRC	Fourth-year MLR resistance
First-year height	-0.659	-0.722
Second-year height	0.317	0.401
Second-year DRC	0.520	0.540
First-year MLR resistance	0.772	0.908
Second-year MLR resistance	0.829	0.978

This greater effect of the males relative to that of the females is expected since there was greater number (6) and diversity (3 species) of the male parents relative to the 2 female parents from *P. deltoides.* The proportionately low male and female interaction (dominance) as compared to the male effect, except for MLR resistance at age 4 in the field, indicates that the genetic effect for most traits in this study was mainly additive. The results of resistance to MLR ages 1 and 2 agree well with those found in the factorial crosses of *P. tremula* and *P. tremuloides* clones, where additive effects in the inheritance were found at the end of the first and second vegetation period (Gallo et al., 1985).

The heritability estimates for MLR resistance in our study are similar to those reported earlier for *P. deltoides* based on clonal and/or open-pollinated progeny tests (Wilcox and Farmer, 1967; Farmer and Wilcox, 1968; Farmer, 1970b), but higher than the mean family heritability estimate (0.38) reported by Nelson and Tauer (1987) for an open-pollinated progeny test. Also, the heritability estimates for growth traits are similar to those reported for *P. deltoides* (Wilcox and Farmer, 1967; Farmer and Wilcox, 1968; Farmer, 1970a, and b; Mohn and Randall, 1971; Nelson and Tauer, 1987).

The estimates of heritability appropriate for mass selection were moderate to high, except for the DRC measurements (*Table 2*). The estimates for MLR resistance were particularly high, ranging from 0.45 at age 4 to 0.98 at age 2. The lower estimate at age 4 was due to the predominance of the dominance genetic effect. If this dominance variation was the result of hybrid vigour, it might suggest that its expression at the later stage of growth was probably related to developmental homeostasis in response to the heterogeneous environment in the field (Lerner, 1954). The greatest increase for estimates of family heritability relative to individual tree heritability was in DRC, the trait with the lowest individual heritability. With a single exception of the resistance to MLR at age 4, the standard errors for heritabilities were smaller than the estimates themselves. The large standard error of individual heritability for resistance to MLR at age 4 was probably due to the prevalence of a dominance genetic effect. In addition, a greater number of the female and male parents would be needed to increase the precision of this factorial test (Pederson, 1972). In view of the fact that the heritability appropriate for mass selection is high for MLR resistance and moderate for height growth, the gains from screening MLR resistant and outstandingly tall clones/trees in plantations and/or wild stands would be substantial if trends in variance components and family ranks continue. Thus, mass selection would be effective for a long-term breeding program to increase the height growth and resistance to MLR in *Populus.*

There is a pattern of higher genetic correlations than the corresponding phenotypic correlations (*Table 3*), especially for the second-year height with the first-year resistance to MLR. Most likely, this is due to greater negative environmental correlations between the traits. The pattern for height growth was different at ages 1 and 2 (*Table 3*). The genetic correlations between first-year height and all other nursery traits were negative and high. Thus, an early selection at age 1 in the nursery for height could not be combined with the other nursery traits. In contrast, the genetic correlations between second-year height and all other traits were positive and varied between moderate to high. These results suggest a significant contribution of the environmental variance to the performance of intra- and inter-specific crosses in *Populus.*

The perfect genetic correlation for MLR resistance between the first- and the second-year, (*Table 3*) and high phenotypic correlations of MLR resistance at age 4 to that at ages 1 and 2 (*Table 4*) suggest that effective selections can be made for MLR resistance during the first year of growth in the nursery. The improvement of both height and resistance to MLR can be effective at age 2 due to the positive and moderate genetic correlation (0.34) between these traits and their moderate (0.45) and high (0.98) heritabilities. In comparison, the simultaneous improvement of DRC and resistance to MLR will be less effective, due to the low heritabilities of DRC (0.17 and 0.24) and their moderate genetic correlations (0.36 and 0.57) to MLR resistance.

Our results suggest that in future improvement of *Populus,* great care should be placed on the selection of clones, such as from the interspecific crosses between *P. deltoides* and *P. maximowiczii,* and *P. deltoides* and *P. nigra.* We observed great variation among families within interspecific crosses, particularly in DxN crosses for MLR resistance, and among individuals within families. Therefore, significant genetic gains could be made by family and within family selection. In addition, a combination can be achieved between the fast growth and high resistance to MLR by selective breeding of MLR resistant clones with high ability for growth, particularly for the DxM clones. Whether the pattern of growth and MLR resistance at the young age in our study will be maintained as the trees mature is unknown. Our estimates for genetic parameters for growth traits and MLR resistance are based on parents coming from different species. Evolution of *Melampsora* rust populations adapted to interspecific poplar hybrids in due course may require re-estimation of these genetic parameters in future, assuming that the *Melampsora* rust populations, at present, are adapted to the species but not the hybrids. We feel, however, that the estimates presented here will be valuable for selective breeding purposes, when used with due caution. The assessment of this field trial will be continued to monitor possible trends in variance components and family ranks that could influence the estimates of genetic parameters.

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Rooting Acacia mangium Cuttings: Effects of Age, Within-Shoot Position and Auxin Treatment

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Summary

The possibilities of vegetatively propagating *Acacia mangium* through rooted cuttings were examined, focusing on 3 main factors, namely: (i) the age of the donor plant, comparing 6-month-old seedlings to sprouts from a mature stump, (ii) the original within-shoot position of the cutting before collection and (iii) the auxin treatment applied to the cuttings. These 3 factors were shown to influence greatly the capacity of the cuttings for rooting. The best scores in terms of rooting rates were obtained for the plant material collected from (i) the seedlings, (ii) the upper part of the shoot close to the terminal bud and (iii) when treated with auxin. The only interaction confirmed by statistical tests was between the age of the donor plant and the auxin treatment, with a greater auxin induced increment of the rooting rates for the cuttings from seedlings.

The results obtained tend to demonstrate that, although capable of improvement by optimizing the investigated factors, the potential of *Acacia mangium* to be propagated by rooted cuttings remains rather limited, especially when starting from mature material.

Key words: *Acacia mangium*, adventitious rooting, auxin, **cuttings**, maturation, vegetative propagation, within-shoot position.

FDC: 165.44; 161.4; 232.5; 176.1 *Acacia mangium.*

Introduction

Acacia mangium Willd., an arborescent species belonging to Leguminosae (Mimosoideae), is native to northern Australia (Queensland), western parts of Papua New Guinea and eastern provinces of Indonesia (Irian Jaya and Maluku) from sea level up to 720 m (Gunn and Midgley, 1991). It has been recognized as a valuable forest tree species since its initial introduction into Sabah (Malaysia) in 1966, where it has been demonstrated to thrive quite well, even on very acid and infertile soils whose fertility can be restored thanks to its natural nitrogen fixing ability. In such poor but rather frequent site conditions, it has been shown to outperform all the other fast growing forest tree species, especially in situations of proliferating weeds with which it competes successfully. The early vigorous growth of this short-lived pioneer enables it to reach commonly 20 m to 25 m in height within 10 years to 15 years in Sabah, with a wood production averaging 25 m^3/ha/year to 30 m^3/ha/year, despite the mediocre genetic value of the material planted so far (Sim, 1986). Owing to this remarkable potential, which accounts for the establishment of industrial plantations all over South-East Asia mainly for pulpwood production, it appears obvious as a matter of urgency to concentrate efforts on tree improvement of *A. mangium* with a view of improving the genetic quality of the planting stock. Progress in that field is just beginning and although simple breeding strategies based on sexual propagation seem objectively well adapted to the situation (Monteuuis and Nasi, 1992), the vegetative propagation option is also worth special attention. Theoretically, it can be used for mass "bulk" vegetative propagation of a restricted number of juvenile genotypes of presumably high genetic value — derived for example from controlled pollinations — (Wong and Haines, 1992), or for producing clones, either to establish clonal seed-orchards, or to develop clonal plantations, especially from genotypes selected from clonal tests of advanced generation families