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SPECIATION IN THE *PENIOPHORA CINEREA* COMPLEX

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ABSTRACT

Mating tests were performed *in vitro* to determine interfertility patterns among eastern North American populations of *Peniophora cinera*, and two sympatric sibling species of the *P. cinerea* complex in Europe. No intersterile groups were detected in eastern North America. Reproductive isolation between the two European species reported previously by Hallenberg was verified. Since one sibling species is apparently restricted to the wood of *Fagus sylvatica*, speciation accompanied by substratum specialization is indicated. Intercontinental pairings showed that American *P. cinerea* is partially reproductively isolated from the two European sibling species.

Key Words: Basidiomycota, fungi, mating factors, *Peniophora*, speciation

Peniophora cinerea (Pers. : Fr.) Cooke is a species complex of corticioid fungi inhabiting the wood of dead, attached and recently detached hardwood limbs in North America (Farr *et al.*, **1989**), Europe (Boidin, **1965**; Eriksson *et al.*, **1978**), Asia (Rattan, **1977**), Australasia (Cunningham, **1963**), and Africa (Doidge, **1950**).

Hallenberg (**1986**) performed mating tests with European isolates of *P. cinerea*. Using the formation of hyphae with clamp connections as the criterion for interfertility, he detected two sibling species. The "*Fagus*-type" sibling species is known from Denmark, Romania and Spain, and occurs on the wood and bark of *Fagus sylvatica* L. The "main-type" species is known from Austria, France, Norway, Romania, and Sweden; and occurs on the wood and bark of a variety of hardwoods, e.g., *Alnus, Fagus, Tilia,* and *Ulmus* spp.

Hallenberg (**1986**) also found that homokaryons from Canada were partially interfertile with those of both the "main-" and "*Fagus*-types" from Europe. Hallenberg and Larsson (**1991**) recently demonstrated differences in protein electrophoresis profiles among European "main-" and "*Fagus*-types," and North American populations.

The purposes of the present study were: 1) to ascertain whether sibling species exist in *P. cinerea* in northeastern North America, and 2) to determine the degree of reproductive isolation between the isolates from North America and those from Europe in order to suggest a pattern of speciation.

MATERIALS AND METHODS

Isolates.—Seventeen basidiomata of *P. cinerea* were collected on a variety of hardwood substrata from Pennsylvania, New York, and Virginia betwen May 1988 and August 1989 (TABLE I). Fifteen single-basidiospore isolates were obtained from each individual (discrete dikaryon), and maintained on MEA (malt extract agar: 15 g/L agar, 15 g/L malt extract) slants at 5 C. After identifying the mating types of each individual, one homokaryon of each type was retained. Single-basidiospore isolates of the European "main-" and "*Fagus*-type" species were obtained from Dr. Nils Hallenberg, Gothenburg University, Sweden (TABLE II).

Pairing procedure.—Mating tests were performed by placing small bits of inoculum taken from the margin of actively growing homokaryotic, simple-septate tester mycelia 2–3 mm apart on MEA plates. Four sib pairings were carried out on a single plate, one at each of four poles. For non-sib pairings, two pairings were carried out on a single plate, each at opposite poles.

Nine sib homokaryons were paired in all combinations to identify mating types. Following 3–5 da incubation at 25 C, plates were examined macroscopically and then microscopically for the presence of hyphae with clamp connections. If fewer than four mating types were found, additional sib homokaryons were paired against those of known mating type until the fourth type was retrieved. For determination of mating type fac-

TABLE I

NORTH AMERICAN INDIVIDUALS USED IN THE MATING STUDIES

Individual number[a]	Genotype	Tester number	Genotype	Substratum	Locality
2215 [1107656]	A1A2 B1B2	2215/2	A1 B2	*Syringa vulgaris* L.	Bloomsburg, PA
		2215/3	A2 B1		
2220 [1107657]	A3A4 B3B4	2220/1	A3 B3	*Ligustrum vulgare* L.	Bloomsburg, PA
		2220/6	A4 B4		
2231 [1107658]	A5A6 B5B6	2231/1	A5 B5	*L. vulgare*	Bloomsburg, PA
		2231/5	A6 B6		
2232 [1107659]	A7A8 B7B8	2232/2	A8 B7	*Quercus alba* L.	Bloomsburg, PA
		2232/5	A7 B8		
2238 [1107660]	A9A10 B3B9	2238/1	A9 B9	*S. vulgaris*	Benton, PA
		2238/5	A10 B3		
2244 [1107661]	A11A12 B10B11	2244/2	A11 B11	*Cornus florida* L.	Bloomsburg, PA
		2244/11	A12 B10		
2249 [1107662]	A13A14 B12B13	2249/1	A13 B12	*L. vulgare*	Bloomsburg, PA
		2249/12	A14 B13		
2250 [1107663]	A15A16 B14B?	2250/4	A15 B14	*Celtis occidentalis* L.	Bloomsburg, PA
		2250/5	A16 B14		
2251 [1107664]	A17A? B15B16	2251/5	A17 B15	*Tilia americana* L.	Bloomsburg, PA
		2251/6	A17 B16		
2252 [1107665]	A18A19 B17B18	2252/1	A18 B17	*Rhus typhina* L.	Levittown, PA
		2252/11	A19 B18		
2254 [1107666]	A20A21 B19B20	2254/3	A20 B20	*S. vulgaris*	Wappingers Falls, NY
		2254/9	A21 B19		
2255 [1107667]	A22A23 B21B22	2255/1	A22 B21	*Salix babylonica* L.	Wappingers Falls, NY
		2255/3	A23 B22		
2256 [1107668]	A24A25 B23B24	2256/1	A24 B23	*L. vulgare*	Wappingers Falls, NY
		2256/7	A25 B24		
2257 [1107669]	A26A27 B8B25	2257/1	A26 B25	*Acer platanoides* L.	Wappingers Falls, NY
		2257/2	A27 B8		
2258 [1107670]	A28A29 B8B26	2258/1	A28 B26	*L. vulgare*	Poughkeepsie, NY
		2258/5	A29 B8		
2259 [1107671]	A30A31 B27B28	2259/1	A30 B27	*S. vulgaris*	Fredericksburg, VA
		2259/2	A31 B28		
2265 [1107672]	A32A33 B29B30	2265/2	A33 B29	*Acer saccharinum* L.	Bloomsburg, PA
		2265/5	A32 B30		

[a] Four digit numbers are the author's collection numbers; seven digit numbers in brackets are herbarium accession numbers for the National Fungus Collections, U.S. Dept. Agric., Beltsville, Maryland.

TABLE II

EUROPEAN INDIVIDUALS USED IN THE MATING STUDIES

Species	Individual number	Tester number[a]	Substratum	Locality
P. cinerea "Main-type"	GB 1442	1442/1,4	*Rhamnus*	Västergötland, Sweden
	GB 1469	1469/2	hardwood	Iasi, Romania
	GB 1483	1483/1,6	*Tilia*	Iasi, Romania
	GB 1761	1761/1	*Fraxinus*	Västergötland, Sweden
	GB 1810	1810/1	*Betula*	Roussillon, France
	GB 2026	2026/1	*Fagus*	Jutland, Denmark
P. cinerea "*Fagus*-type"	GB 1007	1007/3,5	*Fagus*	Bistrita-Nasaud, Romania
	GB 1474	1474/3	*Fagus*	Brasov, Romania
	GB 1477	1477/1	*Fagus*	Iasi, Romania
	GB 1484	1484/1	*Fagus*	Neamt, Romania
	GB 1488	1488/3	*Fagus*	Brasov, Romania
	GB 1788	1788/1	*Fagus*	Huesca, Spain
	GB 1910	1910/1,5	*Fagus*	Jylland, Denmark

[a] When two testers are listed, they are fully compatible (A≠ B≠)

tors (TABLE I), North American testers from each individual were paired in all combinations. For intercontinental pairings, two fully compatible testers from each American individual were used, e.g., A1B2 and A2B1. When two European testers were used, they were fully compatible; otherwise, one tester was used per European individual.

Following approximately 5 da incubation for non-sib American pairings and 7–12 da incubation for the remaining pairings, interactions were described macroscopically, i.e., presence of a junction line or dikaryotic fringe, and examined microscopically for the presence of clamp connections.

RESULTS

Sib matings among 17 American individuals confirmed the report by Vandendries (**1937**) that *P. cinerea* is bifactorial. A≠ B≠ pairings produced a distinct fringe composed of hyphae bearing clamp connections at the periphery of each homokaryon. A= B≠ pairings showed a fringe of restricted, granular mycelial growth; the hyphae formed neither clamps nor hook cells. A≠ B= pairings showed a narrow line of compact aerial mycelium along the junction or zone of contact. Junction line hyphae formed false clamps infrequently. A= B= pairings showed no macroscopic or microscopic changes, and testers did not intermingle.

All four mating types were identified in 15 of the 17 American individuals. Individual 2250 yielded three mating types, and 2251 only two. A total of 33 A factors and 30 B factors were detected. Mating factor sharing was minimal (TABLE I); even individuals 1–2 m apart, e.g., 2215 and 2231, showed no sharing. Factor B3 is shared by 2220 and 2238, approximately 18 miles apart. Factor B8 was shared by individuals 2232, 2257, and 2258; 2257 and 2258 were only about 7 mi apart from each other, but 130 mi from 2232. With the exeption of testers with common factors, all non-sib pairings were fully compatible and displayed the characteristic fringe of clamped hyphae.

The results of non-sib, intraspecific pairings for both European species are shown in TABLE III. All non-self pairings resulted in dikaryon formation, although in four cases clamps were formed sparsely along the junction line betwen testers (±JL). Roughly one-third of all pairings displayed limited nuclear migration, with clamp connections formed either at the junction line only (+JL), or in a sector emanating from the line (+SEC).

Matings betwen the "main-" and "*Fagus*-type" European species were negative (TABLE III). This verifies the report of intersterility by Hallenberg (**1986**), with the following qualification. Hallenberg reported sparse clamp connections in a few interspecific pairings; all but one (1007/3 × 1442/1) involved testers not used in the present study. After several attempts, no clamp connections could be located in 1007/3 × 1442/1 pairings.

Intercontinental pairings (TABLE III) resulted in reactions ranging from full dikaryotization with

TABLE III

RESULTS OF PAIRINGS AMONG AMERICAN, "MAIN-TYPE" AND "*FAGUS*-TYPE" EUROPEAN SIBLING SPECIES OF *P. CINEREA*

Species pair	Total number of pairings	Number of pairings leading to:							
		+FR[a]	+HFR	+SEC	+JL	±SEC	±JL	−JL	−NI
American × main-type (Europe)	198	44	3	5	9	0	4	75	58
American × *Fagus*-type (Europe)	252	88	5	6	18	7	22	44	62
Main-type (Europe) × main-type (Europe)	28	18	0	4	5	0	1	0	0
Fagus-type (Europe) × *Fagus*-type (Europe)	36	23	1	2	7	0	3	0	0
Main-type (Europe) × *Fagus*-type (Europe)	72	0	0	0	0	0	0	6	66

[a] Abbreviations: +FR = full dikaryotization, fringe composed of clamped hyphae, indicating bilateral nuclear migration; +HFR = fringe composed of clamped hyphae at edge of one tester only, possibly indicating unilateral nuclear migration, with no intermingling of testers; +SEC = a junction line formed from which emanated a sector of clamped hyphae; +JL = a junction line formed, rarely with brownish pigments, composed of hyphae with abundant, true clamp connections; ±SEC = as in +SEC, but sector hyphae with simple septa, false clamps, and scattered true clamps; ±JL = as in +JL, but hyphae in line with simple septa, false clamps, and scattered true clamps; −JL = junction line formed, hyphae mostly with simple septa, false clamps rare; −NI = no junction line, no intermingling of testers, no fringe, hyphae with simple septa only.

bilateral nuclear migration as seen in A≠ B≠ sib pairings (+FR) to no observable homokaryon interaction similar in appearance to A= B= sib pairings (−NI). Intermediate reactions included apparent interruptions in nuclear migration (−JL, ±JL, +SEC, ±SEC, +HFR) and clamp connection formation (false clamps in ±JL and ±SEC). The reactions are characterized and abbreviations explained in TABLE III.

DISCUSSION

Pairings among homokaryons from seventeen individuals suggest that *P. cinerea* represents a single species in northeastern North America. Intersterile groups may exist, but an additional survey with a broader scope would be needed to detect them. If such groups exist among the populations sampled, the isolating mechanism, such as that reported for *Pleurotus eryngii* (DC.: Fr.) Quél. (Cailleux *et al.*, **1981**), must be operative after dikaryon formation and, therefore, would be undetectable by the methods employed in the present study. Reproductive isolation between the two sibling species of *P. cinerea* in Europe reported by Hallenberg (**1986**) is confirmed (TABLE III).

The early European and American populations of *P. cinerea* were probably fragments of a larger ancestral population system, but their divergence has yet to result in complete genetically-based reproductive isolation. Allopatric speciation is a generally accepted mode of speciation in vertebrates (Mayr, **1970**) and many plants (Grant, **1981**), and appears to be operative in many fungi as well (Brasier, **1987**; Burnett, **1983**). It is consistent with the theory of allopatric speciation that given a sufficiently effective extrinsic physical barrier to gene flow (which the Atlantic Ocean is presumed to be for a species with hyaline, thin-walled basidiospores), geographically isolated populations undergoing gradual divergence can retain full or partial capacity to form dikaryons *in vitro*. Support for this can be drawn from reports (Anderson *et al.*, **1980**; Bresinsky *et al.*, **1987**; Bruehl *et al.*, **1975**; David and Boidin, **1984**; Flynn, **1986**; Fox and Wong, **1990**; Fries and Neumann, **1990**; Hallenberg, **1984**; Nobles and Frew, **1962**) of full or partial interfertility between populations separated by oceans or large land masses.

Based on the results presented herein, it is suggested that after European and American populations began their divergence, a speciation episode occurred in Europe where a phenotype adapted for utilization of the wood of *Fagus sylvatica* became reproductively isolated from the

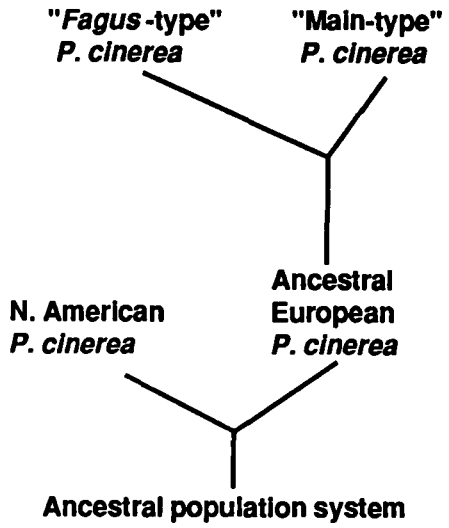

FIG. 1. Hypothetical speciation scheme for European and eastern North American *P. cinerea*. The scheme is supported by the mating studies reported here, and by the protein studies of Hallenberg and Larsson (**1991**).

generalized or "main-type" (FIG. 1). There are numerous examples (Anderson *et al.*, **1973**; Fries, **1985**; Hedger *et al.*, **1987**; Leuchtmann and Clay, **1988**; McKeen, **1952**; Perkins *et al.*, **1976**; and Worrall *et al.*, **1983**) of "habitat" or host specialization in fungi, demonstrating either concomitant reproductive isolation or genetic differentiation. It therefore seems reasonable to hypothesize that substratum preference for *F. sylvatica* may have been involved in the formation of European sibling species of *P. cinerea*. Although many species of fungi have apparently arisen through host or substratum specialization, other cases exist (Saliba and David, **1988**) where substratum preference appeared not to have played a role.

Speciation in European *P. cinerea* could have occurred allopatrically, with later migration resulting in zones of sympatry. Alternatively, speciation via substratum specialization in Europe may have occurred sympatrically. Sympatric speciation has been questioned by Mayr (**1970**) and others, but there is an increasingly convincing body of empirical and theoretical evidence supporting its importance, especially under the regimen of habitat specialization (Rice and Salt, **1990**; Tauber and Tauber, **1989**). Sympatric speciation has gained its best support from studies implicating linkage or pleiotropy between incompatibility mechanisms and habitat specialization in plants (Macnair and Christie, **1983**) and insects (Feder *et al.*, **1988**).

Reproductive isolation between American and European populations is weak, but is nearly complete between the "*Fagus*-" and "main-type" European sibling species (TABLE III). Other workers have shown that sympatric populations of closely related species, or those of sympatric species, can be reproductively isolated from each other while maintaining at least partial ability to mate with distant, allopatric populations (Boidin and Lanquetin, **1984**; Meinhardt *et al.*, **1984**; and Weresub and Gibson, **1960**). More pronounced isolation betwen sympatric populations as opposed to allopatric ones may be akin to the concept of character displacement in ecological theory (Brown and Wilson, **1956**).

It is not implied here, however, that recently-formed sympatric species would display more genetic differences than would allopatric species or semispecies. Actually the reverse appears to be true (Vilgalys and Johnson, **1987**). It is interesting to note here that Lessios and Cunningham (**1990**), working with sea urchins, have suggested that the strength of reproductive isolation and the degree of genetic divergence need not be correlated.

The protein profiles for *P. cinerea* isolates published by Hallenberg and Larsson (**1991**) indicate that the two European sibling species are more similar to each other than either is to the American population. This lends support to the notion that the strength of reproductive isolation and the degree of genetic divergence need not be correlated. The protein profiles also provide molecular support for the speciation scheme, proposed on the basis of mating studies, depicted in FIG. 1.

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