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SEQUENCE OF MACROMYCETES ON DECAYING BEECH LOGS

MORTEN LANGE

Institut for Sporeplanter, Copenhagen University*

Development of the macromycete flora of windfall beech logs in different stages of decay were studied over 10 years. The occurrence of 48 species found on more than six logs are discussed in relation to five 5-year periods of progressing decomposition. The first period has several distinctive species confined to hard bark and fresh wood. Also the second period with desquamating bark has distinctive taxa. Polyporaceous species have a slight dominance in this period, while saprophytic agarics are more frequent in the later periods. Many species, including *Armillaria mellea*, *Fomes fomentarius* and other necrotrofic parasites are met in all 5-year periods. The final stage of decay is characterized by slow invasion of species of the forest floor.

Strødam is a nature reserve in the southern part of Grib Skov, Zealand. The reserve is under supervision of a committee set up by the University of Copenhagen, Faculty of Science. The main part of the reserve is old stands of beech. Many standing trees have attacks of *Fomes fomentarius*, and every year new windfalls are added to the large number of fallen logs which are left on the forest floor. The present study deals with the development of the macromycete flora during the advancing decay of the logs. Sixteen logs, which were selected for an entomological study, had been dated, so that the year of growth stop was known. The logs were suited also for a mycological study. The 16 logs were 1–18 years old counting from the year of growth stop.

The logs were observed over a ten year period. A number of additional logs were included during the study, so that the last two years observations cover 27 logs. One of the original logs has been excluded from the tabulated results, due to uncertainty of the dating.

All logs were windfalls. Most of the trees have been uprooted, with a distinct root plate, some boles are, however, broken above ground. This factor, as well as the shape of the bole, provide for a great variation in soil contact, which again influences the decomposition process. The selected trees are 100–200 years old. The diameter at 1 m above the base varies from 50 cm to 85 cm. Many boles are divided in two or three. The decomposition of logs have been studied by several workers. In this presentation, I prefer to follow the classification proposed by Muhle & LeBlanch (1975). They define five phases of decay, distinguished primarily on the characteristics of the bark and of the log surface as indicated here in slightly modified form:

1. bark firmly attached to wood, wood solid,
2. bark surface desquamating, wood solid or locally softened,
3. bark partly lost, breaking into pieces, wood softened,
4. bark mostly lost, wood breaking into pieces, charcoal-like,
5. bark lost, log broken up, wood completely soft.

* Mailing address: Rønne bærvej 66, DK 2849 Holte, Denmark.

Every log shows a certain variation. Sections with soil contact decompose faster than the elevated parts. Also, most boles will have small areas in stages 4 or 5 already from the first year. However, according to my observations, I find it justified to ascribe five years development to each phase.

The macromycetes were observed 2–8 times per year in 1980–1989. The observations covered the whole log and its branchings to 10 cm diam. but not the root plate. Of course the development of the fungus flora differs much from year to year. This is limited by placing the observation days in optimal periods. Observations in 1981 were not optimally placed due to other assignments.

In the present study, macromycetes include Agaricales s.l., Gasteromycetales, Aphyllophorales with exception of most of the truely resupinate forms, larger Discomycetes, larger stromatic Pyrenomycetes, and larger tremellaceous fungi. Only presence of a species was noted, and the results recorded here indicate presence in an observation year.

Nomenclature follows Moser (1983), Jülich (1984) and Dennis (1981). However, species concept and nomenclature in *Pluteus* follows Orton (1986). Selected specimens of most of the observed taxa are deposited in herbarium C.

RESULTS

Table I records the average number of species on the logs for each of the ten years. The number of observations is 2–4 in the first five years, 6–8 in the last five years. The larger number of inspections in the last years is mainly due to increase in off-season observations, adding but little to the averages calculated. Variation in the development of the flora in the ten years complicates the comparision of the yearly number of species. This variation pattern appears most clearly from the figures for the 15 original logs given in the two lower rows. It is notable that the high figures for 1980 and especially for 1989 reflect rich seasons.

Table II records the number of species observed on each of the logs of the ten observation years. The scheme shows the results for logs of same age of decay in 28 vertical columns. The serial number and the year of growth stop are shown to the left. The total number of species for each log is given to the right. These figures demonstrate remarkable variations. For

Table I. Average yearly number of species on the logs. The table shows the observation years, the corresponding number of observations, the number of logs included, their average age of decay and their average number of species. The two last rows give the similar figures for the original series of 15 logs (14 in 1980).

Year	80	81	82	83	84	85	86	87	88	89
no. obs.	3	2	3	3	4	6	8	6	6	7
no. logs	14	16	17	17	17	17	20	20	26	26
av. age	9.4	10.1	10.5	11.5	12.5	13.5	12.5	13.5	12.2	13.2
av. sp.	11.4	6.8	8.9	10.5	12.5	12.1	12.6	12.9	12.5	16.7
av. age orig. ser.	9.4	10.7	11.7	12.7	13.7	14.7	15.7	16.7	17.7	18.7
av. sp.	11.4	7.1	9.7	11.2	13.9	12.6	14.9	13.8	12.5	15.7

Table II. Number of species on the logs arranged after age of decay, 1 to 28 years. Number of 'log units' for each year is indicated in the second row. The ruled table gives the number of species of each log. Log serial number and year of growth stop is given to the left. Total number of species observed on each log is shown to the right. Figures below show average species number per year, number of 'log units' in 5-year groups, and average species number in these groups.

age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
no. logs	8	10	9	9	5	7	10	10	9	8	7	7	8	9	11	10	7	6	7	7	7	6	5	2	2	2	1	1	
18-81	3	4	3	6	9	12	14	19	27																				
17-80	2	3	7	1	11	8	15	10	17	31																			
13-79	4	3	7	13	13	15	16	20	27	24	46																		
16-78	10	9	8	7	10	14	16	19	11	23	34																		
12-76	12	12	20	26	32	28	38	20	26	29	77																		
3-74	2	1	5	11	14	14	13	12	14	19	43																		
9-73	5	6	4	4	17	10	7	9	11	12	33																		
15-73	25	16	19	22	21	29	20	26	15	24	65																		
1-73	13	8	12	13	11	7	12	13	9	10	31																		
27-73	21	21	32																										
26-87	10	14	19	7-72	6	6	7	10	10	12	13	11	13	16	33														
24-87	7	16	19	4-68	11	7	9	10	13	9	12	8	14	15	21														
22-86	10	17	21	14-67	13	9	9	11	7	12	12	10	8	10	28														
25-85	18	21	26	8-66	6	10	7	16	9	9	10	14	12	29															
21-85	4	8	8	15	21	5-66	9	5	10	6	10	12	17	13	11	16	34												
20-85	4	5	12	18	24	11-66	18	8	9	10	11	7	13	10	8	10	36												
19-85	5	10	17	24	27	10-63	19	5	7	12	16	17	13	11	11	10	40												
23-83	12	17	21	2-61	13	6	7	6	7	8	10	5	6	5	22														
	4.9	8.3	10.9	13.1	10.4	11.3	14.6	13.8	15.9	16.6	16.6	15.1	14.0	13.3	11.3	13.3	10.6	11.0	9.7	11.6	11.3	11.0	11.6	9.5	10.5	7.5	6.0	5.0	
	41 - 9.5					44 - 14.5					42 - 13.8					37 - 11.4					22 - 11.0					4 - 6.5		

the 16 logs observed through 9–10 years the range is from 21 species to 77 species. The average species number for these logs is 38.

The yearly averages for the 28 years are significantly low for the first 2–3 years and also low for the last 10–11 years. The last five years include but very few logs. In the lower row of the table the results are calculated for 5-year periods corresponding to the phases of decay defined above. The figures indicate the number of 'log units' in each 5-year group and corresponding average number of species.

The second period shows the highest average species number, closely followed by the third period. The two logs most rich in species (nos 12 & 15) have maximum numbers in their tenth and twelfth year respectively. The figures for these two logs weigh heavily in the calculated averages. Also in this table, the good seasons, 1980 and 1989, can be traced. (High figures in years 4, 7, 16, 23.)

The species found most frequently on the logs are recorded in Table III. It is limited to taxa observed on six logs or more, a total of 48 species. As shown in column I, six of these species are found on 20 logs or more. Column II indicates the constancy of the species by giving the sum of the number of 'log units' on which the species has been found in each of the ten observation years. Three species have been recorded on more than ten logs per year, viz.

Table III. Frequency of species in 5-year periods of decay. The table includes all species found on at least six logs. I. Number of logs on which the species were found. II. Sum of number of logs per year. III. First and last observation year. The six last columns: Sum of number of logs per year distributed on 5-year periods, and recorded as percentage of observations possible. Corresponding number of 'log units', see Table II.

	I	II	III	1–5	6–10	11–15	16–20	21–25	26–28
Armillaria mellea	20	62	1–28	27	36	38	30	27	50
Ascocoryne sarcoides coll.	18	42	1–25	27	27	14	22	23	
Ustulina deusta	15	71	1–23	22	45	43	43	32	
Fomes fomentarius	24	147	1–23	63	98	93	78	41	
Bulgaria inquinans	7	8	1–2	20					
Hypoxylon fragiforme	7	15	1–4	37					
Schizophyllum commune	7	12	1–4	29					
Chrondrostereum purpureum	6	7	1–4	17					
Trametes hirsuta	9	12	1–6	27	2				
Neobulgaria pura	8	15	1–8	32	8				
Exidia glandulosa	8	11	2–9	22	5				
Pleurotus ostreatus coll.	12	27	1–8	51	14				
Datronia mollis	7	11	2–12	20	5	2			
Phlebia radiata	15	26	2–15	46	14	2			
Pholiota adiposa	7	17	1–12	20	16	5			
Trametes gibbosa	6	8	3–13	10	5	7			
Bjerkandera adusta	20	57	1–20	56	50	17	14		
Stereum hirstum	17	54	2–22	51	41	26	3	9	
Panellus serotinus	16	37	2–21	39	27	7	14	4	
Oudemansiella mucida	15	40	1–24	32	30	12	19	9	
Calocera cornea	10	19	4–15	7	30	7			
Mycena speirea	9	19	4–16	7	18	17	3		
Kuehneromyces mutabilis	6	14	4–19	2	16	10	8		
Fomitopsis pinicola	13	41	2–16	22	43	26	5		
Polyporus varius	15	43	4–20	10	52	21	19		
Trametes versicolor	15	31	2–23	22	30	12	8	4	
Coprinus micaceus	20	70	2–23	34	68	36	22	14	
Pseudoclitocybe cyathiformis	6	14	6–16		16	14	3		
Pluteus gracilis	13	24	6–22		25	14	16	4	
Peziza avernensis	15	35	1–21	17	16	26	24	4	
Xylaria hypoxylon	19	77	2–23	20	54	57	38	23	
Merulius tremellosus	10	44	4–21	2	34	45	22	4	
Mycena crocata	15	56	5–25	2	30	48	41	32	
Pluteus umbrosus	6	10	5–23	2	5	10	3	9	
Pluteus phlebophorus	16	67	6–27		32	64	46	32	25
Marasmius alliaceus	22	109	2–28	24	75	67	76	73	100
Mycena haematopus	19	96	2–28	10	57	64	65	59	75
Ganoderma applanatum	12	67	5–23	2	41	43	57	41	
Pluteus cervinus	20	101	1–27	12	41	71	73	86	75
Mycena galericulata	14	59	6–28		16	48	46	55	75
Conocybe subpubescens	15	37	5–25	2	23	21	27	32	
Hypholoma fasciculare	8	20	4–27	7	14	10	3	18	25

(Table III continued)

	I	II	III	1–5	6–10	11–15	16–20	21–25	26–28
Lycoperdon gemmatum	13	22	4–25	2	16	12	11	23	
Polyporus brumalis	6	15	3–24	2	5	10	8	23	
Psathyrella hydrophila	7	29	7–23		9	19	27	32	
Galerina unicolor	10	35	6–25		23	26	22	27	
Pluteus salicinus	6	12	9–26		5		14	18	25
Lycoperdon pyriforme	13	55	6–28		11	31	49	73	75
Lactarius subdulcis	7	12	12–26			7	5	27	25

Fomes fomentarius, Marasmius alliaceus, and *Pluteus cervinus. Mycena haematopus* is the only other species close to this number.

The distribution on age groups is shown in the following seven columns. Column III gives first and last year of appearance. It is striking, that more than half of the species were found already in the first or second year, and that almost half of the species had an age span of 20 years or more. Only eight species cover ten years or less. With the exception of *Lactarius subdulcis,* all species listed are found before the logs have been decaying for ten years. Some of the species may be falsely credited with an early appearance, growing on small parts of the boles in advanced stages of decay. It has, however, been seen much more frequently, that typical late-stage species are found on rather fresh, bark-covered wood. Such early specimens are often dwarfish.

The table is grouped in six sections. The first of these includes four species, which are frequent in all five full 5-year age groups. In the remaining sections, the species are arranged after their highest frequency in the age groups, calculated as the percentage of records possible in the group. The corresponding number of 'log units' is given in Table II. It will be seen that this number is largely of same size in the first four periods, while significantly lower in the fifth period. Figures from the sixth period are based on four 'log units' only and thus of little significance. This last group is generally disregarded in the following.

The four species in the first section are found to have but slight preference for any of the stages of decay. Three of these species are well known necrotrofic parasites on living beech but they also thrive well on strongly decayed wood. *Fomes fomentarius* usually appears in the second year and can produce new fruit-bodies for 20 years. From the 15th year, the fruit-bodies tend to be few and small. It has not been noted on one log where *Ganoderma applanatum* is dominant. *Ustulina deusta* follows the same pattern with a very constant occurrence on a number of logs, while totally absent from others. *Armillaria mellea* is found on all logs more than eight years old but with very large variation in the yearly occurrence (e.g. 3 logs in 1988, 17 logs in 1989). *Ascocoryne sarcoides* is commented on below.

Sixteen species dominant on logs in the first 5-year period, form the largest of the sections. Half of these species occurs exclusively – or almost so – in this period. *Bulgaria inquinans* is most restrictive, confined to fresh bark in years 1–2, associated with the slightly more long-lived *Hypoxylon fragiforme* and *Schizophyllum commune.* Also *Neobulgaria pura, Exidia glandulosa, Datronia mollis,* and *Phlebia radiata* are mainly confined to the hard bark. *Bulgaria inquinans* and *Chondrostereum purpureum* are the only species with highest frequency

in the first year. The latter species is a true parasite. The most frequent fungus in this part of the section is *Pleurotus ostreatus*, culminating in years 2–4. Like *Trametes hirsuta* the species decomposes fresh wood. The last four species in the section are found fruiting through at least 20 years with high frequencies also in the second 5-year period. Correspondingly, they have no clear relation to the firm bark which characterize the section. The same holds true for *Pholiota adiposa*.

The second 5-year period has nine dominant species. Most selective for the period is *Calocera cornea*, which has a strong majority of its occurrences in years 7–11. The most frequent species in the section is *Coprinus micaceus*. It has some preference for the duff, which accumulate under the decaying bark. Also the optima of *Pluteus gracilis*, *Mycena speirea*, and *Pseudoclitocybe cyathiformis* have connections to the stages of bark decay typical for the period. The three polyporaceous species in the section have their optima in accordance with the stage of decay of the wood.

The fungus flora of the three last periods where the bark gradually disappears have much in common. The procentual margins on which most of these species are classified in the three sections can hardly be considered as significant. Some of these species could have been referred to the group of omnipresent species, notably *Xylaria hypoxylon*, *Marasmius alliaceus*, *Mycena crocata*, and *M. haematopus*. They are, however, all rather sparse in the first period.

Merulius tremellosus and *Pluteus phlebophorus* could be mentioned as typical for the years 11–15. Among the three species listed in section 4, only *Ganoderma applanatum* shows figures with traces of significance. It is confined to rather few logs but with a high constancy of appearance. Section 5 has no less than 11 members. Even if some procentual margins are narrow, it suggests an increase in the occurrence of a series of agarics in this stage of decay, where the bark is lost and the wood is distintegrating. True dominants in section 5 are probably only the two *Lycoperdon* species and *Lactarius subdulcis*, which species is the only mycorrhizal fungus frequent enough to be included in the table. The total list of species includes several mycorrhiza formers, i.a. *Xerocomus chrysenteron*, *X. porosporus*, *Laccaria amethystina*, *L. laccata*, all found on very strongly decayed logs.

Also some species generally growing on litter in the forest floor are typical for this last stage of the decay. *Clitocybe* spp., *Lepista nebularis*, *L. nuda*, *Cystolepiota sistrata*, and several others, recorded on a few logs each.

In the total list there are a few species without relation to the decay process, growing in or on moss: *Galerina vittaeformis*, *Rickenella fibula*, *R. setipes* are most common, found on 4–5 logs each. A similar, insignificant group is made up of species growing on beech mast, on beech leaves, or on decaying remains of other fungi.

The determination of two species in the list has left some doubt. *Coryne sarcoides* includes both this species and *C. cylichnium*. Unripe specimens of these species are difficult to separate. From my notes it appears that the true *C. sarcoides* probably is confined to the first two periods, growing on bark, while the remaining records most likely represent *C. cylichnium* on strongly decayed wood. Figures for *Pleurotus ostreatus* include several records referred to *P. pulmonarius*. However, intermediate forms are met with, and the two species are both found on the same logs in the same periods of decay.

CONCLUSIONS

The macromycetes delt with here belong in two major groupings. A group of 9–10 species are clearly thriving on the bark, and correspondingly restricted to the first 10–15 years of the decay period. Most typical and most restricted among these species are *Bulgaria inquinans* and *Hypoxylon fragiforme* but also two or three other ascomycetes seem strictly confined to the firm bark. The species typical for the desquamating bark are rather few, and have a less well defined biology, *Calocera cornea* and *Mycena speira* being most typical. Of course, almost all the other species found in the first 5–10 years will actually grow on – or break through the bark but they are supposed to be true wood decomposers, with their mycelium mainly in the wood. They are thus the first links in the chain of true wood decomposing fungi. Most outstanding is a polyporaceous series with *Chondrostereum purpureum* and *Trametes hirsuta* as the most restrictive members of the early stage, followed by *Datronia mollis, Trametes gibbosa, Bjerkandera adusta, Polyporus varius, Fomitopsis pinicola, Trametes versicolor,* and *Ganoderma applanatum,* with *Fomes fomentarius* as the only member being frequent throughout. The polyporaceous series is declining after the bark has started to disappear. *Fomes* and *Ganoderma* are still frequent in the last two 5-year periods, while *Polyporus brumalis* seems to have a culmination in the latest phase.

There is a similar series of wood decomposing agarics. It starts with the agressive saprophytes: *Pleurotus ostreatus, Pholiota adiposa, Panellus serotinus,* and *Oudemansiella mucida,* all found dominant in the period of fresh bark and hard wood. It continues with a series of *Mycena* species: *Mycena crocata, M. haematopus,* and *M. galericulata,* with dominance in age groups 3, 4, and 5 respectively, and a similar sequence of *Pluteus* species: *P. phlebophorus, P. umbrosus, P. cervinus,* and *P. salicinus.* Several other agarics have a more or less well defined place in the total sequence, with *Armillaria mellea* and *Marasmius alliaceus* as equivalents to the omnipresent *Fomes fomentarius.*

The fact that many frequent species appear over a long series of years makes a true divsion of the sequences of occurrence somewhat illusive. There is, however, a reasonable good correspondence to the stages of decay defined here.

The fungi thriving on the bark characterize the first phase and continues with new members in the second period when the bark is desquamating.

The wood decomposing fungi have a very pronounced and continuous polyporaceous series, culminating in the second period and hereafter becoming more sparse, while the last three periods have agarics as the typical members.

It all ends up with a slow invasion of species from the forest floor degrading the scattered remains of the logs.

DISCUSSION

With few exceptions, the species recorded here as frequent on the beech logs are confined to deciduous wood. Several of them have preference for beech, viz. *Neobulgaria pura, Ustulina deusta, Trametes gibbosa, T. versicolor, Polyporus varius, Ganoderma applanatum, Pluteus gracilis.* Four species are found exclusively on beech, viz. *Hypoxylon fragiforme,*

Oudemansiella mucida, Marasmius alliaceus, and *Mycena crocata.* The last three species seem confined to logs and branches of beech, while they are absent from beech stumps. Some species found very sparingly on the logs studied are reported as frequent on stumps. *Xylaria polymorpha* found on one log only, *Meripilus giganteus* noted on two logs. Also *Trametes versicolor* and *Hypholoma fasciculare* are probably much more frequent and abundant on stumps.

It is quite reasonable that these two biotopes have a different fungus flora. The perfect soil contact of the stump, and its open, cut surface give rich possibilities for the intrusion of fungi, and the progress of the decomposition is judged to be much faster. Undoubtedly the spatial development of the mycelia is quite different in the two types of substrate. An analysis of the specific mode of decay could, however, not be included in this study, without interfering with its main objective – the sequence of the occurrence of the macromycetes on undisturbed fallen logs.

There are very important recent contributions to the biology of decay of beech wood caused by macromycetes. Several such studies are reviewed by Cooke & Rayner (1984: 234–237) and new evidence is added by Coates & Rayner (1985).

Studies of the same scope as the present one are not very many. Jahn (1979) summarizes most of these in a brief synthesis. He also underlines the differences between the mycoflora on stumps and on logs.

More recent publications by Runge (1980) and Kreisel & Müller (1987) add some more facts to this summary. These authors distinguish three phases of the development of the mycoflora: Initital phase, Optimal phase, and Final phase. They are largely corresponding to the first, second, and third-fourth decay period described here. I have not adopted this terminology. The final phase is logically the period when the fungus flora of the litter and the mycorrhiza formers invade the decomposed remains of the log or stump, and whether the second or third decay period should be termed optimal is not a clearcut matter. Undoubtedly, the initial phase is characterized by a series of species confined to this stage but the species occurring in the later phases all have so long periods of appearance that the categorization is extremely fluent.

References

COATES, D. & RAYNER, A.D.M. (1985). Fungal population and community development in beech logs. I–III. *In* New Phytol. 101: 153–183.

COOKE, R.C. & RAYNER, A.D.M. (1984). Ecology of saprotrophic fungi. London.

DENNIS, R.W.G. (1981). British Ascomycetes. Vaduz.

JAHN, H. (1979). Pilze die an Holz wachsen. Herford.

JÜLICH, W. (1984). Die Nichtblätterpilze, Gallertpilze und Bauchpilze. *In* Gams, Kl. Kryptog.fl. 2b/1. Stuttgart.

KREISEL, H. (1961). Die Entwicklung der Mykozönosen an Fagusstubben auf Norddeutsche Kahlschlagen. *In* Fedde's Repert. sp. nov. Beih. 139: 227–232.

KREISEL, H. & MÜLLER, K.-H. (1987). Das Pleurotetum cornucopiae, eine Pilzgesellschaft an toten Ulmenstammen in Gefolge des Ulmensterbens. *In* Arch. Nat. schütz. Landsch. forsch. Berlin 27 (1): 17–15.

MOSER, M. (1983). Die Röhrlinge und Blätterpilze. *In* Gams, Kl. Kryptog.fl. 2b/1. Stuttgart.

MUHLE, H. & LEBLANCH, F. (1975). Bryophyte and lichen succession on decaying logs. I. *In* J. Hattori bot. Lab. 39: 1–33.

ORTON, P.D. (1986). Pluteaceae: *Pluteus & Volvariella. In* Br. Fung. Fl. 4.

RUNGE, A. (1980). Pilz-Assoziationen auf Holz in Mitteleuropa. *In* Z. Mykol. 46: 95–102.