For. Path. 33 (2003) 105–112

ISSN 1437–4781

Distribution of *Heterobasidion annosum* intersterility groups in Poland

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Summary

Specimens of *Heterobasidion annosum* were collected in 104 different stands in 43 regions of Poland. Pure cultures originating from 439 collections were identified in mating tests. Three intersterility groups, P, S and F, of *H. annosum* were found. Their occurrence in Poland was connected with the natural distribution of the main hosts: *Pinus sylvestris*, *Picea abies* and *Abies alba*, respectively. P was the most common intersterility group of *H. annosum* in Poland, causing mortality in Scots pine plantations and root rot in older stands. It was also isolated from *Betula pendula, P. abies, Larix decidua, Fagus sylvatica* and *Carpinus betulus*. The S group was present in the southern and north-eastern parts of the country, causing root and butt rot mostly in spruce stands. The F group occurred in the south of Poland, in the mountains, highlands and lowland up to the northern border of the distribution of fir. It was found only on stumps, old dead trees and logs. There was no evidence of damage caused by the F group on *A. alba* trees.

1 Introduction

Heterobasidion annosum (Fr.) Bref is one of the most important basidiomycetes causing root and butt rot in forest trees. In Europe, it consists of three intersterility groups showing different host preferences. Recently, Niemelä and Korhonen (1998) suggested raising the three intersterility groups of *H. annosum* to the specific levels and proposed the following names: P group – *H. annosum* (Fr.) Bref *sensu stricto*; S group – *H. parviporum* Niemelä and Korhonen; and F group – *H. abietinum* Niemelä and Korhonen. The P group attacks primarily pine species, the S group is a pathogen of Norway spruce (*Picea abies* (L.) Karst.) and Siberian fir (*Abies sibirica* Ledeb.), and the F group occurs on European silver fir (*A. alba* Mill.) (Korhonen 1978; Stenlid and Swedjemark 1988; Capretti et al. 1990; Korhonen et al. 1997).

In Poland, *H. annosum* causes the biggest economic losses in Scots pine (*Pinus sylvestris* L.) stands especially on previously agricultural soil (Sierota 1987, 1995; Mańka 1998). The occurrence of the three intersterility groups of *H. annosum* in Poland has been described previously and preliminary results on their distribution have been presented (Żółciak 1992; Łakomy 1996; Łakomy et al. 2000).

In this study, we identified the intersterility group of a relatively large number of *H. annosum* isolates originating from different areas, types of forest and host species in Poland. Special attention was paid to the occurrence of the F group because of the northern border of fir distribution in Europe is in southern Poland.

Received: 21.1.2002; accepted 24.10.2002; editor: J. Stenlid.

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2 Materials and methods

2.1 Sampling and isolation

The study material was collected during 1999–2001, comprising 439 *H. annosum* specimens from 104 different stands localized in 43 Forest Districts or National Parks (Table 1, Fig. 1). Stands were investigated for the presence of pathogen. Basidiocarps and wood samples from stumps, logs and dead or living trees were collected. From living trees, wood samples were taken using a Presler's borer.

The host species were: *P. sylvestris* 189 collections; *P. abies* 144; *A. alba* 68; *Betula pendula* Roth. 35; *Fagus sylvatica* L. 8; *Larix decidua* 5 and *Carpinus betulus* L. 1.

Single-spore cultures were made from 145 basidiocarp specimens. Fresh basidiocarps were dried in paper bags for 2–3 weeks at room temperature. For homokaryotic single spore isolation, a thin layer of basidiocarp pores was cut off and dragged along the 1% malt-agar surface on a Petri dish. After 2-day incubation at 23°C, single germinating spores were transferred to fresh medium using Pasteur pipette at 20× magnification under a microscope (Korhonen et al. 1992).

Decayed wood was stored in plastic bags at +4°C and heterokaryotic mycelia were isolated onto 1% malt-agar with 20 mg/l Benomyl to omit the contamination with other saprotrophs (Piri et al. 1990).

2.2 Observation of disease

H. annosum impact and symptoms occurring on trees were observed in each stand. The decay column on infected Norway spruce stems was also measured when removing wind-fallen and wind-broken trees or during routine thinning. The decayed part of the stem was cut by saw into 1-m sections until the decay was smaller than 10% of the cut surface.

2.3 Mating test

Intersterility groups were determined by pairing homokaryotic and heterokaryotic isolates with homokaryotic tester strains. Four testers from each intersterility group, P, S or F, were paired with each isolate. The testers originated from different parts of Europe: P from Finland (Siuntio, 91065; Kirkkonummi, 93252/2), Switzerland (Zürich, 87087), Italy (Tirrenia, 1.1.3); S from Finland (Kirkkonummi, 93254/2; 92044/5), Estonia (Vormsi, 93142/2), Italy (Vicenza, 87075/2); F from Italy (Vallombrosa, 1.3.1; La Secchia, 3.2.2), Greece (Menalon Mt., 93315) and Slovenia (Sneznik, 92216). The pairings were made in the centre of Petri dishes, on 1.5% malt-extract agar (Merck, Darmstadt Germany). The distance between two inocula was 1 cm. Incubation was carried out at 25°C in light. The tester mycelia were examined for the presence of clamp connections, indicating heterokaryosis. Observations were made directly through the bottom of the Petri dish at magnification of 100–200 × 3 weeks after inoculation and additionally 1–2 weeks later. The external appearance of tester mycelia was also evaluated and the morphology of the interaction zone between the two colonies was observed. In cases of unclear results, subcultures were taken from the contact area. The presence of clamp connections in subcultures was checked after 7–8 days (Chase and Ullrich 1983).

3 Results

Altogether 251 out of 439 identified specimens belonged to the P group (Table 1). This group was isolated mostly from *P. sylvestris* (186) and also from *B. pendula* (34), *P. abies* (19), *F. sylvatica* (8), *L. decidua* (3) and *C. betulus* (1). The P group caused the most severe damage in Scots pine plantations on previously agricultural soils, mainly in the

Table 1. **The *Heterobasidion annosum* specimens identified (for locality numbers refer to the map in Fig. 1)**

No.	Forest district	Number of stands	Number of isolates	Tree species	*Hetero-basidion annosum* IS group		
					P	S	F
1	Suwałki (54°08′N, 22°56′E)	3	14	*P. sylvestris*	5		
				P. abies		9	
2	Pomorze (54°05′N, 23°23′E)	1	4	*P. sylvestris*	4		
3	Giżycko (54°04′N, 21°51′E)	2	5	*P. abies*		5	
4	Pisz (53°37′N, 21°48′E)	2	7	*P. abies*		7	
5	Olsztyn (53°46′N, 20°26′E)	2	6	*P. abies*		4	
				P. sylvestris	2		
6	Lidzbark (53°08′N, 19°46′E)	2	10	*P. abies*		8	
				P. sylvestris	2		
7	Łomża (52°51′N, 22°06′E)		6	*P. sylvestris*	6		
8	Białowieża (52°50′N, 23°32′E)	2	6	*P. abies*		6	
9	Słowiński National Park (54°44′N, 17°12′E)	1	2	*P. sylvestris*	2		
10	Osusznica (53°52′N, 17°23′E)	1	8	*P. abies*	8		
11	Tuczno (53°16′N, 16°11′E)	3	12	*P. sylvestris*	9		
				B. pendula	3		
12	Strzelce Krajeńskie (52°47′N, 15°33′E)	1	3	*P. abies*	3		
13	Smolarz (52°30′N, 15°50′E)	4	10	*P. abies*	2		
				P. sylvestris	8		
14	Krucz (52°50′N, 16°22′E)	3	17	*P. sylvestris*	15		
				B. pendula	2		
15	Podanin (52°75′N, 16°73′E)	4	19	*B. pendula*	6		
				L. decidua	3		
				P. sylvestris	10		
16	Solec Kujawski (53°02′N, 18°16′E)	3	18	*P. sylvestris*	15		
				B. pendula	3		
17	Łopuchówko (52°35′N, 17°08′E)	4	18	*B. pendula*	2		
				C. betulus	1		
				F. sylvatica	5		
				P. abies	2		
				P. sylvestris	8		
18	Zielonka (52°30′N, 17°02′E)	5	22	*P. sylvestris*	15		
				B. pendula	4		
				F. sylvatica	3		
19	Babki (52°23′N, 16°58′E)	2	15	*P. sylvestris*	13		
				B. pendula	2		
20	Wielkopolski National Park (52°22′N, 16°93′E)	3	10	*P. sylvestris*	10		
21	Międzyrzecz (52°36′N, 15°34′E)	3	13	*P. sylvestris*	11		
				B. pendula	2		
22	Skwierzyna (52°38′N, 15°31′E)	4	10	*P. sylvestris*	7		

Table 1. **Continued**

No.	Forest district	Number of stands	Number of isolates	Tree species	*Heterobasidion annosum* IS group P	S	F
				B. pendula	3		
23	Syców (51°19′N, 17°30′E)	2	10	*A. alba*			1
				P. abies	4		
				P. sylvestis	5		
24	Siemianice (51°15′N, 17°54′E)	2	29	*A. alba*			12
				P. sylvestris	13		
				B. pendula	4		
25	Lubin (51°22′N, 16°14′E)	3	7	*P. sylvestris*	7		
26	Złotoryja (51°12′N, 15°47′E)	3	10	*P. abies*		10	
27	Śnieżka (50°50′N, 15°38′E)	2	8	*P. abies*		8	
28	Szklarska Poręba (50°49′N, 15°25′E)	2	10	*P. abies*		10	
29	Karkonoski National Park (50°46′N, 15°42′E)	4	18	*B. pendula*	3		
				P. abies		15	
30	Kozienice (51°35′N, 21°31′E)	2	4	*P. sylvestris*	4		
31	Świętokrzyski National Park (50°52′N, 20°43′E)	3	11	*A. alba*			9
				L. decidua			2
32	Łagów (50°48′N, 20°45′E)	1	5	*P. sylvestris*	3		
				A. alba			2
33	Krasnystaw (50°37′N, 23°15′E)	2	3	*P. abies*		3	
34	Roztoczański National Park (50°31′N, 23°27′E)	3	10	*A. alba*			10
35	Józefów (50°27′N, 23°15′E)	1	5	*P. sylvestris*	5		
36	Narol (50°22′N, 23°32′E)	1	4	*P. sylvestris*	4		
37	Strzyżów (49°56′N, 21°48′E)	1	5	*A. alba*			5
38	Rymanów (49°26′N, 22°02′E)	1	3	*P. abies*		3	
39	Wetlina (49°08′N, 22°29′E)	2	5	*A. alba*			3
				P. abies		2	
40	Sucha (49°40′N, 19°27′E)	3	16	*A. alba*			4
				P. abies		12	
41	Węgierska Górka (49°42′N, 19°15′E)	5	25	*A. alba*		4	9
				P. abies		10	2
42	Limanowa (49°30′N, 20°14′E)	2	5	*A. alba*			5
43	Nowy Targ (49°25′N, 20°05′E)	4	11	*P. abies*		8	
				P. sylvestris	3		
	Total	104	439		251	124	64

north-western part of Poland. The mortality in such stands (second generation of pine) started sometimes 3 or 4 years after planting. In three cases, we observed 2-year-old pines killed by *H. annosum*. The mortality gaps spread very quickly for the next 5 years. In older

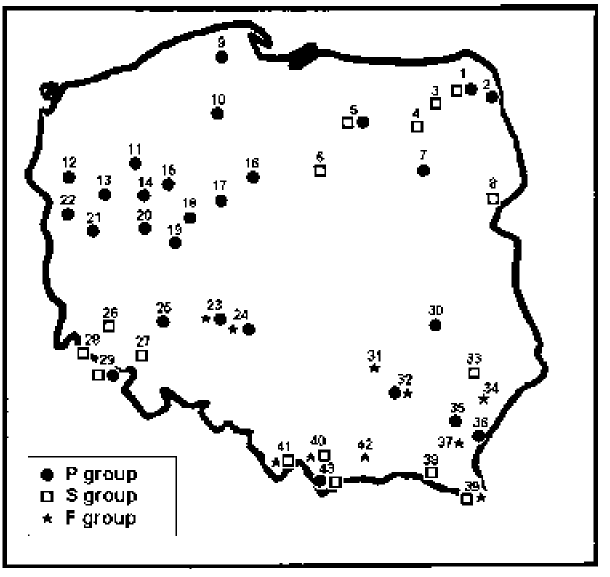

Fig. 1. Collection localities in Poland (for locality numbers refer to Table 1)

stands, the dying of Scots pine was generally slower than in young stands. The basidiocarps appeared 1 or 2 years after tree death. Occasionally, they were present on dying trees. Particularly big sporocarps appeared usually on trees growing on previously agricultural soils. By contrast, on old forest sites, the sporocarps were small, often resupinate and appeared on roots and root collar under the litter and soil, and they were never found on older trees. The extension of butt rot was limited in pine stems and was never more than 1 m, except in one case where the decay reached up to 1.7 m. *P. abies* was attacked by the P group mostly outside of its natural distribution. Only in one case, in a mixed stand of fir–spruce–pine, the P group was found on spruce in the natural distribution of this tree (locality no. 23, Table 1, Fig. 1). On deciduous trees, the P group was isolated only from stumps except in the case of birch, where sporocarps were observed on dead old trees. In one case, we found a 10-year-old *B. pendula* infected by P group.

Of the 124 isolates belonging to the S group, 120 were isolated from spruce and four from fir. Basidiocarps were formed rather seldom on dead trees or fresh stumps. They usually occurred on old stumps and lying logs. The morphology of basidiocarps was typical for the European S group with small pores and velvety upper side of the basidiocarp margin. Decay in *P. abies* stems extended sometimes up to 4–5 m and was often the cause of windfalls or windbreaks. No symptoms of disease were seen in spruce crowns.

The F group isolates occurred especially on *A. alba* (60 collections), but was recorded also from *P. abies* (2) and *L. decidua* (2). Basidiocarps were found on old fir stumps (decayed), lying logs and in a few cases on 160-year-old dead trees. No disease symptoms were observed on growing *A. alba*. The basidiocarps appeared commonly in dense and humid fir stands but were rather seldom in thinned, very old (180-year-old) *A. alba* stands or in mixed *F. sylvatica–A. alba* stands. This group was present on *A. alba* in the mountains, highlands and lowland at the northern border of the distribution area of *A. alba* in Europe.

The F group was also isolated from Norway spruce in a mixed beech–spruce–fir stand and in one case from a stump of *L. decidua* in a mixed larch–fir–beech stand.

In two cases, the S and F groups occurred in the same stand (locality nos. 40 and 41, Table 1, Fig. 1). In both cases, it was a mixed spruce–beach–fir stand. In one stand (fir–spruce–pine), we found both P and F groups (locality no. 23, Table 1, Fig. 1). In this stand, the F group was isolated from a dead fir and the P group from spruce stumps.

4 Discussion and conclusion

The distribution of the P, S and F groups in Poland was closely related to the natural occurrence of Scots pine, Norway spruce and European silver fir, respectively. The host preferences of the intersterility groups were comparable to those observed in earlier studies in Europe (Korhonen et al. 1992; Capretti et al. 1994; Munda 1994; Tsopelas and Korhonen 1996; La Porta et al. 1998). Scots pine stands contribute to 70% of Polish forests and the P group occurs almost in the whole country. It was isolated from several tree species, both coniferous and deciduous. Among the deciduous trees, the P group was common on birch. This phenomenon was also described by Korhonen et al. (1992), Sierota (1995), Łakomy (1998), Łakomy et al. (2001), and birch may play an important role as a pathogen source and aid in spreading of the fungus in mixed pine–birch forests on poor sites, where birch is commonly planted together with pine. The observation of early pine mortality in second-generation stands growing on previously agricultural soils was also described by Sierota (1995, 2001) and Łakomy (1998). In Poland, in the first pine generation on such sites, mortality usually occurs 11–13 years after planting (Sierota 1995, 2001). The high mortality of pine is probably caused by unfavourable site conditions for this species, in particular, high content of nitrogen, higher pH than in forest soil, lack of antagonistic microorganisms and mycorhizal fungi, and very dense spacing during the planting. Scots pine roots in these sites grow vertically and the probability of root contact, which could transfer the pathogen, is relatively high (Sierota 1987, 2001). Rönnberg and Vollbrecht (1999) described circumstances where the mortality of larch due to *Heterobasidion* infection on infested sites appeared also 2 years after planting.

The occurrence of the S group is limited to the south and north-east of Poland. The role of this group in timber losses was emphasized by Łakomy et al. (2001) after investigating the occurrence of rot in stumps of wind-fallen and wind-broken trees. Representatives of this group were also isolated from *A. alba* in the mountains. However, they were rare (four isolates) and inhabited only stumps and lying logs. The S group is not only specialized to Norway spruce but also to Siberian fir (Korhonen et al. 1997) . Korotkov (1978) showed that in mixed Norway spruce–Siberian fir stands, the incidence of *H. annosum* on fir was higher than on spruce. Twelve mixed stands of spruce and fir were sampled in our study; the S group was found only in one stand on fir, occurring on stumps or logs.

The F group proved to be rather common in pure *A. alba* and mixed stands in the mountains, highlands and also in lowland, although the earlier investigations pointed out that this group is rather rare in Poland (Łakomy 1996; Łakomy et al. 2000). The role of the F group as a root pathogen of fir was not confirmed. A few fresh stumps with annosum rot as well as basidiocarps on dead trees suggest that the trees could be attacked when alive. However, no damage in young fir regeneration or in older fir stands was recorded. We did not observe a situation similar to that in the Italian peninsula, Greece and Bulgaria where the firs are frequently attacked by the F group (Capretti et al. 1994; Tsopelas and Korhonen 1996; La Porta et al. 1998). In Italy, the death of trees was promoted by long dry periods, which caused stress to the trees. Soil conditions probably also played a part in disease development in the southern part of the peninsula, as most of the silver fir plantations were established on previously agricultural lands or pasturelands that are normally conducive to the disease (Capretti et al. 1998). In Poland, *A. alba* grows in different site and climatic conditions, and its relationship with the F group resembles the situation in Slovenia where the F group was defined as non-pathogenic saprobe (Munda 1994). La Porta et al. (1998) suggested that the F group displays lower fitness to fir in colder and moister climate. In our infection experiments (Werner and Łakomy 2002), F group isolates showed similar virulence on fir, pine and spruce, but lower than those of P and S isolates on pine and spruce. The F isolates were the most virulent on fir, but differences were not statistically significant.

The most probable reason of the low pathogenicity that the F group shows on *A. alba* in central Europe is genetic resistance of the local provenances of this tree. Different forest management may also influence the *H. annosum* incidence in fir stands. Whether the relatively low pathogenicity could be also connected with the post-glacial expansion of *A. alba* from south to north of Europe needs further investigations.

Acknowledgements

The authors are grateful to Dr KARI KORHONEN and Dr PAOLO CAPRETTI for providing pure cultures of *H. annosum* and to ANNA RATAJCZAK and ARLETA ŚWIETLIK for technical assistance. The Polish Committee for Scientific Research financially supported this study, grant no. 5 P06H 044 15.

Résumé

Distribution des groupes interstériles de Heterobasidion annosum en Pologne

Des échantillons de *Heterobasidion annosum* ont été récoltés dans 104 peuplements de 43 régions de Pologne. Les cultures pures de 439 récoltes ont été identifiées par test de croisement. Trois groupes interstériles, P, S et F de *H. annosum* ont été trouvés. Leur existence en Pologne a été reliée à la répartition naturelle des principaux hôtes : *Pinus sylvestris, Picea abies* et *Abies alba*, respectivement. Le groupe P était le plus répandu provoquant des mortalités dans les plantations de pin sylvestre et des pourritures racinaires dans les peuplements plus âgés; il a été aussi isolé sur *Betula pendula, Picea abies, Larix decidua, Fagus sylvatica* et *Carpinus betulus*. Le groupe S était présent dans le sud et le nord-est du pays, provoquant des pourritures de racines et de pied surtout en pessières. Le groupe F se trouvait dans le sud de la Pologne, dans les montagnes, les régions hautes ou basses jusqu'à la limite nord de l'aire du sapin; il n'a été trouvé que sur souches, arbres âgés morts et troncs abattus; il n'y a pas d'indication de dégâts par le groupe F sur *Abies alba*.

Zusammenfassung

Verbreitung der Intersterilitätsgruppen von Heterobasidion annosum in Polen

In 43 Regionen Polens wurden an 104 verschiedenen Standorten Proben von *Heterobasidion annosum* (Fruchtkörper und infiziertes Holz) gesammelt. Reinkulturen aus 439 Kollektionen wurden mit Kreuzungstests bestimmt. Es wurden alle drei Intersterilitätsgruppen (P, S und F) von *H. annosum* nachgewiesen. Ihr Vorkommen in Polen steht in Zusammenhang mit der natürlichen Verbreitung der jeweiligen Hauptwirte *Pinus sylvestris, Picea abies* und *Abies alba*. Als häufigste Intersterilitätsgruppe in Polen wurde die Gruppe P nachgewiesen, diese verursacht das Absterben von *Pinus sylvestris* in Pflanzungen und Wurzelfäule in älteren Beständen. Die Gruppe P wurde auch von *Betula pendula, Picea abies, Larix decidua, Fagus sylvatica* und *Carpinus betulus* isoliert. Die Intersterilitätsgruppe S kommt in den südlichen und nordöstlichen Teilen des Landes vor, wo sie Wurzel- und Stammfäulen vorwiegend in Fichtenbeständen verursacht. Die F-Gruppe wurde in Südpolen nachgewiesen, wo sie im Gebirge, im Hügelland und im Tiefland bis zur nördlichen Verbreitungsgrenze der Weisstanne vorkommt. Sie wurde nur an Stümpfen, alten toten Bäumen und liegenden Stämmen gefunden, und es gibt keine Hinweise auf Schäden an *Abies alba* durch die F-Gruppe.

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