

Variability in the Genus *Populus* in Sensitivity to *Melampsora* Rusts

By J. PINON

Laboratoire de Pathologie forestière, I.N.R.A.—C.R.F.,
F-54280 Champenoux

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Summary

Several *Melampsora* species are responsible for poplar leaf rusts. Poplar species belonging to the same section (or to related sections) are generally subject to the same rust species, but it appears a large variability in poplar reaction to a defined rust at different genetic levels: species, provenance and clone. The present paper attempts to sum up the principal trends in this poplar variability in sensitivity to rusts.

While our knowledge is still short for *Turanga*, *Leucooides* and *Leuce* sections, much more is known on species belonging to the *Aigeiros* and *Tacamahaca* sections and their hybrids because of their world-wide use in poplar cultivation. Many data are available, even at the clonal level, versus rusts due to *M. allii-populina*, *M. larici-populina* and *M. medusae*. Attention is drawn on the importance for poplar breeding of the existence of physiological races within *M. larici-populina* and *M. medusae* that can counteract some resistances.

Key words: *Populus*, *Melampsora*, sensitivity, variability.

Introduction

The genus *Populus* is native to the northern hemisphere (North America, Europe, North Africa and Asia). Nearly forty species belong to this genus which is subdivided into five sections. Many fast growing poplar species have great potential ecological amplitude and have been successfully introduced in the southern hemisphere (South America, South Africa and Australasia). In native stands, poplar competes well with adversities, especially diseases, as a result of natural selection and a broad spectrum of genetic diversity. Up to now, no record exists of natural stands badly damaged by rust.

Quite early (17th and 18th centuries in Europe) farmers, and later tree-breeders, selected individual trees for faster growth, form and wood quality. Ease of vegetative propagation (dormant cuttings) of black and balsam poplars provided a means to quickly multiply such superior trees which were planted as genetically homogeneous stands. Such artificial plantations were infected by leaf rusts with more or less severity depending on sites and current year climate. With our present knowledge, it seems that most of the clones cultivated during the last two centuries in Europe were never immune, suggesting mainly a non-specific resistance. More recently tree-breeders have selected interspecific (sometimes intersectional) hybrids and some of these exhibited immunity but, this may be counteracted by the adaptation of physiological races, mainly of *M. larici-populina* and *M. medusae*. Year by year, genetic diversity of poplar is enhanced by new combinations, including crosses between allopatric species.

During the same time, diversity among rusts genotypes was explored and rusts (species, pathotypes) were transferred between continents. All those events expanded the scope and scale of interactions between various hosts and pathogens, increasing our knowledge on a world-wide scale, especially for sections *Aigeiros* and *Tacamahaca*.

Around the world, breeders and pathologists have collected observations on poplars' variability to rust, most of the time under natural infection in nurseries or plantations and in some occasions after inoculation in the laboratory. Only part of this huge amount of information is directly accessible and useful; many data have never been published (some tree-breeders records for instance) or rust species have not been identified. Available information must be accepted with some tolerance because severity of the disease is governed not only by host and parasite genotypes but also by ecological conditions, host physiology and nutrition and presence of other parasites and microorganisms. Also, rating methods and vocabulary are not standardized. In the following we refer most of the time to poplar terminology adopted by KRUSSMANN (1976.)

Sections *Turanga* and *Leucooides*

2.1. Section *Turanga*

Populus euphratica is the main species of this section and many others are often considered as local varieties. Because this species is not widely cultivated and also that natural stands occur often under arid climate (unfavourable to rust development) no general trends have been observed on its variability to rusts. *P. euphratica* is infected with *Melampsora pruinosae* in the Soviet Union (NASYROV, 1962) and China (ZENG DAPENG, 1986) and by *M. pulcherrima* (Anonymus, 1981). *M. tremulae* has been recorded by NASYROV (1962) on *P. ariana*.

2.2. Section *Leucooides*

Section *Leucooides* is native to Eastern Asia. In Japan (CHIBA, 1964) *P. lasiocarpa* tends to be susceptible or very susceptible to *M. larici-populina* but in New Zealand WILKINSON and VAN KRAAYENOORD (1975a, 1975b) introduced a clone which appeared resistant to *M. larici-populina* and was free from *M. medusae*, while *P. wilsonii* was susceptible to *M. larici-populina* and immune to the second rust.

Section *Leuce*

3.1. Subsection *Albidae*

Although native to Europe, North Africa and West Eurasia, white poplar has been introduced on all the continents, often for ornamental purposes or to take advantage of its tolerance to salt and drought. It also appears resistant to many major diseases including rust.

P. alba is free from *M. larici-populina* in Europe and Japan (CHIBA, 1964). This immunity is confirmed in New Zealand (VAN KRAAYENOORD, 1984) for several clones ('BO-2', 'I 40-57', 'I 42-57', 'I 49-51', 'I 59-1', 'Silver'), and varieties (*hickeliana*, *pyramidalis*, *tomentosa*¹⁾) and in Australia (SHARMA and HEATHER, 1976a) for clones (cv. '*caspiica*'),

¹⁾ Considered by some authors as closed to *P. x canescens* (LEMOINE, pers com.)

'marocco, 'maktar') and variety *hickeliana*. Immunity to *M. medusae* is the rule in the U.S.A. (OSTRY and McNABB, 1985) and also for the above clones and varieties in New Zealand and Australia, with the exception of *P. alba* var. *hickeliana* in Australia (SHARMA and HEATHER, 1977).

In Europe, OUDEMANS (1920) listed the common rust species found on *P. alba* as *M. larici-tremulae*, *M. pinitorqua*, *M. rostrupii* and *M. magnusiana*. *P. alba* is the main host of *M. pulcherrima*, a species confined to the Mediterranean margin. In Spain *M. castellana* was added to this list (CABALLERO, 1928) but was never confirmed. Those records are in agreement with data collected outside of the native range of white poplar: *M. larici-tremulae* on variety *bolleana* in China (SHANG and PEI, 1984) and Soviet Union (NASYROV, 1962), *M. aecidioides* (= *M. rostrupii*) in Himalaya (CUMMINS, 1943) and Pakistan (KAHN, 1954). In India, *P. alba* is slightly infected by *M. ciliata* (SUJAN SINGH et al., 1983).

3.2. Subsection *Trepidae*

European aspen (*P. tremula*) is free from *M. larici-populina* in Europe as in Japan (CHIBA, 1964) and New Zealand (VAN KRAAYENOORD, 1984) where the same clones ('CBG', 'FR 1', 'Nelson' and 'W.D.K.') were also free from *M. medusae*. *M. allii-populina* was recorded one time on aspen in Spain (LOSA ESPANA, 1945). *Melampsora* species infecting aspen in Europe are those already mentioned for white poplar (OUDEMANS, 1920; DUPIAS, 1965). To this list MAGNANI (1962) added *M. pulcherrima* after a successful inoculation. Most of the time those species are not very dangerous to aspen and the main problem lies in the contamination of pine with basidiospores emerging from overwintered aspen leaves infected with *M. pinitorqua*.

In North America, subsection *Trepidae* is mainly represented by *P. grandidentata* and *P. tremuloïdes*. In its native range, bigtooth aspen is subject to *M. abietis canadensis* and *M. medusae* (SINCLAIR et al., 1987). Artificial inoculation of *P. grandidentata* with *M. pulcherrima* was successful, while *P. tremuloïdes* was resistant (MAGNANI, 1962). Quaking aspen in North America is a host for *M. medusae* (HUNT, 1929; ZILLER, 1955).

Among asiatic species, *P. davidiana* was found infected with *M. magnusiana* (HIRATSUKA, 1941) and also *M. larici-*

tremulae in China after inoculation (SHANG and PEI, 1984). Reported as *P. sieboldii*, it resists *M. larici-populina* in Japan (CHIBA, 1964). Recently *P. sieboldii* was recorded as a host for *M. osmariensis* (BAGYANARAYANA and RAMACHAR, 1984).

3.3. Sectional hybrids

All the hybrids between clones belonging to sections *Albidae* and *Trepidae* exposed to *M. larici-populina* in Japan (CHIBA, 1964) and in New Zealand (VAN KRAAYENOORD, 1984; WILKINSON and VAN KRAAYENOORD, 1979) proved to be immune; they were also immune to *M. medusae*. Natural and artificial *P. x canescens* hybrids in Europe are subject to the same rust species as their parents. *P. davidiana* crossed with *P. alba* or with *P. x canescens* was successfully inoculated in China (SHANG and PEI, 1984) with *M. larici-tremulae*. Interspecific hybrid aspens (*P. tremula x P. tremuloïdes*) may be infected in Europe by *M. pinitorqua* (RENNERFELT, 1953) but they are free from *M. medusae* in the U.S.A. (OSTRY and McNABB, 1985). Such hybrids were studied in detail by GALLO et al. (1985) in Germany under infection due to *M. magnusiana* after they crossed eight aspens and six quaking aspens. Rating infection on a 1 to 7 scale, the average of all families was 3.82 with a very significant range of variation between families (from 1.1 to 6.1). The most resistant hybrid families were obtained by crossing quaking aspens and the most susceptible from crossing aspens. Resistance was genetically governed, exhibiting a strong general combining ability and also some specific combining ability. The low dominance variance indicates polygenic inheritance and additive genetic effects.

Section *Aigeiros*

4.1. *Populus nigra*

The most common rust species on *P. nigra* is *M. larici-populina*. In Europe, CELLERINO et al. (1986) compared 27 Italian provenances (350 clones altogether) for their reaction to *M. larici-populina* and *M. allii-populina*. It appeared difficult to distinguish provenances based upon resistance but, on the other hand, a large range of reaction was found between clones. In Belgium, probably under ambient *M. larici-populina* infection, STEENACKERS

Table 1. — Reaction of major clones to *M. allii-populina*, *M. larici-populina*, *M. medusae*.

	<i>M. allii-populina</i>			<i>M. larici-populina</i>								<i>M. medusae</i>			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CDN
<i>P. nigra</i>															
ITALICA		+													
FARSI			R	+		S	HR	VS	VS			NS	I/R		
POURTET			R	MS	R										
SEMPERVIRENS								VS	VS			NS	I/NS		
VEREECKEN			R		VS	VS									
<i>P. deltoïdes</i>															
CAROLIN			VS	MR	R										
CHAUTAGNE				MS/S									R		
FRIMLEY													S		
HARVARD			R	MR	R								R/S		
LINCOLN			I		I										
LUX			R	*	R								S		
MARQUETTE			R		R										
ONDA			R	R	R								S		
PEORIA			R	R	R										

P. x euramericana	M. allii-populina			M. larici-populina								M. medusae			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CDN
AGATHE F		MS		VS		VS									
ALLESTEIN			R		R	S/VS	MR								
ALTICHIERO				*					*				S/VS		
BELLINI		MS	R	MS/VS	MS				VS				VS		
BELLOTTO		MS	R	*	R										
BIETIGHEIM		MS	R	VS	S	VS	MR								
BLANC DU POITOU		+	R	*	R	MR/MS	R		S				VS		
BL COSTANZO		MS	MR	S/VS	MS				VS				S		
BOCCALARI		R	R	VS	MS				VS		MS/S		S		
BRABANTICA			S/VS	VS	R	*	R								
BRANAGESI		MR	MR		MR										
BUCHIG		MS	R	S	MR										
CAMPEADOR			R		R										
CANADA BLANC			R		MR									MS	
CAPPA BIGLIOWA		J	R		MS										
CARPACCIO		MR	R	*	R				*				VS		
CIMA		MS	S	*											
CULASSO		I		VS											
DOLOMITEN			R		MS	MS/S	R								S
DORSKAMP		MS/MR	MR	R	MR	R			I				R		
DROMLING			MR		MR	S									
ECKHOF		I		MR		R/MS	R			MR					
EUGENII		+		MR		*	MR	VS	VS			S	S	R	
FIEROLO			R		I				R				S		
FLACHSLANDEN		R	R	R	R	R	VR								
FLEVO		MS/R	R	I/R	I	R			I/R				R		
FLORENCE BIONDI		S		MS/VS		S									
FORNDORF		MR		MS		S	MR		VS						

	M. allii-populina			M. larici-populina								M. medusae			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CDN
GATTONI		R	R	S	MR										
GAVER		R	I	I	I										
GELRICA	S		S	MR/MS	R	*	MR		VS	R					
GHOY		I/MR	R	I	R										
GIBECO		MR	R	I	I										
GRANDIS	S	R			R	MS/S	MR			R					
GUARDI			MR						S				S		
GUARIENTO		R		S					S				VS		
MARFF		MR		MR		S	R		VS					S	
MEIDEMIJ		MR	R	VS	MS	VS	MR		VS						
I-30									VS				S/VS		
I-45/51		I/MR	R	S		S/VS			VS	R	S		VS	R	
I-65									VS				VS		
I-74-D									S				VS		
I-78									VS				VS		
I-92/40						NR	NR		S				VS		
I-154		I/R	MR*	R	R	R	VR/R	*	R	VR		*	R		
I-214		I/MR	R	S	MR	MS	R	*	S	MR/S	MR/MS	*	VS		
I-262		R	R	S	MR	MS	MR								
I-455		R		S/VS		R/MS	MR	*	VS	MR/S		*	VS		
I-488			R		MS	MS/S	R/MR	VS	VS			VS	VS		
ISIERES		MR	R	*	R										
JACOMETTI			R		I	MS	R			MR/S				R	
LAEVI GIATA			R		MR				VS				S		
LAMPERTHEIM		S				VS									
LEIPZIG	S	S	MS	MS	VS	S/VS	R		VS	S/VS			S		
LINGENFELD		I	R		MR/MS	MR									
LONGHI									S				S		
LONS		MS	VS	+	R	MS/S	MR								
LUISA AVANZO		I	R	*	R				*				VS		

	M. allii-populina			M. larici-populina								M. medusae			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CDN
MARILANDICA			MS		R	S	MR		VS						
NEGRITO DE GRANADA									VS					R	S
NEUPOIZ	MR	I	MS	MR/MS	R	MR/MS	R		VS						
NE 222		MS	MS	MS			VS								
OGY		R	R	*	I									R	S
OSTIA			R		MR	VS									
PACHER			R		R				S			VS			
PAN			R		MS										
PRIMO		MR/S	S	I	R										
REGENERATA	MR		MS		R	*		VS	VS	MR		VS	S		S
RINTHEIM		MS	R		MR										
ROBUSTA	R	MS/S	R	S/VS	MR	S	S		VS	MR			R		S
SAN GIACOMO			R		MS										
SAN MARTINO			R	MR/MS	R				R		MR/MS		S		
SCHIAVONE									S			MS	S		
SEROTINA	S					VS		S	VS	R/VS			VS		
SPIJK				*		MS			I				VS		
STECKBY		R		MS		S									
TARDIF DE CHAMPAGNE		MS		S/VS		S/VS	MR		VS						
TASMAN		MS		R					I				R		
TIEPOLO		MS	R	*	R				*				S/VS		
TRIPLO		MR	R	MR	R				R		MR		R		
VENEZIANO		MR	R	MR	R				R				VS		
VERONESE				*					*				S/VS		
VIRGINIE DE FRIGNICOURT		R		MS		MS	R								
VIRGINIE DE NANCY		+	R	S	R	S/VS	S								

	M. allii-populina			M. larici-populina								M. medusae			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CDN
P. trichocarpa															
BLOM			R	S	R	R									
COLUMBIA RIVER		I		S											
FRITZI PAULEY		I	R	MS	R	R/MS			S				I		
HEIMBURGER		I	R	MR	R										
TRICHOBEL		+	S/VS	MS/S											
P. maximowiczii x															
P. trichocarpa															
ANDROSCOGGIN	R	I	I	S	MS	MR/MS									
P. deltoides x															
P. trichocarpa															
BARN		I	R	I	I	MR			I				VS		
BORGH									I				VS		
DONK		I	R	I	R	R			I				VS		
NL 1656									I				R		
NL 1783									I				R		
P. trichocarpa x															
P. deltoides															
BEAUPRÉ		MR/S	R	I	R				I				S		
BOELARE		MS	R	I	R				I				VS		
HUNNEGEM		MS		MS/S					VS						
RAP		I	I	*	R										
RASPALJE		R/MS	R	MS	R				S				S		
UNAL		MR	I	S/VS	R				R				VS		
P. maximowiczii x															
P. berolinensis															
GENEVA	R		I			MR/MS	VR		S				R		
OXFORD	R					MR/MS			VS	VS			S		
P. maximowiczii x															
P. nigra															
ROCHESTER	R	I	R	S/VS	S	MS	R		VS				S		

	M. allii-populina			M. larici-populina								M. medusae			
	EUROPE			EUROPE				AUSTRAL.		ASIA		AUSTRAL.		N. AM.	
	A	F	I	F	I	NL	PL	AUS	NZ	J	K	AUS	NZ	USA	CND
P. deltoides x P. maximowiczii ERIDANO		R	I		R				R				R		
P. nigra x P. laurifolia STRATHGLAS									VS	VS				R	

Levels of resistance : I = immune, R = resistant, S = susceptible, V = very, M = moderately.

+ presence of the M. species on the clone

* reaction changing according to pathotypes

Geographical origin of the observations:

Europe : A = Austria, F = France, I = Italy, NL = the Netherlands, PL = Poland

Australasia : AUS = Australia, NZ = New Zealand

Asia : J = Japan, K = Korea

North America (N. AM.) : USA, CND = Canada

Origin of the records:

Austria: DONAUBAUER (1966).

France: TARIS (1968), LEMOINE et PINON (1978), LEMOINE, PINON, (1986), PINON (1986), PINON (1987), PINON and PEULON (1988), PINON TERRASSON (unpublished), PINON and BACHACOU (1984), PINON et al. (unpublished).

Italy: ANSELMI et al. (1986), BENES et al. (1986), MAGNANI (1965).

The Netherlands: VAN VLOTEN (1949), VAN DER MEIDEN (1961 and 1963), GULDEMOND (1966), KOLSTER (1967).

Poland: KRZAN (1978 and 1982).

Australia: SHARMA and HEATHER (1976 a and b), HEATHER et al. (1980).

New Zealand: WILKINSON and VAN KRAAYENOORD (1975), VAN KRAAYENOORD (1984), LATCH and WILKINSON (1980).

Japan: CHIBA (1964).

USA: OSTRY and McNABB (1985), WIDIN and SCHIPPER (1981).

Canada: HUBBES et al. (1983).

Korea: HWANG et al (1980), JEONG et al. (1981).

See complementary comments in § 4.3.

(1972a) rated clones between 2 and 5 on a 0 to 5 scale, while MUHLE-LARSEN (1964) found a few clones to be immune among collections in Grammont, Wageningen and Germany. In France, PINON and TEISSIER DU CROS (1976) compared clones from Czechoslovakia, Italy, Hungary, Rumania, French Alps and selections from the Rhône, Loire and Garonne Valleys. The Hungarian clones appeared more infected and the best clones came from the Rhône and Durance valleys. Within the Alps, the percentage of infected leaves ranged between 38% and 75% among the various progenies tested. A positive and significant correlation was established between parents and progenies within the alpine families. Most of the time, the level of infection (mainly due to *M. larici-populina*) of the progenies was intermediate between those of their parents. Only in a few instances was it higher than that of the most susceptible parent. In such cases, progenies were especially vigorous and it was thought that they are earlier infected by the inoculum. This large diversity of clonal reactions to *M. larici-populina* was confirmed in different countries. In Japan (CHIBA, 1964) six clones ranged from resistant to susceptible, in Poland (KRZAN, 1982) 25 clones were considered moderately resistant and 5 resistant. On the other hand, VAN KRAAYENOORD (1984) described 5 susceptible clones and 31 very susceptible. This contrast between the Polish and New Zealand data may reflect both diversity in clones and important differences in both inoculum pressure and in its date of onset. A few common clones were examined in the dif-

ferent countries and their comparative reactions are given in table 1.

M. allii-populina has been described several times on *P. nigra* in Europe, including its formae speciales *muscaridis-populina* (VIENNOT-BOURGIN, 1937). In France, among 61 clones submitted in 1974 to a mixed infection (*M. larici-populina* and *M. allii-populina*), none was infected only by *M. allii-populina* and five exhibited mixed infection while the majority were subject only to *M. larici-populina*. Clonal reactions to those two rusts are poorly correlated (CELLERINO et al., 1986). Records from Australia (SHARMA and HEATHER, 1976) denote some susceptibility to *M. medusae* while in New Zealand (WILKINSON and VAN KRAAYENOORD, 1979) *P. nigra* appeared resistant or immune. There is no relation between the reaction of clones to *M. larici-populina* and to *M. medusae*. Eleven clones of *P. nigra* var. *thevestina* from Turkey and three of *P. nigra* were judged susceptible to the former species in New Zealand, but also were resistant to the latter.

Outside of its native range, *P. nigra* may act as host for some other rusts: *M. ciliata* in India (SUJAN SINGH et al., 1983) and *Uredo tholopsora* in China (CUMMINS, 1951). MAGNANI added *M. pulcherrima* to this list after inoculation. Still to be confirmed is the presence of *M. rostrupii* (OUDEMANS, 1920).

4.2. *P. deltoides*

Because of its high value in poplar cultivation both as a pure species and, more often, hybridized with *P. nigra* or *P. trichocarpa*, *P. deltoides* has been carefully studied and much data are available from its native range and also from Europe and Australasia.

In North America, *M. medusae* is the major rust on eastern cottonwood. JOKELA (1966) described populations from the Mississippi River valley in southern Illinois as less susceptible than those from northern Illinois. Altogether 2 percent of the native populations were highly resistant and resistance was highly heritable. THIELGES and ADAMS (1975) examined 228 clones obtained from open pollinated progenies of 76 parent trees growing in a test in Ohio. The mother trees were selected along major river valleys in the northern species range. Highly significant differences appeared between female parent trees and within their progenies. Heritability (broad sense) was again high. Missouri and Illinois provided the most resistant families and clones, the most susceptible originating from Indiana, Ohio and Pennsylvania. Comparing 11 provenances, OSTRY and McNABB (1986) found a large range of reaction from immune (Indiana) to severe infection with defoliation throughout the crown (South Dakota). Slight infection characterized provenances from Northern Illinois, Pennsylvania and Kansas. Because of the limited and uneven distribution of *M. medusae* in Europe (South-

West of France, Spain and Portugal) limited information is available there. DUPIAS (1943) detected this rust on *P. deltoides* ssp. *angulata*. TARIS (1975) indicated that some cultivars ('Alabama', 'I 74-51', 'Carolin' and 'Angulata de Chautagne') were occasionally infected by *M. medusae*. Accidental introduction of this rust in Australasia gave rise to many observations, including some on European clones. In Australia (SHARMA and HEATHER, 1976) experimental clones ranged from resistant to very susceptible, with susceptibility being the most frequent situation. ELDRIDGE et al. (1973) compared 13 provenances (54 families). Very significant differences appeared within families (0% to 52% of healthy leaves) but there was only a minor effect between families. The best provenances came from the southern area: Louisiana, Tennessee and Southern Illinois.

Introduced in Europe, Asia and Australasia, eastern cottonwood is subject to leaf rust attacks due to *M. larici-populina* which are quite well documented. In Belgium, STEENACKERS (1972b) examined 3712 seedlings and, according to their origin, he found between 3% (Connecticut) and 75% (Iowa) of plants completely free from rust. Between individuals (STEENACKERS, 1972a) he established a full range of reaction from immunity to high susceptibility. Among many crosses (F1 and F2) he found two (S. 666 and S. 748) completely immune (STEENACKERS, 1972b). In the same country, MUHLE-LARSEN (1964) mentioned that *P. deltoides* provided more immune clones than the other North American related species (*P. sargentii*, *P. fremontii* and its var. *wislizenii*). In eastern cottonwood, he established that resistance was likely dominant and governed by two genes or more. In the Netherlands, KOSTER (1971) examined seedlings from 14 American states for their foliage diseases. There was a pronounced effect of geographical origin. Provenances from northern states (Dakota, Minnesota and Wisconsin) were very susceptible with the exceptions of Vermont and Massachusetts which were moderately resistant. Fair resistance was the rule in the central states (Kansas, Iowa, Illinois, Ohio) and in the southern states (Texas, Louisiana, Mississippi, Tennessee). From the middle western states, only Nebraska was considered susceptible. In France, PINON and TEISSIER DU CROS (1976), observing about thirty clones, got an asymmetric population in which resistance was predominant especially in Missouri clones. This diversity is confirmed in Poland (KRZAN, 1978 and 1982): *P. deltoides* ssp. *angulata* is described as a good source of resistant clones and ssp. *missouriensis* as an intermediate one. In Japan (CHIBA, 1964) a few clones subjected to infection were classified from resistant to susceptible. In Australia (SHARMA and HEATHER, 1976a) clones ranged from immune to very susceptible. Among the 68 clones tested in New Zealand by VAN KRAAYENOORD (1984) 41 were resistant, 16 susceptible and 11 very susceptible. For those clones there does not appear to be a clear relationship between their reaction to *M. larici-populina* and *M. medusae*, which means that selecting for resistance to both is feasible but also that resistance to one rust is not a guaranty of resistance to the other.

In the case of *M. allii-populina*, CELLERINO (1975) pointed out a relationship between resistance to this rust and geographical origin of the host. All the families below 38° latitude were totally resistant. Above this limit, families from Kansas, Nebraska and Minnesota proved to be quite susceptible. Clones well studied for reaction to

different rusts, including those clones often cultivated, are summarized in table 1.

Eastern cottonwood is also subject to *M. ciliata* in India (SUJAN SINGH, 1983). Closely related to eastern cottonwood, *P. fremontii* is subject to *M. larici-populina* in Europe (OUDEMANS, 1920), Japan (CHIBA, 1964) and Australia (SHARMA and HEATHER, 1976a) and to *M. allii-populina* in Czechoslovakia (LEONTOVYC, 1958).

4.3. *P. x euramericana*

At the end of the 17th century, some *P. deltoides* were introduced in Europe where they crossed naturally with the native *P. nigra*. Such hybrids, named *P. x canadensis* or *P. x euramericana*, were propagated, cultivated and still constitute the major basis of European poplar cultivation. Most of our knowledge deals with their behaviour to *M. allii-populina*, *M. larici-populina* and *M. medusae*. Many clones were exchanged and some are now represented on all continents, thus providing a large mass of information. We have tried to sum it up (Table 1) taking into consideration both old and recent selections, including some of practical use for cultivation and some mainly useful to pathologists who study both host and parasite variability. Most of the data come from field observations, sometimes complemented by results from inoculations, especially when clonal reactions are dependent upon the aggressiveness or virulence of rust pathotypes. Taken into account were only those records for which rust identification seemed quite exact. Sometimes, field contaminations resulted from a mixture of rust species, such as *M. allii-populina* and *M. larici-populina* in central and southern Europe, and *M. larici-populina* and *M. medusae* in Australasia. In such cases, cross-checking between different observations helped to determine the relative importance of the two rusts. Even for the same clone, scores from different authors are not necessarily strictly similar or directly comparable for several reasons such as time of observation, level of inoculum pressure, pathotypes, host physiology, previous infection with other foliar parasites (*Marssonina brunnea* for example) and methods and scales of rating symptoms. In many publications, numerical data were converted by the authors into a variable number (4 to 7) of qualitative classes. Such presentation is posted in table 1 as it was in the original publication. When data were presented only as numerical figures (for example in the Netherlands, Italy and sometimes in France) we converted the maximum level of infection reported in the experiment into value "100". Then the range 0 (immune) to 100 (heavy infection) was divided in six classes as follows: 0 = immune, 1 to 10 = resistant, 11 to 25 = moderately resistant, 26 to 50 = moderately susceptible, 51 to 75 = susceptible, 76 to 100 = very susceptible. When some diversity of reaction was described for specific clone x rust species interactions, we reported this information.

4.4. Other sectional hybrids

Two hybrids *P. fremontii* x *P. nigra sempervirens* examined in New Zealand (WILKINSON and VAN KRAAYENOORD, 1975b) were immune to *M. larici-populina*, one being susceptible to *M. medusae* and the second resistant. In Japan (CHIBA, 1964) and New Zealand (VAN KRAAYENOORD, 1984) *P. charkoviensis* x *P. nigra* were susceptible to very susceptible to *M. larici-populina*. In this last country, as in the U.S.A. (OSTRY and McNABB, 1985) no significant attack by *M. medusae* was recorded.

Section *Tacamahaca*

5.1. *Populus maximowiczii*

In Japan, CHIBA and NAGATA (1972) examined growth and infection by *M. larici-populina* of 30 clones derived from the progenies of artificial crosses. After eight years of observation, highly significant differences were found among clones which ranged between 2.0 and 4.9 on a 1 to 5 scale. Resistance was highly heritable (broad sense) and growth in diameter was correlated with infection severity. CHIBA (1984) studied 124 clones from four provenances (Northern Hokkaido, Kitami, Tokachi and Southern Hokkaido). A full range of scores was recorded among clones and the southern Hokkaido provenance was significantly more resistant availing the selection of 37% of the clones from this provenance. Eleven clones from Japanese origin tested in New Zealand (VAN KRAYENOORD, 1984) were generally resistant there despite a few that were found to be susceptible in earlier reports (WILKINSON and VAN KRAYENOORD, 1975 and 1979). In Belgium, STEENACKERS (1972a) obtained scores ranging between 2 and 4 while 3 clones observed in Poland were very resistant (KRZAN, 1982).

It seems that *M. allii-populina* has never been described on *P. maximowiczii* while *M. medusae* was found on it by HIRATSUKA (1939), but immunity to *M. medusae* is very common according to WILKINSON and VAN KRAYENOORD (1975 and 1979), VAN KRAYENOORD (1984) and SCHREINER (1951).

5.2. Other asiatic species

Other Asiatic species from the *Tacamahaca* section are quite often included in susceptibility tests but usually with a limited number of clones which does not provide statistical information on the variability of host reaction.

P. ciliata is subject to *M. ciliata* in Pakistan (QURAIISHI and JAMAL, 1969) and in India (SUJAN SINGH et al., 1983). Out of its native range this species is moderately resistant (KRZAN, 1982) to very susceptible (WILKINSON and VAN KRAYENOORD, 1975a) to *M. larici-populina*. This rust was also recorded on *P. koreana* in Japan (CHIBA, 1964) and on *P. laurifolia* and *P. suaveolens* (= *P. cathiana*) in Poland (KRZAN, 1982). MAGNANI (1962) did not succeed with positive inoculations of *P. koreana* with *M. pulcherrima*.

P. simonii and its var. *fastigiata* is mainly susceptible to *M. larici-populina* in Japan (CHIBA, 1964) and in New Zealand (WILKINSON and VAN KRAYENOORD, 1975a). In New Zealand *P. simonii* is also subject to *M. medusae* while *P. ciliata* and *P. laurifolia* are free from it.

P. szechuanica is resistant to *M. larici-populina* and immune to *M. medusae* (VAN KRAYENOORD, 1984). Different reports from New Zealand gave evidence of some variability within *P. yunnanensis* for reaction to *M. larici-populina* (resistant to susceptible) while it is resistant to *M. medusae*. In India (SUJAN SINGH, 1983) moderate infection is attributed to *M. ciliata*, and MAGNANI (1962) in Italy obtained infection with *M. pulcherrima* after inoculation. While all the authors who compared clonal reaction of different species between young and adult trees obtained a good correlation, WILKINSON and VAN KRAYENOORD (1979) mentioned that one male clone of *P. yunnanensis* susceptible to *M. larici-populina* in the nursery was very resistant when older.

5.3. *P. trichocarpa*

In its native range, black cottonwood is essentially infected by *M. occidentalis* (ZILLER, 1955) though some records

deal with *M. medusae* (HEPTING, 1971) or its synonym, *M. albertensis* which was not successfully inoculated by MOLNAR and SIVAK (1964). HSIANG et al., (1985) explored the variability of reaction of 14 clones to various isolates of *M. occidentalis*. No interaction between clones and isolates appeared despite significant differences among host and rust genotypes.

M. allii-populina is uncommon on *P. trichocarpa*; we found in France only light infection on one clone while examining about 900 genetically different individuals. The most dangerous rust in Europe is without any doubt *M. larici-populina*. Several authors described wide variability in reaction to this rust among provenances, families and individuals. In Belgium, STEENACKERS (1972a) scored clones between 2 and 5 on his 0 to 5 scale and described variability between clones of the same family (full-sib). Most of the seeds introduced by KOSTER (1986) in the Netherlands gave rise to susceptible plants but some resistance was detected in a limited number of seedlings from British Columbia, Washington, Oregon, Idaho and Montana. This effect of geographical origin on the reaction to *M. larici-populina* was also documented in Germany and France. From seeds collected at 79 sites in the U.S.A. and Canada, WEISGERBER (1975) concluded that infection was nil or slight in the coastal provenances while continental provenances were heavily infected, notwithstanding a few exceptions. PINON (1976 (unpublished) recorded important and significant differences between provenances with a marked susceptibility (up to the death of one year old cuttings) of provenances from east of the Cascade mountain range. Nevertheless, even within very susceptible families there was opportunity to select individuals with useful tolerance. In Poland, among 22 clones, KRZAN (1982) described one as very resistant, two resistant, 4 moderately resistant, 13 susceptible and 2 very susceptible. In New Zealand (WILKINSON and VAN KRAYENOORD, 1975b; VAN KRAYENOORD, 1984) the trend was the same: susceptibility: sometimes high, is the rule but it is generally possible to detect some resistant clones. Most of the clones studied were immune or resistant to *M. medusae*. Only one clone was exposed to *M. ciliata* inoculum and it was declared moderately infected (SUJAN SINGH et al., 1983).

5.4. Other american species

Here again, variability is still to be explored within species. *M. larici-populina* may slightly infect *P. candicans* (KRZAN, 1982; WILKINSON and VAN KRAYENOORD, 1975b) and *P. angustifolia* (OUDEMANS, 1920; VAN KRAYENOORD, 1984). *P. candicans* is susceptible to *M. medusae* in New Zealand (WILKINSON and VAN KRAYENOORD, 1975b) and WEHMEYER (1947) recorded *M. occidentalis* on *P. angustifolia*.

P. balsamifera and *P. tacamahaca* are generally accepted as synonyms. Observations in Japan (CHIBA, 1964), Poland (KRZAN, 1982) and New Zealand (WILKINSON and VAN KRAYENOORD, 1975a) generally denote susceptibility, sometimes high, of this species to *M. larici-populina*. *M. medusae* does not appear dangerous either in Australasia or in North America. A few other rust species were reported on balsam poplar: *M. allii-populina* (DUPIAS, 1965), *M. occidentalis* (ZILLER, 1974) and *M. rostrupii* (OUDEMANS, 1920).

5.5. Sectional hybrids

Tree breeders sometimes have crossed species from section *Tacamahaca*. Among 6 *P. maximowiczii* x *P.*

laurifolia clones, 5 are resistant to *M. larici-populina* and one is moderately resistant (KRZAN, 1982). *P. tacamahaca* x *P. trichocarpa* hybrids are susceptible (KRZAN, 1982) to very susceptible (VAN KRAAYENOORD, 1984) to the same rust.

Some hybrids between American and Asiatic species exist. *P. koreana* x *P. trichocarpa* are scored susceptible to *M. larici-populina* in Japan (CHIBA, 1964) and New Zealand (VAN KRAAYENOORD, 1984) but in the latter country these are immune to *M. medusae*. *P. trichocarpa* x *P. koreana* hybrids exhibit some variation in behaviour to *M. larici-populina* (KRZAN, 1982).

Intersectional Hybrids

Crossing species of different sections was accomplished by some tree breeders, especially KOSTER in the Netherlands and STEENACKERS in Belgium, giving rise to very vigorous hybrids. These exhibit a wide range of reaction to diseases, and immunity to rusts is not uncommon. Such clones are also of great help to pathologists when determining pathotypes. For those clones which are well cultivated and studied, information on their behaviour is given in table 1.

6.1. *P. deltooides* x *P. trichocarpa*

Most of the Dutch intersectional hybrids are this combination. In New Zealand (VAN KRAAYENOORD, 1984) they are immune to *M. larici-populina* but very susceptible (most of the time) to *M. medusae*. On the contrary, hybrids selected in the U.S.A. are, in New Zealand, (WILKINSON and VAN KRAAYENOORD, 1975b) badly affected by *M. larici-populina* which is also confirmed by Japanese (CHIBA, 1964) and Polish (KRZAN, 1982) observations. In fact, such American hybrids were originally selected for resistance to *M. medusae* (OSTRY and McNABB, 1985).

6.2. *P. trichocarpa* x *P. deltooides*

Crosses between these species were made by STEENACKERS in Belgium. In New Zealand they suffer from *M. medusae* (VAN KRAAYENOORD, 1984). The same author ranged them from immune to very susceptible to *M. larici-populina* (see also Table 1). French observations indicate some infection by *M. allii-populina*, likely due to the eastern cottonwood parentage, sometimes pronounced but generally not too dangerous. Reaction of such hybrids may also change according to pathotypes. In fact, among 18 Belgian clones selected for high resistance to *M. larici-populina*, WILKINSON and VAN KRAAYENOORD (1979) found, in New Zealand, 9 clones susceptible to this rust, 9 susceptible to *M. medusae* but five resistant to both rust species. So there appears to be a large potential of selection for rust resistance within hybrids between *P. deltooides* and *P. trichocarpa* (whatever may be the direction of the crosses) but resistance or immunity on one continent is not necessarily a guaranty on another, because of the existence of physiological races and an apparent independence of genes for resistance to *M. larici-populina* and to *M. medusae*.

6.3. Other hybrids from *P. deltooides*

Thirty three *P. deltooides* x *P. balsamifera* clones exposed to *M. allii-populina* in Italy (ANSELMINI and CELLERINO, 1978) ranged from 15.5% to 100% of infected leaf area (mean = 52%). A few other clones of this type were observed elsewhere; 'NC 7168' had light infection with *M. medusae* in the U.S.A. (OSTRY and McNABB, 1985), and 'NC 5261' moderate to high infection, confirming the variability of

this botanical type and its sometimes high susceptibility (WIDIN and SCHIPPER, 1981). Again, as female parent, *P. deltooides* has been involved in other crosses but the limited number of clones do not allow generalizations: *P. deltooides* x *P. simonii* very resistant to *M. larici-populina*, three clones of *P. petrowskiana* (= *P. deltooides* x *P. laurifolia*) susceptible (KRZAN, 1982) and *P. deltooides* x *P. yunnanensis* immune to *M. larici-populina* and *M. medusae* in New Zealand (VAN KRAAYENOORD, 1984).

6.4. Hybrids from *P. nigra*

P. nigra, both as male or female parent, does not seem able to increase resistance to *M. larici-populina*. In Japan, hybrids of *P. nigra* with *P. maximowiczii*, *P. trichocarpa* and *P. laurifolia* proved to be susceptible to *M. larici-populina* (CHIBA, 1964). It was also the case in New Zealand (WILKINSON and VAN KRAAYENOORD, 1975b) for *P. nigra* x *laurifolia* (cv. 'Frye' and 'Rumford') and for *P. nigra* x *trichocarpa* (cv. 'Andover' and 'Roxbury') but all four clones were free from *M. medusae*. In Poland (KRZAN, 1982), in their reaction to *M. larici-populina*, various hybrids were described as follows: *P. nigra* x *P. simonii* moderately resistant, *P. nigra* x *P. laurifolia* resistant to very susceptible, *P. nigra betulifolia* x *P. trichocarpa* ('NE-296') very susceptible and *P. laurifolia* x *P. nigra* susceptible to very susceptible. Immunity to *M. medusae* was commonly observed in New Zealand (VAN KRAAYENOORD, 1984) for *P. nigra* x *P. maximowiczii* (and reciprocal) and for *P. koreana* x *P. nigra*.

6.5. Other hybrids

One clone of *P. x acuminata* (= *P. angustifolia* x *P. sargentii*) examined by KRZAN (1978) in Poland, was resistant to *M. larici-populina*. Between sections *Aigeiros* and *Tacamahaca* some trispecific hybrids were created and observed for rust. Twenty five clones of *P. x euramericana* x *P. balsamifera* proved to be quite resistant to *M. allii-populina* (ANSELMINI and CELLERINO, 1978). A few other clones were examined in different countries and are included in table 1.

Hybridization of section *Leuce* with other sections is often difficult. Nevertheless some exceptions exist. Clones from Delbo and Delmark series (*P. deltooides* x *P. alba*), *P. alba* x *P. nigra*, *P. alba* x *P. yunnanensis* were free from *M. larici-populina* and *M. medusae* in New Zealand (VAN KRAAYENOORD, 1984). But *P. alba* x *P. berolinensis* and *P. alba* x *P. nigra* were successfully inoculated with *M. larici-tremulae* in China (SHANG and PEI, 1984). It thus seems that *P. alba* may determine the susceptibility or the resistance of the hybrid.

Concluding Remarks

Our present knowledge of host variability to rust is still practically nonexistent for sections *Leucoides* and *Turanga*, and sparse for section *Leuce*. At least in Europe, we are beginning to plant aspen, and that requires us to learn more about the reactions of aspen species and hybrids to various rusts, and to establish the genetic basis for these reactions.

We know more about sections *Aigeiros* and *Tacamahaca*, and our knowledge increases with the recent interest in poplar rusts in North America and Asia. But merely studying variability will never have any productive end. Artificial gene arrangements become more numerous because of "traditional" selection to which may be added new progress in biotechnology, including suppression of

incompatibility barriers and somaclonal variants. In addition, rusts are rapidly-evolving organisms and the existence of many physiological races must be taken into account to adequately define clonal behaviour.

Despite this large natural variability and its potential for artificial expansion, economic and technological constraints tend to reduce the number of genotypes which are cultivated, often as monoclonal stands creating risky situations. To reduce the risk, selecting for higher levels of resistance may be dangerous ("boom and bust cycles", loss of horizontal resistance) and it is often proposed to cultivate multiclinal varieties. With this option we shall have to not only continue our explorations of host and pathogen variability, but also learn how to manage it, in regard to host-rust-environment interactions, towards the creation of more stable systems.

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Nuclear and Extranuclear Genetic Effects in F₁ Reciprocal Hybrids between *Pinus strobus* and *P. peuce*

By I. BLADA

Forest Research Institute, Bucharest 11, Romania

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Summary

Three *P. peuce* and one *P. strobus* parents were reciprocally crossed. The 6 families were artificially inoculated with *C. ribicola* then transplanted in the field. The results after 9 years of testing are, as follows: (1) Nuclear gene effects in hybrids were significant in height growth and highly significant in blister rust resistance; (2) Extranuclear gene effects were highly significant in blister rust resistance, diameter, basal area and volume growth rate; (3) There is evidence that the parent 62 of *P. strobus* is a carrier and transmitter of extranuclear genes involved in blister rust resistance and in some growth traits such as, diameter, height growth, basal area and volume growth rate; (4) The superiority in blister rust resistance, diameter, basal area and volume growth, due to extranuclear genes effects was about 218%, 34%, 80% and 88%, respectively.

Key words: *Pinus strobus*, *P. peuce*, *Cronartium ribicola*, reciprocal hybrids, nuclear genes, extranuclear genes, genetic correlations, phenotypic correlations.

Introduction

For many decades, the chromosomal theory of heredity has been the cornerstone of genetics. Consequently, concentration on the study of chromosome heredity led to

the exclusion of investigations of the extranuclear complement of the cell. But, as far back as 1909, CORRENS and BAUER (cited from JINKS, 1964) found instances of non-Mendelian inheritance of some flowering plants. Although correctly interpreted as examples of extranuclear heredity, this and other exceptions aroused little interest. However, for some decades the cell was recognized as an integrated unit whose properties were more than a mere composite of its nuclear and extranuclear contents (JINKS, 1964).

Extranuclear or maternal effects were found both in plants and animals. The most common maternal effect in plants is caused by a variation in seed size. It is well known that seeds of different sizes may vary in speed of germination and in subsequent growth rate. Some authors (HOUGH, 1952; SCHELL, 1960; GREEN, 1971; BRAMLETT et al., 1983) have shown that fast germinating seeds yield seedlings that initially grow more vigorously than those from smaller seeds, but this initial difference may decrease or disappear after several months or after a few years.

Maternal effects were most often considered of little importance in tree improvement programmes, and BARNES and SCHWEPPEHAUSER (1978) had shown that these effects