For. Path. 37 (2007) 374–386 doi: 10.1111/j.1439-0329.2007.00516.x

Occurrence of *Heterobasidion* basidiocarps on cull pieces of Norway spruce left on cutting areas and in mature spruce stands

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Summary

Fruiting of *Heterobasidion* on cull pieces and stumps of Norway spruce was investigated in cutting areas and mature spruce stands located in southern Finland. Cull pieces of variable size and showing butt rot were left on three clear-cut areas and in one thinned stand. Additionally, a part of the cull pieces was transported to mature forest sites with closed canopy. During the succeeding 3–4 years the cull pieces were investigated annually for sporocarps of *Heterobasidion*, and the area of actively sporulating pore layer of each sporocarp was measured. Root bases of spruce stumps in the logging areas were excavated and sporocarps found on the stumps also measured. At the onset of the experiment, *Heterobasidion* spp. were isolated from 76% of the cull pieces showing butt rot; 85% of the isolates were identified as *H. parviporum* and 15% as *H. annosum s.s.* During the following 3–4 years sporocarps were found on 20% of the 1938 cull pieces where Heterobasidion butt rot was initially detected visually. Sporocarp formation was promoted by advancement of butt rot, increasing cull piece diameter and end-to-end ground contact, but restricted by the colonization of the cull piece by *Stereum sanguinolentum*. Between-site differences were significant but could not be explained by differences in tree cover. At the end of the investigation period the average sporulating area of *Heterobasidion* sporocarp per metre of cull piece was higher than the average sporulating area per stump at three of four logging sites. Hence, leaving cull pieces containing Heterobasidion butt rot at logging areas in southern Finland can considerably increase local production of *Heterobasidion* spores.

1 Introduction

Present forestry guidelines in Finland recommend increasing the amount of decayed wood in managed forests to ensure biodiversity. In particular, the amount of high diameter decaying wood is deficient in managed forests (Edman et al. 2004; Jonsson et al. 2005). Therefore, it is recommended to leave a certain amount decaying large-diameter stem wood like fallen trunks and dead standing trees on the site at final cutting. In addition, it is recommended to leave 5–10 living large-diameter trees standing per hectare. Later, some of these trees may fall in storms, increasing the amount of coarse woody debris on the site. Leaving coniferous logs with bark in larger amounts than 10 m^3/ha on forest sites is prohibited because bark beetles may proliferate on them.

Previously, cull pieces of Norway spruce [*Picea abies* (L.) Karst.] with butt rot were commonly left on cutting areas. As *Heterobasidion parviporum* Niemelä & Korhonen and *H. annosum* (Fr.) Bref. *sensu stricto* are the most common fungi causing butt rot of Norway spruce in many parts of Europe, a large proportion of decayed cull pieces of spruce are inhabited by these fungi. Such logging residues can provide substrate for fruiting and spore production by *Heterobasidion*. Schütt and Schuck (1979) showed that *Heterobasidion* sporocarps can appear as soon as 1 year after logging but the frequency is generally highest and size biggest 3–4 years after logging. However, it is not known whether the numbers of

Received: 26.8.2006; accepted: 19.3.2007; editor: E. Donaubauer

sporocarps occurring on logging residues could significantly increase local spore production. Neither is it known whether *H. parviporum* and *H. annosum* show differences in sporocarp production on logging residues.

Our aim was to compare spore production by *Heterobasidion* occurring in cull pieces of spruce to that on spruce stumps in the same logging area, assuming that the quantity of spore production is related to the actively sporulating pore layer area of the fruit bodies. Aerial spread of *Heterobasidion* is believed to take place mainly by basidiospores, conidia having probably a minor significance in contributing to the aerial inoculum (Redfern and Stenlid 1998). Additionally, we investigated the effect of various factors on sporocarp production in a field trial lasting for 4 years at eight locations.

2 Material and methods

2.1 Field sites and experimental design

The experiment was carried out on four logging sites and in four forest sites (Table 1). Three logging sites were clear-cut (stand age ca. 80 years), and one was thinned (ca. 60 years). Two logging sites were situated in Bromarv (south-western Finland), one in Hausjärvi (southern Finland) and one in Vehkalahti (south-eastern Finland). Norway spruce was the dominant tree species on all sites. The size of the logging sites varied between 2.8 and 5.6 ha. Logging was performed in August 2000 (Vehkalahti and Bromarv K) or August 2001 (Bromarv A and Hausjärvi) (Table 1). Butt rot frequency on the logging sites varied from 30% to 41%. Cull pieces were left by the harvester close to the stumps from which they originated, and their distribution on the logging areas therefore corresponded to the distribution of butt rot in the stand. A part of the cull pieces was placed lying flat on the ground with end-to-end ground contact, a part was placed with one end in contact with the ground, and the rest of the cull pieces were placed on other logs without ground contact. All stumps on the logging sites were mapped, marked and evaluated visually for the presence of butt rot.

To investigate the effect of forest cover on the fruiting of *Heterobasidion* and other fungi, a part of the cull pieces were moved from clear-cutting areas in Bromarv to four forest sites. These were mature spruce stands, over 100 years old, with closed canopy, situated in Siuntio, Mäntsälä, Sipoo (southern Finland) and Ylämaa (south-eastern Finland). Cull pieces were transported from Bromarv to Sipoo in December 2001 and to the other sites in April 2002. They were placed on a ca. 1-ha area at each site (Table 1).

All experimental areas were situated on moderate slopes (differences in elevation <20 m). Healthy-looking cull pieces were left as controls on each experimental site. All cull pieces were GPS-mapped and marked with a numbered label. Dimensions (diameter and length), degree of ground contact (end-to-end contact, one end contact, no contact) and bark condition (intact, partly removed, completely removed) were recorded. Altogether 2077 cull pieces with signs of decay and 442 healthy-looking controls were included in the study (Table 1).

2.2. Decay characteristics

In the autumn, 2–3 months after logging, two discs, ca. 5 cm thick, were cut from one end of each cull piece. The first disc was discarded. The second was used for assessments of decay characteristics: measurement of the advancement of butt rot and isolation of *Heterobasidion*. Butt rot caused by *Heterobasidion* was identified visually on the basis of the bluish or grey-coloured zone surrounding the decayed inner part (Greig 1998) and microscopically on the basis of the occurrence of typical conidiophores on the sample discs

Table 1. **Experimental areas and treatments**

Location	Total area (ha)	Logging		Date when cull pieces distributed	Area where cull pieces distributed (ha)	Number of cull pieces		Stumps		
		Type	Date			Total	With butt rot	Sound	With butt rot	
									Number	%
Logging sites										
Vehkalahti	5.6	Clear-cut	2000 August	At logging	5.6	644	590	1085	453	29.5
Bromarv K	2.8	Clear-cut	2000 August	At logging	2.8	732	713	330	173	34.4
Bromarv A	2.3	Clear-cut	2001 August	At logging	2.3	281	251	570	391	40.7
Hausjärvi	5.3	Thinning	2001 August	At logging	5.3	462	315	310	167	35.0
Forest sites										
Sipoo	>20	Not within 70 years		2001 December	1	100	60	–	–	–
Ylämaa	>20	Not within 70 years		2002 April	1	100	53	–	–	–
Mäntsälä	>20	Not within 70 years		2002 April	1	100	49	–	–	–
Siuntio	>20	Not within 70 Years		2002 April	1	100	46	–	–	–
Total					20	2519	2077	2295	1184	

after incubation (see Isolation and identification of *Heterobasidion* species). Butt rot caused by *Armillaria* species (*A. borealis* Marxmüller & Korhonen and *A. cepistipes* Velenovsky) was identified visually only: fibrous, more or less soft and wet rot with dark brown colour, or holes in heartwood, and usually a sharp limit between the rot and intact wood. Stereum sanguinolentum-type rot was identified visually by its reddish-brown colour. This rot usually occurred as small spots in the sapwood and was in some cases possibly caused also by other fungi. The decay-causing agent in a small number of discs with butt rot could not be identified.

The decayed area on the discs was determined by measuring of the diameter of the disc and its decayed parts; the average of two perpendicular measurements was calculated. The ratio between the decayed area and disc area was used as a measure of the advancement of butt rot (i.e. proportion of decayed volume) in a cull piece.

2.3 Isolation and identification of *Heterobasidion* species

After cutting, each sample disc was placed into a plastic bag, incubated at room temperature for 5–7 days, and thereafter stored for up to 1 week at +4°C. Incubated discs were examined under a dissecting microscope for conidiophores of *Heterobasidion* spp. Abundance of conidiophores was classified into five classes: (i) conidiophores not found, (ii) a single conidiophore colony, i.e. conidiophores on an area smaller than 3 cm^2, (iii) sparse conidiophores here and there on the disc, (iv) conidiophores in moderate number and (v) conidiophores abundant. The fungus was isolated by picking conidiophores off under a dissection microscope, and the *Heterobasidion* species identified using mating tests (Mitchelson and Korhonen 1998). Isolates were cultured on malt extract agar containing 2% Bacto malt extract and 1.5% Bacto agar (Difco Laboratories, Becton, Dickinson & Co., Sparks, MD, USA) in Petri dishes.

2.4 Fruit body survey

Randomly selected cull pieces (1/3 or 1/4 of total number) were investigated each September from 2002 to 2004 and actively sporulating (white) pore layers of *Heterobasidion* fruit bodies drawn onto a transparent foil that was later scanned and subjected to image analysis to obtain area counts. In September 2002, pore layers of both 2001 and 2002 were recorded; pore layers of 2001 were identified by their brownish colour compared to the white appearance of the current year pore layers. In total, this procedure resulted in 2720 records on the annual existence of fruit bodies from 2077 cull pieces in the course of the study.

To estimate spore production by *Heterobasidion* occurring on the spruce stumps on the site, a random sample (1/3 or 1/4 of total per year) of stumps showing butt rot was also investigated for the presence of *Heterobasidion* fruit bodies. Root bases were excavated and active fruit bodies measured as described above. With few exceptions, no stumps or cull pieces were investigated twice during the course of this study, because it was considered that the investigation could affect fruit body production of the fungus.

2.5 Statistical analyses

Statistical analyses were performed using spss 14.0 for Windows (SPSS Inc., Chicago, IL, USA). Fruit body occurrence on cull pieces (expressed as a binary variable) was analysed by logistic regression. Statistically significant regressors were ranked according to the maximum odds ratio for a regressor (OR_{max}). OR_{max} expresses the maximum proportional increase in odds when only the level of the categorical regressor (or the value of the

continuous regressor) is changed and the values of all the other regressors are constant. For a categorical regressor $OR_{max} = \exp(b_{max} - b_{min})$, where b_{max} is the largest and b_{min} is the smallest regression coefficient for the levels of the regressor. For a continuous regressor $OR_{max} = \exp[|b| (x_{max} - x_{min})]$, where $|b|$ is the absolute value of the regression coefficient and $x_{max} - x_{min}$ is the range of the values of the regressor. The value of OR_{max} does not depend on parameterization of a categorical regressor or on scaling of a continuous regressor. The variation in pore layer area on cull pieces with fruit bodies was analysed using ANOVA.

3 Results

Cull pieces varied significantly in length and diameter (Table 2). Among the cull pieces with decay, more than one-third of the cull piece volume generally was decayed at the beginning of the experiment (Table 2). Heterobasidion butt rot was identified visually on 1938 cull pieces (93% of the total of 2077) and conidiophores appeared on 1572 cull pieces (76%). Of the *Heterobasidion* pure cultures isolated from conidiophores, a subsample of 902 isolates were identified by mating tests: 85% were identified as *H. parviporum* and 15% as *H. annosum s.s.* Relative prevalence of these two species varied considerably between the experimental sites (Table 2). Cull pieces infected by *H. parviporum* contained significantly more decay than those infected by *H. annosum s.s.* (63% *vs.* 34% of volume, respectively, $p < 0.0005$, data not shown). Armillaria-type butt rot was recognized on 2.6%, and unidentified rot types on 1% of the cull pieces. *Stereum sanguinolentum*-type decay was recognized on 57% of the cull pieces. It was common in the sapwood, and in most cases was obviously a result of infection by spores to the end of the cull piece after logging.

Over 3–4 years after logging *Heterobasidion* fruit bodies were found on cull pieces at every experimental site. However, there was considerable variation between sites: the number of cull pieces producing fruit bodies varied on different sites from 4% to 30% of the total number of cull pieces with initial butt rot (Table 3). In total, fruit bodies were found on 395 cull pieces with initial butt rot, corresponding to 19% of the total number of cull pieces in that category (Table 3), and to 20% of the cull pieces where Heterobasidion butt rot was detected visually, and to 25% of the cull pieces where *Heterobasidion* was identified on the basis of conidiophores. Among the 1938 cull pieces where Heterobasidion butt rot was visually detected, fruit bodies developed on 23% of the pieces having end-to-end contact to the ground (i.e. on 337 of 1475), on 15% of the cull pieces having one-end ground contact (51 of 341), and on 4.9% of the cull pieces without ground contact (six of 122).

The fruit bodies were mostly small, with a pore layer of <10 cm^2, but when present, there were usually several fruit bodies (up to 42) on the same cull piece. The largest fruit body found on cull pieces had an active pore layer area of 224 cm^2 (Table 3). The fruit bodies found on stumps were, depending on the cutting area, three to 10 times larger than those present on the cull pieces (Table 3). Small fruit bodies were also found on seven (1.6%) of the total of 442 initially sound-looking cull pieces.

The average pore layer area per log metre exceeded the average pore layer area per stump on three sites at the end of the investigation period, while on one site (Bromarv A) the areas were equal (Fig. 1). During the first 3 years after cutting, the active pore layer area of the fruit bodies on cull pieces increased. On two sites the logs were investigated in four successive years; on one of these sites (Vehkalahti) the pore layer area decreased in the fourth year from the maximum recorded in the third year, whereas on the other site (Bromarv K) the pore layer area increased also during the fourth year. Considerable differences were observed between the average pore layer area per log metre found on different sites (Table 3).

Table 2. **Cull piece properties at experiment onset**

	Cutting areas				Forest sites			
Variable	Vehkalahti	Bromarv K	Bromarv A	Hausjärvi	Sipoo	Ylämaa	Mäntsälä	Siuntio
Length (cm)								
Average	119	119	46	122	83	58	75	69
Range	22–643	20–2200	18–140	11–850	21–165	23–105	47–113	34–108
Diameter (cm)								
Average	32	26	26	22	25	24	21	22
Range	9–61	8–60	10–46	9–51	11–48	14–38	14–35	15–35
Mean volume of decay (% of total volume)	63	45	38	39	43	48	55	50
Decay types recognized (number of cull pieces)								
Heterobasidion butt rot	585	689	187	282	52	45	52	46
Armillaria butt rot	9	27	3	13	0	0	0	3
Stereum sanguinolentum rot	214	412	211	218	47	25	19	29
Other type	2	7	1	30	0	1	0	0
Heterobasidion species								
Cull pieces with *H. parviporum* (%)	93	93	78	56	n.d.	n.d.	n.d.	n.d.
Cull pieces with *H. annosum* (%)	7	7	22	44	n.d.	n.d.	n.d.	n.d.

Table 3. **Some characteristics of fruit bodies of *Heterobasidion* found on cull pieces and stumps**

	Cutting areas				Forest sites				
Variable	Vehkalahti	Bromarv K	Bromarv A	Hausjärvi	Sipoo	Ylämaa	Mäntsälä	Siuntio	Sum
Cull pieces									
Cull pieces with *Heterobasidion* fruit bodies									
Number of cull pieces with butt rot initially	179	144	11	31	13	7	7	3	395
Percentage of cull pieces with butt rot initially	30	20	4	10	22	13	14	7	
Number of initially sound-looking cull pieces	0	0	0	3	4	0	0	0	7
Number of *Heterobasidion* fruit bodies									
Average per cull piece, when present	7	9	5	14	8	9	17	5	
Range, when present	1–51	1–60	1–12	1–37	1–18	2–17	2–42	2–7	
Pore layer area of individual fruit bodies									
Average area (cm^2)	5.8	6.0	1.4	5.5	1.6	0.4	1.9	5.0	
Range (cm^2)	0.05–161	1.8–159	0.1–23	0.05–224	0.05–31	0.05–9.3	0.05–28	0.05–88	
Stumps									
Average pore layer area of individual fruit bodies (cm^2)	21	32	7.3	57					

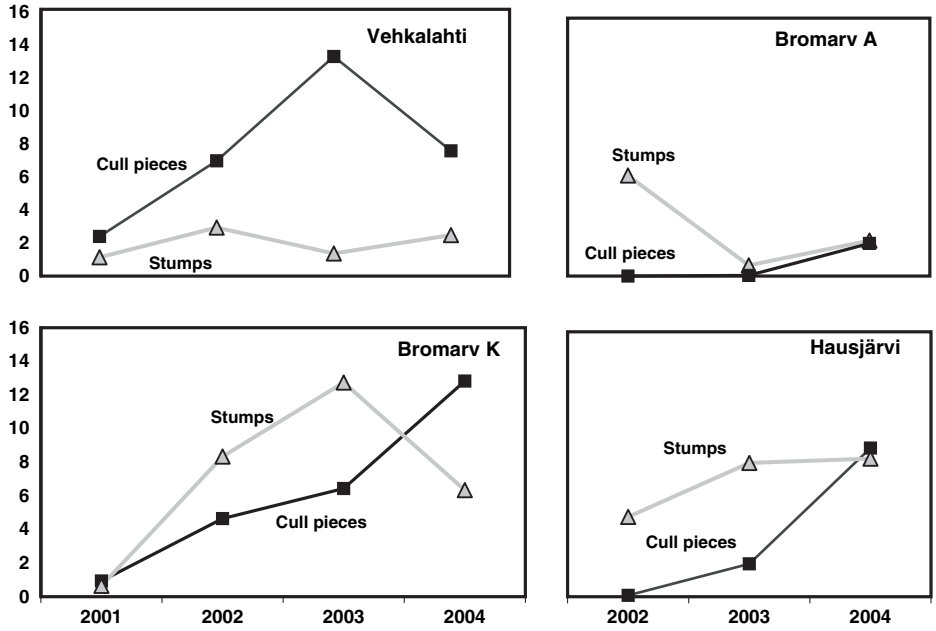

Fig. 1. Pore layer area of *Heterobasidion* fruit bodies on stumps and cull pieces during the experimental follow-up at each of the four cutting sites: Vehkalahti, Bromarv A, Bromarv K and Hausjärvi. Results are presented as average values per stump and per metre of cull pieces. During the experiment all cull pieces and all stumps of the sites were investigated

The advancement of butt rot in the cull piece was the most forceful variable (odds ratio 47; Table 4) in a logistic regression analysis explaining the occurrence of fruit bodies on cull pieces. This analysis included all 2720 annual fruit body records (from the 2077 cull pieces with initial decay) and the presence of fruit bodies was treated as a binary-dependent variable (1 = presence, 0 = absence). Other significant variables explaining the occurrence of *Heterobasidion* fruit bodies were cull piece diameter, abundance of *Heterobasidion* conidiophores on sample discs, site, year, contact of the cull piece with ground and presence of decay caused by *S. sanquinolentum*. Fruit bodies appeared most probably on large-diameter cull pieces, which were extensively colonized by *Heterobasidion*, in which *S. sanguinolentum* was absent and which were positioned with an end-to-end contact to the ground (Table 4). The presence of *S. sanguinolentum* significantly decreased the formation of *Heterobasidion* fruit bodies, although its overall influence was low according to the model (odds ratio 1.7). Cull piece length, bark injuries or *Heterobasidion* species causing decay did not affect fruit body formation. Forest cover did not affect the occurrence of fruit bodies when included as a categorical covariate (1 = clear-cut, 2 = thinned and 3 = mature) in a separate logistic regression analysis.

Variation in pore layer area on cull pieces was investigated in an ANOVA. In this analysis, the cull pieces without fruit bodies were excluded. The analysis revealed that advancement of butt rot in the cull piece, size of cull piece (length and diameter), site and year significantly influenced pore layer area (logarithmically transformed) formed by *Heterobasidion* (Table 5). While cull piece length was not a significant variable when fruit body occurrence was examined (Table 4), it turned out to be a significant variable explaining the logarithm of the summed pore layer area of fruit bodies on the cull pieces (Table 5).

Table 4. **Logistic regression model explaining the variation of *Heterobasidion* fruit body occurrence on cull pieces**

Variable	*B*	SE	Significance	OR_{max}[1]
The advancement of butt rot in cull piece (range: 0.00–1.00)[2]	3.85	0.410	0.000	47
Cull piece diameter (range: 8–61 cm)	0.058	0.008	0.000	21
Abundance of *Heterobasidion* conidiophores[2]				
Conidiophores not found	−2.18	0.323	0.000	13
Single conidiophore colony	−2.58	1.105	0.000	
Sparse conidiophores	−1.46	0.260	0.019	
Conidiophores moderately	−0.64	0.145	0.000	
Conidiophores abundantly	0.00		0.000	
Site				
Vehkalahti (clear-cut)	1.91	0.630	0.000	9
Bromarv K (clear-cut)	2.22	0.631	0.002	
Bromarv A (clear-cut)	0.50	0.703	0.000	
Hausjärvi (thinning)	2.16	0.659	0.478	
Sipoo (mature)	2.10	0.678	0.001	
Mäntsälä (mature)	1.08	0.734	0.002	
Ylämaa (mature)	1.43	0.728	0.140	
Siuntio (mature)	0.00		0.050	
Year				
2001	−1.96	0.213	0.000	7
2002	−0.71	0.167	0.000	
2003	−0.24	0.164	0.000	
2004	0.00		0.144	
Degree of ground contact of the cull piece				
Cull piece on ground with end-to-end contact	1.54	0.447	0.000	4.7
Cull piece on ground with one-end contact	0.98	0.474	0.001	
Cull piece without ground contact	0.00		0.038	
Stereum sanguinolentum rot not found[2]	0.53	0.135	0.000	1.7
Constant	−8.04	0.830	0.000	

Total n = 2720. The model of type: $p/(1 - p) = \exp(B_o + B_1{*}X_1 + B_2{*}X_2 + ...)$ predicts correctly 96% of 'clean' cull pieces and 37% of fruit body-carrying cull pieces. The variable groups are listed according to their odds ratio. Cox & Snell $R^2 = 0.240$; Nagelkerke $R^2 = 0.414$.

[1]Maximum odds ratio for a regressor, for instance $e^{3.85}/e^{o} = 47$ or $e^{o}/e^{-2.58} = 13$ or $e^{0.058*61}/e^{0.058*8} = 21$.

[2]These variables were determined from sample discs taken from the cull pieces at experiment onset.

According to this analysis (where cull pieces without fruit bodies were excluded), the abundance of *Heterobasidion* conidiophores on sample discs, degree of the cull piece ground contact, and presence of *S. sanguinolentum* had no significant effect on the pore layer formation.

4 Discussion

At the beginning of the experiment, Heterobasidion butt rot was identified visually on sample discs cut from 1938 cull pieces but conidiophores of *Heterobasidion* were found on only 1572 discs (81%). The true number of cull pieces containing Heterobasidion butt rot was probably between these two figures, because some visually identified Heterobasidion butt rot may have been caused by other fungi and, on the other hand, some sample discs from cull pieces with Heterobasidion butt rot may not have produced conidiophores.

The occurrence of butt rot was high on all the harvested sites (Table 1), which is not unexpected for spruce stands in southern Finland (Tamminen 1985). Also, the high

Table 5. ANOVA **of the logarithm of the pore layer area of sporocarps found on cull pieces**

Source	d.f.	*F*	Significance
Corrected model	23	5.33	0.000
Intercept	1	33.21	0.000
Advancement of butt rot in cull piece	1	25.88	0.000***
Cull piece diameter	1	16.43	0.000***
Cull piece length	1	9.40	0.002**
Site	7	4.91	0.000***
Year	3	3.38	0.018*
Site*Year	10	0.93	0.506
Error	430		
Total	454		
Corrected model	453		

Cull pieces without any sporocarps at any year during the experiment were excluded from the analysis.
$R^2 = 0.222$ (adjusted $R^2 = 0.180$). $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

frequency of *Heterobasidion*, and of *H. parviporum* in particular, as a causal agent of butt rot is typical for the region. In all, *Heterobasidion* spp. were isolated from 76% of the sample discs showing butt rot; 85% of the isolates were *H. parviporum* and 15% *H. annosum s.s*. The proportion of *H. annosum* was unusually high, 44%, in Hausjärvi. A possible explanation is that sandy soils and pine forests with root rot caused by *H. annosum* are common in this region, presumably providing a high local inoculum pressure of *H. annosum*. However, the study site itself was relatively fertile, representing a typical spruce site in Finland.

In the present study, incidence of *Heterobasidion* sporocarps on cull pieces containing Heterobasidion butt rot ranged from 4% to 30% on different sites. These figures are lower than reported by SCHÜTT and SCHUCK (1979) from two sites in Germany. They investigated decayed Norway spruce logs left in the forest and found *Heterobasidion* sporocarps on 26% and 50% (depending on site) of the logs over a 4-year period after cutting. In our study, the highest sporulating pore layer area (13 cm^2 per log metre; Fig. 1) was found in Vehkalahti 3 years and in Bromarv K 4 years after logging. This value is considerably lower than that observed by SCHÜTT and SCHUCK (1979) in Germany, where they found on one site maximally 88 cm^2 and on the other 123 cm^2 of sporocarp area per log metre within 4 years after logging. The large difference can only partly be explained by differences in measuring the fruit bodies; SCHÜTT and SCHUCK (1979) measured the area of the total sporocarp, whereas in the present work, the area of the active pore layer was measured.

A great majority, if not all, of the fruit bodies found on cull pieces during this study probably originated from *Heterobasidion* infections already present before logging, as judged from the very low fruit body occurrence on initially sound-looking cull pieces, i.e. on seven of 442 initially sound-looking cull pieces (Table 3). Even these few fruit bodies have not necessarily emerged from aerial infections of the cull pieces, but may have originated from incipient decay that was initially present but was not detected at the beginning of the study. In comparison with some other common wood-decay fungi, such as *S. sanguinolentum* or *Phlebiopsis gigantea* (Fr.) Jülich, *Heterobasidion* species are not important storage-decay fungi in initially sound spruce timber (VON PECHMANN et al. 1967). Hence, we consider that leaving healthy-looking cull pieces of spruce on cutting areas infested with *Heterobasidion* does not notably support the spread of this fungus.

Logistic regression analysis (Table 4) revealed a high number of factors that possibly affect fruit body formation of *Heterobasidion* on cull pieces. It was not surprising to find

that advancement of butt rot and abundance of *Heterobasidion* conidiophores on sample discs were among the most forceful variables affecting fruit body formation on cull pieces. Advancement of decay was considerably higher in cull pieces where *H. parviporum* occurred, compared to cull pieces where *H. annosum* was found (63% *vs.* 34% of cull piece volume). This result is in agreement with earlier studies, which showed that *H. parviporum* is better adapted to Norway spruce (e.g. VASILIAUSKAS and STENLID 1998). Even though in our logistic regression analysis the species of *Heterobasidion* did not explain fruit body occurrence (Table 4), it can be concluded, that cull pieces decayed by *H. annosum s.s.* are less likely to produce fruit bodies than cull pieces decayed by *H. parviporum*, because of the generally smaller amount of decay caused by the former.

Cull piece size may affect the fruit body formation in several ways. A large cull piece can support a large mycelium that may be needed for fruit body production. Also, moisture and temperature conditions are more stable in larger than in smaller pieces. The results obtained here suggest that moisture conditions in the cull pieces are critical for fruit body production. Compared to stumps, which are partially inside the soil, cull pieces are certainly more susceptible to drying, and hence contact between the cull piece and the ground is essential for fruiting of *Heterobasidion*. The larger pore layer area of individual fruit bodies found on stumps compared to that found on cull pieces (Table 3) may reflect more favourable conditions for the fungus in stumps. On the other hand, not all stumps provide favourable niches for fruit body formation. The fruit bodies of *Heterobasidion* in Finnish forests almost always develop in non-exposed positions; they can be found in hollows under roots of stumps and dead trees, under moss cover on the root collar and under logs lying on the ground. Where soil contact with stump roots and the root collar is tight, fruit body formation may be prevented. Instead, logs lying on the ground usually offer suitable non-tight niches for fruit body development.

Variation in the numbers of fruit bodies on different sites is difficult to explain but agrees with results reported earlier (SCHÜTT and SCHUCK 1979). Considerable differences in fruit body formation were found between two experimental sites in southern Germany. Considering that forest cover (clear-cut *vs*. closed canopy) has a strong influence on the microclimate, it is surprising that no clear differences were observed in fruit body formation by *Heterobasidion* in the present work, on cull pieces placed in clear-cut areas and in mature spruce forests with closed canopies.

Presence of *S. sanguinolentum* had a small (odds ratio 1.7, Table 4) but significant effect on fruiting of *Heterobasidion* on cull pieces. This is noteworthy, as *S. sanguinolentum* occurred generally only on small areas of the sample discs examined.

Only 37% of the fruit body-carrying cull pieces were classified correctly with the model presented in Table 4. Also, the low values of Cox & Snell and Nagelkerke R^2 suggest that all important variables ruling fruit body formation by *Heterobasidion* on cull pieces were not included in the logistic regression analysis. One important missing group of variables in these data was obviously that describing chemical and physical characteristics of the cull piece wood. Differences in susceptibility of individual trees to root rot are known to be considerable (DELATOUR et al. 1998). Differences between individual strains of *Heterobasidion* and even local populations may also contribute to variations in occurrence of fruit bodies on cull pieces.

Differences between the sets of variables significant in the two statistical models (Tables 4 and 5) reflect the fact that cull pieces without fruit bodies were omitted in the ANOVA. In ANOVA the lack of significance of the variables *Heterobasidion* abundance, presence of *S. sanguinolentum* and ground contact, was due to exclusion from the data set of most cull pieces that produced sparse conidiophores on sample discs, were inhabited by *S. sanguinolentum* and had incomplete ground contact. It is, however, surprising that cull piece length did not explain fruit body formation in the logistic regression analysis (Table 4), despite being a significant variable in the ANOVA explaining pore layer size when

formed (Table 5). When included in the logistic regression, cull piece length was clearly not significant ($p = 0.40$, data not shown).

The results obtained in this study clearly indicate that, if cull pieces of Norway spruce with butt rot are left in the forest, remaining in contact with ground, and if the decay is caused by *Heterobasidion* spp. (as it usually is in southern Finland), the probability of fruiting of *Heterobasidion* on such cull pieces is relatively high, at least during the first 4 years after cutting. Figure 1 shows that the sporulating fruit body area per metre of cull piece can be considerable compared to that found on stumps, and in some cases values on cull pieces even exceeded those on stumps. As it can be supposed that spore production is related to the actively sporulating area of fruit bodies, these data show that leaving decayed cull pieces can markedly increase local spore production by *Heterobasidion* and hence support the spread of this pathogen to surrounding forests, through fresh stumps in particular. The density of *Heterobasidion* spores on a stump surface may be a crucial factor in disease spread because normally only heterokaryotic mycelia are able to cause the disease (Korhonen and Stenlid 1998), and a prerequisite for heterokaryon formation is that two compatible homokaryotic mycelia, each of them originating from a basidiospore, can meet in the stump. A high spore density on the stump surface may also lead to formation of several heterokaryons enabling selection of the most competitive ones (Swedjemark and Stenlid 2001). This aspect is relevant also when fresh stumps are treated with protectants because the protectants usually do not give 100% control of *Heterobasidion* infection. Moreover, there is some indication that spores of *Heterobasidion* may infect saplings of the next spruce generation already at the age of ca. 10 years (Piri and Korhonen 2001). If sporulation on cull pieces continues until saplings have reached that age, these logging residues may contribute also to the direct infection of the next spruce generation on the site.

Logging practices have recently changed in Finland, and decayed cull pieces of spruce are not generally left in the forest. When the harvester driver recognizes butt rot in the spruce being cutt, the stem is usually cut into 3 m long pieces until a sound cross-section appears. The rotten timber is then removed from the forest and, depending on the extent of the decay, used for chemical pulping or as fuel wood. Based on the results obtained in this study this practice appears reasonable. The need for increasing decaying spruce wood in managed forests, to support biodiversity, should preferably be fulfilled by leaving sound spruce wood or spruce trees damaged by factors other than Heterobasidion root rot.

Acknowledgements

We are grateful to Hannu Rantanen, Ismo Kyngäs, Anu Kajosaari and Rauni Björkman for their skilful help with the field and laboratory work. Kaija Puputti and Pentti Kananen are acknowledged for arranging the cull pieces and field sites at Bromarv and Hausjärvi. We also want to thank Anja Romu, UPM-Kymmene, for arranging the Vehkalahti field site and Metsähallitus for providing the mature forest sites for our use. Kiti Müller is thanked for checking the language and Thomas Kirisits for constructive criticism.

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