Variability in pathogenicity of *Melampsora allii-populina* expressed on poplar cultivars

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Summary

A collection of 42 isolates of *Melampsora allii-populina* was established. Fourteen isolates were collected from various poplar cultivars over several French localities and 28 isolates from the alternate hosts (*Allium* spp., *Arum* sp. and *Muscari comosum*) obtained from nature or after inoculation. These isolates were inoculated in the laboratory on a large range of poplar cultivars belonging to several species. No isolate proved pathogenic on all cultivars and many qualitative interactions were observed between isolates and cultivars. This is the first evidence for the existence of physiological races within this fungus. No link was found between pathogenicity on poplar and on the alternate hosts.

Among the inoculated cultivars, at least three were susceptible to all isolates (Beaupré, Candicans and Robusta), whereas the following showed qualitative reactions to the inoculated isolates: Altichiero, Carpaccio, Cima, Fritzzi Pauley, I 154, Isières, Luisa Avanzo, NL 2842, Rap and Spijk. Race-specific resistance to *M. allii-populina* (i.e. resistance to some races of the pathogen, but not to the others) has been found in two North American species (*Populus deltoides* and *Populus trichocarpa*) which have never coevolved with this fungus. The results are discussed in comparison with *Melampsora larici-populina*.

1 Introduction

Rust fungi are known to exhibit variability in pathogenicity and generally described as composed of *formae speciales* (according to the range of species infected) and as physiological races (according to the range of cultivars infected) (MCINTOSH and WATSON 1982; AGRIOS 1988). This is well known in the genus *Melampsora* Castagne.

The first evidence for the variability in pathogenicity in a *Melampsora* species was given by FLOR (1935) who described physiological races within *Melampsora lini* (Schum.) Desm. Poplars may be infected by various *Melampsora* species and VAN VLOTEN (1949) first reported the existence of physiological races within *Melampsora larici-populina* Kleb. More recently, many new races were discovered within this species when complete resistance (i.e. resistance to all known races of the pathogen) of selected cultivars was broken down (STEENACKERS 1982; PINON and BACHACOU 1984; PINON et al. 1987; PINON and PEULON 1989; PINON and LEFEVRE 1994; STEENACKERS et al. 1994; PINON 1995).

MAGNANI (1965) reported a possible variability in pathogenicity on poplar within *M. allii-populina* Kleb. and suggested the possible existence of physiological races. He studied isolates from different geographical origins and found differences in pathogenicity between them. However, no clear qualitative interactions between clones and isolates were described. In a review on the variability in the susceptibility to *Melampsora* rusts within the genus *Populus*, PINON (1992) reported conflicting conclusions from various authors about the susceptibility of cultivated poplar clones to *M. allii-populina*. The inconsistency of the behaviour of some cultivars suggested the possible existence of races within *M. allii-populina*.

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Variability in *M. allii-populina* has also been described according to the pathogenicity on the alternate hosts. VIENNOT-BOURGIN (1937) described two *formae speciales*: f. sp. *allii-populina*, which was pathogenic on *Arum* spp. and *Allium* spp. and f. sp. *muscaridis-populina*, which was pathogenic only on *Muscari comosum* Mill. and *Allium sphaerocephalum* L. Furthermore, the author reported the presence of thin spinules at the apex of the urediniospores of the f. sp. *muscaridis-populina*. Later, DUPIAS (1965) suggested the existence of a third *forma specialis*, f. sp. *typica* which was pathogenic on *Allium* spp., *Arum* spp. and *M. comosum*. This latter statement is questionable, since the poplar leaves studied by DUPIAS could have borne teliospores of both f. sp. *allii-populina* and f. sp. *muscaridis-populina*.

In the present study, we have tested the pathogenicity of various isolates of *M. allii-populina* collected from poplar and from the alternate hosts on a wide range of poplar cultivars in order to determine the presence of physiological races.

2 Materials and methods

2.1 Poplar cultivars

The cultivars to be inoculated were chosen among (1) those which were currently infected in nature by *M. allii-populina* and (2) those whose behaviour towards *M. allii-populina* appeared inconsistent according to the literature (PINON 1992; PINON and VALADON 1997). These cultivars belong to various species from sections *Aigeiros* and *Tacamahaca* of genus *Populus* L. and their intra- and inter-sectional hybrids (Table 1). The plants were propagated from dormant cuttings planted in a greenhouse in 5-l containers in a mixture of peat and sand (1/1) complemented with limestone (to adjust pH around 5.5) and fertilized with Nutricote Total 13.13.13.2 (Fertil, Paris, France).

2.2 Alternate hosts

*Arum italicum* Mill. was collected from the field in nature and transplanted in the nursery, while seeds and bulbs of *Allium cepa* L., *M. comosum* and *A. sphaerocephalum* were purchased and grown in the greenhouse in the same substrate used to grow poplars.

2.3 Isolates from poplar

The poplar isolates were collected from naturally infected leaves (Table 2). Each isolate was derived from an individual uredinium selected from one leaf. The isolates were cultured in

<p>| Table 1. Poplar species and cultivars tested for their reaction to <em>Melampsora allii-populina</em> isolates |</p>
<table>
<thead>
<tr>
<th>Populus species</th>
<th>Cultivars</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. × euramerica (Dode) Guinier</td>
<td>Altichiero, Cima, Carpaccio, Bellini, Bellotto, Büchig, Ghoy, I 154, I 214, Issières, Luisa Avanzo, Primo, Rintheim, Robusta, Spijk, Tiepolo, Véronèse</td>
</tr>
<tr>
<td>P. nigra L.</td>
<td>Italica</td>
</tr>
<tr>
<td>P. trichocarpa Torr. &amp; Gray</td>
<td>Fritzi Pauley</td>
</tr>
<tr>
<td>P. trichocarpa × P. deltoides Bartr.</td>
<td>Beaupré, Boelare, Rap, Raspalje, Unal</td>
</tr>
<tr>
<td>P. trichocarpa × P. maximowiczii Henry</td>
<td>NL 2842</td>
</tr>
<tr>
<td>P. candidans At.</td>
<td>Candidans</td>
</tr>
</tbody>
</table>
Variability in *M. allii-populina* pathogenicity

**Table 2. Origin of the isolates of *Melampsora allii-populina* collected from poplar**

<table>
<thead>
<tr>
<th>Isolate</th>
<th>Cultivar</th>
<th>Locality</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALT B</td>
<td>Altichiero</td>
<td>Bordeaux</td>
<td>1989</td>
</tr>
<tr>
<td>BPR G</td>
<td>Beaupré</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>BPR N</td>
<td>Beaupré</td>
<td>Nancy</td>
<td>1989</td>
</tr>
<tr>
<td>BLN G</td>
<td>Bellini</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>BLT G</td>
<td>Bellotto</td>
<td>Guémené-Penfao</td>
<td>1988</td>
</tr>
<tr>
<td>BLR G</td>
<td>Boelare</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>CND G</td>
<td>Candicans</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>CRP B</td>
<td>Carpaccio</td>
<td>Bordeaux</td>
<td>1989</td>
</tr>
<tr>
<td>214 G</td>
<td>1214</td>
<td>Guémené-Penfao</td>
<td>1988</td>
</tr>
<tr>
<td>ITL NT</td>
<td>Italica</td>
<td>Nantes</td>
<td>1988</td>
</tr>
<tr>
<td>PRM G</td>
<td>Primo</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>RNT G</td>
<td>Rintheim</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
<tr>
<td>RBS NT</td>
<td>Robusta</td>
<td>Nantes</td>
<td>1988</td>
</tr>
<tr>
<td>UNL G</td>
<td>Unal</td>
<td>Guémené-Penfao</td>
<td>1989</td>
</tr>
</tbody>
</table>

the laboratory by inoculating healthy leaves of the cultivar Robusta which was susceptible to all isolates of *M. allii-populina*. Because *M. larici-populina* was also present on several poplar cultivars, all isolates were inoculated on the cultivar Beaupré which was, at this time, totally resistant to *M. larici-populina* and susceptible to all isolates of *M. allii-populina*. All the isolates were partially dehydrated at 5°C under vacuum in a desiccator for 1 week, and then cryopreserved in liquid nitrogen until further use.

### 2.4 Isolates from the alternate hosts

Isolates were either collected from naturally infected alternate hosts in April–May, or obtained after artificial inoculation of the alternate hosts (Table 3). Poplar leaves bearing telia on their lower surface were collected in September–October and over-wintered in the nursery in baskets made of plastic mesh. The leaves bearing telia were transferred to the laboratory in March–April, when telia were ready to germinate. Container-grown alternate hosts were inoculated in the laboratory. For each individual plant a separate source of inoculum was used (i.e. leaves from one poplar cultivar collected in one place). Leaves bearing telia were soaked in tap water for 3 h and then laid on a plastic net placed over the alternate host, telia facing the plants to be inoculated. The poplar leaves were then covered with wet filter paper and each container was wrapped with a plastic bag for one night. Plants were incubated in a growth room at approximately 20°C under fluorescent light (16-h photoperiod, 25 μmol/m²·s). Aecia developed 2–3 weeks later. Isolates were obtained from individual aecia and cultured on the susceptible poplar cultivar Beaupré and subsequently provided unrediniospores for the pathogenicity test on poplar cultivars.

### 2.5 Morphological features

Urediniospore morphology of isolates originated from various alternate hosts and from poplars were compared using light and scanning electron microscopy. For scanning electron microscopy, the urediniospores were frozen at −60°C and then freeze-dried at −10°C for 24 h, allowed to reach room temperature, mounted on aluminium stubs with conductive glue containing graphite (Leit C, Boiziau Distribution, Selles-sur-Cher, France), and then overlaid with a 10-nm conducting carbon coat (metallizer Balzer’s CED/020, Boiziau.
Table 3. Origin of the isolates of *Melampsora allii-populina* from alternate hosts

<table>
<thead>
<tr>
<th>Alternate host</th>
<th>Isolate</th>
<th>Natural infection (locality)</th>
<th>Artificial inoculation (cultivar/locality)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Allium vineale</em> L.</td>
<td>4</td>
<td>Nancy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Fontainebleau</td>
<td></td>
</tr>
<tr>
<td><em>Allium cepa</em> L.</td>
<td>3</td>
<td>Nancy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 gr</td>
<td></td>
<td>Beaupré/Nancy</td>
</tr>
<tr>
<td></td>
<td>A 51</td>
<td></td>
<td>Isières/Nancy</td>
</tr>
<tr>
<td></td>
<td>A 3</td>
<td></td>
<td>Isières/Nancy</td>
</tr>
<tr>
<td></td>
<td>E 4</td>
<td></td>
<td>Robusta/Guéméné</td>
</tr>
<tr>
<td></td>
<td>N 2</td>
<td></td>
<td>Isières/Guéméné</td>
</tr>
<tr>
<td></td>
<td>O 1</td>
<td></td>
<td>Ghoy/Guéméné</td>
</tr>
<tr>
<td><em>Arum italicum</em> Mill.</td>
<td>6</td>
<td>Nancy</td>
<td></td>
</tr>
<tr>
<td><em>Arum maculatum</em> L.</td>
<td>9</td>
<td>Fontainebleau</td>
<td></td>
</tr>
<tr>
<td><em>Allium sphaerocephalum</em> L.</td>
<td>A 52</td>
<td></td>
<td>Isières/Nancy</td>
</tr>
<tr>
<td></td>
<td>C 5</td>
<td></td>
<td>Robusta/Nancy</td>
</tr>
<tr>
<td></td>
<td>D 5</td>
<td></td>
<td>Beaupré/Nancy</td>
</tr>
<tr>
<td></td>
<td>G 5</td>
<td></td>
<td>Ghoy/Guéméné</td>
</tr>
<tr>
<td></td>
<td>L 5</td>
<td></td>
<td>Beaupré/Guéméné</td>
</tr>
<tr>
<td></td>
<td>N 5</td>
<td></td>
<td>Isières/Guéméné</td>
</tr>
<tr>
<td><em>Muscari comosum</em> Mill.</td>
<td>10</td>
<td>Fontainebleau</td>
<td></td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Nancy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>D 1</td>
<td></td>
<td>Beaupré/Nancy</td>
</tr>
<tr>
<td></td>
<td>D 3</td>
<td></td>
<td>Beaupré/Nancy</td>
</tr>
<tr>
<td></td>
<td>H 1</td>
<td></td>
<td>Beaupré/Guéméné</td>
</tr>
<tr>
<td></td>
<td>L 3</td>
<td></td>
<td>Beaupré/Guéméné</td>
</tr>
<tr>
<td></td>
<td>N 1B</td>
<td></td>
<td>Isières/Guéméné</td>
</tr>
<tr>
<td></td>
<td>O 4</td>
<td></td>
<td>Ghoy/Guéméné</td>
</tr>
<tr>
<td></td>
<td>R 1</td>
<td></td>
<td>Beaupré/Nancy</td>
</tr>
<tr>
<td></td>
<td>S 4</td>
<td></td>
<td>Robusta/Guéméné</td>
</tr>
<tr>
<td></td>
<td>T 1B</td>
<td></td>
<td>Robusta/Nancy</td>
</tr>
</tbody>
</table>

Distribution). The urediniospores were examined under a Stereoscan 90B scanning electron microscope (Cambridge Instrument, Cambridge, UK) operating a 25 kV.

2.6 Pathogenicity tests on poplar

Urediniospore suspensions were prepared in water agar (0.1 g/l) and adjusted to 10 000 spores/ml. After shaking, the spore suspension was sprayed, using a compressed air spraying device, on leaf disks cut from leaves of poplars grown in the greenhouse. A first test was performed on six 12-mm diameter disks per isolate. Any negative or doubtful reaction was confirmed by a second test on 30-mm diameter disks. The disks were floated on water in Petri dishes, abaxial surface uppermost. The Petri dishes were incubated at 20°C under constant illumination (fluorescent light, 25 μmol/m² × s). During the 2 weeks following the inoculation the disks were observed daily to detect symptoms: absence of symptoms or necrotic flecks in the case of incompatibility, or uredinia formation in the case of compatibility.
Variability in *M. allii-populina* pathogenicity

3 Results

3.1 Morphological features

All the isolates, whether they were collected from poplar or from alternate hosts, exhibited the same morphology under the microscope. When inoculated on poplar, isolates from *M. comosum* and *A. sphaerocephalum* produced typical urediniospores—smooth at the apex and echinulate on the remaining wall. The observation of urediniospores of *M. allii-populina* f. sp. *muscaridis-populina* with a scanning electron microscope did not reveal the presence of any spinules at the apex of the spores as described by VIENNOT-BOURGIN (1937) (Fig. 1). Our observation was confirmed by G. DUPIAS (pers. com.) on his own specimens of *M. allii-populina* f. sp. *muscaridis-populina*. Thus, it seems that the description of special morphological features for this forma specialis is questionable. Furthermore, an examination of specimens from VIENNOT-BOURGIN’s herbarium did not reveal the presence of any spinules at the apex.

3.2 Pathogenicity of the isolates collected from poplar

Of the 24 cultivars inoculated, none appeared completely resistant to all isolates. Sixteen cultivars became infected with all isolates: Beaupré, Bellini, Bellotto, Boelare, Büchig, Candicans, Ghoy, I 214, Italica, Primo, Raspalje, Rintheim, Robusta, Tiepolo, Unal and Véronese. On the other cultivars, a wide range of reactions was observed, ranging between susceptibility and complete resistance depending on the isolate. Eight cultivars (NL 2842, Luisa Avanzo, Cima, Carpaccio, Altichiero, Fritz Pauley, Isières, and I 154) proved to be susceptible only to some isolates and displayed different interaction patterns with the isolates tested (Table 4). The 14 isolates were assigned to nine different pathogenicity groups according to their virulence on the eight cultivars. Compared with leaf disc tests with *M. larici-populina*, some reactions were unstable.

3.3 Pathogenicity of the isolates collected from alternate hosts

Some cultivars appeared susceptible to all isolates from alternate hosts: Beaupré, Robusta, Candicans, I 154, and Isières. The same range of reactions was observed as with the isolates

![Fig. 1. Scanning electron micrograph of urediniospores of *Melampsora allii-populina* f. sp. *muscaridis-populina*. The spores are typically smooth at the apex and echinulate on the remaining wall.](image)

Bar = 20 μm
Table 4. Interactions between isolates of Melampsora allii-populina from poplar and poplar cultivars. NT = not tested; - = no infection; + = slight and irregular infection; ++ = slight (1–10 uredinia per leaf disk) but reproducible infection; +++ = heavy infection and sporulation (more than 10 uredinia per leaf disk); () = test performed only once.

<table>
<thead>
<tr>
<th>Isolate</th>
<th>2842</th>
<th>Luisa Avanzo</th>
<th>Cima</th>
<th>Carpaccio</th>
<th>Altichiero</th>
<th>Fritzi Pauley</th>
<th>Isières</th>
<th>1154</th>
<th>Pathogenicity group</th>
</tr>
</thead>
<tbody>
<tr>
<td>BLT G</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td></td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>A</td>
</tr>
<tr>
<td>ALT B</td>
<td>(-)</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>(-)</td>
<td>+</td>
<td>-</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>BPR G</td>
<td>(-)</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>(-)</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>C</td>
</tr>
<tr>
<td>BPR N</td>
<td>-</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td></td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>D</td>
</tr>
<tr>
<td>CRP B</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>NT</td>
<td>+</td>
<td>+</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>ITL NT</td>
<td>-</td>
<td>-</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>E</td>
</tr>
<tr>
<td>CND G</td>
<td>-</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>RBS NT</td>
<td>(-)</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>UNL G</td>
<td>-</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>NT</td>
<td>++</td>
<td>+++</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>PRM G</td>
<td>-</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td></td>
<td>++</td>
<td>+</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>BLN G</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>-</td>
<td>++</td>
<td>G</td>
<td></td>
</tr>
<tr>
<td>RNT G</td>
<td>-</td>
<td>-</td>
<td>+++</td>
<td>(--)</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>H</td>
<td></td>
</tr>
<tr>
<td>214 G</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>--</td>
<td>++</td>
<td>I</td>
<td></td>
</tr>
</tbody>
</table>

Table 5 summarizes the qualitative interactions found between the eight poplar cultivars and the 42 M. allii-populina isolates collected either from poplar or from alternate hosts, which were clustered in 15 pathogenicity groups.

4 Discussion

These results provide the first clear evidence of the existence of physiological races within M. allii-populina, as was already known for M. larici-populina. Hitherto, no physiological races have been described in M. allii-populina, probably because no loss of complete resistance was reported. In fact, no selection was conducted in Europe for complete resistance to this species, in contrast to M. larici-populina (PINON and VALADON 1997). This is in accordance with the fact that, in the present study, we found no cultivar resistant to all the isolates of M. allii-populina. Several physiological races were found within isolates from both origins (poplar and alternate hosts). The number of virulence per isolate was variable. Some isolates exhibited up to five virulences (e.g. isolates 4, 6, 9 and 10), whereas isolate G5 was found with only two virulences on the range of inoculated cultivars. We found many different combinations of virulences and avirulences. According to the number of interactions found between isolates and cultivars, it may be concluded that more races can exist, as it is the case for M. larici-populina (PINON 1995).

Comparing the virulences found within isolates from both poplar and alternate hosts, it
Table 5. Interactions between isolates of *Melampsora allii-populina* from alternate hosts and poplar cultivars. NT = not tested; - = no infection; + = slight and irregular infection; ++ = slight (1 to 10 uredinia per leaf disk) but reproducible infection; +++ = heavy infection and sporulation (more than 10 uredinia per leaf disk)

<table>
<thead>
<tr>
<th>Origin of the isolate</th>
<th>Inoculated cultivar</th>
<th>NL 2842</th>
<th>Luisa Avanzo</th>
<th>Cima</th>
<th>Carpaccio</th>
<th>Altichiero</th>
<th>Fritzi Pauley</th>
<th>Isières</th>
<th>I 154</th>
<th>Rap</th>
<th>Spijk</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arum maculatum</em></td>
<td>9</td>
<td>+</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>++</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>NT</td>
<td>NT A</td>
</tr>
<tr>
<td><em>Muscaria comosum</em></td>
<td>10</td>
<td>+</td>
<td>-</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>NT</td>
<td>NT A</td>
</tr>
<tr>
<td><em>Allium vineale</em></td>
<td>4</td>
<td>-</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>NT</td>
<td>NT D</td>
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<td>+++</td>
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<td>-</td>
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<td>++</td>
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<td>++ E'</td>
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<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++ J</td>
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<td>++ J</td>
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<td>++</td>
<td>++</td>
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<td>++ J'</td>
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<td>++</td>
<td>++</td>
<td>++</td>
<td>-</td>
<td>++ J'</td>
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<td>-</td>
<td>++</td>
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<td>+</td>
<td>+</td>
<td>+++</td>
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<td>NT K</td>
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<td>+++</td>
<td>++</td>
<td>++ L</td>
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<td>++</td>
<td>++ L</td>
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<td>-</td>
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<td>-</td>
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<td>++</td>
<td>++</td>
<td>++ L</td>
<td></td>
</tr>
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<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++ L</td>
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</tr>
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<td>+</td>
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</tr>
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<td>-</td>
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<td>-</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>-</td>
<td>M'</td>
</tr>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
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<td>+</td>
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<tr>
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<td>-</td>
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<td>++</td>
<td>-</td>
<td>-</td>
<td>N</td>
</tr>
<tr>
<td><em>Allium sphaerocephalum</em></td>
<td>G 5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>++</td>
<td>-</td>
<td>-</td>
<td>O</td>
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</tbody>
</table>

1 = test performed only once.
Table 6. Grouping of isolates of *M. allii-populina* according to their virulence towards eight poplar cultivars. Isolate names in italics correspond to isolates from poplar. NT = not tested; + = virulent; − = avirulent; () = test performed only once

<table>
<thead>
<tr>
<th>Isolate</th>
<th>NL 2842</th>
<th>Luisa</th>
<th>Avanzo</th>
<th>Cima</th>
<th>Carpaccio</th>
<th>Altichiero</th>
<th>Fritzi</th>
<th>Pauley</th>
<th>Isières</th>
<th>I 154</th>
<th>Pathogenicity group</th>
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<td>9, 10, BLT G</td>
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<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>A</td>
</tr>
<tr>
<td>ALT B</td>
<td>(−)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(−)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>B</td>
</tr>
<tr>
<td>BPR G</td>
<td>(−)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>C</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>NT</td>
<td>+</td>
<td>D</td>
</tr>
<tr>
<td>CRP B</td>
<td>−</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>NT</td>
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<td>+</td>
<td>+</td>
<td>NT</td>
<td>+</td>
<td>+</td>
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<td>F</td>
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<tr>
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<td>−</td>
<td>−</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<td>−</td>
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<td>−</td>
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<td>+</td>
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<td>−</td>
<td>−</td>
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<td>−</td>
<td>−</td>
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<td>+</td>
<td>O</td>
<td>Q</td>
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</tbody>
</table>
Variability in *M. allii-populina* pathogenicity

appears that the same races can be found in isolates from both origins (Table 6). Furthermore, no link appeared between the pathogenicity group of the isolates and the *forma specialis* to which they may belong (Table 5). Presently, neither morphological features of ured-inospores, nor pathogenicity on poplar can be used to distinguish the *forma specialis*. This suggests that fungal genes involved in the infection of poplar and of the alternate host may be different.

Comparing the pathogenicity of the isolates from poplar and from the alternate hosts, it may be concluded that, at least three cultivars are susceptible to all isolates: cvs Robusta, Beaupré and Candicans. This result is in accordance with the observation that these cultivars are routinely infected severely in nature by *M. allii-populina* (PINON 1992; PINON and VALADON 1999; J. PINON unpublished data). However, the behaviour of these three cultivars towards physiological races of *M. larici-populina* is not the same (PINON 1995): cv. Robusta is susceptible to all known races, while cvs Candicans and Beaupré can be infected only by isolates having the relevant virulence (virulence 2 and 7, respectively). These results suggest that the genes which confer race-specific resistance to *M. larici-populina* are different from those which confer resistance to *M. allii-populina*.

The following cultivars exhibited race-specific resistance (i.e. resistance to some races of the pathogen, but not to the others) to some isolates of *M. allii-populina* and can thus be used to characterize isolates of this species: cvs NL 2842, Luisa Avanzo, Cima, Carpaccio, Altichiero, Fritzi Pauley, Isières, I 154, Rap and Spijk. These cultivars belong to different botanical types (Table 1). Cultivars Luisa Avanzo, Cima, Carpaccio, Altichiero, Isières, I 154, and Spijk belong to the hybrid *P. × euramericana* (Dode) Guinier (i.e. *P. deltoides* Bartr. × *P. nigra* L.). Cultivar Fritzi Pauley is a pure *P. trichocarpa* Torr. & Gray (native from North America), cv. Rap is a hybrid between this species and *P. deltoides* (native from North America) and cv. NL 2842 is a hybrid between *P. deltoides* and *P. maximowiczii* Henry (from Japanese origin). MAGNANI (1965) described a *P. deltoides* cultivar completely resistant to *M. allii-populina*. Thus, we can conclude that race-specific resistance to *M. allii-populina* is inherited, at least, from both North American species *P. deltoides* and *P. trichocarpa*. In the case of *M. larici-populina*, race-specific resistance was described in *P. deltoides*, whereas none was known in *P. trichocarpa* (LEFÈVRE et al. 1994, 1995). Among the cultivars showing race-specific resistance to *M. allii-populina*, several have already been described to exhibit race-specific resistance to *M. larici-populina*: cvs Carpaccio, Cima, Isières, Luisa Avanzo, NL 2842, Rap and Spijk (PINON 1995). They all inherited their race-specific resistance from their *P. deltoides* parent. This suggests that race-specific resistance to both *Melampsora* species may be found in the same species and in the same cultivars. Furthermore, cv. Beaupré (susceptible to all isolates) has cv. Fritzi Pauley as female parent (V. STEENACKERS, pers. com.), which suggests that race-specific resistance is not necessarily expressed in the interspecific hybrid.

For the two *Melampsora* species we still have no evidence of race-specific resistance in the indigenous host (*P. nigra*) which has co-evolved with the European rust fungi. This situation appears unique since, in many pathosystems, race-specific resistance is commonly found in the native host populations (BURDON 1993, 1994; SICARD 1996). It will be necessary in future to collect many *P. nigra* clones and to inoculate them with various isolates of *M. allii-populina* and *M. larici-populina* to investigate the possible existence of race-specific resistance within *P. nigra*.

With the existence of many different virulences and of two or three *forme speciales*, these results indicate that *M. allii-populina* is a very polymorphic species for its pathogenicity. Consequently, breeding for complete resistance to this species would be very risky.

Acknowledgements

We are grateful to A. Schipfer, D. MASSON, K. EL KARKOURI, and C. VIÉNOT for their technical assistance and to D. LE THIEC for the scanning electron microscopy photograph.
Résumé

Variabilité du pouvoir pathogène de *Melampsora allii-populina* vis-à-vis de cultivars de peuplier

Une collection de 42 isolats de *Melampsora allii-populina* a été constituée pour en étudier le pouvoir pathogène sur divers cultivars de peuplier. D'une part, quatorze isolats ont été prélevés sur divers cultivars de peuplier dans différentes localités en France. D'autre part, vingt-huit isolats ont été obtenus sur des hôtes alternants (*Allium* spp., *Arum* spp. et *Muscari comosum*) infectés naturellement ou inoculés à partir de feuilles portant des téleutosores de *M. allii-populina*. Aucun isolat ne s’est avéré pathogène sur la totalité des cultivars inoculés et de nombreux cas d’interactions qualitatives entre isolats et cultivars ont été mis en évidence. Ces résultats apportent la première preuve de l’existence de races physiologiques chez ce champignon. Aucun lien n’est apparu entre le pouvoir pathogène sur peuplier (virulences) et celui sur les hôtes alternants (formes spéciales). Ceci suggère que les gènes gouvernant le pouvoir pathogène sur ces deux types d’hôtes sont distincts. Parmi les cultivars inoculés, trois au moins ont été infectés par tous les isolats (Beaupré, Candicans et Robusta) alors que d'autres cultivars manifestaient des interactions qualitatives avec les isolats: Altichiero, Carpaccio, Cima, Fritzi Pauley, I 154, Istières, Luisa Avanzo, NL 2842, Rap et Spijk. La résistance spécifique à *M. allii-populina* semble être héritée au moins de deux espèces nord-américaines qui n’ont jamais co-évolué avec le parasite: *Populus deltoides* et *Populus trichocarpa*. Une comparaison est établie avec *M. larici-populina*.

References


Variability in *M. allii-populina* pathogenicity


