Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot

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Fungal fruit bodies were surveyed on a plot area of 1500 m² from 1975–99 (excluding 1980–83) in the fungal reserve La Chaneaz in western Switzerland. Fruit bodies were identified and counted on a weekly basis. Species richness and abundances varied strongly between years. More than 400 species were encountered. Many species were transient; particularly rich years showed species occurring for only one year. This indicates that the number of species will substantially increase if the survey is continued. Within years, the species richness, abundances and periods of fruiting were tightly correlated. The abundance data of species within a year seemed symmetrically distributed over their fruiting period. The relation between species richness and abundances within years was studied by fitting species-abundance plots, known from numerical ecology. The surface area under the curves was taken as a parameter for ecological/fungal diversity. Productivity was correlated with the precipitation from June until October. The time of fruit body appearance was correlated with the temperatures in July and August. As groups, mycorrhizal and saprotrophic species behaved similarly over the years. The productivity of species was compared with their distribution in The Netherlands indicating a correlation between the level of local abundance and the geographic range of species.

INTRODUCTION

Data sets on fungal fruit bodies are special, they only partially represent the fungi living in the substrate. Several reasons exist to study fruit bodies rather than mycelia. Fruit bodies are immediately visible and attract much more attention than mycelia. People are attracted by the sudden appaerance of fruit bodies and their ephemeral beauty. In many countries edible species are picked for food or as a delicacy. Therefore fruit bodies, more than mycelia in general, are important in the context of nature conservation and management. Of course, fruit bodies have specific functional role(s): (1) in the dissemination of spores for the establishment of new mycelia, or perhaps for the genetic adaptation of existing ones or even for the prevention of gene flow (Fries 1981, Gregory 1984); (2) on micro- and macrofauna due to their food value (Avila, Johanson & Bergstrom 1999, North, Trappe & Franklin 1997); and (3) maybe on soil mineralisation if developmentally regulated extracellular enzyme systems and differential resource utilisation as in *Agaricus bisporus* and *Lentinula edodes* (Turner *et al*. 1975, Wood & Goodenough 1977, Ohga *et al*. 2000) are common.

Elaborate and long-term data sets are required to draw any conclusions on the occurrence and the behaviour of fruit bodies, as affected by environmental conditions, such as temperature and precipitation. Important are the number of years of the survey, the protocols for the area to be studied, and the time frequency of recording. Many surveys have already been done. Vogt *et al*. (1992) give an overview of sampling designs and methods used. In some studies transects were used (Wilkins, Ellis & Harley 1937, Ohenoja 1984), in others permanent plots, with or without subplots. Sampling frequency varied from one observation per year (Parker-Rhodes 1951) to a weekly interval (Vogt, Edmonds & Grier, 1981). Egli, Ayer & Chatelain (1997) quantified the loss of recorded species caused by a reduction of the sampling frequency from weekly to monthly intervals. For some purposes 1 yr of sampling is enough, but most questions need longer periods of investigation (Vogt *et al*. 1992). Many studies were focussed on the coherence of the fungal assemblage, the mycocoenosis, and the vegetation. Studies examining the influence of environmental factors on fruit body production have been conducted since the 1930s (Vogt *et al*. 1992). Rainfall and temperature are generally recognized as important factors, but quantifications have hardly been made. The present data set is suited for studying these questions because it is based on a long-term study with a strict and steady protocol. Data were collected in permanent (sub)

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plots and a monitoring frequency of 1 week. The data set is the result of a broader myco-ecological study in the fungus reserve La Chaneaz in western Switzerland. Topics of the study are the effects of mushroom picking (Egli, Ayer & Chatelain 1990), forest management (Egli & Ayer 1997) and microclimate (Kälin & Ayer 1983, Ayer 1990).

The present analysis describes the coherent structure of the data set, and considers species richness, abundance, and phenology. Data on individual species are hardly given but species were grouped in two ways, according to their mycorrhizal versus saprotrophic status and according to their yearly frequency. The relationships with meteorological data are described. Further, an example is given of a comparison with quite another data set: the productivity of species was compared with distribution data of the same species in The Netherlands (Arnolds, Dam & Dam-Elings 1995) to test an ecological 'law' that the local abundance of species is related to the size of their geographic range (Johnson 1998).

MATERIAL AND METHODS

Survey

Mycological data were collected in the 75 ha fungus reserve La Chaneaz in western Switzerland, established in 1975. It is located 600 m above sea level in a typical mixed forest, with deciduous and coniferous tree species, such as *Fagus sylvatica*, *Quercus petraea*, *Picea abies*, *Pseudotsuga menziesii*, *Pinus silvestris*, *P. strobus*, and *Larix decidua*. The plant community (*Galio odorati-Fagetum*) represents a dominating forest type in the Swiss Mittelland and an important and highly frequented habitat for picking mushrooms, especially in the recreational areas around urban regions.

The data set is based on 5 observation plots each of 300 m^2, distributed within the reserve, and surrounded by 2 m high fences to avoid all inconvenient influences by mushroom pickers and large forest animals. From May to November (weeks 21 to 50) all the epigeous fruiting bodies of macromycetes were identified and counted at weekly intervals. To avoid multiple counting of the same fruit bodies, fruit bodies were marked with methylene blue at their first encounter. Voucher specimens of all the fungal species found within this study area are deposited in the mycoherbarium of the Swiss Federal Research Institute WSL.

The survey spanned 25 years, from 1975–99. In 1980–83, as the consequence of a rationalization effort that we now regret, only the edible species were recorded. Thus only 21 years are considered in the detailed analysis.

Climatic data were registered by the automatic surface network of the SMI–MeteoSwiss (Payerne station), in 5 km distance of the fungus reserve. Temperature data represent monthly mean values, precipitation data are monthly sums.

Mathematical

Structure of the data set

The data set was structured into records, entries, and fruit body numbers. A record represents a species in a year; it holds data entries for the weeks with fruiting, and the entries hold the fruit body numbers (Table 1).

Log-transformation

Log-transformation of biological variables often results in better correlations with other variables (Burton 1998). Also, in statistical analysis, normal distributions and homogeneous variance of variables are often required which perhaps can be met by log-transformation. PivotTables were made containing a column with all species and columns for the years of the study holding either fruit body numbers or week (entry) numbers. Averages, variances and medians were calculated for species. Average fruit body numbers were higher than medians. Re-transformed averages of log fruit body numbers were quite similar to the medians. For the period of fruiting (entries with week numbers) the trend was similar but the effect of log transformation was small. In both cases variances of log transformed data were more homogeneous than of non transformed data. When fruit body numbers within records were studied (phenology), the untransformed numbers in the entries were used.

Yearly frequency

Yearly frequency of species is a parameter that it is easy to understand and relatively easy to determine in a data set. The whole range of species was grouped according to the 21 frequency classes. The disadvantages of this parameter are that: (1) its unit, year, is specific for the data set being studied; and (2) it provides for a short discontinous range of numbers between a discrete minimum of 1 and a discrete maximum that equals the total number of years of the survey.

Diversity, productivity

Species-abundance relations can be described in several ways (Magurran 1988). Rather than using or elaborating existing biological models (Preston 1948, Rosenzweig 1995, Harte, Kinzig & Green 1999) we, pragmatically, tried to apply a

Table 1. Structure of the data set; illustration of records, entries and numbers. Two records of *Russula ochroleuca* in a poor (1989) and in a rich (1992) year.

Year	Week number																													Fruit bodies	Entries	Weighted appearance, week number
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50			
1989																					1										1	1	41.0
1992											1	2					3			2	15	28	22	78	68	20	12		6		257	12	43.9

Table 2. Diversity, abundance and phenology data over the years of the study.

	Species richness			Abundance			Phenology		Meteorology	
1	2A	2B	2C	3A	3B	3C	4A	4B	5A	5B
Year	Number of species (records)	Number of mycorrhizal species	Number of saprotrophic species	Number of fruit bodies	Mycorrhizal fruit bodies	Saprotrophic fruit bodies	Number of entries (weeks)	Week number with most fruit bodies	Temperature month 8 °C	Precipitation months 6–10, mm
75	81	54	25	1891	1682	194	221	38	18.0	401.3
76	40	26	13	266	161	98	75	38	16.2	326.4
77	88	61	24	1954	1649	299	251	34	16.1	446.2
78	72	47	22	1253	846	404	238	35	15.7	328.0
79	119	76	37	3802	2478	951	392	37	16.1	319.6
84	38	31	7	668	341	327	125	40	17.1	462.3
85	40	32	8	633	327	306	120	38	17.2	285.5
86	68	46	19	1914	1313	546	245	39	17.4	360.5
87	65	41	22	2251	1109	1106	268	43	17.8	636.3
88	71	48	23	2875	2050	825	273	40	18.4	471.9
89	18	10	8	182	58	124	45	41	18.2	244.8
90	95	64	27	4012	2769	1031	336	40	19.0	468.7
91	55	38	17	830	322	508	145	44	19.7	393.4
92	194	125	60	6006	3861	2080	603	41	20.6	472.4
93	179	119	51	8467	5559	2783	583	40	18.3	609.4
94	162	107	47	8047	4624	3353	472	39	19.6	515.9
95	141	96	41	5972	3362	2529	371	39	18.0	396.1
96	142	88	50	4974	2231	2686	352	41	16.6	412.8
97	157	101	50	5879	2609	2965	459	42	19.3	458.2
98	137	84	50	4507	2079	2397	294	41	18.8	422.1
99	157	98	56	4839	2220	2604	523	43	18.4	544.3

simple statistical model. For all years 5 abundance classes (log values, from minimum to maximum abundances) were applied. The corresponding numbers of species were counted and expressed as log's. Linear regression of log-transformed species numbers (y) on log-abundance classes (x; $y = A + B^*x$) resulted in adequate fits. Fitted A and B values were used to calculate the surface area under the fitted curve. This value was taken for both 'diversity' as well as 'productivity'. The frequently used Shannon index of diversity (Magurran 1988) was calculated for comparison.

With mycorrhizal species as a (sub)assemblage, the same calculations could be made. The saprotrophic assemblage consisted of too few species to obtain satisfactory species-abundance curves; some abundance classes did not contain any species and in several plots the points were scattered irregularly. A productivity parameter was required for saprotrophs for an analysis of the trend seen in Table 2 columns 2B, 2C, 3B and 3C that the number of fruit bodies of saprotrophs, not that of species, increased in time. An estimate was improvised. After preparing the tables required for any species-abundance curve, the sums of the abundance columns were taken, rather than the area under the (incomplete) species-abundance curves. In addition the average abundance was calculated of all saprotrophic species, of the two species that were present in all years, of the 7 most abundant species (7 being the lowest number of species present in 1984) and the maximum abundance of any species (these parameters were progressively better correlated with year number).

Distribution of fruit body numbers (*entries*) *in records, phenology*

For a straight on analysis of as many records as possible, the numbers in the records were divided into three parts, the number before the maximum (front), the maximum number, and the number after the maximum (tail). Only records with fruit bodies in 2 or more weeks and with only one maximum were suited for this analysis (1075 out of 2119). Alternatively, the entries and their fruit body numbers were taken and the 'weighted week number of appearance' was calculated of all 2119 records: the sum of the products of week numbers and fruit body numbers divided by the total number of fruit bodies. For the 1075 records, the weighted appearance was almost equal to the week number in which the maximum number of fruit bodies occurred.

RESULTS

During 21 years, numbers of fruit bodies per mushroom species were counted on a weekly basis. A total of 71 222 fruit bodies belonging to 408 species were seen on the observed area of totally 1500 m^2. Only 8 species were found in all years, 6 being mycorrhizal: *Lactarius blennius*, *Russula cyanoxantha*, *R. fellea*, *R. fageticola*, *R. ochroleuca*, and *Xerocomus badius*; and 2 being saprotrophic: *Collybia butyracea* var. *asema* and *C. dryophila*. The average number of fruit bodies per species and year (per record) equals $71222/2119 = 33.6$. Few records with high numbers contribute strongly to this average. Not surprisingly, the median value is low, it equals 6. If 10-logarithms of the numbers in the records are taken, the average equals 0.860, and, re-transformed it equals $10^{0.860} = 7.3$, quite similar to the median. Log transformation was quite often applied, as described above.

Species richness, abundances and periods of fruiting vary over the years (Table 2 columns 2A, 3A and 4A, respectively) and seem correlated. This gives the impression that merely one phenomenon is encountered: productivity.

Table 3. Yearly frequency of species.

1	2	3	4	5	6
Frequency group	Number of species	Number of mycorrhizal species	Number of saprotrophic species	Number of species with most fruit bodies before week 36	Time of weighted appearance, averaged over species, week number
1	150	102	42	28	38.8
2	53	34	13	2	40.5
3	32	15	17	7	38.6
4	18	14	4	0	39.2
5	23	15	7	6	38.0
6	13	8	5	0	38.9
7	12	8	3	1	38.8
8	20	12	8	2	39.2
9	14	9	3	2	38.8
10	8	5	2	2	37.6
11	7	5	2	1	39.0
12	4	1	2	0	38.5
13	6	2	4	1	36.4
14	7	4	3	1	37.4
15	1	1	0	0	42.3
16	10	7	3	0	39.4
17	4	4	0	0	39.7
18	6	4	2	2	37.2
19	8	7	1	0	38.0
20	4	2	2	0	39.2
21	8	6	2	1	38.3

Species richness and yearly frequency

The numbers of species in the years are given in Table 2 column 2A. In 1989 only 18 species were found and in 1992 the number was as high as 194. The richnesses of the two major ecological groups, mycorrhizal and saprotrophic species, is given in columns 2B and 2C. The number of mycorrhizal species is about twice as high as the number of saprotrophs. 'Species-time' curves show the total number of species in the course of the years (Rosenzweig 1995, Watling 1995, Tofts & Orton 1998). We prefer to give the number of species appearing for the first time in the observation period (Table 4 column 2A). One would expect that this number levels off in time. This is not the case. The number of 'first' species is first of all correlated with 'productivity' of years, less so with year number.

The number of years that species fruited were counted and species were grouped according to their yearly frequency. The number of species in each frequency group is given in Table 3 column 2. The number of species with a frequency of 1 is high and holds the majority of species identified to genus only (a total of 64 species, 48 belonging to *Cortinarius*). As groups, the mycorrhizal and saprotrophic species showed similar patterns (Table 3 columns 3 and 4). The group of species often showing most of their fruit bodies in early summer (Table 3 column 5; phenology section) also showed this common pattern. The log number of species can be plotted against frequency, as done for a grassland/disturbance study of Glenn & Collins (*in* Collins & Benning 1996). Such a plot gradually falls to a level of 0.7 (of $10^{0.7} = 5$ species) for frequencies above 10.

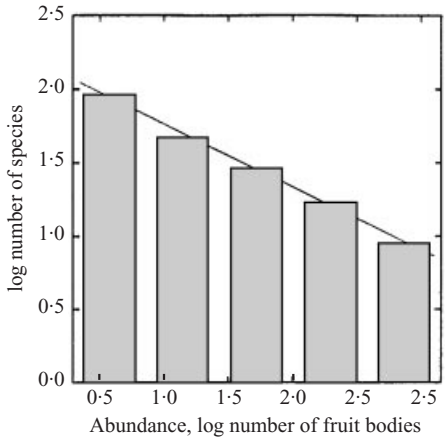

Fig. 1. Species-abundance curve of the rich year 1992. Five abundance classes were taken, the highest class until the abundance of the most abundant species (Table 4 column 3B). The surface area under the curve (Table 4 column 3E) is taken as a parameter for diversity and productivity.

Abundance, diversity and productivity

The easy to understand productivity parameter 'number of fruit bodies per species per year' is ambiguous because the species composition varies over the years. Moreover, each year shows many species with low numbers. These low numbers tend to obscure the differences in productivity between years. This matter has been solved elegantly in biodiversity research where species richness and species abundances are both taken into account in species-abundance curves (Magurran 1988). Typical species-abundance curves

Table 4. Detailed parameters over the years of the study; extension of Table 2.

	Species richness		Diversity/productivity						Phenology		
1	2A	2B	3A	3B	3C	3D	3E	3F	4A	4B	4C
Year	Number of species appearing for first year	Number of species occurring only in 1 year	Log number of species with a single fruit body	Log number of maximum abundance of any species	A value of fitted species-abundance curve	B value of fitted species-abundance curve	Area under fitted species-abundance curve	Shannon index of diversity	Number of species with fruit bodies before week 36	Weighted week number of appearance	Difference in appearance (weeks): saprotrophic–mycorrhizal species
75	81	1	1.204	2.646	1.846	−0.484	3.19	3.095	18	38.1	0.3
76	13	3	1.301	1.643	1.232	−0.481	1.37	2.857	11	37.9	−1.5
77	29	7	1.255	2.685	1.909	−0.505	3.31	3.129	72	34.2	1.3
78	8	0	1.255	2.212	1.623	−0.405	2.60	3.318	49	35.5	−2.0
79	29	7	1.301	2.725	1.916	−0.389	3.78	3.513	33	38.5	0.2
84	2	0	0.954	2.079	1.226	−0.317	1.86	2.686	13	39.0	−2.9
85	1	0	0.954	2.292	1.46	−0.480	2.09	2.631	20	36.6	−2.7
86	3	1	1.146	2.489	1.516	−0.289	2.88	3.164	35	36.8	−1.0
87	5	2	1.041	2.558	1.461	−0.252	2.91	3.116	29	38.8	1.5
88	7	3	1.041	2.698	1.586	−0.308	3.16	3.042	30	38.4	0.8
89	1	1	0.602	1.826	0.954	−0.476	0.95	2.133	4	40.4	2.8
90	18	2	1.255	2.805	1.708	−0.289	3.65	3.348	25	39.1	0.6
91	4	0	1.000	2.356	1.61	−0.480	2.46	2.923	18	39.8	2.9
92	74	33	1.633	2.870	2.192	−0.429	4.52	3.800	55	40.1	0.2
93	33	20	1.602	3.162	2.282	−0.471	4.86	3.516	55	37.7	0.4
94	16	9	1.255	3.046	2.138	−0.420	4.56	3.441	30	39.6	0.7
95	15	10	1.398	2.991	2.058	−0.408	4.33	3.444	18	39.1	−1.2
96	17	8	1.491	2.876	2.093	−0.450	4.16	3.322	40	39.0	0.5
97	22	15	1.477	3.173	2.311	−0.540	4.61	3.307	71	38.9	0.8
98	11	9	1.301	2.880	2.037	−0.418	4.13	3.563	15	40.9	0.0
99	19	19	1.301	2.870	2.144	−0.453	4.29	3.730	76	38.2	1.8

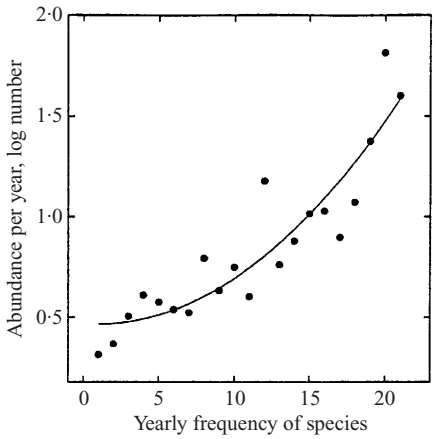

Fig. 2. Relation between the number of fruit bodies (averaged over years) and yearly frequency of species (the number of species involved is given in Table 3 column 2).

were obtained; Fig. 1 shows the curve of a rich year. Columns 3A and 3B in Table 4 give an impression of the left and right side borders of the curves: column 3A contains the number of species with only one fruit body (being the smallest abundance) and column 3B contains the number of fruit bodies of the most abundant species (in all years this value belonged to a single species only). Fitted values of the species-abundance curves are given in Table 4 columns 3C and 3D. The surface area under the fitted curve (column 3E) was taken to characterize the curve with a single parameter only. The Shannon index of diversity is given in column 3F.

The abundances vary strongly among species. If species are grouped to yearly frequency and the abundances averaged accordingly, a clear relationship is seen between abundance and frequency (Fig. 2). Thus yearly frequency can be used to express the productivity of species.

The number of fruit bodies of mycorrhizal species and of saprotrophs are given in Table 2 columns 3B and 3C. The abundance per mycorrhizal species was a bit lower than per saprotrophic species (not shown). In the lasts years of the survey the total numbers of fruit bodies of saprotrophs were higher than those of mycorrhizal species (see Time course below).

Phenology

Fruiting bodies were monitored between week numbers 21 and 50, the ends of months 5 and 12. The start of fruiting varied strongly over the years and over species. The longest period of fruiting of any species in any year showed *Russula cyanoxantha* in 1992. It fruited from week numbers 26 to 45 (20 weeks) but it showed no fruiting in week numbers 36 and 37, thus the number of weeks with fruiting was 18 (being the number of entries in that record). The overall information on the duration of fruiting in the years (total number of entries) is given in Table 2 column 4A. On average, week number 40 at the end of month 9, showed the highest numbers of fruit bodies.

The number of species fruiting in each week of the years were counted (data not shown). Some years had a 'pre-

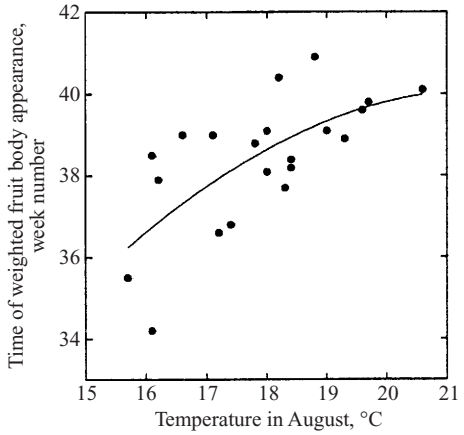

Fig. 3. Relation between the temperature in August and the weighted time of appearance of fruit bodies (Table 4 column 4B).

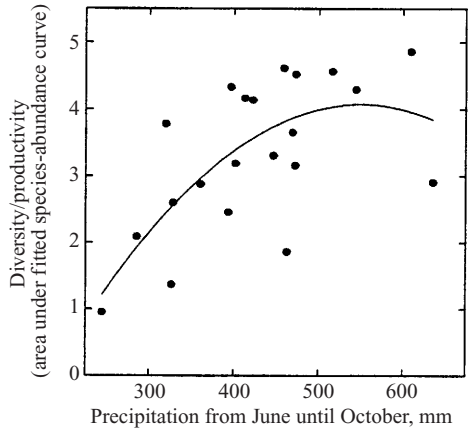

Fig. 4. Relation between the precipitation from June until October and the parameter for diversity and productivity (the area under the fitted species-abundance curve, Table 4 column 3E).

summer' peak, lasting maximally until week 35. Then a dip occurred and the 'autumn' peak appeared. Most years did not show a typical pre-summer peak. The number of species (partly) fruiting up and until week 35 (Table 4 column 4A) was determined. Year 1977 was exceptional; 80% of all species appeared in pre-summer and the distribution in the autumn was irregular. Overall, the pre-summer peak is not very important: (1) the total number of fruit bodies until week 35 is 10886, being only 15% of the total; and (2) the species in column 4A may well have most of their numbers in the autumn.

A 'weighted' week number of fruit body appearance is presented in Table 4 column 4B. For many records, the weighted appearance is very much in between the first and last appearance and similar to the appearance of the highest number of fruit bodies in any week. On average the numbers within a record for front, maximum and tail were 12, 33 and 17, respectively. The three parameters were positively correlated over the records. Distributions within records seem quite regular. It is characterized by the total number of fruit bodies, a maximum number in the middle of the distribution and a time span for fruiting. Two of the three characteristics largely determine the distribution. Some abundant and frequent species showed almost 'normal' distributions. Exceptions were *Mycena pura* and *Russula cyanoxantha*, that showed two peaks in several years. It was impossible to characterize all species; infrequent and unproductive species do not show enough data for entries and fruit bodies.

The number of species was counted that showed most of their fruit bodies in pre-summer in most of the years (Table 3 column 5). Early fruiting species occurred in all frequency groups; an example is *Collybia dryophila*, one of the 8 species that was present in all 21 years. The week numbers with most species fruiting, the week numbers with most fruit bodies and the weighted appearances of individual species were compared. The difference in appearance of mycorrhizal and saprotrophic species is given in Table 4 column 4C. Negative values indicate that mycorrhizal species fruited earlier than saprotrophic species. Over the years many species showed positive correlations with the parameters of appearance in general. This indicates that species showed quite the same sequence of appearance over the years.

Relations with meteorological data

Monthly temperatures show a cyclic patterns over the year. A Gaussian curve fits well to the data, its peak of 19.6 °C lies at month 7.1 (week 27). This is 12 weeks before the peak of fruiting (Table 2 column 4B, Table 4 column 4B). Estimating that the development of fruit bodies takes about 2 weeks, the fruiting peak may be the respons to the temperature in week 37, when it drops below about 14 °C. This temperature level is crossed the other way in spring in week 21, when the first fruit bodies (erratically) appear.

The 'weighted' appearance of fruit bodies (Table 4 column 4B) correlates with the temperatures (Table 2 column 5A) in months 7 and in month 8 (Fig. 3). An increase of 1 ° coincides with a delay of fruiting of almost 1 week. *Cantharellus cibarius* and *Lactarius volemus* were exceptions, they were negatively correlated with the temperatures. Not a delay in fruiting, but a full stop was found at high temperatures. On average this resulted in an early appearance time. The 'negative' effect of temperature on fruiting is not quite apparent in the numbers of species, or in 'productivity'. As groups mycorrhizal and saprotrophic species seem to behave differently: mycorrhizal species fruit earlier (Table 4 column 4C, section Time course below) when summer temperatures are high.

Monthly precipitations show a weak cyclic pattern; the variation over the years is high and the summer peak is less than twice the winter low. Species richness, overall abundances and periods of fruiting (log values of Table 2 columns 2A, 3A and 4A), the average frequency of species (not shown), and diversity parameters (Table 4 columns 3E and 3F) are all correlated weakly with the precipitations of months 10, 8 and 6 (months given in order of impact). Correlation existed also with the total precipitation of months 6 to 10 (Table 2 column 5B). With the total precipitation, all parameters leveled off at a precipitation of about 550 mm (Fig. 4). At this level productivity/diversity is maximal.

Time course

Over the years, the temperature in month 8 increased and the precipitation of months 6–10 showed a tendency to increase. This climate change is typical for the central European region

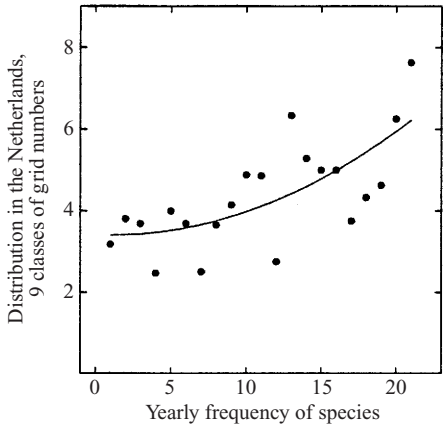

Fig. 5. Relation between the distribution of species in The Netherlands and the yearly frequency, as parameter for abundance, in this study.

(Rebetez & Beniston 1998). The weighted times of fruiting (Table 4 column 4B) correlated with the year numbers of the survey. However, this correlation was weaker than that between time of fruiting and the temperature in month 8. Probably the time course of the survey itself has no effect on the shift in time of fruiting. Similarly, the shift in appearance of saprotrophic versus mycorrhizal species (Table 4 column 4C) correlates with year number, but less so than with the temperature of month 8. Productivity parameters were correlated with year number. This was analyzed in detail in multiple regressions on year number, temperature in month 8 and the precipitation of months 6–10. Precipitation had the highest impact, the influence of year number was small and that of temperature not important. Analyzing the groups of saprotrophic versus mycorrhizal species showed that saprotrophic species reacted to year number in particular and mycorrhizal species much less so. The abundance of saprotrophic species increased with time; not the number of species.

Relation with distribution data from The Netherlands

Of the 408 species of this study, 326 have been fully identified and 82 are identified to genus but not (yet) to species (mainly *Cortinarius* spp.). Of the fully identified species, 257 are mentioned in a list of Dutch wild mushrooms by Arnolds, Dam & Dam-Elings (1995). The list provides distribution data for all species: a virtual grid is laid over The Netherlands and the presence of species is counted in each grid number. Counts are given on an (almost) exponential scale of 1 to 9. All frequent species in the present study occur in The Netherlands. Infrequent species are present in the Netherlands to a lesser extent, the overlap being 70% or higher. Fig. 5 shows the relationship between Dutch distributions and the frequencies in the present study. Of all Dutch species, 2475 'sufficiently documented' species were considered for the establishment of a red list (Arnolds & van Ommering 1996). Of 'our' fully identified species, 122 fall within one of the categories of the Dutch red list: susceptible, vulnerable, threatened, seriously threatened, and disappeared (12 species). On average these species are infrequent and have low abundancies in our present study.

DISCUSSION

The data set is highly structured: species richness, abundance, and the length of the fruiting period in a year, are tightly correlated. This coincides with: (1) the symmetrical distribution of abundance data of species over their fruiting periods; and (2) regular species-abundance distributions over the years (Fig. 1). Regular species-abundance relations are found in all sorts of assemblages, for example of diatoms, higher plants, butterflies etc (Magurran 1988). We assume that, even after 21 yr, the whole spectrum of species richness has not been seen. Many new species may be expected in additional 'productive' years. These years provide for infrequent and unique species (Table 4 column 2B). It was not surprising to find that 'species richness estimators' (Schmit, Murphy & Mueller 1999) did not stabilize to a definite maximum (results not shown).

Productivity varies over the years and probably shows a continuous range of values between its minimum and maximum (both unknown). One may consider that the species of the mushroom assemblage form a continuous range of (potential) productivities. It is not that simple. The least and most productive years are 1989 and 1992, respectively. Given a continuous range of productivities, the 18 species of 1989 would be present in all other years and the number of species with a frequency of one would be 194–179 (being the difference in species of 1992 and the second species rich year 1993). Also, the total number of species in the survey would not exceed the number of 194 in 1992. However, almost each year showed unique species (Table 4 column 2B). Many species are transient; unique species are not the only transient ones. Species may be transient because: (1) they establish themselves for a certain number of years and then disappear from the plot; and (2) their mycelial biomass and the amount of resource they captured fluctuates over the years, independent from the 'productivity' level. Of course our data relate to fruit bodies, not to mycelia, and the mycelia need not be transient at all.

For mycorrhizal fungi, the correspondance between fruit body occurrence and mycelia occurrence in the soil can be measured on the basis of mycorrhizas by molecular methods. The species composition of fruit bodies reflects poorly that of mycorrhizas on the same plot (Gardes & Bruns 1996, Jonsson *et al*. 1999). Many mycorrhizal species do not form fruit bodies or form inconspicuous (*Thelephoraceae* and *Corticiaceae*) or invisible ('*Tuberales*') ones. Dahlberg, Jonsson & Nylund (1997) and Peter, Ayer & Egli (2001) found that about half of the abundance of the ectomycorrhizas was accounted for by species that did not produce conspicuous epigeous fruit bodies.

A rather adequate and simple parameter for the expression of productivity is the number of species. This parameter requires less effort to be measured than the accurate counting of numbers of (identified) fruit bodies and a strict periodical visit of the study site. If this holds for other data sets as well, a quick (re-)analysis of those data can be done because the

accurate identification of species and a list or table showing the presence of species over the years of a study will probably be basic to that study. The best conceivable parameter should characterize the species-abundance relations, for instance the area under the fitted curve (Table 4 column 3E). Compared with other productivity parameters (log numbers of species or of fruit bodies), the area under the curve shows a relatively long range of values, providing for much 'resolution'. However, the length of this range should not be surprising, because the area under the fitted curve is an expression of species richness and of species abundances, two parameters with independent ranges.

To our knowledge, the correlation of the summer temperature with one aspect of phenology, the time of fruiting, has not been found previously. High temperatures in full summer seem to delay fruiting. Temperature is related to the evaporative power of air; the capacity of air to carry water doubles at a temperature increase of 10 °C. Mushroom tissue will desiccate more easily at a high temperature and perhaps this vulnerability causes a delay to the autumn in the development of fruit body initials or their growth into mature, and visible, fruit bodies. We suggest that the species in the assemblage react in a continuous range to temperature for fruit body development and (or) growth. The correlation of precipitation data with productivity parameters has also been demonstrated in other studies (Wilkins & Harris 1946, Wasterlund & Ingelog 1981, Agerer 1985). Fungal species composition seems to be strongly determined by soil chemical properties (Ruehling & Tyler 1990) and vegetation type (Runge 1964). Other factors are the structure and age of the forest stand (Dighton & Mason 1985, Vogt *et al*. 1981), and even the host genotype in the case of mycorrhizal species (Last & Fleming 1985).

The correlation of Swiss 'productivity' data with Dutch 'distribution' data (Fig. 5) supports the biological 'law' of the abundance-distribution relation of species (Johnson 1998). Rare species seem to be threatened with extinction on a (sub)evolutionary time scale. Few data exist for rare species because of their rarity. It is difficult to distinghuish between a specific and a general threat for rare species. Thus, the establishment of red lists is difficult. Such lists will easily over-concentrate on rather abundant and frequent species and will probably be too short.

Mycorrhizal and saprotrophic groups of species behaved similarly. A difference was found with regard to the time of appearance of fruit bodies. In years with high summer temperatures the saprotrophic species reacted with a later appearance (Table 4 column 4C). Another difference was the relatively higher number of fruit bodies of saprotrophs in the later years of the study. The substrates of both groups are quite different. Saprotrophs require litter from (the) previous year(s); mycorrhizal symbionts require photosynthate quickly exudated by young roots (Romell 1938, Last *et al*. 1979). The amounts of substrate available to the fungi will vary over the years. It is difficult to imagine that both substrates vary in phase. Thus, the similarity in diversity/productivity behaviour indicates that the variation in the amounts of substrate is not very relevant. However, the increase of the number of fruit bodies per saprotrophic species in the years indicates a shift in the amount of substrate for these species. Perhaps soil organic matter is accumulating, or, as Arnolds (1991) found, a general nutrient enrichment by atmospheric deposition, in particular that of nitrogen, facilitates the fruiting of saprotrophs.

Knowledge of fruit body productivity is of ecological relevance because of the functional role(s) of fruit bodies. The results are also relevant in a conservational context. Absence in productive years is more alarming than in poor years; this is important for the selection of species for 'red' lists. The results are also interesting for those trying to manipulate the yield of edible mushrooms in forests and in tree plantations of truffles and of other species.

Fruiting starts with the formation of primordia (Clémençon 1997) or primordial undifferentiated stages (Umar & van Griensven 1997). Very little is known about this process in the field. In *Agaricus bisporus*, the formation of the total number of primordia is fixed before any fruit body is visible (Flegg 1979). If this phenomenon is common, it is easy to understand that the appearance of fruit bodies is quite independent from their numbers and that numbers are regularly distributed over the period of appearance. In the field, fairy ring-forming fungi may be suited to study the occurrence of this phenomenon; the position of emerging mushrooms and thus of their primordia can be predicted by observations on fruit body positions in previous years. This offers the possibility of selecting sites for observations. 'Mycelium' mapping and analysis of such data would help in studying the species dynamics in the soil. Primary data related to the present data set await analysis. Experimental field studies have been concentrated on edible mycorrhizal species unsuitable for cultivation, such as truffles (Singer 1965, Rebiere 1967, Hall & Wang 1998), and on 'environmental' effects of fertilization, acid rain, etc. (Jonsson *et al*. 1999). Watering of plots can be used to study the effect of precipitation. Perhaps field experiments can be extended by applying airconditioning in 'greenhouses' on site to study the effect of temperature and the moisture contents of air. Saprotrophic species could be selected for experimental studies. They can often be cultivated (Flegg, Spencer & Wood 1985, Poppe & Heungens 1991) and thus could serve as models in the laboratory and (or) field. The cultivated white button mushroom, *Agaricus bisporus*, seems to react to temperature and moisture (Flegg *et al*. 1985) quite similarly to the assemblage in our plot.

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