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Genetic variation of Melampsora leaf rust resistance in progenies of crossings between and within Populus tremula and P. tremuloides clones

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Summary

A total of 49 families of controlled crosses between and within *Populus tremula* and *P. tremuloides* were investigated concerning their resistance to *Melampsora* leaf rust, presumably caused by *M. magnusiana.* The leaf rust attack was evaluated at the end of both the first and the second vegetation period and showed highly significant genetic variation between the interspecific crossings. The *P. tremuloides* families showed the highest resistance, *P. tremula* families were severely attacked. The interspecific hybrid families showed an intermediate behaviour. A quantitative genetic analysis of the data showed strong additive genetic variation. Therefore, *Melampsora* leaf rust resistance might be incorporated successfully into further breeding programs in aspen and hybrid aspen.

Key words: Populus tremula, P. tremuloides, inter- and intraspecific crossings, *Melampsora* leaf rust, resistance, additive genetic effects.

Zusammenfassung

Insgesamt 49 Familien aus kontrollierten Kreuzungen zwischen und innerhalb der *Leuce*-Pappelarten *Populus tremula* und *P. tremuloides* wurden nach der ersten und zweiten Vegetationsperiode auf Blattrostbefall bonitiert. Untersuchungen an verschiedenen Entwicklungsstadien des Parasiten ergaben, daß *Melampsora magnusiana* als Erreger dieser Rostkrankheit in Betracht kommt. Zwischen den Kreuzungsfamilien bestanden hoch signifikante Befallsunterschiede. *P. tremuloides*-Familien zeigten die größte Resistenz gegen den Pilz, *P. tremula*-Familien waren dagegen am stärksten befallen. Die interspezifischen Hybridfamilien verhielten sich intermediär. Eine quantitativ-genetische Analyse ergab, daß sich die Rostresistenz wie ein quantitatives Merkmal verhält, d.h. sie wird offenbar durch zahlreiche Gene mit additiver Wirkung vererbt. Die Selektion blattrostresistenter Elternbäume führt demnach zu resistenteren Nachkommen. Rostresistenz kann daher mit Erfolg in die weiteren Züchtungsprogramme bei Aspe integriert werden.

1. Introduction

The European aspen *Populus tremula* L. and the north American aspen *P. tremuloides* Michx. of the poplar section *Leuce* Duby, and their hybrids are fast growing hardwood species, which are used in the paper industry as well as for biomass and energy production. Aspens are valuable and tolerant forest tree species for marginal sites. Therefore, they are gaining more and more importance in silviculture. The interspecific hybrids between the two aspen species exhibit often a better growth performance than the parent species, as many hybridization programs have shown (Melchior and Seitz 1966, Hattemer and Seitz 1967, Melchior 1985, Weisgerber 1983).

In connection with the testing of the general performance also the behaviour against the more important fungal diseases should necessarily be known. Aspens can be attacked by a wide range of leaf, twig, branch, and stem diseases (Butin 1957, FAO 1979). One of the commonest, most serious, and widely distributed leaf disease of aspens is the *Melampsora* leaf rust, caused by several species (Gremmen 1954, Pinon 1973, FAO 1979, Butin 1983), which are difficult to distinguish morphologically. Heavy rust infection can result in an early leaf fall, a reduction of increment, an increase of susceptibility to winter frost, an easy entry to other parasites, and a higher mortality of young plants (Butin and Zycha 1973, FAO 1979, Schwerdtfeger 1981, Phillips and Burdekin 1982, Butin 1983). But poplar species show a high genetic variation of resistance to *Melampsora* rust species. These differences should be integrated into breeding programs of aspen.

In the following paper results are given on the genetic variation of *Melamsora* leaf rust infection of crossings between and within *Populus tremula* and *P. tremuloides.* The crossings were made originally with the purpose to study growth performance of families, combining ability and possible heterosis. Results on such traits will be published elsewhere (Gallo and Melchior, in preparation).

2. Materials and Methods

2.1. *Origin of the aspen clones*

For the crossing experiments five female and three male clones of *P. tremula,* and two female and four male clones of *P. tremuloides* were used. The origin of the parent trees is shown in *Table 1.* The clones were selected phenotypically on the basis of their growth performance, stem form

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Table 1. — The parent clones of *Populus tremula* and *P. tremuloides.*

clone nr.	female	male	provenance
Populus tremula **L.**			
Brauna 11	x		Saxony, GDR
Groß-Dubrau 1	x		Saxony, GDR
Wedesbüttel 51	x		East Prussia, USSR
Wedesbüttel 52		x	East Prussia, USSR
Wedesbüttel 66		x	East Prussia, USSR
Wedesbüttel 95	x		East Prussia, USSR
CVS 52		x	Luborec, CSSR
C 61	x		Raztocno, CSSR
Populus tremuloides **Michx.**			
Ihlendieksweg 1		x	Maple, Ontario, Canada
Ihlendieksweg 3	x		Maple, Ontario, Canada
Ihlendieksweg 5	x		Maple, Ontario, Canada
T 428		x	Maple, Ontario, Canada
T 44-60		x	Upper Michigan, USA
T 141		x	New Hampshire, USA

and good combining ability, concerning especially cross fertility, in other breeding programs. Resistance to *Melampsora* leaf rust was no criterion for the phenotypic selection of these aspen clones. Therefore, for the purpose of the present study the trees were considered as random samples of the populations in respect to *Melampsora* leaf rust resistance.

The mother trees and most of the father trees are grown in the clonal archive of the Institute at Grosshansdorf. From the *P. tremuloides* clones T 44—60 and T 428 pollen was collected from selected trees in USA and Canada, respectively.

2.2. *Controlled pollination and mating design*

The clones had been crossed in the greenhouse in February and March 1983, according to a 7 × 7 factorial mating design *(Figure 1)*. The crossings resulted in 49 different families, which belong to four main mating groups, namely two intra- and two interspecific crossing groups.

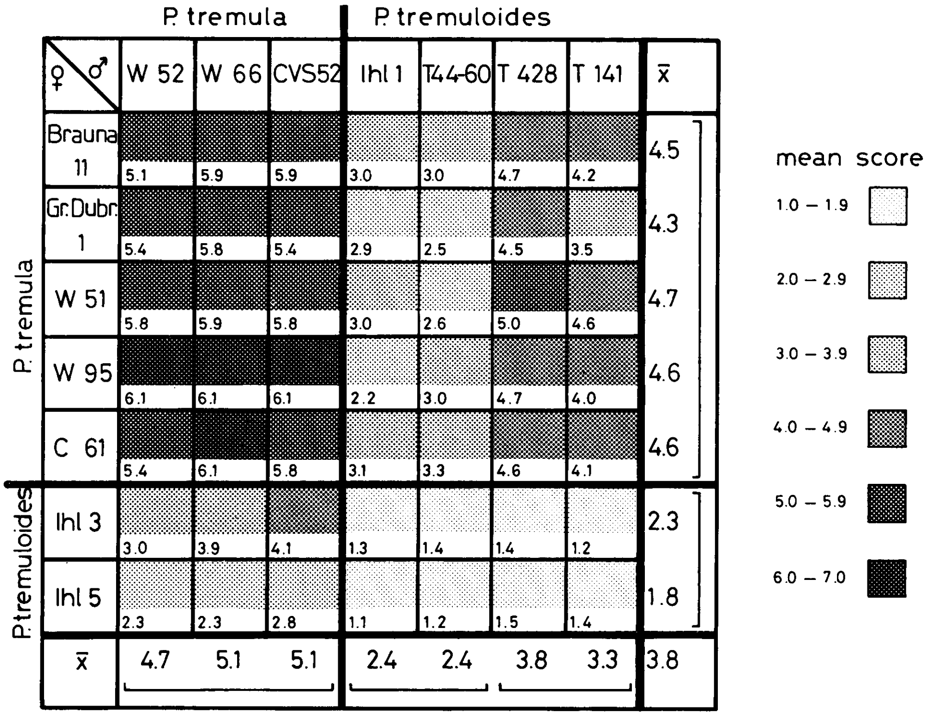
2.3. *Progeny test*

After sowing in May 1983 the seedlings were outplanted in a nursery trial in July 1983. The trial was located in Grosshansdorf, and was planted in a completely randomized blocks design with four replications, 6 × 5 plants of each family (= plot) in each replication, and with a spacing of 20 × 15 cm.

2.4. *Melampsora leaf rust attack*

The maximum of rust infected leaves was observed mostly in September, and the rust attack was scored at that time. In September 1983 only the average rust attack per plot was determined according to the following scale: 0 = no infection; 1 = less than 50% of the leaves of the plot were lightly infected (less than two uredinia per cm^2, single); 2 = more than 50% of the leaves of the plot were lightly infected; 3 = more than 50% of the leaves of the plot were strongly infected (more than two uredinia per cm^2, single or in groups).

The results of 1983 showed significant genetic variation between the families. Therefore, a more detailed examination of the individual trees of the families was conducted in September 1984. For that reason 24 trees per family (= six trees per plot) were scored. Each tree was assigned a single score value according to the following scale from 1 to 7: 1 = no infection; 2 = less than 10% of the leaves show individual uredinia; 3 = 11 to 30% of the leaves show several uredinia widely spread; 4 = 31 to 50% of the



	♀ \ ♂	W 52	W 66	CVS52	Ihl 1	T44-60	T 428	T 141	$\bar{x}$
		P. tremula			P. tremuloides				
P. tremula	Brauna 11	5.1	5.9	5.9	3.0	3.0	4.7	4.2	4.5
	Gr.Dubr. 1	5.4	5.8	5.4	2.9	2.5	4.5	3.5	4.3
	W 51	5.8	5.9	5.8	3.0	2.6	5.0	4.6	4.7
	W 95	6.1	6.1	6.1	2.2	3.0	4.7	4.0	4.6
	C 61	5.4	6.1	5.8	3.1	3.3	4.6	4.1	4.6
P. tremuloides	Ihl 3	3.0	3.9	4.1	1.3	1.4	1.4	1.2	2.3
	Ihl 5	2.3	2.3	2.8	1.1	1.2	1.5	1.4	1.8
	$\bar{x}$	4.7	5.1	5.1	2.4	2.4	3.8	3.3	3.8

mean score

1.0 – 1.9

2.0 – 2.9

3.0 – 3.9

4.0 – 4.9

5.0 – 5.9

6.0 – 7.0

Figure 1. — Mating design, mean infection scores of families, and female and male parents. Parents within a bracket do not differ significantly by Tukey's test ($\alpha = 0.05$).

Table 2. — Characters of *Melampsora* species of the *M. populina* complex on poplars of the section *Leuce* in central Europe.

species	uredinia	urediniospores			paraphyses				teliospores		alternate host	reference
	(mm)	form	length x width (µm)	wall (µm)	form	head length x width (µm)	length (µm)	wall (µm)	length x width (µm)	wall (µm)		
M. larici-tremulae Kleb.	0.5	oval to obovate	15-22 x 10-15	2	head oblong	8-17	40-45	3-5	40-60 x 7-12	1-2	Larix spp.	Gäumann (1959)
	--	oval to oblong	14-23 x 10-16	--	capitate, oblong	8-17	40-45	3-5	--	--	--	Pinon (1973)
	--	ovoid or globoid	14(20)24 x 13(15)19	2	claviform	16-18 x 14.5-16.5	52(59)67	3.2-4.2	--	--	Larix spp.	Cellerino and Anselmi (1979)
M. pinitorqua Rostr.	0.5	oval to elongate	15-22 x 11-16	2	head oblong	20-25 x 12-17	40-50	3-7	20-35 x 7-11	1	Pinus spp.	Gäumann (1959)
	--	ovoid to globoid	14-24 x 10-16	--	capitate	8-17	40-55	--	--	--	--	Pinon (1973)
M. rostrupii Wagner	1	oval, globoid to polygonal	18-25 x 14-18	3	globoid	15-23	50	3-6	25-40 x 5-12	1	Mercurialis perennis	Gäumann (1959)
	1	ovoid, globoid to triangular	17-28 x 14-18	--	capitate, globoid, elliptic	14-25	--	--	--	--	--	Pinon (1973)
	-	ovoid, globoid or angular	15(21.5)29 x 9(17)22	3	capitate, globoid	14-19 x 8-10	40(45)54	3-3.5	--	--	Mercurialis perennis	Cellerino and Anselmi (1979)
M. magnusiana Wagner	0.5	oval to oblong or polygonal	17-24 x 12-18	3	globoid	14-22	40-50	3-5	40-50 x 7-10	1-2	Chelidonium majus, Corydalis cava, C. solida	Gäumann (1959)
	--	ovoid, globoid to triangular	17-24 x 12-19	--	globoid, apex flattened	--	--	--	--	--	--	Pinon (1973)
	--	ovoid, globoid or elongate	9(12)19 x 7(10)15	3	digitate or capitate	14-24 x 13-22	38(45)54	4.5-5.5	--	--	Chelidonium majus, Corydalis solida	Cellerino and Anselmi (1979)
M. spec.	0.5	polygon. 32% elong. 19% elliptic 19% globoid 15% ovoid 15%	18(22)26 x 13(16)19	3.4	globoid, apex flattened	11(18.5)25	--	2(5)11	29(44)56 x 7.5(10)16	1.4	?	present study

leaves show many uredinia, single or in groups; 5 = more than 50% of the leaves are densely covered with uredinia; 6 = all leaves are densely covered with uredinia; 7 = many leaves are brown, dead or already dropped.

As most of the parent clones are growing in the clonal archive of the Institute, their rust attack also was scored in September 1984, using the same scale as for the families. The trees had different ages and grew at various places not far from the progeny trial.

For identification of the *Melampsora* species involved in the leaf disease, leaves with uredinia and urediniospores were collected in autumn, and with telia and teliospores in early spring. Fruitbodies and spores were measured microscopically and compared with data of other authors (e.g. Gäumann 1959, Pinon 1973, Cellerino and Anselmi 1979).

2.5. *Statistical model and methods*

In order to estimate the genetic components of variance the following statistical model, applied to plot means, was assumed:

$$y_{ijk} = \mu + f_i + m_j + fm_{ij} + r_k + e_{ijk}$$

where y_{ijk} = the average score from the cross of the i-th female and the j-th male in the k-th replication
μ = general mean
f_i = an additive effect of the female parent i
m_j = an additive effect of the male j
fm_{ij} = a deviation effect of i x j cross
r_k = an effect due to the replication k
e_{ijk} = plot error,

and where all effects are considered random. The plot error e_{ijk} was divided into σ^2_p = variation due to the interaction between families and replications and into σ^2_w = within plot variation, which was estimated from plots in each cross in each replication and pooled.

The mating design used in this study was similar to the factorial design of experiment II of Comstock and Robinson (1952). Provide the following assumptions (Cockerham 1963) for the genes, which control the rust resistance, are right (1. regular diploid and solely Mendelian inheritance; 2. no environmental correlations among relatives; 3. no linkages; 4. the relatives are not inbred; 5. the relatives can be considered to be random members of some noninbred populations), it could be considered that $\sigma^2_f = \sigma^2_m = 1/4\ \sigma^2_A$ and $\sigma^2_{fm} = 1/4\ \sigma^2_D$, where σ^2_A is the additive genetic variance component and σ^2_D the dominance genetic variance component. Since our trial was established on only one location, in our case would be $\sigma^2_f = \sigma^2_m = 1/4\ (\sigma^2_A + \sigma^2_{AE}$ and $\sigma^2_{fm} = 1/4\ (\sigma^2_D + \sigma^2_{DE})$, where σ^2_{AE} and σ^2_{DE} include the variation due to a possible interaction between genotype × interaction.

For the statistical evaluation the software package GLIM (general linear interactive modelling) was used (Baker and Nelder 1978).

3. Results

3.1. *Identification of the Melampsora species*

Poplars of the section *Leuce* can be attacked by the collective species *Melampsora populina* (Pers.) Lev., which can be divided into several species. Four of them have some importance in Europe (*Table 2*). In most cases *Populus alba, P. tremula* and *P.* × *canescens* are reported as hosts. The four *Melampsora* species can be distinguished morphologically by various characters of their sori, spores and paraphyses. All *Melampsora* species are heteroecious with different alternate host species (*Table 2*), which are suited best for an exact differentiation. If alternate hosts are not available, the differentiation between the fungus species is restricted to spore forms on the poplar leaves, namely uredinia, urediniospores, telia, and teliospores. On this basis the identification of the *Melampsora* species involved in this study has been conducted. Measurements of the fungal structures with relevance to the taxonomic determination are given in *Table 2,* together with data of other authors for comparison.

The traits of our rust material correspond best with the descriptions for *Melampsora magnusiana* Wagner. Very similar characters show only *M. rostrupii* Wagner. But because of the small size of uredinia, size and flattened apices of paraphyses, and size of teliospores we consider the pathogen involved to be *M. magnusiana.* Furthermore, the two species can be distinguished by their alternate hosts *(Table 2),* but only *Chelidonium majus* occurs in the neighbourhood of the poplar trial. Continuous examination of *Ch. majus* plants for the occurrence of *Melampsora* aecidia and aecidiospores during the vegetation period 1984 remained unsuccessful.

It is known that *Melampsora* species can overwinter by mycelium in the host or by urediniospores on poplar leaves on the ground (Butin 1957, Chiba and Zinno 1960). Then, reinfection of the poplars are possible without the alternate host (Zycha 1962, Kraayenoord 1974). One example of this kind of overwintering was observed in 1984. Early in May, the terminal bud of one plant was heavily infected by the *Melampsora* rust. The rust spread on the peduncle of the freshly developped leaf, and from there gradually to other leaves of the respective plant and neighbouring plants. Similar situations were observed also in other plots of the trial. Therefore, we assume that the fungus had overwintered in its dicaryophase by mycelium on the living poplar plant. Additionally, overwintering by urediniospores on dead leaves can be assumed.

Because of the morphological characters studied, the rust fungus will be considered in the following as *Melampsora magnusiana* Wagner.

3.2. *Variation of leaf rust resistance between progenies*

The families show considerable phenotypic differences of the leaf rust attack *(Figure 1).* The mean score values of the families vary between 1.1 and 6.1 with at total average of 3.82 for the trial. In an analysis of variance the highly significant differences between the aspen families were proved *(Table 3).*

On the basis of their mean leaf rust scores the families of the four mating groups are in a good accordance. It be-

Table 3. — Analysis of variance for the different leaf rust scores of the aspen crossings (** : α = 0.01).

source of variation	d.f.	m.s.	variance component (abs.)	(%)
replications	3	1.61 **	---	---
families	48	10.98 **	---	---
female	6	42.52 **	1.490	39.6
male	6	40.56 **	1.420	37.8
female x male	36	0.79 **	0.111	3.0
rest	144	0.35	σ^2_p = 0.269 σ^2_w = 0.466	7.2 12.4

comes very clear that families with nearly no leaf rust infections belong to the intraspecific crossings between *P. tremuloides* clones. On the other hand, families with very high infection scores of more than 5.1 are typical for intraspecific crossings between *P. tremula* clones *(Figure 1)*. The families of interspecific mating groups show an intermediate behaviour to the leaf rust infection. The scores within the interspecific mating groups vary strongly.

Summarizing these results one can state that the *P. tremuloides* families of this trial show a very high resistance to this *Melampsora* species (possibly *M. magnusiana*), whereas the *P. tremula* families are highly susceptible. Interspecific crossings are attacked intermediately.

3.3. *Effect of aspen parents on the leaf rust resistance of progenies*

Considerable differences in the degree of leaf rust attack existed not only between the mating groups, but also between the families on the basis of all female and male parents *(Table 3)*. The variation between the families of a mating group was influenced very strongly by the *P. tremula* and *P. tremuloides* female and male clones used for the crossings. The total means of the families with a distinct clone as female or male parent vary within the respective mating group, particularly within the two interspecific ones *(Figure 1)*. There can clearly be seen that the reaction of a family is affected strongly by the female and male parent clone involved in the respective crossing. With regard to the parent clones two different female parent groups and three different male parent groups can be distinguished *(Figure 1)*. These groups show distinct and significant differences in relation to Tukey's test. All families with *P. tremula* as female parent are separated significantly from families with *P. tremuloides* as female parent. With regard to the male parents all families with a *P. tremula* male parent belong to one group. In the *P. tremuloides* families a group with male parents from Maple and Upper Michigan can be separated from another group with male parents from Maple and New Hampshire *(Figure 1)*.

Concerning the results in the families also the reactions of the original parent clones (grafts of the Institute's archive) were of great interest. The results agree very well with those of the families *(Table 4)*. Also in the older trees of varying ages the *P. tremuloides* clones showed high resistance to this *Melampsora* leaf rust, whereas the *P. tremula* clones were severely attacked. The reactions seem to be independent of the tree age and not to be affected during the vegetation period 1984 by site or other environmental conditions of the clonal archive investigated. Therefore, a juvenile-mature correlation could be assumed for the trait leaf rust resistance.

The scoring of the *Melampsora* leaf rust attack of additional aspen clones in the clonal archive of the Institute (data unpublished) was in good accordance with the previously reported results. Generally the *P. tremula* clones were much more attacked by *Melampsora* than the *P. tremuloides* clones.

3.4. *General and specific combining ability*

As already shown, the aspen parents had a direct and significant influence on the reaction of a given family to the *Melampsora* leaf rust. Therefore, a strong genetic effect for this trait can be assumed. The results show highly significant effects for female and male parents, which contribute to the total phenotypic variation with 39.6% and 37.8%, respectively *(Table 3)*. Although the analysis of variance showed a significant value also for the female × male interaction, its relative variance component was only 3.0% of the total variation. As the variance components for female and male effects correspond to the general combining ability (GCA) and that for the interaction to the specific combining ability (SCA), one can state that in this mating experiment GCA was of greater importance than SCA with respect to the trait leaf rust resistance, what can be seen also in *Figure 1*. These analyses show that an additive mode of gene action can be assumed for the *Melampsora* leaf rust resistance. The score means of the individual families are very well represented by the sum of their respective parent effects (see also *Figure 1*).

Table 4. — *Melampsora* leaf rust attack of parent clones of *P. tremula* and *P. tremuloides* as scored in the clonal archive at Grosshansdorf.

clone nr.	number of scored ramets	age of ramets	mean leaf rust score
Populus tremula			
Brauna 11	2 3 2	18 2 2	6 6 5
Groß-Dubrau 1	1 1 3 1	18 2 2 2	5 6 5 4
W 51	1 1 1	20 18 10	6 6 6
W 52	1 2 1	20 18 10	6 6 7
W 66	1	2	6
W 95	2	2	5
CVS 52	1	18	5
C 61	1	18	6
Populus tremuloides			
Ihl 3	1	2	1
T 141	1 1 6	20 18 2	1 1 1

3.5. *Correlations between traits*

The mean family rust scores were correlated with other characters, as height growth after the first and second vegetation period, and pubescence of the main shoot. There were significant positive and negative correlation coefficients between rust score 1984 and rust score 1983 ($r = 0.60$), height 1983 ($r = -0.70$), height 1984 ($r = -0.73$), and pubescence ($r = 0.77$). These results simulate a relation between the respective characters and the resistance. A more detailed analysis of the trait values of individual trees within a given family revealed that these correlations were masked by the specific traits of *P. tremula* and *P. tremuloides*. In this trial *P. tremula* families were slow growing, had pubescent shoots, and were extremely rust susceptible. On the other hand, *P. tremuloides* families were good growing, were smooth, and rust resistant. The individual trees, particularly those of the interspecific families, showed that these traits presumably are inherited independently. That should be investigated in further experiments.

4. Discussion

The results of these studies show that *Populus tremuloides* clones are highly resistant to *Melampsora* leaf rust, presumably caused by *M. magnusiana,* and that *P. tremula* clones are susceptible to the pathogen. The different behaviour of the aspen species against the *Melampsora* leaf rust was inherited to families of crossings between and within the two species. In these studies the rust resistance behaved as a quantitative character. The low dominance variance indicates polygenic inheritance and additive genetic effects (Falconer 1960), Therefore, *Melampsora* rust resistance is controlled presumably by a large number of genes, which have an additive effect, and can be called "horizontal" (Robinson 1976). This kind of resistance has mostly a higher security against racial variation in the pathogenicity of the parasite. The results agree very well with those in other *Populus-Melampsora*-systems, where also additive effects in the inheritance of rust resistance were found (e.g. Heather, Sharma and Miller 1979, Heather and Chandrashekar 1982, Zycha 1962).

Nevertheless, these results should not be generalized, because they are valid only for the test site. The reaction of the host plants can be influenced by differences in the pathogenicity of the parasite, by genotype-environment interactions, or by the age of the host plants. These relations must be studied before the concept of genetic gain in breeding for resistance can be realized (Stern 1972).

There is no knowledge about the pathogenic variability of *M. magnusiana.* Usually, rust fungi are very variable, and the occurrence of pathogenic races or biotypes is common. As the occurrence of pathogenic races has been proven in other *Melampsora* species (van Vloten 1944, Magnani 1966, Heather, Sharma and Miller 1979), they can be expected in *M. magnusiana,* too. Racial variation can be tested only with a set of aspen clones with different rust resistance on various sites. The reaction of the host plants can also be different, when the other closely related fungal species of the *Melampsora populina*-complex occur in a certain region. This should be investigated in the future together with the aspen breeding program.

In this connection also the genotype-environment interaction should be studied. It is known that resistance can be influenced very strongly by the environmental conditions. Heather and Chandrashekar (1982) pointed out that "in the *Populus-Melampsora* rust system the virulence and aggressiveness expressed by races and the resistance demonstrated by cultivars is very environmentally sensitive". *Populus-Melampsora*-systems show a high temperature sensitivity (Chandrashekar and Heather 1981a), and/or are influenced easily by the light intensity (Chandrashekar and Heather 1981b). The relationship between host and parasite is also dependent from the altitude (Cellerino and Anselmi 1979). In our trial a relatively high stability of the host-parasite relationship can be assumed, because the results of the very hot and dry summer 1983 agree very well with those of the cool and humid summer 1984. Also these results should be confirmed by further trials.

Finally, the observed rust resistance seems to be not affected and altered by the host age, and obviously even not by the age of the leaves. The latter was observed also by Cellerino and Anselmi (1979). Therefore, a strong juvenile-mature correlation in the parent clones can be assumed *(Table 4).* The genetic correlation of the resistance in different stages of host development of the aspen families could not yet be proved. However, an early selection regarding the trait leaf rust resistance seems to be possible and justified.

An estimation of the possible genetic gain was complicated by the failure of some of the genetic assumptions and by problems of the evaluation of score data. The estimation of the different variance components must be considered within these limitations, too. It is clear that on basis of these components high values for heritability would be expected, and even higher than one in the case of individual selection heritability. However, the great proportion of the genetic components compared with the environmental one and the correspondence between the family values within the four mating groups *(Figure 1)* show that the trait leaf rust resistance is under strong genetic control. It should be incorporated successfully into further breeding programs with aspen clones. After Thielges (1982) the breeding strategy ought to improve the host population rather than the individual host tree. In this way a better combination of resistance genes can be obtained and, therefore, better results of the breeding efforts can be expected.

Since many years it is known that some crossings between *P. tremula* and *P. tremuloides* show heterosis in growth characters (e.g. Wettstein 1933). But in contrast to the *Melampsora* leaf rust resistance, the growth characters of the here studied aspen and hybrid aspen crossings and of other ones show a great dominance variance (Gallo *et al.,* in preparation). In future breeding programs, therefore, a combination should be possible between rust resistance and high growth performance by the selection of rust resistant parent clones with high specific combining ability for growth. In other words, the great general combining ability of some parents in the *Melampsora* leaf rust resistance should be properly combined with the great specific combining ability of some parents for growth traits in order to obtain the most resistant and vigorous hybrid aspen families.

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Isozyme Differentiation of Upland and Lowland Picea mariana Stands in Northern Ontario

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Summary

Patterns of allozyme variation among naturally established upland and lowland black spruce (*Picea mariana* (Mill.) B.S.P.) stands were studied from five locations across northern Ontario. Variation in thirteen polymorphic enzyme loci (AAT2, ACO, ALD, GDH, 6PGD1, 6PGD2, LAP1, LAP2, MDH1, MDH2, MDH3, PGI and PGM) was assessed using electrophoretic analysis of gametophytic tissue. The average percentage of polymorphic loci was higher for the five lowland stands (57.3%) compared to the five upland stands (47.5%). In addition, the average heterozygosities of the lowland stands were slightly, but consistently higher ($h = 0.23$) than those of the upland stands ($h = 0.21$). Wright's F_{ST} values calculated over all loci indicated that upland stands were further differentiated from each other ($F_{ST} = 0.069$) than were lowland stands ($F_{ST} = 0.048$). Similarly, Nei's genetic distances were larger between upland stands than among lowland ones; the average distance between all upland/upland pairings was 0.027 as opposed to 0.016 for all lowland/lowland pairings. These results indicate that the five upland stands were more differentiated than the five lowland stands. Discriminant analysis of genotypic frequencies showed that 70 percent of the black spruce trees were correctly classified into upland and lowland categories. Genetic differences between upland and lowland sites may be related to differential survival of seedlings resulting from selective edaphic effects. The distribution of variation appears to reflect more stringent location-specific selection pressures on upland sites, in contrast to the generally more favorable survival conditions for seedlings on the five lowland sites. The greater heterozygosity in the lowland stands may reflect a need for more vigorous growth in response to greater nutrient stresses on trees after seedling establishment.

Key words: edaphic ecotypes, *Picea mariana*, isoenzyme variation.

Zusammenfassung

In natürlichen Hoch- und Tieflandbeständen von *Picea mariana* (Mill.) B. S. P. and 5 Standorten in Nordontario wurden die Variationsmuster der Allozyme untersucht. Die Variation von 13 Isoenzym-Loci (AAT2, ACO, ALD, GDH, 6PGD1, 6PGD2, LAP1, LAP2, MDH1, MDH2, MDH3, PGI und PGM) wurde mittels Gel-Elektrophorese an Endosperm-Gewebe untersucht. Der durchschnittliche Prozentsatz polymorpher Loci war für die 5 Tieflagenbestände höher (57,3 %) als für die Hochlagenbestände (47,5). Außerdem waren die durchschnittlichen Heterozygotiegrade der Tieflagenstandorte zwar geringfügig, aber beständig, höher ($h = 0{,}23$), als die der Hochlagenstandorte ($h = 0{,}21$). Wright's F_{ST}-Werte über alle Loci zusammen berechnet, zeigten, daß Hochlandbestände sich mehr voneinander unterschieden ($F_{ST} = 0{,}069$) als die Tieflandbestände ($F_{ST} = 0{,}048$). Ähnlich waren die genetischen Distanzen nach Nei zwischen Hochlandbeständen größer als zwischen Tieflandbeständen. Der mittlere genetische Abstand zwischen allen Hochland-Hochland-Paarungen war 0,027, gegenüber 0,016 für alle Tiefland-Tiefland-Paarungen. Diese Ergebnisse zeigen, daß die 5 Hochland-Bestände mehr differenziert waren als die 5 Tiefland-Bestände. Eine Diskriminanzanalyse genotypischer Häufigkeiten zeigte, daß 70% der untersuchten *Picea mariana* Bäume korrekt in Hoch- und Tieflandgruppen eingeteilt worden waren. Die genetischen Unterschiede zwischen Hoch- und Tiefland-Standorten können mit den verschiedenen Überlebensraten der Sämlinge, die aus den selektierenden Bodeneffekten resultieren, in Beziehung stehen. Die Variationsmuster scheinen einen stärkeren ortspezifischen Selektionsdruck der Hochlandstandorte, gegenüber den allgemein günstigeren 5 Tieflandstandorten widerzuspiegeln, die den Sämlingen dort generell bessere Überlebensbedingungen bieten. Der höhere Heterozygotie-

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