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Article abstract

European strains of *Armillaria cepistipes* were reported to be interfertile with strains from three American *Armillaria* species known as North American Biological Species (NABS) V (*A sinapina*), NABS X and NABS XI. Such interfertility between species raises some doubts about using different Latin binomials for species capable of mating. This interfertility was reinvestigated by mating 24 haploid isolates of European *A cepistipes* with 23 isolates of A sinapinafrom North America and Asia. Individual pairings were independently performed at least once at Universite Laval, Canada and at INRA Clermont-Ferrand, France. From the 420 interspecific pairings performed at Laval, two were positive and seven were ambiguous for a total of 2.1% of all the pairings. From the 506 pairings made at Clermont-Ferrand, 10 were positive and 24 were ambiguous for a total of 6.7%. The differences in the pairing results may be explained by incubation temperatures, and the different types and concentrations of malt extract used at each laboratory. The low levels of interfertility found between *A. cepistipes* and *A. sinapina* may result from the absence of genetic barriers that are usually present between sympatric species. This low level of interfertility reflects differences in morphology, distribution, and habitat for these two species of *Armillaria* and this supports the retention of different species denominations.

Interfertility between *Armillaria cepistipes* and *A. sinapina*

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European strains of *Armillaria cepistipes* were reported to be interfertile with strains from three American *Armillaria* species known as North American Biological Species (NABS) V (*A. sinapina*), NABS X and NABS XI. Such interfertility between species raises some doubts about using different Latin binomials for species capable of mating. This interfertility was reinvestigated by mating 24 haploid isolates of European *A. cepistipes* with 23 isolates of *A. sinapina* from North America and Asia. Individual pairings were independently performed at least once at Université Laval, Canada and at INRA Clermont-Ferrand, France. From the 420 interspecific pairings performed at Laval, two were positive and seven were ambiguous for a total of 2.1% of all the pairings. From the 506 pairings made at Clermont-Ferrand, 10 were positive and 24 were ambiguous for a total of 6.7%. The differences in the pairing results may be explained by incubation temperatures, and the different types and concentrations of malt extract used at each laboratory. The low levels of interfertility found between *A. cepistipes* and *A. sinapina* may result from the absence of genetic barriers that are usually present between sympatric species. This low level of interfertility reflects differences in morphology, distribution, and habitat for these two species of *Armillaria* and this supports the retention of different species denominations.

Bérubé, J.A., M. Dessureault, S. Berthelay et J.-J. Guillaumin. 1996. Interfertilité entre *Armillaria cepistipes* et *A. sinapina*. PHYTOPROTECTION 77 : 67-74.

Des études ont rapporté que des lignées européennes d'*Armillaria cepistipes* étaient interfertiles avec trois lignées américaines d'*Armillaria* désignées par les termes espèce biologique nord-américaine (NABS) V (*A. sinapina*), NABS X et NABS XI. Une telle interfertilité entre les espèces soulève des doutes au sujet de l'utilisation de binômes latins distincts pour des espèces pouvant se reproduire. Cette interfertilité a été ré-examinée en mettant 24 isolats haploïdes d'*A. cepistipes* européen en présence de 23 isolats d'*A. sinapina* d'Amérique du Nord et d'Asie. Les appariements individuels ont été effectués de façon indépendante au moins une fois à l'Université Laval (Canada) et à l'INRA

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Clermont-Ferrand (France). Des 420 appariements interspécifiques effectués à l'Université Laval, deux étaient positifs et sept étaient ambigus, pour un total de 2,1 % de tous les appariements. Des 506 appariements effectués à Clermont-Ferrand, 10 étaient positifs et 24 étaient ambigus pour un total de 6,7 % des appariements. Les différences dans les résultats de ces appariements peuvent être expliquées par les températures d'incubation, ainsi que par les différents types et concentrations d'extrait de malt utilisés dans chaque laboratoire. Les bas niveaux d'interfertilité trouvés entre *A. cepistipes* et *A. sinapina* peuvent résulter de l'absence de barrières génétiques habituellement présentes entre des espèces sympatriques. Ce bas niveau d'interfertilité reflète des différences entre la morphologie, la répartition et les habitats des deux espèces d'*Armillaria*, et appuie la conservation de dénominations d'espèces distinctes.

INTRODUCTION

Development of a crustose colony morphology after pairing two compatible haploid strains proved to be a useful and highly productive method to determine biological species and later to delineate taxa in the root-pathogenic genus *Armillaria* (Fr.) Staude (Anderson and Ullrich 1979; Kile and Watling 1988; Korhonen 1978). This technique has led to the recognition of at least nine biological species of *Armillaria* in North America and seven species in Europe. Most of these biological species of *Armillaria* have also been linked to morphological taxa and are now referred to by their Latin names (Bérubé and Dessureault 1988, 1989; Guillaumin *et al.* 1989). However, Anderson *et al.* (1980) reported cases of interfertility between isolates of a species from Europe with members of two other rigorously intersterile species from North America. In particular, they reported positive or ambiguous pairings in 4 out of 30 pairings between European *Armillaria* species B (now named *A. cepistipes* Velenovsky), with isolates of North American Biological Species (NABS) V, (now named *A. sinapina* Bérubé & Dessureault), which commonly occurs in the deciduous forests of the province of Quebec. In addition, European *A. cepistipes* was also reported to have a high percentage of interfertily with NABS XI (Morrison *et al.* 1985) which occurs in western Canada. This interfertility brings into question the legitimacy of using two different specific epithets for groups showing partial interfertility. This study was conducted to pair a larger number of isolates from both *A. cepistipes* and *A. sinapina*, allowing the examination and quantification of interfertility.

MATERIAL AND METHODS

Strains used for pairings consisted of 23 monosporous isolates previously labeled as *A. sinapina* and 24 monosporous isolates previously labeled as *A. cepistipes* from Europe, North America, and Asia. The strains and origins are listed in Table 1. The pairings were performed independently at Université Laval in Québec (lat. 46°48' N, long. 71°23' 0), Canada and at INRA in Clermont-Ferrand (lat. 45°45' N, long. 03°06' 0), France. At Université Laval, 863 pairings (420 interspecific, 443 intraspecific) were performed by confronting 21 strains of *A. sinapina* and 20 strains of *A. cepistipes* in all possible combinations of within and between species. The 506 pairings performed at Clermont-Ferrand were done with 23 strains of A. sinapina and 24 strains of *A. cepistipes* in all possible combinations between species. Individual pairings were performed in petri dishes in such a way that the paired mycelia contacted each other (Korhonen and Hintikka 1980). Pairings were grown for at least 21 days in the dark at 20°C at Université Laval and 23-24°C at Clermont-Ferrand. Preparation of growth media differed between the two institutions. At Université Laval, purified malt extract (Difco) at a concentration of 1.25% was used while unpurified baker's malt (Difal) at a concentration of 2% was used at Clermont-Ferrand. The positive or ambiguous pairings were replated twice to confirm results. The combined results of both teams of researchers are reported.

Table 1. Name and origin of *A. cepistipes* and *A. sinapina* strains used in matings

Name	Origin
A. cepistipes	
67.1.1	St-Victor, Puy-de-Dôme, France
79.16.3	Col de la Moreno, Puy-de-Dôme, France
80.38.5	Puy de la Moreno, Puy-de-Dôme, France
80.16.2	Puy de Lachamps, Puy-de-Dôme, France
82.56.4	Trentin, Italy
84.89.3	Schwarzwald, Unterbrand, Germany
84.90.1	Vosges, France
84.91.3	Loffingen, Schwarzwald, Germany
84.93.3	Lizzano, Italy
87.87.1	Moscow, Russia
87.87.2	Moscow, Russia
8509191/5	Lammertal, Austria
88090141/3	Tuusula, Finland
88090211/6	Tuusula, Finland
523M4	Fall, Bayern, Germany
597M3	Blomberg, Bayern, Germany
B8	Bad Tota, Bayern, Germany
B9	Fussen, Bayern, Germany
79.23	Tampere, Finland
79.24	Helsinki, Finland
84.93.1	Lizzano, Italy
81.23.1	Forêt de Tronçais, Allier, France
84.92.2	Vosges, France
472M3	Waalberg, Bayern, Germany
A. sinapina	
JB-05B	Bromont, Québec, Canada
JB-07A	Bromont, Québec, Canada
JB-19E	Lac St-Jean, Québec, Canada
JB-43A	Beauce, Québec, Canada
JB-47A	Beauce, Québec, Canada
JB-66A	Beauce, Québec, Canada
JB-72A	Beauce, Québec, Canada
JB-75B	Beauce, Québec, Canada
MOR-84-14	British Columbia, Canada
MOR-84-1	British Columbia, Canada
48-1	New York, USA
48-5	New York, USA
83.62.1	New York, USA
83.91.1	Petersburg, Alaska, USA
83.92.1	Petersburg, Alaska, USA
83.61.1	Vermont, USA
84.51.1	Vernon, British Columbia, Canada
84.51.2	Vernon, British Columbia, Canada
86.36.3	Dailing, China
86.37.2	Dailing, China
JB-47B	Beauce, Québec, Canada
86.6.1	Hokkaido, Japan
86.7.1	Hokkaido, Japan

RESULTS

Fertility within biological species was quantified by making 210 pairings for both *A. sinapina* and *A. cepistipes*. The results of the intraspecific crosses are shown in Tables 2 and 3.

Intraspecific pairings for *A. sinapina* yielded an overall fertility of 83.8%. Fertility varied from one isolate to another. When paired with all other isolates, strain 86.7.1 gave negative results and was diagnosed as not to belong to *A. sinapina* (Table 2). Strain 86.7.1 was kept for interspecific pairings but was not scored in the final results. Strains JB-47A and 83.92.1 showed the lowest level of fertility with 60% and 65%, respectively. Other strains like JB-19E and 83.91.1 were fertile with all other strains.

Intraspecific pairings of *A. cepistipes* yielded an overall fertility of 81.4 % (Table 3). Five pairings were ambiguous. Fertility varied from one isolate to another. Strain 472M3 gave negative results with all pairings and was diagnosed as not to belong to *A. cepistipes*. It was kept for interspecific pairings but was not scored in the final results. Strain 87.87.1 exhibited very low fertility (11%) with other strains of *A. cepistipes*. Isolate 87.87.2 was from the same fruit body (data not shown) and exhibited normal fertility levels, which lead us to believe strain 87.87.1 to be defective, which sometimes happens when monosporous strains age. Although 87.87.1 was defective, it was scored in the final results. The next lowest level of fertility was 63% with strain 79.24. Other strains like 84.89.3 and 84.90.1 were fertile with all others tested, except for strain 87.87.1 as expected.

Interspecific crosses between isolates of *A. sinapina* and *A. cepistipes* yielded low levels of interfertility (Table 4). Significant differences were observed between results from Université Laval and Clermont-Ferrand. Positive and ambiguous pairings totaled 2.1% at Université Laval while reaching 6.7% at Clermont-Ferrand. However, the most important difference came from the positive pairings which did not include the same strain combinations except for two cases. Pairings MOR-84-1 X 84.89.3 and 79.24 X MOR-84-1 were both evaluated as positive or somewhat positive by both research groups. All other pairings were scored as negative by one research group.

Interfertility was not uniform among strains. For example, *A. cepistipes* strains 67.1.1, 88090141/3, 84.89.3, and 79.23, exhibited 41%, 32%, 23%, and 18% interfertility, respectively, with *A. sinapina* isolates. The majority of the pairings showed little or no interfertility. Similarly, *A. sinapina* strains MOR-84-1 and JB-07A exhibited 26% and 22% interfertility, respectively. No genetic interactions between isolates from different regions are evident from Table 4.

DISCUSSION

The differences in the results of interspecific pairings between the two research groups were unexpected. Although similar low levels of interfertility were observed, the combinations of positive pairings were different from one research group to the other. Since interpretation of positive pairings are usually standard, false interpretation was ruled out as the cause of discrepancy on positive pairings. These discrepancies may be due to the incubation temperatures, and the type and concentration of malt extract used. The media used at Université Laval probably offered minimal growth conditions and may have had an adverse effect on matings. The media used at Clermont-Ferrand was richer, more concentrated, and may have been more favorable for growth. Matings may have had full potential to occur and as well as continued growth afterward under these conditions. Alternative methods should be used, such as presence of clamp connections (Larsen *et al.* 1992) or nuclear migration demonstrated by isoenzyme markers on each strain to screen ambiguous pairings (Rizzo and Harrington 1992).

The low level of interfertility between *A. sinapina* and *A. cepistipes* combined with the high level of fertility within each species supports the use of two distinct Latin names for these species and also reflect differences in morphology, distribution, and habitat. Such low levels of interfertility between species could be explained by the absence of genetic bar-

Table 2. Intraspecific pairings of isolates of *A. sinapina*

	JB-05B	JB-07A	JB-19E	JB-43A	JB-47A	JB-66A	JB-72A	JB-75B	MOR-84-14	MOR-84-1	48-1	48-5	83.62.1	83.91.1	83.92.1	83.61.1	84.51.1	84.51.2	86.36.3	86.37.2	JB-47B
JB-07A	+																				
JB-19E	+	+																			
JB-43A	+	+	+																		
JB-47A	+	+	+	+																	
JB-66A	+	+	+	+	+																
JB-72A	-	+	+	+	+	+															
JB-75B	+	+	+	-	+	-	-														
MOR-84-14	+	+	+	+	+	+	+	+													
MOR-84-1	+	+	+	+	+	+	+	-	+												
48-1	+	-	+	-	+	+	+	+	+	+											
48-5	+	-	+	-	+	+	+	+	+	+	+										
83.62.1	+	+	+	-	+	-	+	+	+	+	+	+									
83.91.1	+	+	+	+	+	+	+	+	+	+	+	+	+								
83.92.1	+	+	+	-	-	-	+	-	+	-	+	+	+	+							
83.61.1	+	+	+	+	-	+	+	+	+	+	+	+	+	+	-						
84.51.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					
84.51.2	+	+	+	-	+	+	+	+	+	+	+	-	+	+	+	+	+				
86.36.3	+	+	+	-	+	+	+	+	+	+	+	-	+	+	-	+	+	+			
86.37.2	+	+	+	-	-	+	+	+	+	+	-	+?	+	+	+	+	+	-	+		
JB-47B	+	+	+	+	-	+	+	+	-	-	-	+?	+	+	+	+	+	+?	+	+	
86.7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Positive interactions (+), questionable interactions (+?) and negative interactions (-).

Table 3. Intraspecific pairings of isolates of *A. cepistipes*

	67.1.1	79.16.3	80.38.5	80.16.2	82.56.4	84.89.3	84.90.1	84.91.3	84.93.3	87.87.1	8509191/5	88090141/3	88090211/6	523M4	472M3	597M3	B8	B9	79.23	79.24
79.16.3	+																			
80.38.5	+?	+																		
80.16.2	-	?	+																	
82.56.4	+	+	+	+																
84.89.3	+	+	+	+	+															
84.90.1	+	+	+	+	+	+														
84.91.3	+	+	+	+	+	+	+?													
84.93.3	+	+	-	+	+	+	+?	+												
87.87.1	-	-	-	-	-	-	-	-	-											
8509191/5	+	+	+	+	+	+	+	+	+	-										
8890141/3	+?	+?	+?	+?	+?	+	+	+?	-	-	+?									
8890211/6	+	+	+	+	+	+	+	+	+	+	+	+								
523M4	+	+	+	+	+	+	+	+	+	-	+	+	+							
472M3	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
597M3	+	+	+	+	+	+	+	+	+?	+?	-	+	+	+	-					
B8	+	+	+	+	+	+	-	?	+	-	+	-	-	+?	-	+				
B9	+	+	+	+	+	+	+	+	+	-	+	+	+	+	-	+	+			
79.23	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	?	+	+		
79.24	+	+	+	+	+	+	+	+	?	-	+	-	-	+	-	+	-	-	+	
84.93.1	+	+	+	+	+	+	+?	+?	-	-	+	+?	+	+	-	+	-	+	+	-

Positive interactions (+), questionable interactions (+?, ?) and negative interactions (-).

Table 4. Interspecific pairings of isolates of *A. sinapina* and *A. cepistipes*

	JB-05B	JB-07A	JB-19E	JB-43A	JB-47A	JB-66A	JB-72A	JB-75B	MOR-84-14	48-1	MOR-84-1	48-5	83.62.1	83.91.1	83.92.1	83.61.1	84.51.1	84.51.2	86.36.3	86.37.2	JB-47B	86.6.1	86.7.1
67.1.1	-?	-?	-	-	-	-?	-?	-+	-+	-	-+	-	-	-	-	-+	-	-?	-	-	-	-	-
79.16.3	-	-	-	-	-	-?	-	-	-	-	?-	-	-	-	-	-	-	-	-	-	-	-	-
80.38.5	-	+-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
80.16.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
82.56.4	-	-	-	-	-	-	-	-	-	-	-	+?-	-	-	-	-	-	-	-	-	-	-	-
84.89.3	-	-	-	-	-	-	-	-	-	-	+?+	-	-	-+	-?	+-	+?-	-	-	-	-	-	-
84.90.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-?	-	-	-	-	-	-	-	-
84.91.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
84.93.3	-	-	-	-	-	-?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
87.87.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8509191/5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8890141/3	-?	-?	-	-	-	-	-	-	-	-	-?	-	-	-	-	-+	-?	-?	-?	-	-	-	-
8890211/6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
523M4	-	+?-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-?	-	-	-	-
87.87.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
597M3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B8	-	-	-	-	-	-	-	-	-	-?	-+	-+	-	-	-	-	-	-	-	-	-	-	-
B9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
79.23	-	-?	-?	-	-	-	-	-	-	-	-	-	-	-?	-?	-	-	-	-	-	-	-	-
79.24	-	-	-	-	-	-	-	-	-	-	++?	-	-	-	-	-	-	-	-	-	-	-+	-
84.93.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-?	-	-	-	-	-?	-	-	-	-
81.23.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-?	-	-	-	-	-
84.92.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
472M3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Positive interactions (+), questionable interactions (+?, ?) and negative interactions (-) are indicated. When two symbols are shown for one pairing, it indicates different results reported by both research teams.

riers that are usually present in sympatric species. It is interesting to note that *A. sinapina* which was initially thought to be found only in North America has been found in Asia (*i.e.* Japan and Manchuria). Similarly, *A. cepistipes* thought to be found only in Europe has been shown to be interfertile with NABS XI from British Columbia (Morrison *et al.* 1985). Thus *A. sinapina* and *A. cepistipes* are considered sympatric in British Columbia. Crosses to evaluate levels of interfertility of British Columbian strains from both species would address this issue.

The low levels of interfertility between two species, such as the one reported in this study, could be useful to understand the genetic system that regulates interfertility or mating systems. A study such as that used by Chase and Ullrich (1990) on *Heterobasidion annosum* (Fr.) Bref. may be done with these two species of *Armillaria*. However, for such a study, the use of colony morphology alone as a criteria for mating could be problematic as demonstrated by our results. Positive or ambiguous matings could be checked using nuclear migration as demonstrated by isoenzyme or DNA analysis.

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