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Dynamics of macrofungi in two moist heathlands in Drenthe, The Netherlands

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SUMMARY

In two plots, dominated by *Erica tetralix* and *Molinia caerulea*, respectively, carpophores of macrofungi were counted during 7 successive years with fortnightly intervals. The changes in the number of species, number of carpophores, carpophore productivity and productivity of dominant species are described and discussed. In addition, the periodicity of some species is treated. It appears that quantitative and qualitative changes in the two stands do not parallel each other. The changes are mainly interpreted as fluctuations, whereas in the *Molinia* stand also successional trends are demonstrated. Also between the investigated species important differences exist. No simple relationships could be found with the prevailing weather conditions.

Key-words: fluctuations, heathlands, macrofungi, periodicity, succession.

INTRODUCTION

This paper is based on mycocoenological research, carried out between 1974 and 1980. Mycocoenology comprises the quantitative and qualitative analysis of communities of larger fungi and the study of relations between these communities and environmental factors under field conditions. This discipline was introduced in The Netherlands by Barkman, who also made important contributions to the methodology (Barkman 1976, 1987).

This paper deals with the results in two plots, in moist heathlands dominated by *Erica tetralix* and *Molinia caerulea*, respectively. The absence of replicate plots does not enable statistical treatment of the data.

The aims of this study are to establish qualitative and quantitative changes in fruiting of macrofungi, and to relate the results to environmental conditions. Few investigations have been carried out in this field in proportion to studies on the dynamics of phanerogamic communities. Fluctuations in fruiting of macrofungi are often much stronger because of (i) the sensitivity of both primordia and mature carpophores to dessication and low temperatures (Ellenberg *et al.* 1986); (ii) the limited life-span of carpophores, for most species in the order of a few days or weeks (Richardson 1970).

Most mycocoenological studies last 2–4 years, which is too short to draw conclusions on the dynamics of the macrofungal flora (Winterhoff 1984). A few studies involve a longer series of observations. Holownia (1983) counted the carpophores of the saprophyte *Collybia peronata* in a *Pinus-Quercus* forest in Poland during 10 successive years. She

found enormous fluctuations; the highest and lowest number of carpophores differing by a factor of over 300. Krieglsteiner (1977) studied six plots of mixed *Abies* forests in southern parts of West Germany during 7 successive years, mainly containing ectomycorrhizal fungi. He found an increase in the number of species by 39 (18% of the total number) in the first year, over 127 (59%) after three years, 172 (79%) after 5 years, to 220 (100%) after 7 years. Runge (1963) studied three plots of Querco-Carpinetum in the western parts of West Germany during 5 successive years. In a single year she found at the least 7–20% of the total number of species and at the most 67–70%.

Besides fluctuations in presumably stable plant communities, a succession of macrofungal communities has been studied in developing forest stands, with special attention to mycorrhizal fungi. It was demonstrated that strong shifts in species composition of symbionts occur. A distinction was made between early and late stage fungi (Dighton & Mason 1985; Dighton *et al.* 1986). For saprotrophic fungi very few quantitative data on succession are available. However, Dighton *et al.* (1986) demonstrated strong changes in saprophyte communities in developing stands of *Pinus contorta* and *Picea sitchensis* in Scotland, for instance a strong increase in *Entoloma cetratum* and *Clitocybe* spp. in deeper litter of older stands.

Nomenclature of phanerogams is after Heukels-Van der Meijden (1983); of mosses after Margadant & During (1982); of fungi after Moser (1983) and Arnolds (1984); of plant communities after Westhoff & Den Held (1969).

MATERIALS AND METHODS

Description of the plots

Research was carried out in two plots each 500 m^2 and numbered 32 and 35 by Arnolds (1981), respectively.

Plot 32 was situated in the nature reserve Holtherzand, 1·5 km east of the village Holthe (municipality of Beilen), in a depression in a heathland area. The plant community was entirely dominated by the grass *Molinia caerulea*, growing in dense tussocks up to 0·6 m high. The coverage of *Molinia* was estimated at 80% in 1974, 75% in 1977 and 70% in 1980. *Erica tetralix* had a cover of $\pm 1\%$. All other herbs and dwarf shrubs covered less than 1%. The coverage of the moss layer decreased from 15% in 1974 to 7% in 1977 and 1% in 1980. Dominant species were *Pohlia nutans, Campylopus fragilis* and *Polytrichum commune*.

Plot 35 was situated in the nature reserve Terhorsterzand 3 km south of Beilen, ± 6 km from plot 32, also in a depression in an extensive heathland area. The community was dominated by the dwarf shrub *Erica tetralix*, forming a closed layer of 20–40 cm height. The coverage of *Erica* decreased considerably from 85% in 1974 to 65% in 1977 and 50% in 1980. *Calluna vulgaris* increased slightly from $\pm 1\%$ in 1974 to $\pm 3\%$ in 1980. *Scirpus cespitosus* ssp., *germanicus* was the only other herbaceous plant covering more than 1%, namely $\pm 4\%$ in all years. The cover of the moss layer varied from 10 to 18%. Dominant species were *Hypnum cupressiforme, Campylopus fragilis, Lophozia ventricosa* and *Gymnocolea inflata*.

Some chemical and physical characteristics of the soil in the two plots are listed in Table 1. More extensive descriptions of the plots and complete relevés of the plant communities were published previously (Arnolds 1981). Phytotaxonomically, the two plots belong to the Ericetum tetralicis typicum (Westhoff & Den Held 1969). However, in plot 32 the original *Erica* community was replaced by a *Molinia* dominated stand, due to lack

Table 1. Some characteristics of vegetation and soil in the studied plots (after Arnolds 1981)

Plot number	32	35
Dominant plant	*Molinia*	*Erica*
Soil type	hydropodzol	hydropodzol
Litter layer thickness (mm)	30–100	30–45
Top soil rich in humus (A1) (m)	0–0·1	0–0·06
Leached sand moderately poor in humus (A2) (m)	0·1–0·2	0·06–0·1
Glacial boulder clay (m)	0·6–1·2	>1·2
Groundwater in summer (m below surface) (m)	0·8–1·1	>1·2
Groundwater in winter (m below surface) (m)	0·4 – +0·05	0·4–0·02
pH H_2O 0–0·05 m	4·2 (4·1–4·4)	3·5 (3·3–3·7)
pH H_2O 0·05–0·1 m	4·1 (4·1–4·2)	4·2 (4·1–4·4)
Organic matter % 0–0·05 m	9·3 (8·9–9·8)	17·1 (14·3–20·6)
Organic matter % 0·05–0·1 m	7·2 (6·3–8·3)	1·6 (1·4–2·0)
C/N ratio 0–0·05 m	26·5 (25·3–28·8)	28·6 (25·5–30·7)
C/N ratio 0·05–0·1 m	31·4 (29·6–32·9)	24·5 (23·5–25·9)
P. Olsen 0–0·05 m (mg kg^{-1} soil)	±27	±32

of appropriate management (grazing, periodical burning, periodical sod cutting) and eutrophication by nitrogen from precipitation (Berendse & Aerts 1984; Berendse 1985). It is not known when *Molinia* had taken over dominance from *Erica*. Circumstantial evidence for this process is the presence of decaying *Erica* twigs in the litter layer. A square of 4 m^2 just outside the plot, where sods were cut in 1972, was dominated by *Erica* during the first years of this study.

Methods

In the plots, carpophores of all macrofungi (as defined by Arnolds 1981, in this case mainly Agaricales) were identified, counted and removed at fortnightly intervals throughout the main fruiting period, from September until November between 1974 and 1980. During the rest of the year inventories were made at more irregular intervals, depending on the weather conditions. Fruiting was not observed during the period January to April and in summer was dependent on periods with heavy rainfall. The productivity of each species was estimated by multiplication of the number of carpophores, with the average dry weight of representative mature carpophores (specific weight according to Arnolds (1981), Appendix A). This is considered to be a better method than determination of the real dry weight at each visit, since many carpophores are then in a very young or very old stage of development. For more exact measurement of productivity a much more intensive monitoring programme is necessary. The data on carpophore numbers and productivity are minimum values since carpophores of some species, e.g. *Mycena sanguinolenta* and *M. galopus*, only last a few days. Consequently, part of the carpophores will have been neglected. Richardson (1970) found in a pine plantation that even ±50% of such ephemeral carpophores will be missed when sampling is done once a fortnight. This cannot be checked in the studied plots due to the methods applied. Incidental observations suggest that 4 or 5 days after a high count of carpophores only a fraction of fresh carpophores is observed again, so that the proportion of overlooked carpophores is much lower than 50%.

Table 2. Species composition of the flora of macrofungi in two plots of 500 m^2 in an *Erica* stand and a *Molinia* stand. tDC = total density of carpophores per 1000 m^2 in the period 1974–1980. mDCv = maximum density of carpophores per 1000 m^2 during one visit in the period 1974–1980

	Erica		*Molinia*	
Taxon	tDC	mDCv	tDC	mDCv
Litter decomposing fungi:				
Clitocybe cf. *agrestis*	—	—	2	2
Clitocybe vibecina	668	126	322	150
Collybia dryophila	1 122	152	—	—
Collybia maculata	28	14	—	—
Cystoderma jasonis var. *jasonis*	8	4	148	34
Cystoderma jasonis var. *purpurascens*	—	—	2	2
Entoloma acidophilum	2	2	—	—
Entoloma cetratum	10	6	—	—
Entoloma conferendum	—	—	108	22
Entoloma fernandae	—	—	18	16
Entoloma helodes	—	—	178	58
Entoloma minutum	—	—	38	28
Entoloma turbidum	22	6	—	—
Entoloma xanthocaulon	—	—	102	66
Galerina atkinsoniana	12	6	134	32
Galerina calyptrata	22	8	18	14
Galerina cinctula	—	—	2	2
Galerina hypnorum	236	36	484	74
Galerina luteofulva	418	92	16	14
Galerina pumila	2	2	—	—
Gymnopilus fulgens	12	4	32	10
Hypholoma elongatipes	6	2	22	12
Hypholoma udum	66	18	—	—
Marasmius androsaceus	14 230	4 270	6	6
Mycena epipterygia	4 372	904	2	2

The removal of carpophores was done in order to prevent double counting. It was noticed in the field that carpophores of some important species, e.g. *Marasmius androsaceus, Mycena epipterygia, Collybia dryophila* and *Clitocybe vibecina,* may persist longer than 14 days. Carpophores of most species are too small to apply a successful method of marking. Removal of carpophores may introduce an unknown effect on subsequent fruiting, although Holownia (1983) demonstrated that removal of carpophores of the litter saprophyte *Collybia peronata* neither influenced their numbers, nor the periodicity.

Vegetation relevés according to the Braun-Blanquet approach were made in the years 1974, 1977 and 1980. Soil samples were taken in 1974 and analysed with standard procedures. For details, see Arnolds (1981).

RESULTS

Floristic composition of mycocoenoses

The taxa of macrofungi found in the two plots during this research, are listed in Table 2 together with two important quantitative parameters, namely the total number of carpophores in the period 1974–1980 (tDC) and the maximum number counted at one visit

Table 2. (*Continued*)

Taxon	*Erica*		*Molinia*	
	tDC	mDCv	tDC	mDCv
Litter decomposing fungi:				
Mycena filopes	12	8	—	—
Mycena galopus	19 964	4 382	542	108
Mycena megaspora	46	10	334	140
Mycena pelliculosa s. *Ricken*	2	2	—	—
Mycena quisquiliaris	—	—	338	240
Mycena sanguinolenta	25 636	5 576	4	2
Mycena vitrea	34	22	16	16
Omphaliaster asterospora	2	2	—	—
Psathyrella fulvescens	4	2	—	—
Rickenella fibula	—	—	2	2
Sphaerobolus stellatus	—	—	50	50
Tephrocybe ambusta	28	18	—	—
Tephrocybe tylicolor	98	46	48	14
Dung inhabiting fungi:				
Ascobolus crenulatus	—	—	60	60
Ascobolus immersus	—	—	300	300
Coprinus miser	34	32	—	—
Coprinus patouillardii	18	18	—	—
Coprinus velox	—	—	110	60
Fimaria porcina	—	—	60	60
Psilocybe coprophila	40	8	—	—
Fungi, parasitic on insects:				
Cordyceps militaris	10	6	—	—
Paecilomyces farinosus	72	34	2	2
Ectomycorrhizal fungi:				
Laccaria laccata	—	—	2	2
Paxillus involutus	—	—	2	2

(mDCv). The latter measure is regarded as the most appropriate criterion for a comparison between plots investigated with a different frequency, or during a different set of years (Barkman 1976; Arnolds 1981). It is an expression of the potential fruiting capacity. However, the mDCv is also dependent on the number of observation years. In the *Erica* stand the mDCv has increased during the years 1977–1980 with 15 litter decomposers (56%), in comparison with the period 1974–1976; in the *Molinia* stand there is an increase of seven species (27%) (cf. Arnolds 1981).

The plots have a moderate mycofloristic similarity: they have 15 litter decomposing taxa (± 55%) in common. The abundance of species often differs considerably and is for most common species, higher in the *Erica* stand.

Besides the litter decomposing fungi some dung inhabiting saprophytes and parasites on insects were found. Their occurrence has to be considered as accidental because the presence of the substrate in a plot is accidental and not bound to the plant community since these animals are able to migrate between different communities. Arnolds (1981) refers to these fungi as alien species. They are neglected in the following paragraphs.

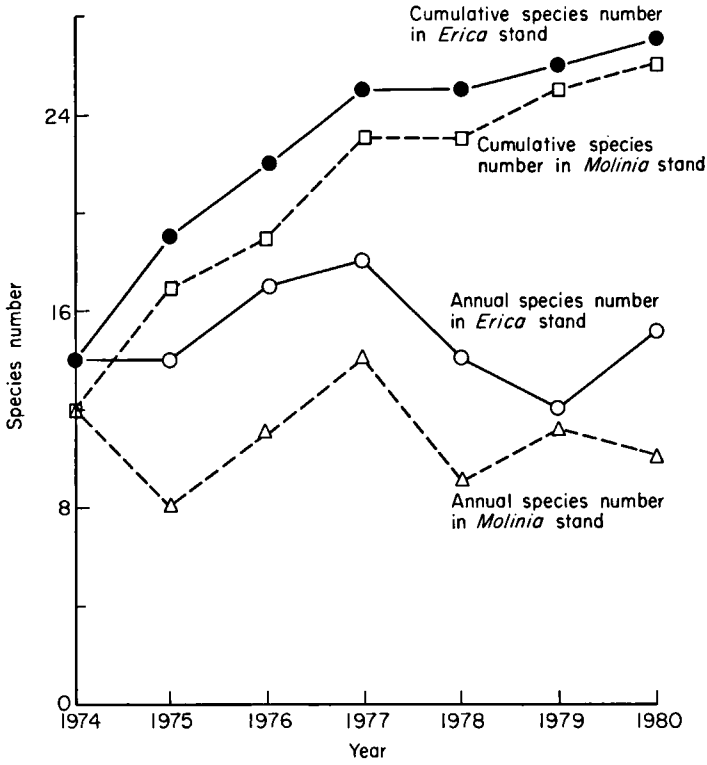

Fig. 1. Cumulative number of species and annual number of species of macrofungi fruiting in a stand of *Erica tetralix* and *Molinia caerulea* in the period 1974–1980.

An intermediate position takes the two species of *Tephrocybe*, growing on litter, but apparently mostly in places enriched by e.g. urine or dead animal bodies (Arnolds 1982). Here they are treated as proper fungi.

In the *Molinia* stand a few ectomycorrhizal species were found, probably associated with roots of *Betula* trees outside the plot. These fungi are also regarded as alien, although *Paxillus* and *Laccaria* may also be active in litter decomposition (Mikola 1956).

Changes in the number of species

The annual number of species in the *Erica* stand varied between 12 and 18 and in the *Molinia* stand between 8 and 14. In the two plots the cumulative number of species approximately doubled in the course of 7 years of observations (Fig. 1). The curves are gradually flattening and the increase from 1977 onwards is relatively small. If the cumulative number of species in 1980 is regarded as the real number of fungal species present, the annual number varies from 31 to 67% of the total number. This demonstrates the necessity of carrying out mycocoenological studies during several successive years, stressed by various authors (Barkman 1976, 1987; Winterhoff 1984; Thoen 1976). For an interpretation of these fluctuations, see p. 298.

Changes in the number of carpophores and productivity

The total number of carpophores in the two plots shows enormous fluctuations (Fig. 2). In the *Erica* stand it ranges from 1, 004/1000 m^2 in 1974 to 21, 492/1000 m^2 in 1978; in the

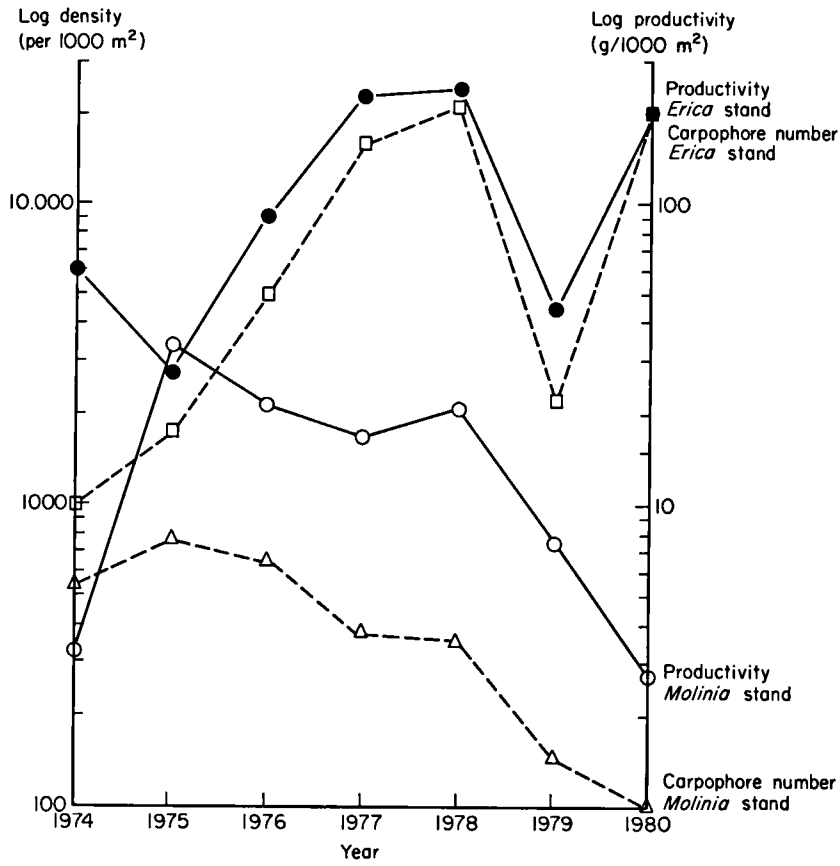

Fig. 2. Changes in number and productivity of macrofungi in a stand of *Erica tetralix* and of *Molinia caerulea* in the period 1974–1980.

Molinia stand from 98 in 1980 to 770 in 1975. The quotient between maximum and minimum number is a measure of the degree of change and is indicated here as the fluctuation factor (FF). It is 20 and 8 in *Erica* and *Molinia*, respectively.

The productivity in the *Erica* stand ranges from 28 g/1000 m^2 in 1975 to 248 g/1000 m^2 in 1978 (FF = 9); in the *Molinia* stand from 2·8 g in 1980 to 35 g in 1975 (FF = 12). Productivity is generally well correlated with carpophore abundance. The larger distance between the two curves in the *Molinia* stand indicates a larger proportion of species with relatively heavy carpophores in that community. The correlation between productivity and carpophore number is disturbed in the year 1974. In the *Erica* stand the productivity is then relatively high, due to the occurrence of *Collybia maculata* with a high specific weight (1286 mg), not found in later years. In the *Molinia* stand the productivity is relatively low, due to the abundance of *Mycena quisquiliaris* with very small and light carpophores (specific weight 0.05 mg), also not present in later years.

No correlation exists between productivity and abundance levels in the two plots. The highest productivity in the *Molinia* stand in 1975 even coincides with the lowest productivity in the *Erica* stand. The latter tends to increase during the period of study whereas the *Molinia* stand shows an opposite trend.

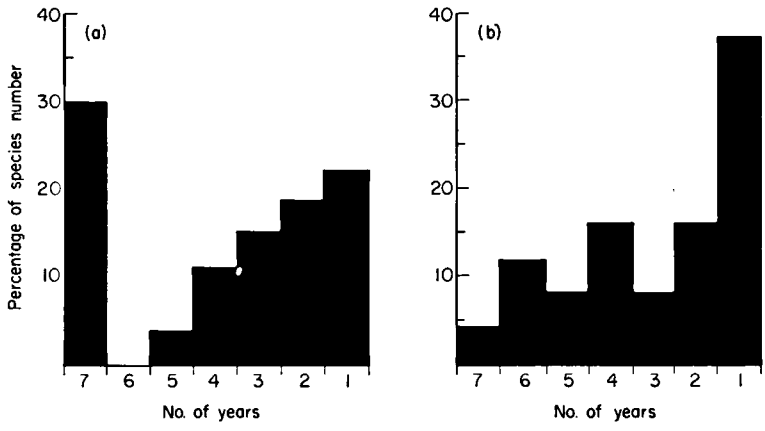

Fig. 3. Changes in species composition of macrofungi in a stand of *Erica tetralix* (a) and of *Molinia caerulea* (b) in the period 1974–1980, expressed as the percentage of the total species number fruiting in a certain number of years.

Table 3. Affinity between the macrofungal flora in different years in two plots of 500 m^2 in an *Erica* stand and a *Molinia* stand. The right-hand side of the matrix presents the number of common species in different pairs of years, the left-hand side the similarity according to the Sørensen index

	1974	1975	1976	1977	1978	1979	1980
A. *Erica* stand							
1974	—	9	11	12	9	9	9
1975	0·64	—	11	11	9	9	11
1976	0·71	0·71	—	13	12	10	10
1977	0·75	0·69	0·74	—	11	10	11
1978	0·67	0·67	0·80	0·71	—	9	10
1979	0·69	0·69	0·69	0·67	0·72	—	9
1980	0·62	0·76	0·62	0·67	0·71	0·67	—
B. *Molinia* stand							
1974	—	4	4	4	3	3	3
1975	0·40	—	7	7	6	4	5
1976	0·35	0·74	—	10	8	5	6
1977	0·31	0·63	0·80	—	9	6	8
1978	0·30	0·71	0·80	0·78	—	5	6
1979	0·26	0·42	0·45	0·48	0·50	—	7
1980	0·27	0·56	0·57	0·67	0·63	0·67	—

Qualitative changes in species composition

Qualitative changes are regarded here as changes in which carpophores of a species are present or absent in a certain year. The number of species present in a certain proportion of the observation period in the two plots is presented in Fig. 3.

Changes in the number of species (p. 296) and species composition may be ascribed to either succession or fluctuations. When succession prevails some steady trend in the change can be expected. This is reflected, for example, by a decreasing number of common species when the first years are compared with later years (Table 3). A more accurate method is the comparison of the similarity between the species composition in different

Table 4. The relation between the total density of carpophores of species of terrestrial macrofungi (tDC, on 1000 m^2) and the number of years in which the species was observed (nY) in two plots of 500 m^2 in an *Erica* stand and *Molinia* stand

Vegetation type	*Erica*				*Molinia*			
nY	1–2	3–4	5–6	7	1–2	3–4	5–6	7
Number of species	12	6	1	8	14	6	5	1
tDC:								
1–19	9	2	—	—	11	—	—	—
20–99	3	4	1	—	2	3	—	—
100–999	—	—	—	3	1	3	5	1
⩾1000	—	—	—	5	—	—	—	—

pairs of years (Table 3). The similarity was calculated using the Sørensen index 2C/A + B. C is the number of common species, A the total number of species in 1 year, B the total number of species in the other considered year. In the *Erica* stand the two measures show relatively little variation, the Sørensen index ranging from 0·62 to 0·80. No trend is visible, indicating a shift in species composition. In the *Molinia* stand the number of common species and the value of the Sørensen index is, on average, lower and subject to more variation; the latter value ranging from 0·26 to 0·80. There is a clear trend towards a lower similarity between more remote years. Consequently, besides fluctuations, some successional changes appear. The only clear successional trend among green plants in this plot is the strong decline of the moss layer (p. 292).

Fluctuations can be explained in two ways: they can be attributed to local invasions and extinctions of species in the plots or to fluctuations of fruiting of mycelia present in the soil throughout the period of research. At present no method is available to test these hypotheses since it is impossible to trace and identify mycelia of saprotrophic agarics in the soil. Probably both processes occur in reality. Most species are probably constantly present as mycelia, since mycelia of saprotrophic agarics are, in principle, perennial and since many striking examples are known of species fruiting on exactly the same locality with intervals of several years (Reid 1974). However, according to Meyer (Ellenberg *et al.* 1986), a large part of the fungal mycelium dies off each winter and is replaced by other micro-organisms. It seems that qualitative changes in the *Molinia* stand are much larger than in the *Erica* stand. In the *Molinia* stand only a single species (*Mycena galopus*) was present in all the years of observation (Fig. 3). No less than 14 species (54%) can be regarded as accidental, fruiting in 1 or 2 years only. In the *Erica* stand eight species (30%) are constant and 11 (41%) accidental.

A positive correlation exists between the abundance of carpophores and the number of years in which a species is fruiting (Table 4). It is to be expected that fruiting approaches zero in rare rather than in abundant species. However, in the *Erica* stand all species with a density of carpophores over 100 are found in all years, whereas in the *Molinia* stand only one species (10%) of that category is found in all years. This difference is partially explained by the successional trends in the *Molinia* stand, as indicated above.

Quantitative changes in species composition

Quantitative changes are changes in abundance of carpophores and/or productivity. The changes in numbers of carpophores in the six most important species in the *Erica* stand are

Table 5. Changes in abundance of six dominant species of macrofungi in a stand of *Erica tetralix* during the period 1974–1980, expressed as the total annual carpophore density per 1000 m^2

Species	1974	1975	1976	1977	1978	1979	1980	Total	Average
Mycena sanguinolenta	132	342	1 598	4 486	11 428	298	8 432	26 716	3 817
Mycena galopus	282	868	2 050	3 956	6 262	1 132	5 414	19 964	2 852
Marasmius androsaceus	118	302	562	5 818	2 206	146	5 078	14 230	2 033
Mycena epipterygia	212	132	294	1 048	1 108	540	1 038	4 372	625
Collybia dryophila	26	8	164	488	284	30	122	1 122	160
Clitocybe vibecina	122	46	134	226	28	58	54	641	92

presented in Table 5. The fluctuation factor is often very high, with a maximum of 87 in *Mycena sanguinolenta* and a minimum of 8 in *Clitocybe vibecina* and *Mycena epipterygia*. High and low abundance values of the studied species are often correlated: 1977, 1978 and 1980 were in general very favourable years. Apparently, fruiting in many agarics is promoted or suppressed by a similar complex of environmental factors. However, important exceptions occur. For example, *Clitocybe vibecina* had its lowest abundance in 1978, which for most other species was a peak year.

The relative importance of each species in various years is better expressed as its proportional contribution to the annual productivity (Fig. 4). It appears that this contribution is very variable, indicating that strong specific reactions to environmental conditions also exist.

The changes in the number of carpophores in the six most important species in the *Molinia* stand are presented in Table 6. Changes are relatively even larger than in the *Erica* stand. The fluctuation factor can only be calculated for *Mycena galopus* and amounts to 11 in that species. Because of the large qualitative fluctuations in the *Molinia* stand it is hardly useful to calculate the contribution of various species to the total annual productivity. The resulting curves should give a rather chaotic picture.

Periodicity

The periodicity is the rhythm of fruiting throughout the years. Fruiting of all agarics is restricted to some part of the year (Höfler, 1954), but varies from year to year within that potential period. Our data are too scanty to describe the course of periodicity during all 7 years and to correlate these data with environmental conditions. However, it is possible and useful to present graphs of the average (or specific) periodicity, calculated by adding the numbers of carpophores found in a certain month during all the years of observation and dividing the resulting figure by the total number of observed carpophores (Fig. 5) (Arnolds 1982).

Maximum fruiting in the *Erica* stand ranges from summer (July and August) in *Mycena sanguinolenta* and *Marasmius androsaceus* until late autumn (November) in *Clitocybe vibecina*. The numbers of carpophores in the *Molinia* stand are too low to present similar graphs. However, the periodicity of *Mycena galopus* and *Clitocybe vibecina* shows a comparable temporal pattern.

CONCLUSIONS AND DISCUSSION

The composition of the macrofungal flora and the carpophore productivity in the *Erica* and the *Molinia* stands are very different, although the soil and climatological conditions

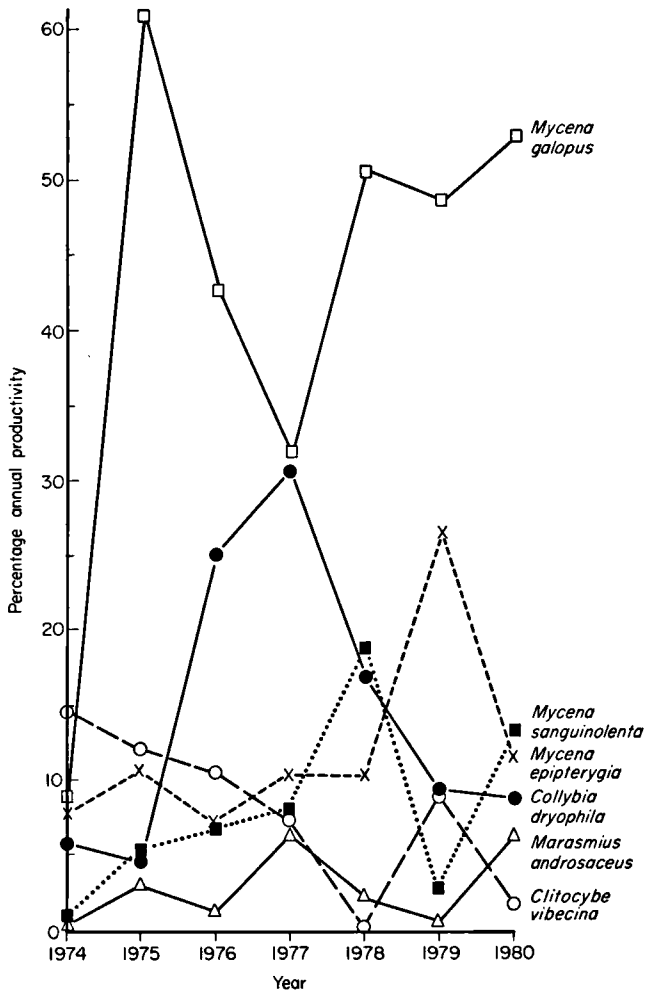

Fig. 4. Changes in carpophore productivity of six dominant species of macrofungi in a stand of *Erica tetralix* in the period 1974–1980, expressed as the percentage of the total carpophore productivity in each year.

Table 6. Changes in the abundance of six dominant species of macrofungi in a stand of *Molinia caerulea* during the period 1974–1980, expressed as the total annual carpophore density per 1000 m^2

Species	1974	1975	1976	1977	1978	1979	1980	Total	Average
Mycena galopus	64	222	122	20	62	26	36	1 282	183
Mycena megaspora	—	246	32	18	34	2	2	334	48
Clitocybe vibecina	—	—	—	24	230	60	8	322	46
Entoloma helodes	—	84	56	30	6	2	—	178	25
Cystoderma jasonis	6	—	82	58	2	—	—	148	21
Entoloma conferendum	10	30	44	10	8	—	6	108	15

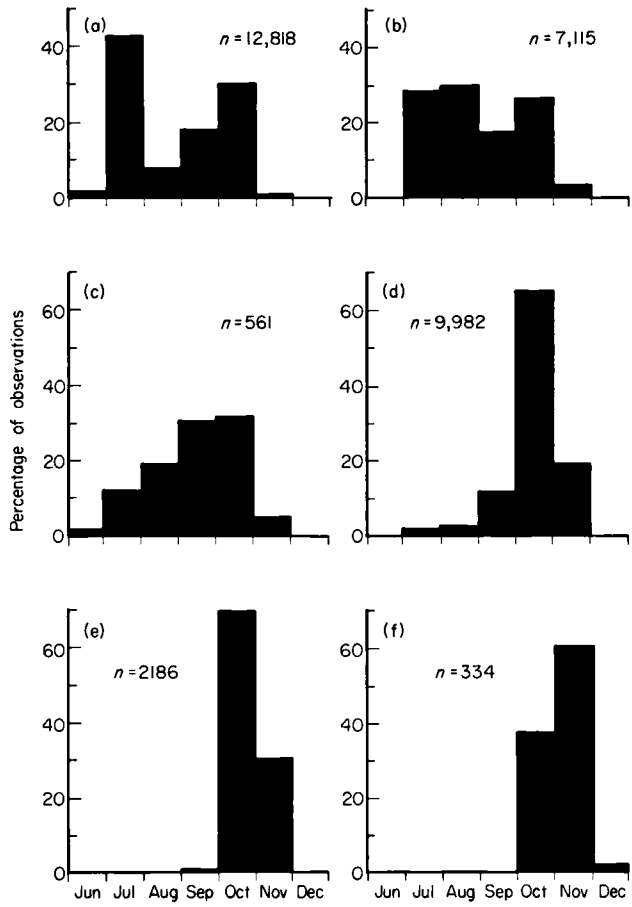

Fig. 5. Average seasonal periodicity of six dominant species of macrofungi in a stand of *Erica tetralix* in the period 1974–1980, expressed as the percentage of the total number of carpophores found in a certain month during the period of observations: (a) *Mycena sanguinolenta*, (b) *Marasmius androsaceus*, (c) *Collybia dryophila*, (d) *Mycena galopus*, (e) *Mycena epipterygia*, (f) *Clitocybe vibecina*.

Table 7. Monthly amounts of precipitation (mm) from April until December, at Wijster, in the period 1974–1980

Year	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1974	12	48	77	117	91	129	115	92	138
1975	74	66	30	94	33	99	30	79	49
1976	7	76	33	70	30	58	32	81	76
1977	77	56	57	74	131	54	57	154	67
1978	17	21	83	53	73	76	33	47	106
1979	87	86	56	48	59	57	45	73	146
1980	49	46	112	178	63	50	99	96	65

are rather similar (Table 1). The differences are apparently caused in the first place by the dominant plant species. The high productivity in the *Erica* stand indicates a dominant role of agarics in the litter decomposition. The low productivity in the *Molinia* stand might indicate a lower decomposition rate of litter, but Rouwenhorst *et al.* (1985) have found, in field experiments, a faster decomposition of *Molinia* litter instead. Therefore, the process may be dominated by other organisms. Small ascomycetes of the *Helotiales* were observed in large quantities and may be important in this respect. They were not involved in the mycocoenological studies. In the *Erica* stand hardly any ascomycete was seen.

A striking difference between the stands is also that qualitative changes in *Molinia* are much larger than those in *Erica* (Fig. 3). This may be caused by the much lower average abundance of the dominant species in *Molinia;* increasing the chance of absence of carpophores in 1 year or another, and by the successional trends in this mycocoenosis (p. 298).

In the two plots opposite trends in carpophore productivity are found (Fig. 2). In the *Molinia* stand the productivity had a tendency to decrease, whereas in the *Erica* stand the productivity tended to increase during the observation period. The increase in the latter stand may be caused by ageing and degradation of the *Erica* plants, increasing the amount of available litter.

Most mycocoenological studies last only 2–4 years (Winterhoff 1984). From the present study it appears that such a period may be adequate for a representative (although incomplete) knowledge on the species composition, at least when the intensity of sampling (once a fortnight) is comparable. For insight into quantitative changes a longer period is necessary.

Qualitative and quantitative fluctuations are usually mainly attributed to weather conditions in the period of potential carpophore formation (e.g. Wilkins & Patrick 1940; Thoen 1976). Precipitation is considered the most important factor, especially in summer and early autumn, when soils dry out easily. Wet periods are often succeeded by strong fruiting (e.g. Thoen 1975; Kriegsteiner 1977). Temperature is also important, since growth of the mycelium of most saprotrophic agarics takes places between ± 5°C and 30°C (Bohus 1957).

Figures on the monthly precipitation at Wijster from April until December during the period of study are given in Table 7. According to my experience, monthly precipitation sums are a good indication for general moisture conditions in grass and heathlands (Arnolds 1981), although the distribution and intensity of rain within a month has some influence as well. No correlation with the carpophore productivity can be found. For instance, 1974 and 1977 are years with high summer precipitation. However, in both plots productivity was low in 1974 and high in 1977 (Fig. 2). The same applies to early fruiting species only, such as *Mycena sanguinolenta* and *Marasmius androsaceus* (Table 5). Precipitation in September and October of 1977 was rather low, but productivity was high. Productivity in 1979 was much lower, although the amount of precipitation was hardly lower.

Between the two plots large differences exist as well: in 1975 the productivity in the *Erica* stand was the lowest for 7 years, but in the *Molinia* stand it was highest. Similar differences occur between species. If all species would have a similar response to weather conditions the curves of percentage productivity in Fig. 4 should be approximately horizontal lines on different levels. However, the contribution to total productivity varies strongly from year to year.

In the studied plots a correlation exists between the periodicity and the degree of fluctuation; early fruiting species, such as *Mycena sanguinolenta,* have a higher

fluctuation rate than late species, e.g. *Clitocybe vibecina*. Apparently, weather conditions (especially moisture conditions) are more often favourable in late autumn than in summer, although low temperatures can be a limiting factor in late autumn.

Mycelia need a period of growth with favourable temperatures and moisture in spring and summer before fruiting is possible (Hueck 1953; Meyer in Ellenberg *et al.* 1986). Also with these factors no correlation was found. Various authors (e.g. Becker 1956; Thoen 1971; Wilkins & Patrick 1940) claim that a warm, dry summer is favourable for fruiting in the next autumn. In both 1975 and 1976, summer was dry and warm, but the effect on fruiting in the two plots was very different (Figs 1, 2). In general, 1976 was a much more productive year in grassland communities than 1975, although autumn precipitation was much higher in the latter year (Arnolds 1975).

According to Guminska (1962) and Thoen (1971), fruiting is also influenced by the process in the preceding year, a 'bad' year being very frequently succeeded by a 'good' year. Also this rule is not true in the investigated plots: in the *Erica* stand 1974 and 1975 are successive low-productive years, 1977 and 1978 successive high-productive years.

Apparently, the actual and preceding weather conditions cannot give a simple, satisfactory explanation for the dynamics of fruiting in the studied plots. Fruiting seems to be influenced by other factors as well, possibly by interactions with other micro-organisms and animals and by litter productivity by plants.

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