

Somatic compatibility in *Amylostereum areolatum* and *A. chailletii* as a consequence of symbiosis with siricid woodwasps

IBEN MARGRETE THOMSEN¹* AND JØRGEN KOCH²

¹ The Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

² Department of Plant Biology, The Royal Veterinary and Agricultural University, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Denmark

Somatic compatibility is used to identify clones or vegetative compatibility groups (VCG) in fungal populations. For basidiomycetes, VCGs have normally been associated with either homothallic, non-outcrossing fungi or root decay fungi spreading by vegetative growth. A special instance is provided by the symbiotic relationships between woodwasps and the fungi *Amylostereum areolatum* and *A. chailletii*. This association results in clonal propagation, as the wasps (*Sirex* sp. and *Urocerus* sp.) transfer arthrospores of *A. areolatum* or *A. chailletii* during ovipositing in conifers. Identical isolates of the symbiont are normally carried by all the female offspring of one wasp. The presence of clones of *A. areolatum* and *A. chailletii* was tested through somatic compatibility shown in pairings of heterokaryons obtained from wasps, basidiocarps and wood. Isolates found more than 100 km apart within Denmark belonged to the same vegetative compatibility groups. In addition, *A. areolatum* isolates from Sweden and Lithuania were compatible with a Danish clone, in spite of the barrier of the Baltic Sea. The association between woodwasps and fungi thus creates dispersive clones or VCGs which are stable across time and space. The dispersal through basidiospores may be considered of less importance for *A. areolatum*, but common in *A. chailletii*.

A self–non-self rejection mechanism known as somatic or vegetative incompatibility operates to delimit individual genotypes from one another in many fungal species. This ability of fungi to recognize self and reject genetically different isolates has been widely used in studies of clonal populations. Somatic incompatibility tests have been carried out to determine the presence of clones and their distribution (e.g. Stenlid, 1985; Dahlberg & Stenlid, 1990). Pairings of somatically incompatible mycelia are often made with both totally unrelated mycelia and sib-related mycelia composed by mating single spore homokaryons (only basidiomycetes). This led to the discovery that unrelated isolates showed stronger incompatibility reactions than sib-related isolates, i.e. somatic incompatibility reactions always occurred between different strains of fungi, but the reactions were less marked between closely related isolates (Adams, Todd & Rayner, 1981; Coates, Rayner & Todd, 1981; Boddy & Rayner, 1982; Rayner & Turton, 1982; Sharland & Rayner, 1986).

Fungal isolates which are somatically compatible may also be considered a vegetative compatibility group or VCG (Leslie, 1993). VCGs can be defined as either territorial or dispersive clones (Anderson & Kohn, 1995). They used the basidiomycete *Armillaria gallica* as a example of a fungus having territorial clones, i.e. the equivalent of genets occupying discrete territories. In contrast, the homothallic ascomycete *Sclerotinia sclerotiorum* was described as having dispersive

clones, i.e. the genets are scattered in small, discontinuous units spatially disconnected from their points of origin (Anderson & Kohn, 1995). One conclusion in relation to these extremes in clonal population types was that territorial clones spread through vegetative growth and cannot disperse abruptly from place to place. No clone will, therefore, become frequent in the larger population, if the fungus is heterothallic. This is of course due to the fact that any dispersal across longer distances must happen by basidiospores as the result of a sexual process. Dispersive clones are, therefore, normally linked to clonal propagation in homothallic or asexual fungi.

Homothallic basidiomycetes may thus create dispersive clones, one example being *Stereum sanguinolentum* which is normally non-outcrossing. One basidiospore may colonize a wound on a standing tree, and the resulting mycelium can produce new fructifications without going through mating with another homokaryon. Rayner & Turton (1982) showed that monospore isolates obtained from basidiocarps (collected at one site) as well as isolations from their woody substrates could be divided into 'interaction groups'. Within groups the isolates mingled freely, whereas between groups antagonistic reactions occurred. The isolates within a group were therefore considered to have originated from a common source of basidiospores. The presence of clones or vegetative compatibility groups of *S. sanguinolentum* arising from basidiospore infection has also been shown in a recent study (Vasiliaskas & Stenlid, 1998).

A striking and exceptional case of dispersive clones in heterothallic basidiomycetes is that of fungi transferred by

* Corresponding author.

woodwasps. *Amylostereum areolatum* (Fr.) Boidin and *A. chailletii* (Pers.: Fr.) Boidin are symbionts of siricid woodwasps, e.g. *Sirex juvencus* (L.) and *Urocerus gigas* (L.). The vegetative propagation of these fungi takes place through the formation of arthrospores in special glands (intersegmental sacs) in the female woodwasp. These spores, or oidia, are inserted into the wood of conifers during the egg laying of the wasp. The fungus then grows through the wood and are later acquired by the new females through a rather complicated process, so that it is present in their glands just before emergence (Francke-Grosmann, 1957). These fungi may, therefore, be spread to new resource units by a purely vegetative process without going through sexual recombination.

Basidiocarps of *A. areolatum* and *A. chailletii* may, however, also be found with varying frequency. Both fungi are tetrapolar heterothallic, and basidiospore derived heterokaryons are, therefore, separate genets. In Europe, basidiocarps of both fungi have been found in several countries, but some countries have only recorded finds of *A. chailletii*. In Australia, where *A. areolatum* has been introduced with the woodwasp *Sirex noctilio*, basidiocarps have not as yet been recorded, and in northern America *A. chailletii* fruitbodies have been found in some areas but not in others despite the presence of woodwasps (Gilbertson, 1984). In any case, the existence of basidiocarps shows that sexual recombination and production of basidiospores is a possible method of dispersal in addition to woodwasps as vectors. The ability of the basidiospores of *A. areolatum* to colonize freshly cut disks of spruce wood has been shown by Pechmann *et al.* (1967). Thus, the populations of *A. areolatum* and *A. chailletii* may arise from both vegetative and sexual propagation.

The existence of closely related isolates in *Amylostereum* species has been touched upon in earlier studies (Pechmann *et al.*, 1967; Gaut, 1970; Talbot, 1977) but no direct research into somatic compatibility as proof of clonal propagation has been published. The aim of the present study was to establish the population structure of *A. areolatum* and *A. chailletii* in relation to both clones (VCGs) and genets arising from sexual recombination.

MATERIALS AND METHODS

Collections of isolates of *Amylostereum areolatum* and *A. chailletii* were made for tests of somatic compatibility. The isolates of *A. areolatum* and *A. chailletii* from Denmark were obtained from basidiocarps, via wood isolations or from the woodwasp species *Sirex juvencus* and *Urocerus gigas* reared or captured during flight seasons. The isolates were collected by the author from 1992 to 1995 or came from the culture collection (CP) at the Department of Plant Biology, The Royal Veterinary and Agricultural University. Altogether, less than twenty basidiocarps of *A. areolatum* were collected, 14 of which yielded isolates. In addition, 11 isolates were obtained from *S. juvencus* woodwasps and six came from wood. Almost 100 basidiocarps of *A. chailletii* were collected, of which 50 yielded isolates. Another nine isolates of *A. chailletii* came from *U. gigas* woodwasps, and 10 from wood. Most isolates came from within 100 km from Copenhagen, but some came from Jutland more than 200 km away. The Swedish and

Lithuanian *A. areolatum* isolates were supplied by R. Vasiliauskas and J. Stenlid, from the wood of wounded *Picea abies*, and were part of a larger collection (Vasiliauskas & Stenlid, 1999). The Lithuanian isolates came from two different sites 100 km apart.

Isolations from Danish basidiocarps were made by cutting small pieces of the tramal layer with a sterilised razor blade and transferring them aseptically to Petri dishes containing Potato Dextrose Agar (PDA). Wood isolations were made by removing small pieces of wood with a sterile gouge and placing them on PDA. Isolations from woodwasps were done after killing the insects which were then cut open, so that the glands containing the oidia were exposed. The spore masses were transferred aseptically to Petri dishes with PDA.

All isolates were maintained on PDA, which was also used for the somatic compatibility tests. The first experiment, however, showed that growth rates of isolates, especially of *A. areolatum*, were often so slow that confrontation never happened. All isolates were, therefore, transferred to Petri dishes with bean pod agar (BPA) beforehand. This treatment speeded up the growth rate of the *Amylostereum* isolates, and the tests could then be carried out on PDA. The same effect could be obtained by adding thiamine hydrochloride (5 m l^{-1}) to the PDA on which the cultures were kept before testing.

Inoculations were made with 7 mm plugs cut from the edge of growing cultures. Tests were made on PDA in 9 cm Petri dishes with two, three or four isolates per dish and at least two replicates of each test. In tests with four isolates two test methods were used. The plugs were either placed in the four 'corners' of a square ($2.5 \times 2.5 \text{ cm}$) in the middle of the dish or two and two at the opposite edges of the dish. In tests with three isolates the plugs were placed at the corners of a triangle with a side length of 2.5 cm. Each isolate was thus confronted with two other isolates simultaneously. Tests with only two isolates were carried out to check questionable cases, and when somatic compatibility was registered. The inoculation plugs were placed 1.5–2 cm apart at the edge of the dish, so that the reaction could be seen over the whole width of the dish. This was found to facilitate easy reading of the reactions, as the agar immediately adjacent to the plug often became darker, a well known characteristic of these fungi (Stalpers, 1978).

The dishes were incubated at room temperature (18–20 °C) for 2 to 3 wk. In some cases longer time was needed, as some isolates grew out vigorously enough but were slow in growing right up to the opposing isolates. Interactions between two mycelia were regarded as compatible when a continuous mycelial mat was formed between isolates, corresponding well to that of self-pairing controls. Incompatible reactions were generally characterized by the appearance of brown demarcation lines and sparse mycelial growth in confrontation zones.

RESULTS

In the initial tests, isolates of *A. areolatum* were included in tests of *A. chailletii* strains and vice versa. Confrontations between the two *Amylostereum* species gave a strong incompatibility reaction in the shape of a broad demarcation

Table 1. DK clone A, *A. areolatum*. All isolates in this clone were fully compatible. In addition to the Danish isolates one Swedish and two Lithuanian isolates also belonged to this VCG. Isolates 55 and 531–544* came from the same pile of wood. All isolates originated on *Picea abies*. The site letters refer to the designations on the maps (Figs 1–3).

ID	Substr	Year	Site	9	12	17	20	37	55	56	59	62	679	832	886	955	531	532	539	540	541	544	215	236	282
9	B. carp	1992	DKl	+																					
12	B. carp	1992	DKr	+	+																				
17	B. carp	1992	DKr	+	+	+																			
20	B. carp	1992	DKr	+	+	+	+																		
37	B. carp	1993	DKs	+	+	+	+	+																	
55	B. carp	1993	DKf	+	+	+	+	+	+																
56	B. carp	1994	DKg	+	+	+	+	+	+	+															
59	B. carp	1994	DKc	+	+	+	+	+	+	+	+														
62	B. carp	1994	DKr	+	+	+	+	+	+	+	+	+													
679	Wood	1983	DKo	+	+	+	+	+	+	+	+	+	+												
832	B. carp	1988	DKi	+	+	+	+	+	+	+	+	+	+	+											
886	B. carp	1990	DKa	+	+	+	+	+	+	+	+	+	+	+	+										
955	B. carp	1992	DKt	+	+	+	+	+	+	+	+	+	+	+	+	+									
531	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+								
532	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
539	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+						
540	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					
541	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
544	Wasp	1994	DKf	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
215	Wood	1994	LIH	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
236	Wood	1995	LIV	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
282	Wood	1994	SEB	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

* B. carp, Basidiocarp; DK, Denmark; LI, Lithuania; SE, Sweden; +, Fully compatible.

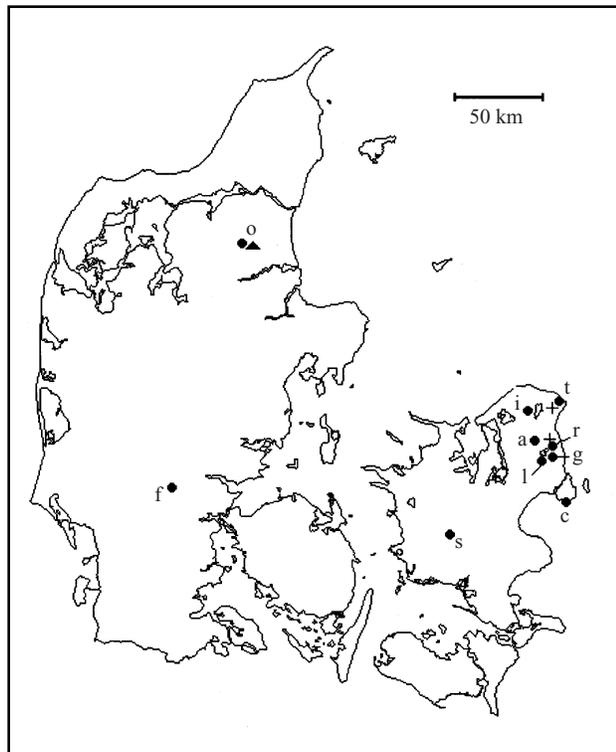


Fig. 1. Map of Denmark showing distribution of *A. areolatum* clones DK-A (●), DK-B (+) and DK-C (▲). Sites t, r and o yielded two clones and are marked twice.

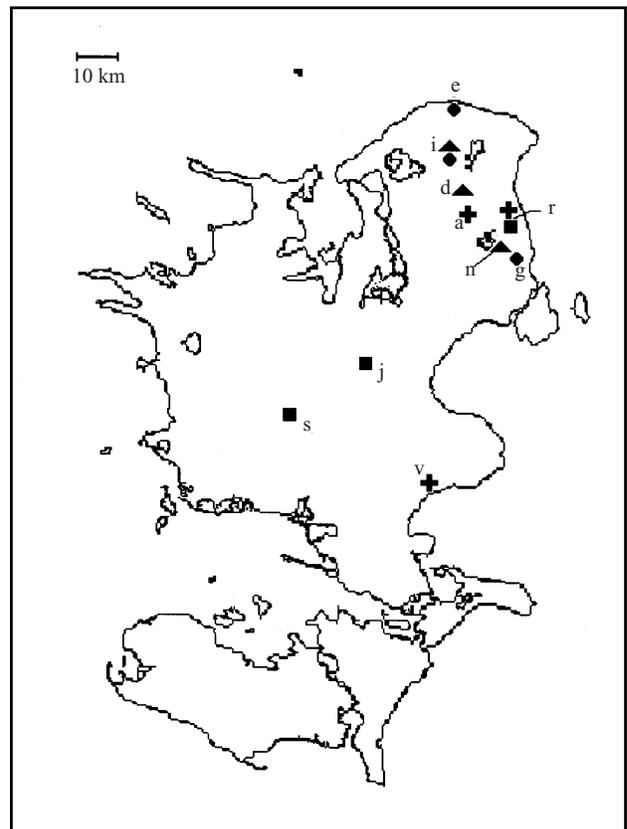


Fig. 2. Map of eastern Denmark (except Bornholm) showing distribution of *A. chailletii* clones DK-1 (■), DK-2 (●), DK-4 (+) and DK-5 (▲). The DK-3 clone came from site r. Sites i and r both yielded two clones and are marked twice.

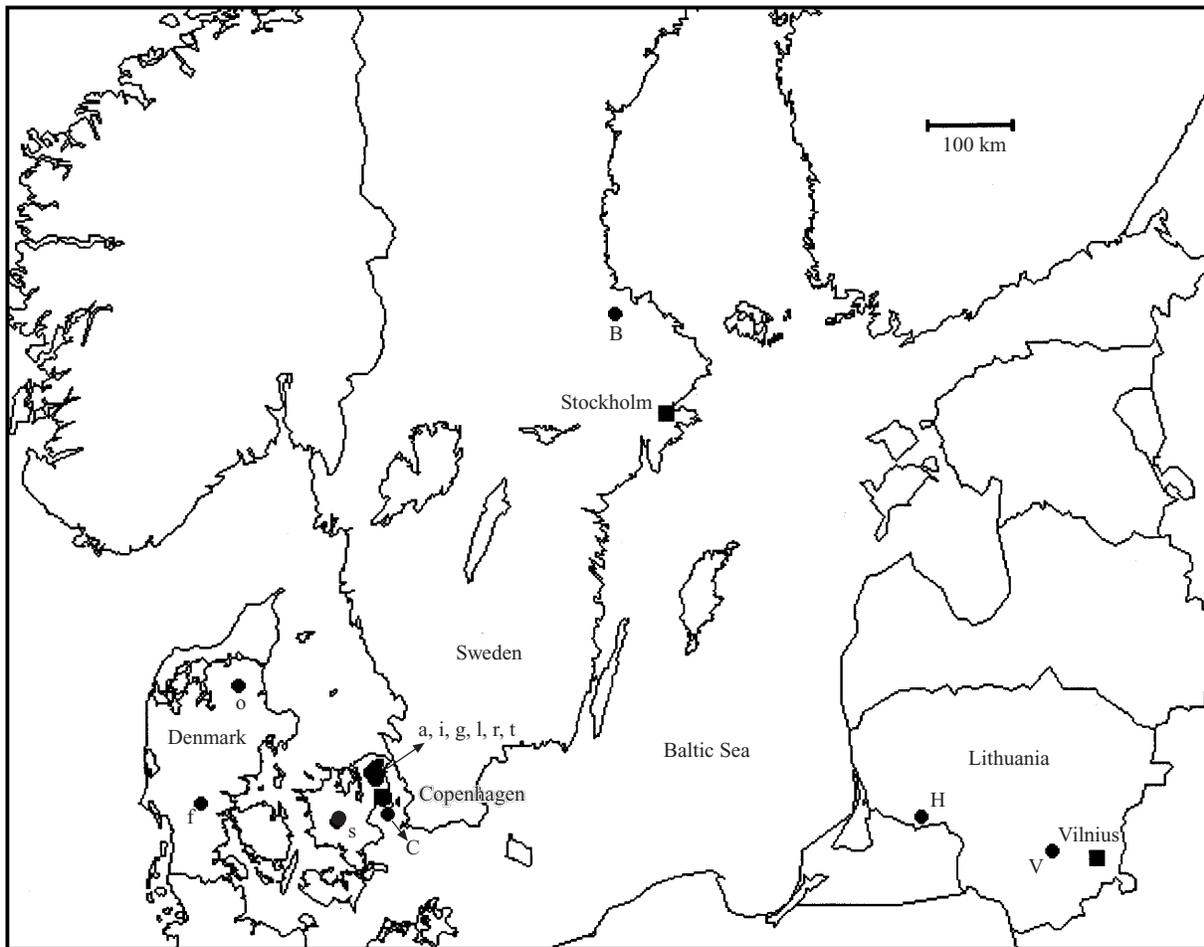


Fig. 3. Map of relevant parts of the Baltic area showing distribution of the *A. areolatum* clone DK-A (●) in Denmark, Sweden and Lithuania. The six sites (a, i, g, l, r and t) in North Zealand are marked with one large dot.

line seen as a strongly discoloured, brown zone on the lower side of the Petri dish. In confrontations between somatically incompatible isolates within the same species the same type of incompatibility reaction but less strongly marked could be found. The free intermingling of mycelia with no antagonistic reaction was observed in both species. Tests among three and more isolates were transitive: When one isolate mingled with two or more others, the latter were also compatible in all combinations. In general, for both *A. areolatum* and *A. chailletii* the extremes of somatic incompatibility were easy to read, as strong incompatibility reactions occurred quickly and within 2 wk, and the free intermingling of clones was even and constant. However, especially for *A. chailletii* a range of intermediate reactions could also be observed. In the following the two species are treated separately.

Amylostereum areolatum

Within *A. areolatum* there was a high degree of somatic compatibility between isolates. Most of the isolates found belonged to two large clones. *Sirex juvencus* woodwasps reared from logs from the same tree always carried the same clone of *A. areolatum*. Such woodwasp isolates were also compatible with basidiocarps of the fungus found on the same

logs. Fruitbody and woodwasp isolates from geographically separate areas of Denmark were somatically compatible in several cases. Furthermore, somatic compatibility could also be found between isolates from woodwasps, basidiocarps and wood obtained over a period of more than 10 yr (1983–1994).

The largest group of somatically compatible strains comprised 19 Danish isolates, mostly from basidiocarps (Table 1). One isolate, however, came from wood, and six isolates came from woodwasps reared from the same log. Most of the isolates had been found from 1992 to 1994, but one isolate (no. 679) was from 1983 and two others from 1988 and 1990. Half the isolates came from North Zealand within a 50 km radius, but all the woodwasp isolates, two fruitbody isolates and the wood isolate were from Jutland (200 km away and across water), and one isolate was from Central Zealand about 75 km away from the main group (Figs 1–3, circles). This clone (DK-A) was also compatible with the Swedish and Lithuanian isolates.

The other Danish clone (DK-B) contained at least five isolates, two of which were from wasps reared from the same log (Table 2). The three woodwasp strains were from 1994, and the logs were from the same forest (Fig. 1, site r). The two fruitbody isolates were from 1987 and both from the same site in another forest 25 km away (Fig. 1, site t). Another group of

Table 2. DK clones B and C of *A. areolatum*. The reaction between clone B and C were inconclusive as to compatibility. Both were incompatible with clone A. All isolates originated on *Picea abies*.

ID	Substr	Year	Site	782	784	545	547	550	678	680	681
782	B. carp	1987	DKt	+	*						
784	B. carp	1987	DKt	+	+						
545	Wasp	1994	DKr	+	+	+					
547	Wasp	1994	DKr	+	+	+	+				
550	Wasp	1994	DKr	+	+	+	+	+			
678	Wood	1983	DKo	?	?	?	?	?	+		
680	Wood	1983	DKo	?	?	?	?	?	+	+	
681	Wood	1983	DKo	?	?	?	?	?	+	+	+

* +, Fully compatible; ?, Ambiguous reaction.

isolates (DK-C) gave ambiguous results in compatibility tests with the DK-B clone (Table 2). However, according to DNA tests they were a different VCG (Vasiliauskas, Stenlid & Thomsen, 1998). The isolates in DK-C (nos 678, 680 and 681) had been obtained from wood in 1983 together with no. 679 (site o), but the latter belonged to clone DK-A as described above.

Amylostereum chailletii

Somatic compatibility occurred much more rarely in this species, especially amongst fruitbody isolates, but several cases of somatically compatible isolates from geographically separate areas of Denmark were found (Table 3). In one instance, isolates found almost 10 yr and 75 km apart constituted a VCG. Isolates from woodwasps reared from logs of the same tree were typically one clone, although four logs cut from one large stem yielded two batches of wasps with different strains. In addition, isolates from wood and basidiocarps taken from the same tree were compatible as expected.

Each *A. chailletii* VCG typically included only a few isolates.

Apart from five isolates from woodwasps reared from the same tree (DK-3), all other clones found had only three isolates. The isolates were mostly found 20–30 km apart, but in a couple of cases up to 75 km apart. Three of the VCGs were mixtures of fruitbody, wood and wasp isolates, while one clone had only fruitbody isolates (DK-5). The time spans between finds of isolates belonging to the same VCG were 1–5 yr, except for one case where 8 yr separated one isolate from the others (DK-4).

The incompatibility between clones was not tested in all combinations, only with sufficient isolates to verify the division into separate VCGs (see Table 3). In contrast to the examples of compatibility between distant isolates described above, many isolates from wood or basidiocarps found on the same sample plots or within a few kilometres of each other showed strong incompatibility reactions. Thus, most of the Danish *A. chailletii* isolates were incompatible (results not shown).

In addition to the clear cases of somatic compatibility or incompatibility, intermediate reactions were quite common. They fell into three categories. One type produced a thin but clear brown line seen from below and also a zone of no growth of aerial mycelium. Such confrontation reactions were scored as incompatible, although the demarcation line was much weaker than the clearcut cases. A second type produced a confrontation zone with sparse growth of aerial mycelium and almost invisible brown specks, but no brown line. Zones with no aerial mycelium could also occasionally be seen in self confrontations, but rarely with brown colours along the zones. After repeated tests, this type of reaction was scored as (partially) compatible. The third type showed intermediate interactions. The confrontation zone had no aerial mycelium, and the brown pigmentation on the lower side of the Petri dish was weak and broken. Tests showing these reactions were considered inconclusive, but tending towards incompatibility. If Petri dishes with isolates showing the last reaction were left for additional weeks, the brown line became clearer.

Table 3. Danish clones of *A. chailletii*. Most isolates originated on *Picea abies*. Isolates 77 and 953 were from *Pseudotsuga menziesii*. The woodwasp which yielded isolate 554, was found ovipositing on *Larix*. The site letters refer to the map in Fig. 2.

Clone	ID	Substr	Year	Site	10	40	53	530	554	966	534	535	538	546	559	22	77	724	942	953	962
DK-1	10	B. carp*	1992	DKr	+																
	40	B. carp	1993	DKs	+	+															
	53	B. carp	1993	DKj	+	+	+														
DK-2	530	Wasp	1994	DKe		–	–	+													
	554	Wasp	1995	DKi		–		+	+												
	966	B. carp	1992	DKg		–		+	+	+											
DK-3	534	Wasp	1994	DKr	–	–	–	–			+										
	535	Wasp	1994	DKr		–	–	–	–	–	+	+									
	538	Wasp	1994	DKr	–	–	–	–			+	+	+								
	546	Wasp	1994	DKr	–	–	–	–			+	+	+	+							
DK-4	559	Wasp	1995	DKr		–	–	–	–		+	+	+	+	+						
	22	B. carp	1993	DKv	–	–	–	–	–	–	–	–	–	–	–	+					
	77	Wood	1993	DKr	–	–	–	–	–	–	–	–	–	–	–	+	+				
DK-5	724	Wood	1985	DKa							–	–				+	+	+			
	942	B. carp	1992	DKd		–	–	–	–	–									–	+	+
	953	B. carp	1992	DKi		–	–	–	–	–									–	+	+
	962	B. carp	1992	DKn	–						–	–	–						–	+	+

* B. carp, basidiocarp; +, Fully compatible; –, Incompatible; Blank, Not tested.

Interpretation was, however, made difficult by the fact that brown lines finally (after 10–12 wk) appeared all over the bottom of the dish as a general phenomenon unrelated to the test.

DISCUSSION

The presence of clones in the populations of *Amylostereum areolatum* and *A. chailletii* was very likely in the light of their symbiosis with woodwasps and the vegetative spread entailed by this association. It was somewhat surprising, however, that isolates found more than 100 km apart within Denmark were somatically compatible. In addition, isolates of *A. areolatum* from Denmark, Sweden and Lithuania were compatible with each other. Thus, the barrier of the Baltic Sea did not prevent clones from dispersing.

A similar spatial distribution of clones in non-outcrossing populations of *Stereum sanguinolentum* has recently been established (Vasiliauskas & Stenlid, 1998). The presence of one VCG in Sweden, Lithuania and Finland was explained by long-range dispersal of basidiospores. For *A. areolatum* and *A. chailletii*, however, the clonal distribution must be attributed to the association with woodwasps. Possible explanations could be the ability of wasps to fly long distances and the fact that the development of the larvae in the wood may take several years. As a result of the long life cycle, these insects are often transported in felled timber or finished wood products and may thus emerge a long distance from their origin. In addition, the clones may be considered as stable and long lived. In this respect these *Amylostereum* species resemble territorial clones rather than dispersive clones. Once the fungi have gained access to a resource unit via woodwasps, they may continue to grow long after the new generation of wasps has emerged. Fructifications may be seen on old logs left in the forest, any woodwasp emergence holes being several years old. The stability of the clones showed in that both geographically separate isolates and isolates collected more than 10 yr apart could still belong to the same clone.

A. chailletii yielded clones more rarely, and the number of isolates in a clone was small compared to *A. areolatum*. The tests of somatic compatibility often gave ambiguous reactions. A pattern with many intermediate reactions indicates a concurrent spread of *A. chailletii* by basidiospores, as the pattern is reminiscent of the reactions seen in sib-related isolates. The frequency of basidiocarps of *A. chailletii* in Denmark undoubtedly reflect that fructifications are made by both vegetatively propagated isolates and isolates originating as a result of basidiospore infection. The latter case would usually be the result of mating between two basidiospores. Another possibility, however, is that mycelium from a single basidiospore infecting a wound or a cut surface meets mycelium already present as a result of woodwasp inoculation. If the woodwasp originated mycelium donated a nucleus to the homokaryotic basidiospore mycelium (the Buller phenomenon), a new genet would also arise. If the basidiospores of these basidiocarps of different origin subsequently interbreed, a population would arise consisting of genetically related genets as well as totally unrelated genets, and the original clones carried on by woodwasps. In contrast, the much rarer

occurrences of *A. areolatum* basidiocarps is consistent with the total dominance of clones found in this species.

The existence of vegetative compatibility groups of *A. areolatum* and *A. chailletii* may prove very useful in future research into the population structures of these fungi. The ratio of clones and genetically separate isolates may reveal whether spread through woodwasps dominates, and/or basidiospore infection is common. Pairing of isolates from different areas and countries could yield information on the distribution of woodwasps originating from a common ancestor. As woodwasps, especially *Sirex noctilio*, have been introduced in various parts of the world, the history of such introductions could be traced as already hinted by Talbot (1977). Another interesting research subject is whether any degree of relatedness could be found between the same fungal species of symbiont carried by different species of woodwasps.

The symbiotic association between woodwasps and *A. areolatum* and *A. chailletii* was thought to promote vegetative spread of these fungi. The results presented illustrate this theory and the consequence of the wasp/fungus relationship on the population structure of *A. areolatum* and *A. chailletii*. These two fungi may thus be considered to constitute an unusual example of vegetative compatibility groups or dispersive clones in basidiomycetes.

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