Mycologia, 89(1), 1997, pp. 24–36.

Somatic incompatibility in basidiomycetes

James J. Worrall [1]

College of Environmental Science and Forestry, State University of New York, Syracuse, New York 13210

Abstract: Somatic incompatibility regulates allorecognition (recognition of nonself) and allorejection following somatic contacts in many groups of organisms. The occurrence of somatic incompatibility and the resolving power of allorecognition probably reflect an evolutionary balance between the costs and benefits of somatic integration with conspecific neighbors and intramycelial anastomoses. In basidiomycetes, somatic incompatibility appears to function primarily in the dominant somatic phase, the secondary mycelium, and is clearly distinct from two other incompatibility systems, sexual incompatibility and intersterility. In laboratory studies, closely related mycelia are apparently recognized as self in many cases. However, allorecognition is almost always evident between different secondary mycelia from nature. Somatic incompatibility has therefore played an important role in concepts of individualism in fungi. In practice, somatic incompatibility in the strict sense (failure of anastomoses and genetic and cytoplasmic isolation) is usually inferred from mycelial incompatibility (macroscopic lines between colonies that can be interpreted as agonistic responses). Although the genetic mechanism is still unclear, multiple loci appear to be involved.

Key Words: Basidiomycota, population, vegetative compatibility

Somatic incompatibility refers to the prevention of effective fusion and integration following allorecognition (recognition of nonself) between genetically distinct, conspecific tissues when isogenic (self) contacts result in such fusion (Grosberg, 1988; Rayner et al., 1984). "Somatic" specifies a nonreproductive domain, distinguishing the system from sexual incompatibility. This review will first consider the occurrence of somatic incompatibility in other organisms, briefly discuss evolution of the phenomenon, and then focus on the basidiomycetes.

Accepted for publication August 26, 1996.

[1] Email: jworrall@mailbox.syr.edu

A WIDESPREAD PHENOMENON

Somatic incompatibility, under various names and with varying details, appears to be widespread in biology. In animals, cellular slime molds and plants, it regulates fusion of tissues, which would result in a chimera of genetically distinct tissues in the case of nonself fusions. In acellular slime molds and fungi, it regulates fusion also at a more intimate level, determining whether fusion or hyphal anastomosis result in effective cytoplasmic continuity and nuclear exchange.

Slime molds.—Somatic incompatibility has been documented in protists such as acellular (Lane, 1981) and cellular slime molds (Buss, 1982), where it regulates fusion among (pseudo)plasmodia. In the myxomycetes, distinct loci govern fusion vs. post-fusion compatibility. All loci must be homogenic for compatibility. In *Physarum polycephalum,* a difference at a single post-fusion locus led to selective enclosure and evacuation of one of the two types of nuclei following fusion (Lane and Carlile, 1979).

Animals.—Somatic incompatibility systems are common in colonial and some other animals in groups such as Porifera, Cnidaria and Bryozoa (Grosberg, 1988). Fusing of colonies *in situ* and success of experimental grafts require close relationship of the pair due to a requirement for identity at highly polymorphic loci. When somatic compatibility permits nonself fusion, a chimera results, as in tissue or organ transplants.

In motile, noncolonial invertebrates, somatic incompatibility is uncommon and tissue can generally be grafted indiscriminantly (Crampton and Hurst, 1994). However, in vertebrates, a phenomenon known as histocompatibility is particularly important in organ transplants and tissue grafts, as well as in the immune response. A series of highly polymorphic loci known as the major histocompatibility complex (MHC) must be isogenic for full tissue compatibility (Klitz et al., 1992).

Plants.—Like most noncolonial animals, plants often can be grafted indiscriminantly, even between species and genera in some cases. However, intraspecific graft (somatic) incompatibility is not uncommon (Andrews and Marquez, 1993). For instance, it has caused problems in establishing conifer seed or-

chards. The phenomenon is not easily predictable and has not been clearly elucidated genetically, but is thought to be controlled by multiple genes with additive effects.

Asco- and deuteromycetes.—In this group of fungi, mating-type heterokaryons formed as part of the sexual cycle are usually restricted to the ascogonium and ascogenous hyphae. The dominant somatic phase is a haploid homokaryon. Somatic incompatibility, often referred to as heterokaryon or vegetative (in)compatibility, regulates success of hyphal anastomoses and heterokaryon formation in this phase.

Understanding of somatic incompatibility and its genetic control is further along in this group than in most others because of genetic analysis of a variety of ascomycetes and cloning of several genes involved (Bégueret et al., 1994; Glass and Kuldau, 1992; Leslie, 1993). Multiple loci (often referred to as *het* loci) are generally involved; up to 17 loci have been found in *Podospora anserina* (Glass and Kuldau, 1992). Each locus has two or more alleles. Typically, two homokaryons must be homoallelic at all loci for full compatibility. In some fungi, the mating-type locus functions also as one of the somatic incompatibility loci. Sometimes, specific alleles at two different loci interact ("nonallelic" interaction) to cause incompatibility. According to a model developed to explain the phenomenon in molecular terms (Bégueret et al., 1994), allelic *het* genes code for polypeptides, homomeric complexes of which perform some primary cellular function. In incompatible heterokaryons, heteromeric complexes poison the cell. Nonallelic genes function similarly, except that only certain heteromeric complexes, coded by different loci, are poisonous.

Somatic compatibility in asco- and deuteromycetes is often detected directly by heterokaryon formation, often using nutritional mutants. When somatic compatibility permits heterokaryon formation, nuclei usually migrate and heterokaryotic growth may occur. In some species, however, heterokaryosis is limited to the fusion cells (Glass and Kuldau, 1992). In many species, a macroscopic line of demarcation, often called a barrage, appears between somatically incompatible mycelia (Leslie, 1993). The line is often pigmented and may be a sparse zone with raised mycelium on either side. In the line, numerous hyphal anastomoses degenerate and die. Thus, the line often represents a barrier to exchange of cytoplasm and nuclei. However, the line does not always correspond with heterokaryon incompatibility (Ford et al., 1995). It is therefore useful to distinguish the phenomenon by the term mycelial incompatibility (Kohn et al., 1991). In work on some species, most notably *Cryphonectria parasitica,* mycelial incompatibility has been the primary criterion of somatic incompatibility. DsRNA, associated with hypovirulence in this fungus, can be transmitted between some mycelially incompatible isolates, further evidence that such incompatibility does not necessarily preclude a functional cytoplasmic bridge.

Genetic diversity is generally greater between than within somatic compatibility groups, but substantial genetic variation, e.g., pathogenic races, may exist within groups in some cases (Jacobson and Gordon, 1991). DNA fingerprints often correspond with somatic or mycelial compatibility groups, but in some cases do not (see below under Somatic Incompatibility and Relatedness).

EVOLUTION OF SOMATIC INCOMPATIBILITY

There are many potential advantages and disadvantages of nonself fusion and integration. As Rayner (1991a) wrote, "Of all the challenges which a fungal mycelium faces during its potentially infinite life span, the one arguably bringing the most powerful combination of risk and promise to the welfare of the selfish genes it contains is an encounter with another mycelium of the same or related species." Advantages of fusion with contiguous conspecifics derive mainly from an increase in size, making available greater resources and faster reproduction. The size structure of some fungal populations suggests that survivorship is low at small sizes (Holmer and Stenlid, 1991; Worrall, 1994), such that a rapid increase in size would improve the chances of survival.

Potential costs of nonself fusion are several. First, one genome may be disproportionately represented in progeny at the expense of another genome that contributed to success of the soma, a phenomenon known as somatic cell parasitism (Buss, 1982). A related form of nuclear warfare is genomic replacement, in which one set of nuclei replaces the other after anastomosis. This has been detected mostly when at least one of the pairs is a homokaryon (Rayner et al., 1984; Rizzo and Harrington, 1992; Rizzo and May, 1994), probably because somatic incompatibility between unlike heterokaryons generally prevents nuclear invasion. Genomic replacement also characterizes the selective evacuation of nuclei described for a slime mold above. Quantitative modelling suggests that conspecific, parasitic nuclei could account for evolution of somatic incompatibility (Malik, 1996). Also, nonself fusion may facilitate transmission of conventional parasites such as mycoviruses. Finally, heterogeneity achieved by sexual recombination may be lost: at the extreme, complete fusion of a population would severely limit expression of the

variability inherent in the population, partially nullifying natural selection. This role for somatic incompatibility was supported by Lane (1981) because of the existence of pleiotropic genes in some ascomycetes that affect both somatic and sexual compatibility and the limited effectiveness of post-fusion incompatibility in preventing virus spread in fungi. Theoretical modelling also suggests that preservation of evolved adaptations is sufficient for evolution of somatic incompatibility (De Boer, 1995). One or more of these disadvantages appear to provide selective forces for recognition and rejection of nonself, or at least rejection of any but close kin.

It is not known whether these allorecognition and rejection phenomena arose by convergent evolution (Esser and Blaich, 1973) in each group or as a primitive trait that has developed somewhat differently in the groups. It has been argued that the immune system in vertebrates is better adapted for graft rejection than for preventing spread of pathogens, suggesting that allorecognition is a primitive trait (Lane, 1981). In either case, somatic incompatibility appears to be play a role in maintaining phenotypic diversity among genotypically distinct individuals in a population and in avoiding conspecific and conventional parasitism.

OVERVIEW OF SOMATIC INCOMPATIBILITY IN BASIDIOMYCETES

Somatic incompatibility and the life cycle.—Consideration of a homobasidiomycete will illustrate how somatic incompatibility fits in the life cycle in relation to other incompatibility systems. As a mycelium grows, it is likely to encounter many other mycelia. Three known incompatibility systems govern the outcome of these interactions (Anderson et al., 1992; Brasier, 1987; Rayner and Todd, 1982a). If the juxtaposed mycelia are of different species not closely related, intermingling of hyphae or various forms of antagonism may occur. Alternatively, the two mycelia may be of the same species (FIG. 1). First, assume that both are primary (unmated, homokaryotic) mycelia. If they are sexually compatible (different mating-type alleles), anastomosis and nuclear exchange (plasmogamy) occur. The resultant mycelium is said to be secondary (mated, heterokaryotic, often dikaryotic), and the two component nuclei may ultimately undergo karyogamy. Alternatively, the primary mycelia may be either sexually incompatible or from intersterile populations, in which cases hyphal anastomoses, if they occur, do not result in a secondary mycelium.

Once established, the secondary mycelium may confront further mycelia of the same species (FIG. 1). A primary mycelium may receive nuclei from the secondary mycelium, assuming sexual compatibility and interfertility (see Relationship with Other Incompatibility Systems, below). If a secondary mycelium is encountered, the interaction depends on somatic compatibility. If the mycelia merge and hyphal anastomoses persist between them, they are said to be somatically compatible. This is the rule for clonally related mycelia and may occur in other cases, especially with close kin. If anastomoses fail and a zone of inhibition forms between the secondary mycelia, the mycelia are said to be somatically incompatible.

Several features distinguish somatic incompatibility from sexual incompatibility and intersterility systems in the basidiomycetes (TABLE I). It is somatic in that it does not normally interfere with sexual compatibility of primary mycelia and in that somatic incompatibility can occur between secondary mycelia that contain sexually compatible nuclei. Unlike sexual incompatibility, somatic incompatibility is associated with genetic difference and is thus a heterogenic incompatibility system. Unlike intersterility, which prevents matings between members of intersterile populations (biological species), somatic incompatibility does not prevent mating and operates at the level of the individual.

Although strict definitions have always varied, a comparison of earlier and current literature suggests that usage of terms describing the nuclear condition of a mycelium has evolved. A heterokaryon is an association of unlike nuclei in a common mycelium (Raper, 1953). In practice, the term was formerly not applied to secondary mycelia, but to other associations of nuclei. Currently, and in this review, 'heterokaryon' is used more broadly to include secondary mycelia (except diploids, of course). Earlier, the term "dikaryon" was applied to secondary mycelia even when the conjugate nuclei were not strictly paired nor the hyphae possessing clamp connections, the condition to which "dikaryon" is more often restricted today. Accordingly, the more inclusive term "heho" (heterokaryon-homokaryon) has been used recently to describe pairings that have been referred to as "di-mon" (dikaryon-monokaryon) (Angwin and Hansen, 1993). Logical extensions of that terminology used here are ho-ho and he-he pairings.

Somatic vs. mycelial incompatibility.—Once a neighbor is identified as nonself (allorecognition) and rejected for integration (somatic incompatibility) competition and invasive growth become a possibility. Many organisms apparently obviate this outcome by agonistic behavior. Some colonial animals fight aggressively when allorecognition systems identify a conspecific neighbor as nonself (Grosberg, 1988). Similarly, so-

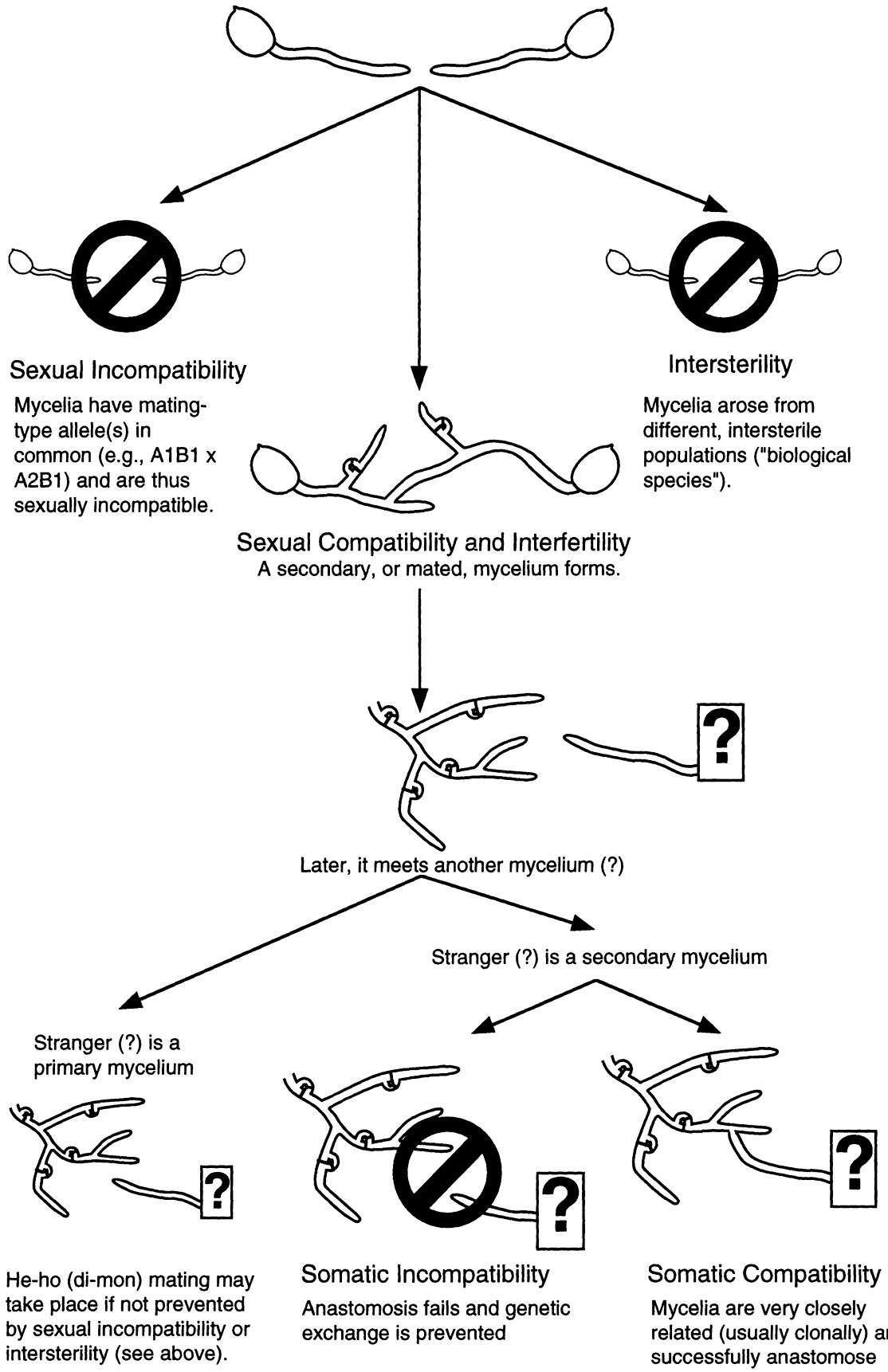

FIG. 1. Somatic incompatibility relative to other incompatibility systems in the life cycle of a representative homobasidiomycete.

TABLE I. Incompatibility systems in basidiomycetes

Type	Definition	Function	Genetic nature of incompatibility
Sexual incompatibility	Mating incompatibility between nuclei with identical alleles at any mating-type locus.	Prevents formation of secondary (heterokaryotic, usually dikaryotic) mycelium and subsequent sexual reproduction.	homogenic
Somatic incompatibility	Mycelial rejection between genetically dissimilar, usually secondary, mycelia.	Maintains individuality of mated mycelia; usually prevents genetic exchange.	heterogenic
Intersterility	Mating incompatibility, regardless of mating-type alleles, between individuals from different, intersterile, populations ("biological species") or species.	Limits gene flow between sympatric populations; may permit sympatric speciation.	heterogenic

matic incompatibility in fungi is often accompanied by or similar to combative interactions between species, including pigment formation, raised lines of dense mycelium, sparse zones, etc. (Rayner and Todd, 1982b). That reaction, often referred to as mycelial incompatibility in ascomycetes, may be viewed as agonistic behavior, as in somatically incompatible animals. Indeed, it is often called a line of antagonism.

Thus, allorecognition may trigger two reactions that have different implications and should be distinguished (Rayner, 1991b). One is prevention of successful, somatic anastomoses and the accompanying cytoplasmic and nuclear exchange. The term somatic incompatibility, as applied to basidiomycetes, should be restricted to this reaction to conform with other groups of organisms. The other, macroscopic interaction may be called mycelial incompatibility. Mycelial incompatibility has been the most common criterion in evaluating somatic incompatibility in basidiomycetes, but it has not been widely recognized as a distinct reaction. Although it appears likely that mycelial incompatibility and genetic and cytoplasmic isolation are generally associated, as described below, they have been related in too few basidiomycetes to be certain of the implications in all.

ELUCIDATION OF THE PHENOMENON

Although several workers had previously noted lines of demarcation when pairing different isolates of the same species, Irene Mounce (1929) was the first to study the phenomenon in detail and established the essence of the concept that we have today. Using 47 isolates of *Fomitopsis pinicola,* she found that a zone of inhibition almost invariably formed between isolates. It varied from a sparse zone between the mycelia, sometimes bordered on one or both sides by thickened aerial mycelium, to a dense line of submerged, dark, sclerotial tissue forming a wall between the mycelia. The latter was termed a line of demarcation. When a mycelium was paired with itself, the colonies grew together and eventually looked like a single colony. Also, isolates sometimes merged when: a) an isolate from wood was paired with a tissue isolate from a basidioma on the same tree; b) tissue isolates from two basidiomata on the same tree were paired; c) a polysporous isolate was paired with a tissue isolate of the parent or with a polysporous isolate from another basidioma on the same tree. When two isolates from a single tree formed a line of demarcation, she hypothesized that they arose from separate infections and confirmed this by detecting different sets of mating-type alleles in monosporous isolates from two basidiomata on the same tree.

In pairings of monosporous cultures, lines of demarcation were usually associated with failure to mate (detected by clamp connections). However, some pairings resulted in both clamps and lines of demarcation, and some resulted in neither.

The same phenomenon was detected in *Phaeolus schweinitzii* (Childs, 1937). Isolates from different trees, usually distinguishable morphologically, formed lines of demarcation between them, except in one case of three trees separated by 7–10 m. When isolates were from the same tree, lines were not formed. In contrast to Mounce's study, lines never formed between monosporous isolates. Like Mounce, Childs interpreted morphological differences and lines of demarcation as evidence that the mycelia varied as individuals originating from different basidiospore pairs.

Similarly, tissue isolates of various forms (now considered species) of *Phellinus igniarius sensu lato* intermingled only when paired with isolates from the same tree (Verrall, 1937). When isolates from one tree failed to intermingle, diffuse brown discolora-

tion could be found in the wood between the isolation points. Verrall concluded that these mycelia represented separate infections. Lines of demarcation formed in virtually all pairings between different mycelia, whether monosporous or secondary, but they were fleeting in sexually compatible matings of single-spore isolates within a form.

Childs (1963) later studied the same phenomenon in *Phellinus sulphurascens* (as *Poria weirii,* Douglas-fir form). He identified expanding disease centers in a young stand. Simple centers yielded isolates that merged with one another without forming lines of demarcation. Paired isolates from different centers usually formed distinct lines of demarcation. In some cases, two or more centers with distinct mycelia had become contiguous and formed a composite center. On the other hand, some centers over 30 m apart were inhabited by mycelia that merged completely when paired. The mycelium had apparently grown that distance in previous stands and caused isolated centers where conditions facilitated contact of roots with infested residues.

Both in wood in nature and in culture, allorecognition usually triggers a zone of antagonism. In wood, antagonism may take the form of a diffuse, more or less pale zone line (Verrall, 1937). This phenomenon has been contrasted with zone lines in wood arising from other causes (Rayner and Todd, 1982b). In culture, it is generally characterized as a sparse zone between the colonies, often accompanied by pigment formation and sometimes massing of the mycelia adjacent to the line.

MAINTAINING INDIVIDUALITY: *SEMPER INTACTUS*

The distribution of incompatible mycelia in nature and consistent association of markers such as mating-type alleles (see Relatedness below) suggest that the phenomenon functions to genetically isolate secondary mycelia. Snider (1965) concluded, based on nuclear migration experiments with *Schizophyllum commune,* that dikaryons "barricade" themselves effectively against entry of a third type of nucleus. Dikaryons could function as nuclear donors but not as recipients, a pattern also observed in studies of nuclear migration across mycelial incompatibility barriers (Coates et al., 1985). A large mycelium of *Armillaria gallica,* estimated to be well over 1000 yr old, was genetically stable, despite the frequent exposure to other, conspecific mycelia that must have occurred (Smith et al., 1992). In diploid-haploid pairings of the same fungus, Carvalho et al. (1995) found no evidence of haploid nuclei invading the diploid hyphae, although the reverse occurred.

Rayner and Todd (1979) looked for evidence of cytoplasmic and nuclear exchange in mycelially incompatible pairings and found none. They synthesized dikaryons of *Trametes versicolor* and paired them, resulting in zones of antagonism. After dedikaryotization and testing the resulting monokaryons against parent monokaryons to identify mating-type alleles, only the original nuclear types were recovered from the paired dikaryons. In addition, they added radioactive rubidium to one side of a pair, incubated, and then made an autoradiograph of the Petri dish. With selfpaired, compatible isolates, the tracer was distributed throughout the dish. When the mycelia were incompatible, the tracer remained on one side. Thus, mycelial incompatibility was shown to be associated with somatic incompatibility in the strict sense.

These results are consistent with the concept that somatic incompatibility effectively prevents introgression of foreign nuclei and cytoplasm in secondary mycelia. Primary mycelia, on the other hand, commonly accept donor nuclei, even during pairings in which mycelial incompatibility is observed (see Relationship with Other Incompatibility Systems, below).

Microscopical studies of anastomosis also show an association between mycelial and somatic incompatibility in most secondary mycelia that have been studied (Adams et al., 1981; Anderson, 1984; Aylmore and Todd, 1986; Barrett and Uscuplic, 1971; Rayner and Todd, 1979; Rizzo et al., 1995; Wilson, 1991). These studies indicate that anastomosis does occur, but is followed by degeneration or aberrant, limited development of fusion cells. Subtending hyphae may also develop abnormally, forming chains of vesicles, and eventually degenerate and die. In *Rhizoctonia solani* this is called the "killing reaction." Pigment accumulation in the medium and sometimes in hyphal walls often occurs. Presumably this killing of anastomosed hyphae is responsible for preventing the exchange of cytoplasm and nuclei, as discussed above. Anastomoses may be rare in somatically incompatible pairings, particularly after the reaction develops (Wilson, 1991).

An exception to the rule is *Heterobasidion annosum* (Hansen et al., 1993b). In this fungus, the heterokaryon is not a strict dikaryon; some hyphae are clamped and some have simple septa. Evidence suggests that at least some of the simple-septate hyphae are homokaryotic. In pairings that showed mycelial incompatibility, anastomoses were observed between simple-septate hyphae that did not lead to cell disruption. Some heterokaryotic hyphae from such pairings were shown to contain nuclei from both heterokaryons (Hansen et al., 1993b). The variable distribution of nuclei in this species apparently permits what amount to he-ho or ho-ho pairings at a hyphal

level between secondary mycelia. There is some evidence that this phenomenon may occur in the field (T. C. Harrington, unpublished results).

Somatic incompatibility has played a major role in development of concepts of the fungal individual. Based on earlier work and its interpretation, a concept arose suggesting that a genetically heterogeneous mycelium, a genetic mosaic, may arise by more or less unrestricted anastomosis and function as a physiological and ecological unit, or individual. Since mycelial incompatibility has been detected in most species that have been studied and associated with somatic incompatibility in some cases, the concept has since emerged that secondary mycelia of basidiomycetes maintain their individuality in every sense, genetic, physiological and ecological, by the process of somatic incompatibility (Rayner et al., 1984; Rayner and Todd, 1979).

SOMATIC INCOMPATIBILITY AND RELATEDNESS

Two facts about somatic incompatibility and relatedness can be stated unequivocally. First, somatically incompatible isolates are genetically different. Somatic incompatibility, usually inferred from mycelial incompatibility, is definitive evidence of and is usually quite sensitive to genetic difference. Second, colonies of the same genotype are somatically compatible. The uncertainty lies in the reliability of the assumption that somatically compatible isolates are of the same genotype.

Natural secondary mycelia that are thought to be genetically distinct are generally incompatible. For instance, field evidence suggests there is no tree-to-tree somatic growth of *Phaeolus schweinitzii* as there is with other root pathogens, and mycelia from different trees, even adjacent ones, are incompatible (Barrett and Uscuplic, 1971; Childs, 1937). Isolates of *Clitocybe nebularis* from fairy rings, which can be up to 40 m diameter, were compatible within fairy rings but incompatible among rings (Dowson et al., 1989). In many species, compatible isolates are morphologically uniform and distinguishable from other, incompatible isolates (Barrett and Uscuplic, 1971; Rishbeth, 1978; Verrall, 1937). In several studies, isolates that were compatible had the same molecular-genetic characters, which differed in incompatible isolates (DeScenzo and Harrington, 1994; Holmer et al., 1994; Smith et al., 1994). Other markers of field isolates such as mating-type alleles and isoenzyme patterns support the concept that different genotypes are almost always mycelially incompatible (Falk and Parbery, 1995; Kay and Vilgalys, 1992; Kile, 1983; Korhonen, 1978; Rizzo and Harrington, 1993; Sen, 1990; Stenlid, 1985). Thus, with field isolates of most species, it appears that reasonable confidence, with a margin for error, can be placed in the assumption that mycelially compatible isolates are of the same genotype.

Occasional anomalous results have been reported. Intransitiveness (incongruent results among pairings in a population, e.g., A=B and A=C, but B≠C) has been observed in a few cases (Jacobson et al., 1993; Malik, 1996). In other cases, poor correspondence was found between somatic incompatibility and other indicators of identity. For instance, certain mycelia of *Suillus granulatus* were compatible but had different RAPD markers (Jacobson et al., 1993). In both *P. schweinitzii* and *F. cajanderi,* pairs of morphologically distinguishable isolates were found to be compatible (Adams and Roth, 1967; Barrett and Uscuplic, 1971). Similarly, mycelial compatibility was observed between isolates of *Armillaria* spp. that differed by one mating-type allele (Kile, 1983; Korhonen, 1978).

A variety of factors may account for such anomalies. First, intransitiveness could arise if differences between isolates at more than one locus are necessary for detectable incompatibility (Malik, 1996). Second, somatic mutation may occur. In the example of *S. granulatus* above (Jacobson et al., 1993), there is reason to suspect that somatic mutation or recombination may be involved in some of the variation observed, at least in RAPD markers. For instance, two isolates collected at the same point, two years apart, differed at only 1 of 47 markers; most other isolates showed many more differences. Third, the techniques may not be adequate to detect somatic incompatibility or molecular-genetic differences. For example, mycelial incompatibility may vary in degree and depend in part on the medium used. Regarding the example above, *S. granulatus* reportedly gives relatively variable and indistinct reactions in mycelial compatibility pairings (Fries, 1987), which would make identification of genets by such pairings difficult. Similarly, a molecular technique or region of DNA may not be suitable for detecting variability or may be subject to inconsistent results (Smith et al., 1994). Fourth, work with ascomycetes suggests that a high level of inbreeding in small, isolated populations and/or a low number of segregating determinants may lead to frequent, independent origin of compatibility types (Anderson and Kohn, 1995; Kohn, 1995).

Pairings of synthetic secondary mycelia have been examined to study the relationship between mycelial incompatibility and relatedness. The species vary considerably, but the general trend is for more distantly related secondary mycelia to express incompatibility more frequently (TABLE II) and intensely. The results with *P. schweinitzii* (Barrett and Uscuplic,

TABLE II. Frequency of somatic incompatibility among pedigreed secondary mycelia

Type of pairing	Example	Species	Frequency of incompatibility (%)	Reference
Nonsibcomposed, unrelated mycelia	1a2a × 3a4a[a]	*Coprinus cinereus*	100	(May, 1988)
		Armillaria luteobubalina	100	(Kile, 1983)
		Phaeolus schweinitzii	90[b]	(Barrett and Uscuplic, 1971)
Nonsibcomposed mycelia having 1 or 2 of 4 mating alleles in common	1a2a × 3a– [c]	*A. luteobubalina*	90	(Kile, 1983)
Sibcomposed mycelium with unrelated field isolate	1a1b × 2	*Fomitopsis cajanderi*	100	(Adams and Roth, 1967)
		P. schweinitzii	85	(Barrett and Uscuplic, 1971)
Sibcomposed mycelia from different parents	1a1b × 2a2b	*Echinodontium tinctorium*	95	(Wilson, 1991)
		P. schweinitzii	62	(Barrett and Uscuplic, 1971)
Sibcomposed mycelia from same parent but no nucleus in common	1a1b × 1c1d	*Marasmius androsaceus*	100	(Holmer and Stenlid, 1991)
		Pleurotus ostreatus	96	(Kay and Vilgalys, 1992)
		F. cajanderi	83	(Adams and Roth, 1967)
		Armillaria spp.	44–55[d]	(Kile, 1983; Korhonen, 1978)
Sibcomposed mycelia from same parent, one nucleus in common	1a1b × 1a1c	*F. cajanderi*	65	(Adams and Roth, 1967)
Nonsibcomposed mycelia with one nucleus in common	1a2a × 1a3a	*Coprinus cinereus*	92	(May, 1988)
		Phaeolus schweinitzii	63	(Barrett and Uscuplic, 1971)
Sibcomposed mycelium with parental field isolate	1a1b × 1	*Collybia subnuda*	98	(Murphy and Miller, 1993)
		Phellinus sulphurascens	93	(Hansen, 1979)
		Pleurotus ostreatus	90	(Kay and Vilgalys, 1992)
		F. cajanderi	59	(Adams and Roth, 1967)
		Phaeolus schweinitzii	18	(Barrett and Uscuplic, 1971)
		Marasmiellus praeacutus	15	(Murphy and Miller, 1993)
Nonsibcomposed mycelia with one nucleus in common, the other nuclei being sib-related	1a2a × 1b2a	*Phellinus gilvus*	50	(Rizzo et al., 1995)

[a] Numbers refer to secondary mycelia from the field; letters refer to their single-spore progeny. For example, 1a is a single-basidiospore isolate from the parental mycelium 1. Synthetic secondary mycelia are indicated by the component single-spore isolates.

[b] Incompatibility in these pairings would have been absolute but for one aberrant isolate.

[c] Some pairings, including all compatible ones, involved a common parent.

[d] It was not explicitly stated that no monosporous isolates were in common.

1971) are complicated by uncertainty in detecting heterokaryon formation (*P. schweinitzii* does not form clamps). Behavior of field isolates was most closely approximated by nonsibcomposed, unrelated heterokaryons, which were incompatible in all cases except for one anomalous isolate. Results with *Trametes versicolor* (Todd and Rayner, 1978) and *Bjerkandera adusta* (Rayner and Todd, 1979) are somewhat unusual in that 100% of pairings among synthesized dikaryons were incompatible, regardless of relatedness (data not shown). Only the intensity of the reaction (as indicated by pigment production) varied.

In basidiomycetes, mycelial incompatibility is usually not a strict, binary character. The visual intensity of mycelial incompatibility usually varies among pairings and media affect its appearance and detection. It is unlikely that the threshold of detection of mycelial incompatibility coincides precisely with somatic incompatibility in the strict sense. Techniques that permit detection and identification of nuclei following pairings will be necessary to determine the significance of the variability in mycelial incompatibility.

RELATIONSHIP WITH OTHER INCOMPATIBILITY SYSTEMS

Confusion sometimes arises because of failure to adequately distinguish compatibility systems and because there is, in fact, interaction among the systems

that is still not well understood. We will first consider interactions between somatic and sexual incompatibility systems.

Since somatic incompatibility arises between dissimilar mycelia, why does it not interfere with sexual compatibility, preventing somatogamy? The hypothesis of "sexual override" may be useful in understanding this phenomenon (Rayner et al., 1984; Rayner and Todd, 1979). According to this hypothesis, somatic incompatibility is usually suppressed or overcome in sexually compatible homokaryons. Still unaccounted for is the formation of heterokaryons in hemicompatible (A≠, B= and A=, B≠) matings of fungi with bifactorial mating systems (Parag, 1965; Raper, 1953; Swiezynski and Day, 1960). Stable heterokaryons that lack clamp connections and are infertile commonly form in common-A (A=, B≠) matings. Perhaps override occurs in cases of hemicompatible as well as fully compatible (A≠, B≠) matings.

If the hypothesis is accurate, it appears that in some cases sexual compatibility fully suppresses somatic and mycelial incompatibility. In other cases, mycelial incompatibility is apparent but is "leaky," permitting plasmogamy. The specific cases of he-ho and ho-ho pairings where the interaction occurs are discussed separately below.

He-ho pairings.—A heterokaryon will generally contribute a nucleus to a homokaryon in a he-ho pairing, assuming sexual compatibility. Such pairings may be quite common in nature (see discussion in May, 1988).

He-ho pairings are often accompanied by mycelial incompatibility, the frequency and intensity depending on the relatedness between the isolates. For instance, in *Fomitopsis cajanderi, Phellinus gilvus, P. igniarius, P. sulphurascens* (the Douglas-fir form of *P. weirii*), *P. weirii* and *Coprinus cinereus,* such pairings between unrelated isolates resulted in mycelial incompatibility in almost all cases (Adams and Roth, 1967; Hansen, 1979; May, 1988; Rizzo et al., 1995; Verrall, 1937). However, in cases where it was checked, heterokaryotization was usually not prevented by somatic incompatibility. It is not always clear whether mycelial incompatibility in he-ho pairings represents an ephemeral response that may break down, permitting plasmogamy, or forms after plasmogamy, delimiting the two secondary mycelia. Pairings between homokaryons and the parent heterokaryons almost always resulted in mycelial incompatibility in *Phellinus igniarius* and *Fomitopsis cajanderi,* but in *Phaeolus schweinitzii* the reaction was absent or weak (Adams and Roth, 1967; Barrett and Uscuplic, 1971; Verrall, 1937). Pairings in which the heterokaryon and homokaryon shared a common nucleus (which would normally result in the new heterokaryon having nuclei identical with those in the first heterokaryon) usually gave no or weak reactions in *P. schweinitzii, Stereum gausapatum* and *C. cinereus,* but in *T. versicolor* and *F. cajanderi* such pairings gave 50–60% incompatibility (Adams and Roth, 1967; Barrett and Uscuplic, 1971; Boddy and Rayner, 1982; May, 1988; Todd and Rayner, 1978). Mycelial incompatibility that occurs in these cases presumably results directly from the interaction between hetero- and homokaryons rather than between the heterokaryons after nuclear acceptance and migration. In contrast, mycelial incompatibility developed only after nuclear migration in he-ho crosses in *Phellinus gilvus* (Rizzo et al., 1995). In *Echinodontium tinctorium,* mycelial incompatibility occurred in about half of the pairings between monokaryons and sibcomposed dikaryons from the same parent (Wilson, 1991). Incompatibility did not prevent dikaryotization of the monokaryon except when the reaction was intense (accompanied by pigment formation). In *Trametes versicolor,* mycelial incompatibility was consistently observed in he-ho pairings, but clamp connections formed on the monokaryon in 78% of cases (Todd and Rayner, 1978). In pairings where the monokaryon was a component of the dikaryon, initial antagonism sometimes broke down and complete fusion occurred.

In some species of *Phellinus* (which do not form clamps), mycelial incompatibility is so consistently present in he-ho crosses and absent in ho-ho crosses (assuming unrelated isolates in both cases) that heterokaryon formation between homokaryons can be detected by pairing the subculture with an unrelated homokaryon. If mycelial incompatibility is observed, the subculture is a heterokaryon; if no incompatibility is observed, the subculture is a homokaryon (Angwin and Hansen, 1993; Rizzo et al., 1995).

In some he-ho pairings, "track" formation was observed (Angwin and Hansen, 1993; May, 1988; Rayner and Todd, 1979). These narrow lines of antagonism radiated into the original homokaryon, dividing it into sectors. By subculturing, the sectors could be shown to represent incompatible heterokaryons formed by contribution of alternate nuclei from the original heterokaryon.

Ho-ho pairings.—In some fungi, reactions interpretable as mycelial incompatibility occur between some homokaryons. Most commonly and most intensively, they occur when the homokaryons are sexually incompatible by virtue of mating-type alleles (Coates et al., 1981; Mounce, 1929; Verrall, 1937). Such reactions may be less intense than those between secondary mycelia (Hansen, 1979). Besides representing somatic incompatibility (expressed in the absence of

sexual compatibility, see discussion of sexual override above), such reactions may be an indication of intersterility (see below). They may also represent the "sexual barrage" or restricted heterokaryon frequently seen in common-B matings (A≠, B=) in species with bifactorial mating systems (Parag, 1965; Raper, 1953; Rizzo et al., 1995; Wilson, 1990).

On the other hand, cases are known of homokaryons that apparently form a normal secondary mycelium despite lines of antagonism. For instance, sibling ho-ho pairings in *Phellinus weirii* often resulted in line formation (Angwin and Hansen, 1993). The presence of a line was generally associated with sexual incompatibility, but some pairs formed heterokaryons despite intense line formation. Mounce (1929) observed frequent and definite lines of aversion in ho-ho pairings. When clamp connections were formed, the line was either absent or relatively light in color. The lines were generally black only in pairings that did not form clamp connections. In *Rhizoctonia solani,* sexually compatible matings are generally manifested by tufts of heterokaryotic hyphae that arise from a line of antagonism between the homokaryons (Anderson, 1984).

Somatic incompatibility and intersterility.—Rayner and Todd (1979) expressed concern, which has proven to be well founded, that somatic incompatibility would be confused particularly with intersterility since both fall under the term "heterogenic incompatibility." However, their functions are very different (FIG. 1, TABLE I). Homokaryons from intersterile populations often exhibit a reaction similar to mycelial incompatibility when paired. It has therefore been hypothesized that intersterility is a failure of sexual override of somatic incompatibility (Rayner et al., 1984). The intersterility system may prevent sexual override, but in any case seems to trigger the same rejection phenomenon as does somatic incompatibility. More study is needed, however, to determine whether the incompatibility associated with intersterility is expressed as is somatic incompatibility. For instance, does anastomosis occur at all in pairings of intersterile isolates? Somatic and mycelial incompatibility seem to be generally triggered after anastomosis. At least in *Rhizoctonia solani,* intersterility is a prefusion phenomenon.

Because of its importance as an agricultural pathogen, work on the population biology and incompatibility systems of *Rhizoctonia solani* has progressed somewhat independent of that on other basidiomycetes. Although the terminology is different in this group, the incompatibility systems may be similar. There are a number of "anastomosis groups" that differ in pathology and in other respects; these groups appear to represent distinct intersterility groups or species (Vilgalys and Cubeta, 1994). Anastomosis does not occur between groups. Within a group, anastomosis occurs but, in pairings between different isolates, is followed by a "killing reaction" involving cells around the point of fusion. Macroscopically this is manifested as a line of antagonism, and occurs in he-he, ho-ho, and he-ho pairings. The killing reaction and line of antagonism apparently represent somatic incompatibility. Although mating behavior varies among the anastomosis groups, paired homokaryons with different H factors (for heterokaryon) generally produce a tuft of heterokaryotic hyphae at the line (Anderson, 1984). This homogenic incompatibility system can be interpreted as the sexual incompatibility system, and the H-factors as mating-type alleles.

MECHANISM AND GENETIC BASIS

Little is known of the physiological mechanisms of somatic incompatibility. Oxidizing conditions and phenoloxidases such as laccase have been detected in zones between incompatible mycelia (Hansen et al., 1993b; Li, 1981).

The genetic basis of somatic incompatibility must be understood to fully assess its utility as a tool in population studies and its influences on population structure (Anderson and Kohn, 1995). In the few cases for which there is evidence, mycelial compatibility appears to be controlled primarily by nuclear genes that are not linked with sexual compatibility loci. Pairings between heterokaryons of *Coprinus cinereus* that differed only in mitochondrial genotype indicated that mycelial incompatibility depends primarily on nuclear genes, but there was some apparent influence of mitochondria in one case (May, 1988). Studies of sexual and mycelial compatibility among pedigreed mycelia provide evidence that somatic incompatibility is controlled by at least some loci unlinked to the mating-type loci (Hansen et al., 1993a; Rizzo et al., 1995).

Because of the frequency of mycelial incompatibility among field isolates and even among closely related, pedigreed heterokaryons, multiple loci and/or multiple alleles have been thought to control somatic incompatibility in many cases. Difference at any locus would lead to incompatibility, but in most cases mycelial incompatibility is more intense with greater genetic difference.

An approach that has been used in several studies is to build pedigreed heterokaryons in which one nucleus is kept constant in all mycelia. This permits variation due to one set of nuclei to be analyzed in secondary mycelia without confounding variation from

the conjugate nucleus. In *Heterobasidion annosum,* when the varied nuclei were unrelated (e.g., 1a2a × 1a3a, 1a4a × 1a5a, etc.; see TABLE II for convention used in designating nuclei), mycelia reacted like field isolates, giving strong and consistent mycelial incompatibility in pairings with one another (Hansen et al., 1993a). When the varied nuclei were from a single family, i.e., sibrelated with one another but not with the common nucleus (e.g., 1a2a × 1a2b, 1a2c × 1a2d, etc.), incompatibility was often less distinct and about 10–20% of pairings were compatible. The results suggested that incompatibility was controlled by 3 or 4 loci, at least one of which was multiallelic (Hansen et al., 1993a).

At least in several *Phellinus* species, a single locus may play a major role in mycelial incompatibility (Hansen et al., 1994; Rizzo et al., 1995). Rizzo et al. (1995) conducted he-he pairings like those in the second experiment on *H. annosum* described above. Approximately half the isolates merged with one another but gave strong incompatibility reactions with the other half, which in turn merged with one another. This suggested a single heterozygous locus in the family's parent heterokaryon. When fully sibrelated heterokaryons were paired (e.g., 1a1b × 1c1d, but in some cases with common nuclei), three groups were found, corresponding again to a single locus (SC) that, in a family of inbred heterokaryons could exist as SC1/SC1, SC1/SC2 or SC2/SC2. However, weak incompatibility was frequent within the groups in the second experiment, suggesting that other loci contributed, but no pattern was evident. Similar results were found for *Phellinus weirii* (Hansen et al., 1994). In *Pleurotus ostreatus,* three or more loci apparently regulate mycelial incompatibility, although in some lines a single locus seemed to have a major effect (Malik, 1996; Malik and Vilgalys, 1994).

Genetic analysis of mycelial incompatibility is complicated by its dependence on media, the variability in degree of the phenomenon, and the uncertainty as to what level of mycelial incompatibility indicates somatic incompatibility. Further work that involves detection of nuclear identity following he-he pairings is necessary to elucidate the genetic control of somatic incompatibility.

ACKNOWLEDGMENTS

This review incorporates useful suggestions provided by J.B. Anderson, T.C. Harrington, L.M. Kohn and several anonymous reviewers.

LITERATURE CITED

Adams, D. H., and L. F. Roth. 1967. Demarcation lines in paired cultures of *Fomes cajanderi* as a basis for detecting genetically distinct mycelia. *Canad. J. Bot.* 45: 1583–1589.

Adams, T. J. H., N. K. Todd, and A. D. M. Rayner. 1981. Antagonism between dikaryons of *Piptoporus betulinus. Trans. Br. Mycol. Soc.* 76: 510–513.

Anderson, J. B., and L. M. Kohn. 1995. Clonality in soilborne, plant-pathogenic fungi. *Ann. Rev. Phytopathol.* 33: 369–391.

———, ———, and J. F. Leslie. 1992. Genetic mechanisms in fungal adaptation. Pp. 73–98. *In: The fungal community: Its organization and role in the ecosystem.* Eds., G. C. Carroll and D. T. Wicklow. Marcel Dekker, Inc, New York.

Anderson, N. A. 1984. Variation and heterokaryosis in *Rhizoctonia solani.* Pp. 367–382. *In: The ecology and physiology of the fungal mycelium.* Eds., D. H. Jennings and A. D. M. Rayner. Cambridge University Press, Cambridge.

Andrews, P. K., and C. S. Marquez. 1993. Graft incompatibility. Pp. 183–232. *In: Horticultural reviews.* Ed., J. Janick. Vol. 15. J. Wiley & Sons, New York.

Angwin, P. A., and E. M. Hansen. 1993. Pairing tests to determine mating compatibility in *Phellinus weirii. Mycol. Res.* 97: 1469–1475.

Aylmore, R. C., and N. K. Todd. 1986. Cytology of non-self fusions and somatic incompatibility in *Phanerochaete velutina. J. Gen. Microbiol.* 132: 581–591.

Barrett, D. K., and M. Uscuplic. 1971. The field distribution of interacting strains of *Polyporus schweinitzii* and their origin. *New Phytol.* 70: 581–598.

Bégueret, J., B. Turcq, and C. Clavé. 1994. Vegetative incompatibility in filamentous fungi: *het* genes begin to talk. *Trends Genet.* 10: 441–446.

Boddy, L., and A. D. M. Rayner. 1982. Population structure, inter-mycelial interactions and infection biology of *Stereum gausapatum. Trans. Br. Mycol. Soc.* 78: 337–351.

Brasier, C. M. 1987. The dynamics of fungal speciation. Pp. 231–260. *In: Evolutionary biology of the fungi.* Eds., A. D. M. Rayner, C. M. Brasier and D. Moore. Cambridge University Press, Cambridge.

Buss, L. 1982. Somatic cell parasitism and the evolution of somatic tissue compatibility. *Proc. Natl. Acad. U. S. A.* 79: 5337–5341.

Carvalho, D. B., M. L. Smith, and J. B. Anderson. 1995. Genetic exchange between diploid and haploid mycelia of *Armillaria gallica. Mycol. Res.* 99: 641–647.

Childs, T. W. 1937. Variability of *Polyporus schweinitzii* in culture. *Phytopathology* 27: 29–50.

———. 1963. *Poria weirii* root rot. *Phytopathology* 53: 1124–1127.

Coates, D., A. D. M. Rayner, and L. Boddy. 1985. Interactions between mating and somatic incompatibility in the basidiomycete *Stereum hirsutum. New Phytol.* 99: 473–483.

———, ———, and N. K. Todd. 1981. Mating behaviour, mycelial antagonism and the establishment of individuals in *Stereum hirsutum. Trans. Br. Mycol. Soc.* 76: 41–51.

Crampton, W. G. R., and L. D. Hurst. 1994. True kin recognition, in the form of somatic incompatibility, has

multiple independent origins. *Anim. Behav.* 47: 230–234.

De Boer, R. J. 1995. The evolution of polymorphic compatibility molecules. *Mol. Biol. Evol.* 12: 494–502.

DeScenzo, R. A., and T. C. Harrington. 1994. Use of (CAT)5 as a DNA fingerprinting probe for fungi. *Phytopathology* 84: 534–540.

Dowson, C. G., A. D. M. Rayner, and L. Boddy. 1989. Spatial dynamics and interactions of the woodland fairy ring fungus, *Clitocybe nebularis*. *New Phytol.* 111: 699–705.

Esser, K., and R. Blaich. 1973. Heterogenic incompatibility in plants and animals. *Advances in Genetics* 17: 107–152.

Falk, S. P., and D. G. Parbery. 1995. *Armillaria luteobubalina* population structure in horticultural plantings in Victoria, Australia. *Mycol. Res.* 99: 216–220.

Ford, E. J., R. V. Miller, H. Gray, and J. E. Sherwood. 1995. Heterokaryon formation and vegetative compatibility in *Sclerotinia sclerotiorum*. *Mycol. Res.* 99: 241–247.

Fries, N. 1987. Somatic incompatibility and field distribution of the ectomycorrhizal fungus *Suillus luteus* (Boletaceae). *New Phytol.* 107: 735–739.

Glass, N. L., and G. A. Kuldau. 1992. Mating type and vegetative incompatibility in filamentous ascomycetes. *Ann. Rev. Phytopathol.* 30: 201–224.

Grosberg, R. K. 1988. The evolution of allorecognition specificity in clonal invertebrates. *Quart. Rev. Biol.* 63: 377–412.

Hansen, E. M. 1979. Sexual and vegetative compatibility in *Phellinus weirii*. *Canad. J. Bot.* 57: 1573–1578.

———, J. Stenlid, and M. Johansson. 1993a. Genetic control of somatic incompatibility in the root-rotting basidiomycete *Heterobasidion annosum*. *Mycol. Res.* 97: 1229–1233.

———, ———, and ———. 1993b. Somatic incompatibility and nuclear reassortment in *Heterobasidion annosum*. *Mycol. Res.* 97: 1223–1228.

———, ———, and ———. 1994. Somatic incompatibility in *Heterobasidion annosum* and *Phellinus weirii*. Pp. 323–333. *In: Proceedings of the eighth IUFRO root and butt rot conference.* Eds., M. Johansson and J. Stenlid. Swedish University of Agricultural Sciences, Uppsala.

Holmer, L., L. Nitare, and J. Stenlid. 1994. Population structure and decay pattern of *Phellinus tremulae* in *Populus tremula* as determined by somatic incompatibility. *Canad. J. Bot.* 72: 1391–1396.

———, and J. Stenlid. 1991. Population structure and mating system in *Marasmius androsaceus* Fr. *New Phytol.* 119: 307–314.

Jacobson, D. J., and T. R. Gordon. 1991. *Fusarium oxysporum* f. sp. *melonis*: a case study of diversity within a forma specialis. *Phytopathology* 81: 1064–1067.

Jacobson, K. M., O. K. Miller Jr., and B. J. Turner. 1993. Randomly amplified polymorphic DNA markers are superior to somatic incompatibility tests for discriminating genotypes in natural populations of the ectomycorrhizal fungus *Suillus granulatus*. *Proc. Natl. Acad. U.S.A.* 90: 9159–9163.

Kay, E., and R. Vilgalys. 1992. Spatial distribution and genetic relationships among individuals in a natural population of the oyster mushroom *Pleurotus ostreatus*. *Mycologia* 84: 173–182.

Kile, G. A. 1983. Identification of genotypes and the clonal development of *Armillaria luteobubalina* Watling & Kile in eucalypt forests. *Aust. J. Bot.* 31: 657–671.

Klitz, W., G. Thomson, N. Borot, and A. Cambon-Thomsen. 1992. Evolutionary and population perspectives of the human HLA complex. Pp. 35–72. *In: Evolutionary biology.* Eds., M. K. Hecht, B. Wallace and R. J. MacIntyre. Vol. 26. Plenum, New York.

Kohn, L. M. 1995. The clonal dynamic in wild and agricultural plant-pathogen populations. *Canad. J. Bot.* 73: S1231-S1240.

———, E. Stasovski, I. Carbone, J. Royer, and J. B. Anderson. 1991. Mycelial incompatibility and molecular markers identify genetic variability in field populations of *Sclerotinia sclerotiorum*. *Phytopathology* 81: 480–485.

Korhonen, K. 1978. Interfertility and clonal size in the *Armillariella mellea* complex. *Karstenia* 18: 31–42.

Lane, E. B. 1981. Somatic incompatibility in fungi and Myxomycetes. Pp. 239–258. *In: The fungal nucleus.* Eds., K. Gull and S. G. Oliver. Cambridge University Press, Cambridge.

———, and M. J. Carlile. 1979. Post-fusion somatic incompatibility in plasmodia of *Physarum polycephalum*. *J. of Cell Sci.* 35: 339–354.

Leslie, J. F. 1993. Fungal vegetative compatibility. *Ann. Rev. Phytopathol.* 31: 127–150.

Li, C. Y. 1981. Phenoloxidase and peroxidase activity in zone lines of *Phellinus weirii*. *Mycologia* 73: 811–821.

Malik, M. 1996. The genetics and evolution of somatic self/non-self recognition in the oyster mushroom *Pleurotus ostreatus*. Ph.D. Dissertation, Duke University. Durham, North Carolina. 217 pp.

———, and R. Vilgalys. 1994. Towards the genetic basis of somatic incompatibility in *Pleurotus ostreatus*. Pp. 132. *In: Abstracts, Fifth Int. Mycol. Congr., 14–21 August 1994.* Vancouver, British Columbia.

May, G. 1988. Somatic incompatibility and individualism in the coprophilous basidiomycete, *Coprinus cinereus*. *Trans. Br. Mycol. Soc.* 91: 443–451.

Mounce, I. 1929. Studies in forest pathology. II. The biology of *Fomes pinicola* (Sw.) Cooke. *Can. Dept. Agric. Bull.* No. 111, New Series: 1–65.

Murphy, J. F., and O. K. Miller. 1993. The population biology of two litter decomposing agarics on a southern Appalachian mountain. *Mycologia* 85: 769–776.

Parag, Y. 1965. Common-B heterkaryosis and fruiting in *Schizophyllum commune*. *Mycologia* 57: 543–561.

Raper, J. R. 1953. Tetrapolar sexuality. *Quart. Rev. Biol.* 28: 233–259.

Rayner, A. D. M. 1991a. The challenge of the individualistic mycelium. *Mycologia* 83: 48–71.

———. 1991b. The phytopathological significance of mycelial individualism. *Ann. Rev. Phytopathol.* 29: 305–323.

———, D. Coates, A. M. Ainsworth, T. J. H. Adams, E. N. D. Williams, and N. K. Todd. 1984. The biological consequences of the individualistic mycelium. Pp. 509–540. *In: The ecology and physiology of the fungal mycelium.*

Eds., D. H. Jennings and A. D. M. Rayner. Cambridge University Press, Cambridge, United Kingdom.

———, and N. K. Todd. 1979. Population and community structure and dynamics of fungi in decaying wood. Pp. 333–420. *In: Advances in botanical research.* Ed., H. W. Woolhouse. Vol. 7. Academic Press, London.

———, and ———. 1982a. Ecological genetics of basidiomycete populations in decaying wood. Pp. 129–142. *In: Decomposer basidiomycetes: their biology and ecology.* Eds., J. C. Frankland, J. N. Hedger and M. J. Swift. Cambridge University Press, Cambridge.

———, and ———. 1982b. Population structure in wood-decomposing basidiomycetes. Pp. 109–128. *In: Decomposer basidiomycetes: their biology and ecology.* Eds., J. C. Frankland, J. N. Hedger and M. J. Swift. Cambridge University Press, Cambridge.

Rishbeth, J. 1978. Infection foci of *Armillaria mellea* in first-rotation hardwoods. *Ann. Bot.* 42: 1131–1139.

Rizzo, D. M., and T. C. Harrington. 1992. Nuclear migration in diploid-haploid pairings of *Armillaria ostoyae. Mycologia* 84: 863–869.

———, and ———. 1993. Delineation and biology of clones of *Armillaria ostoyae, A. gemina* and *A. calvescens. Mycologia* 85: 164–174.

———, and G. May. 1994. Nuclear replacement during mating in *Armillaria ostoyae* (Basidiomycotina). *Microbiology* 140: 2115–2124.

———, R. M. Rentmeester, and H. H. Burdsall Jr. 1995. Sexuality and somatic incompatibility in *Phellinus gilvus. Mycologia* 87: 805–820.

Sen, R. 1990. Intraspecific variation in two species of *Suillus* from Scots pine (*Pinus sylvestris* L.) forests based on somatic incompatibility and isozyme analysis. *New Phytol.* 114: 607–616.

Smith, M. L., J. N. Bruhn, and J. B. Anderson. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* 356: 428–431.

———, ———, and ———. 1994. Relatedness and spatial distribution of *Armillaria* genets infecting red pine seedlings. *Phytopathology* 84: 822–829.

Snider, P. J. 1965. Incompatibility and nuclear migration. Pp. 52–70. *In: Incompatibility in fungi.* Eds., K. Esser and J. R. Raper. Springer-Verlag, New York.

Stenlid, J. 1985. Population structure of *Heterobasidion annosum* as determined by somatic incompatibility, sexual incompatibility and isoenzyme patterns. *Canad. J. Bot.* 63: 2268–2273.

Swiezynski, K. M., and P. R. Day. 1960. Heterokaryon formation in *Coprinus lagopus. Genet. Res.* 1: 114–128.

Todd, N. K., and A. D. M. Rayner. 1978. Genetic structure of a natural population of *Coriolus versicolor* (L. ex Fr.) Quél. *Genet. Res.* 32: 55–65.

Verrall, A. F. 1937. Variation in *Fomes igniarius* (L.) Gill. *Univ. Minn. Agric. Expt. Sta., Techn. Bull.* 117: 1–41.

Vilgalys, R., and M. A. Cubeta. 1994. Molecular systematics and population biology of *Rhizoctonia. Ann. Rev. Phytopathol.* 32: 135–155.

Wilson, A. D. 1990. The genetics of sexual incompatibility in the Indian paint fungus, *Echinodontium tinctorium. Mycologia* 82: 332–341.

———. 1991. Somatic incompatibility in dikaryotic-monokaryotic and dikaryotic pairings of *Echinodontium tinctorium. Canad. J. Bot.* 69: 2716–2723.

Worrall, J. J. 1994. Population structure of *Armillaria* species in several forest types. *Mycologia* 86: 401–407.