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Effects of temperature and rainfall on fruiting of macrofungi in oak forests of the Mediterranean area

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ABSTRACT

The results of a study on the effects of weather (rainfall and minimum, mean, and maximum temperatures) on fruiting of macrofungi in a number of oak forests of Tuscany (central Italy) are reported. The fungal parameters (total number of species and total number of carpophores) were examined for statistical correlations with annual and seasonal temperature and rainfall and with temperature and rainfall in the 5-, 10-, 15-, and 30-day periods before the date of the sampling. It was found that abundant annual rainfall was necessary for the fungal mycelium to fruit. Spring rainfall in particular seemed to be related to the number of species found in autumn. Rainfall was the main influence on fruiting in the most important fruiting period (autumn). Highly significant correlations were found between the number of carpophores and rainfall in the 30 days preceding sampling.

INTRODUCTION

The quantity of recent research on macrofungi, which are fungi that produce carpophores visible to the naked eye and larger than 1 mm in size (Arnolds, 1981), is indicative of the interest these organisms have aroused in the scientific community. The aspects investigated range from systematics and evolution to morphology and ecology. The aim of applied ecologists is the conservation of the environment in which these important components of forest ecosystems grow (Arnolds, 1999). For species such as *Armillaria mellea* (Vahl.: Fr.) Kummer and *Heterobasidion annosum* (Fr.) Bref., the phytopathological aspect has been studied (Last and Fleming, 1985). For fungi of economic value (*Boletus* spp., *Pleurotus* spp., *Tuber* spp., etc.), attempts have been made to find strategies to increase production (Hall et al., 1998; Salerni and Laganà, 2000). The study of macrofungal communities has also recently been included in environmental biomonitoring programs since changes in composition of the fungal community seem to reflect and prelude changes in the ecosystem to which they belong (Jakucs, 1988; Arnolds, 1991; Fellner and Peskova, 1995). All these studies are based on the presence and abundance of carpophores. It is therefore surprising how little is known about the mechanisms regulating fungal fruiting (Last and Fleming, 1985; Ohenoja, 1995).

Temperature and rainfall are regarded as two major factors for macrofungal production (Arnolds, 1981). In northern and central Europe, many authors studied the relations between these two parameters and fungal production. Becker (1956) and Heim (1969) found that alternation of dry and wet periods favored fruiting. Bujakewicz (1969) reported that too much water inhibited fruiting of soil species (mycorrhizal fungi and humus and litter saprotrophs). Lange (1978) studied fruiting of macrofungi for 10 years in permanent areas in beech woods of Denmark and concluded that rain was a major factor for this process. Thoen (1976) came to the same conclusion after studying the effect of rain and soil temperature on the presence of carpophores in conifer woods in the period June to December.

In southern Europe, studies of this type have been few. Barluzzi et al. (1992) studied fungal communities in several chestnut woods in Tuscany (central Italy) and found that the main production period was autumn, but with large variations from year to year, which differed from those observed by the same authors in communi-

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Table 1
Main characteristics of the 10 permanent stations (CS = clayey schist; S = sandstone; PC = polygenic conglomerates; CL = cavernous limestone; AS = argillites and siltites)

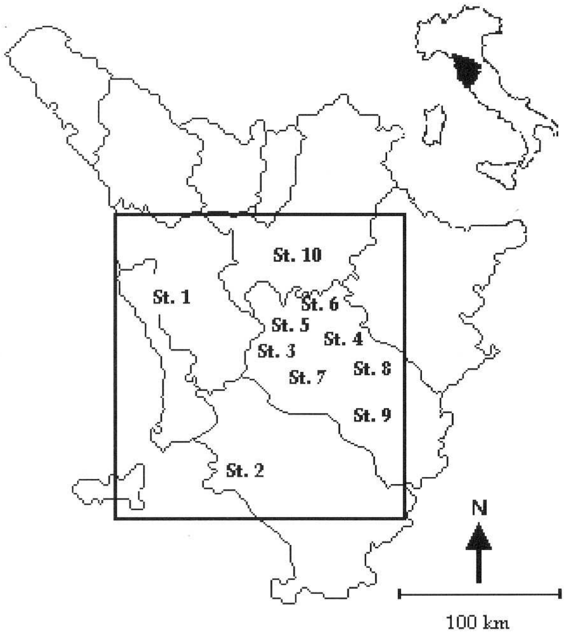
	1	2	3	4	5	6	7	8	9	10
Altitude (m)	250	5	140	490	470	280	440	430	440	190
Exposure	NE	WNW	WNW	SE	SE	NNW	SE	SSE	WNW	NW
Slope (°)	variable	5	15	12	2	8	15	14	17	15
Substrate	CS	S	CL	CL	CL	CL	PC	PC	PC	AS
Soil pH	5.8	5.3	7.0	6.8	6.8	6.8	5.4	5.2	5.2	7

ties of evergreen oak woods (De Dominicis and Barluzzi, 1983; Perini et al., 1989). However, no direct correlation has yet been found between these parameters and fungal fruiting (Arnolds, 1988; Eveling et al., 1990; Laganà et al., 2000).

The aim of the present study was to investigate the extent to which temperature and rainfall influence fruiting of fungal species found in oak forests of the Mediterranean area.

MATERIALS AND METHODS

Ten permanent stations were chosen in oak woods of central-southern Tuscany (Fig. 1) and were sampled throughout the period 1992–1997. These ecosystems ranged over a large geographical area in which oak woods are the most common dominant type of forest (Arrigoni, 1972). Stations 1 and 2 were on the coast (Fig. 1) in woods in which *Quercus ilex* prevails. In St. 1, *Q. ilex* grew together with tree species such as *Q. pubescens*, *Sorbus torminalis*, *Fraxinus ornus,* and pines. In St. 2, the tree layer was dominated by *Q. ilex* and there were sporadic specimens of *Q. suber.* The other stations were inland. Stations 3–6 were in woods dominated by *Q. pubescens* and *Q. cerris.* As well as these two oaks, Sts. 7–9 also had *F. ornus*, *Pyrus pyraster,* and *Q. ilex*. Station 10 contained two types of vegetation: a more Mediterranean type with *Q. ilex, Phillyrea, Arbutus unedo, Erica scoparia, Q. pubescens,* and planted pines; and a more mesophilous type with *Acer campestre*, *S. torminalis*, *Q. cerris*, *Ulmus,* and *Crataegus*. The main characteristics of the stations are shown in Table 1.



Vertices Coordinates (UTM ZONE 32 ED 50)

	EAST	NORTH		EAST	NORTH
NW	604830	4847110	NE	721920	4847110
SE	721920	4726340	SW	604830	4726340

Fig. 1. Map of the study area with location of the 10 permanent monitoring stations.

The study period ranged from two (Sts. 2–6, 10) to three years (Sts. 1, 7–9). Sampling was both qualitative (floristic) and quantitative (carpophore counts per 1000 m^2 as suggested by Arnolds [1981]). Observations were once a month in all stations and more frequent in St. 10 during the period of peak production. Each taxon was attributed to a trophic group (mycorrhizae, humus saprotrophs, litter saprotrophs, wood saprotrophs, and parasites), as suggested by Arnolds et al. (1995). The weather variables considered were total rainfall and daily minimum, mean, and maximum temperatures, and were obtained from the weather stations nearest to the study areas. Correlations between meteorological variables and number of species and carpophores were analyzed by the Pearson linear coefficent.

RESULTS

The results of samplings carried out in the ten stations during two or three years of observation are summarized in Table 2. The greatest number of species was observed

Table 2

Summary of mycological sampling (M = mycorrhizal species; Sh = humus saprotrophs; Sl = litter saprotrophs; Sw = wood saprotrophs; P = parasites)

		St. 1			St. 2		St. 3		St. 4		St. 5		St. 6		St. 7			St. 8			St. 9			St. 10	
		1995	1996	1997	1996	1997	1992	1993	1992	1993	1992	1993	1992	1993	1994	1995	1996	1994	1995	1996	1994	1995	1996	1996	1997
No. species	Tot	25	59	72	73	73	72	69	77	68	106	69	39	59	62	46	132	79	67	137	83	69	84	181	27
	M	2	14	13	22	18	29	32	30	26	49	36	12	25	14	18	71	24	30	68	23	24	35	122	14
	P	1	3	1	2	2	1	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1	1	3	1
	Sh	5	5	9	8	12	12	6	14	12	16	6	7	5	7	5	6	15	8	14	11	6	11	25	0
	Sl	6	11	13	5	12	14	13	12	13	16	12	12	11	11	4	13	12	7	17	15	12	9	16	8
	Sw	11	24	34	34	23	12	14	10	16	16	15	6	15	28	19	39	24	19	37	30	26	25	15	4
No. carpophores	Tot	822	1233	872	523	1412	701	1109	641	875	1654	967	542	1669	2252	491	2747	3776	931	4100	1983	1381	1698	15,544	517
	M	5	74	26	119	118	148	230	254	253	272	192	17	82	26	79	1228	113	161	1485	99	144	219	11,741	401
	P	10	78	39	40	73	2	1	2	0	600	0	0	0	0	0	0	6	1	0	7	12	4	42	1
	Sh	55	74	60	32	89	35	26	71	42	243	13	25	10	38	5	45	114	103	291	62	12	248	779	0
	Sl	544	361	147	68	132	218	669	147	390	345	438	407	1353	358	54	540	1852	30	1397	372	344	477	2786	83
	Sw	208	643	592	258	983	245	164	121	189	159	324	88	221	1818	353	871	1667	585	923	1380	869	547	180	32

in 1996 in St. 10 (181 fungal species) and the smallest in 1995 in St. 1 (25 species). The greatest number of carpophores was counted in the first year in St. 10 (15,544 carpophores). This cannot be attributed to the greater frequency of observations in this station, because the subsequent year only 517 carpophores were counted.

Figure 2 shows the mean temperature and total rainfall data recorded each month during the observation period, along with the number of species found in each station. Only two graphs were plotted for Sts. 3–6 and 7–9 because they were relatively close to each other and the meteorological data were from two weather stations only. All 10 stations showed a similar fruiting pattern: A maximum number of species was recorded in autumn (September–December) when temperatures were mild and rain abundant (mean 12 °C and 352 mm, respectively). In winter (January–February), when it was colder and rainfall was generally less abundant (mean 8 °C and 102 mm), no

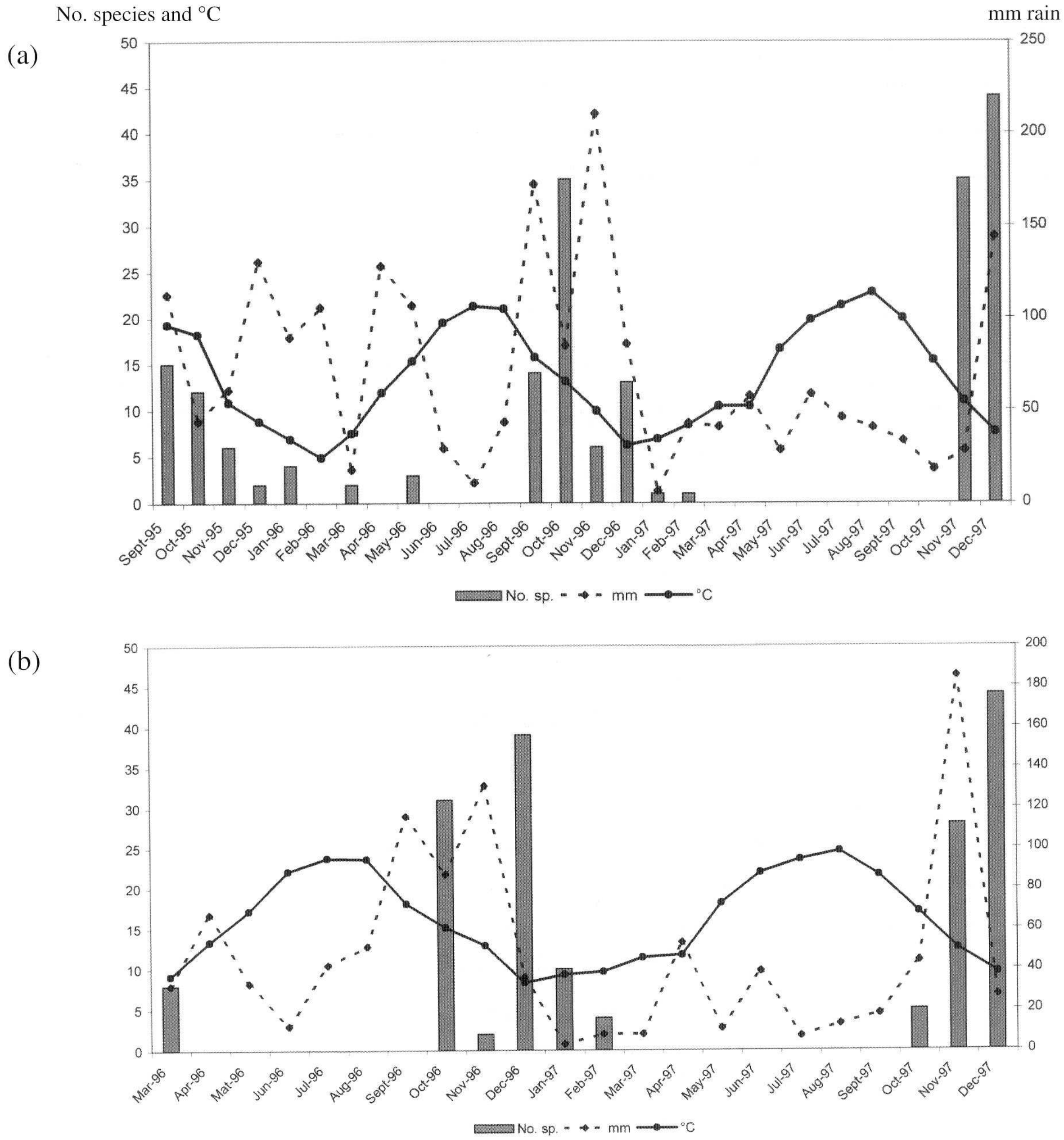
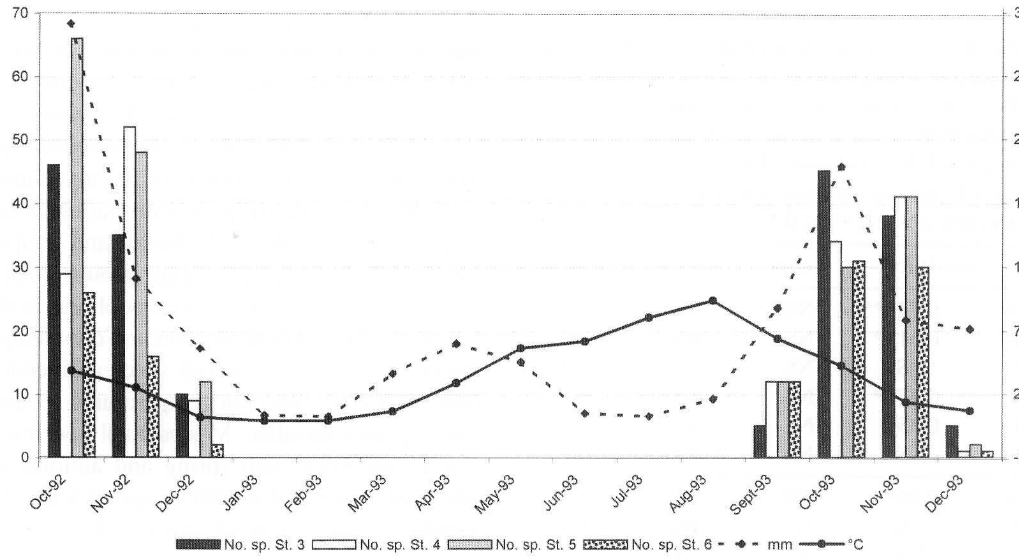


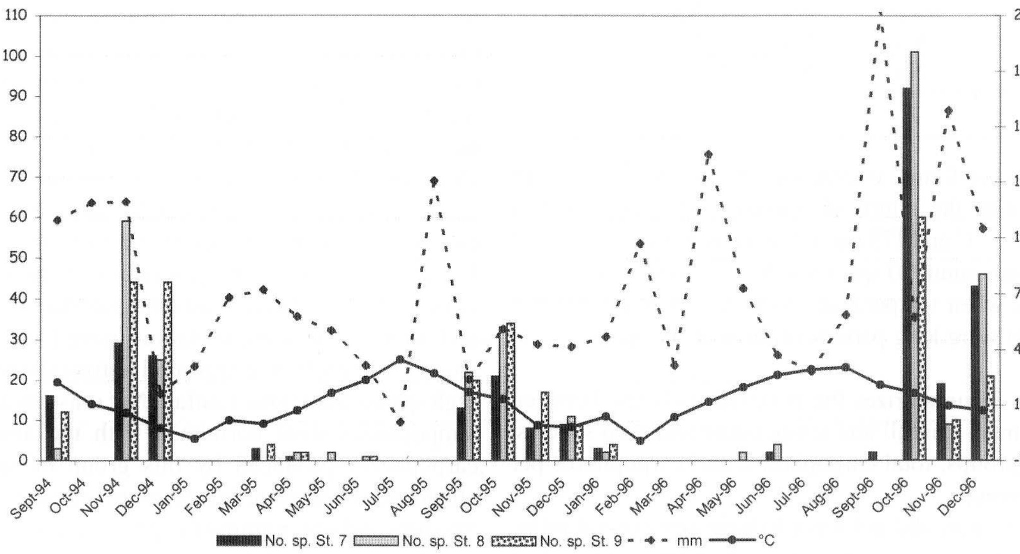
Fig. 2. *This and facing page.* Graph of mean monthly temperature, total monthly rainfall mm, and number of species in the study period. (a)—St. 1, (b)—St. 2, (c)—Sts. 3–6, (d)—Sts. 7–9, (e)—St. 10.

(c)



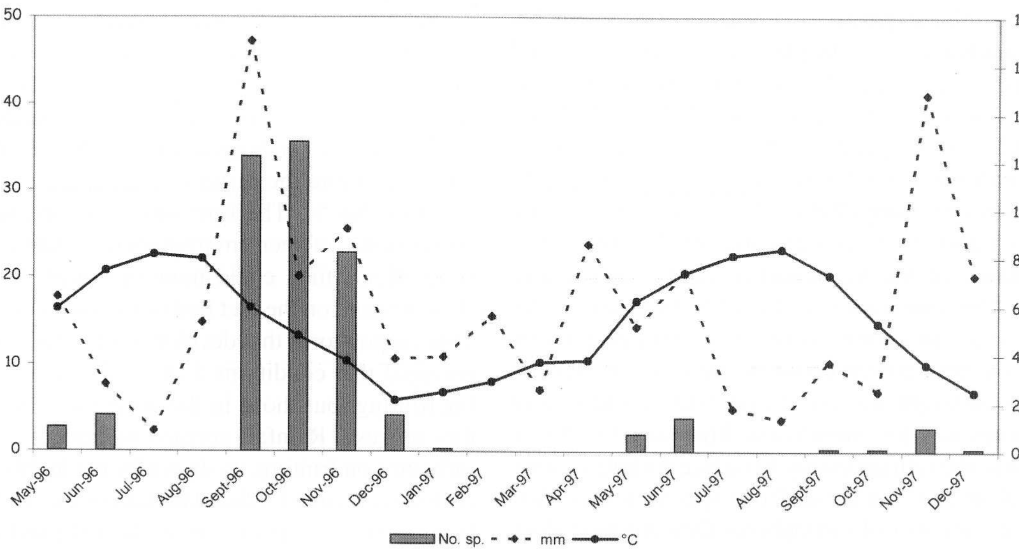
70
60
50
40
30
20
10
0
320
270
220
170
120
70
20
-30
Oct-92
Nov-92
Dec-92
Jan-93
Feb-93
Mar-93
Apr-93
May-93
Jun-93
Jul-93
Aug-93
Sept-93
Oct-93
Nov-93
Dec-93
No. sp. St. 3
No. sp. St. 4
No. sp. St. 5
No. sp. St. 6
mm
°C

(d)



110
100
90
80
70
60
50
40
30
20
10
0
220
190
160
130
100
70
40
10
-20
Sept-94
Oct-94
Nov-94
Dec-94
Jan-95
Feb-95
Mar-95
Apr-95
May-95
Jun-95
Jul-95
Aug-95
Sept-95
Oct-95
Nov-95
Dec-95
Jan-96
Feb-96
Mar-96
Apr-96
May-96
Jun-96
Jul-96
Aug-96
Sept-96
Oct-96
Nov-96
Dec-96
No. sp. St. 7
No. sp. St. 8
No. sp. St. 9
mm
°C

(e)



50
40
30
20
10
0
180
160
140
120
100
80
60
40
20
0
May-96
Jun-96
Jul-96
Aug-96
Sept-96
Oct-96
Nov-96
Dec-96
Jan-97
Feb-97
Mar-97
Apr-97
May-97
Jun-97
Jul-97
Aug-97
Sept-97
Oct-97
Nov-97
Dec-97
No. sp.
mm
°C

Table 3
Correlations (r-value) between number of species and total number of carpophores and their division among the trophic groups (M = mycorrhizal species; Sh = humus saprotrophs; Sl = litter saprotrophs; Sw = wood saprotrophs; P = parasites) and annual rainfall (R), minimum (T min), maximum (T max), and mean (T mean) annual temperature. Statistical significance: NS: $p > 0.1$; * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.01$

		R tot	T min	T max	T mean
No. species	Tot	0.54***	NS	NS	NS
	M	0.51**	NS	NS	NS
	P	NS	NS	NS	NS
	Sh	0.47**	NS	NS	NS
	Sl	0.35*	NS	NS	NS
	Sw	NS	NS	0.70***	0.45**
No. carpophores	Tot	0.36*	NS	NS	NS
	M	NS	NS	NS	NS
	P	NS	NS	NS	NS
	Sh	0.44**	NS	NS	NS
	Sl	NS	NS	NS	NS
	Sw	NS	NS	0.59***	NS

species were found, except for certain taxa in St. 1. In spring, with the return of warmer and wetter weather (mean 15.5 °C and 175 mm), fruiting resumed to a limited extent (maximum 20 species in St. 10). In summer (July–August), when temperatures were higher (mean 22 °C) and there were long periods of drought, no species were found.

Table 3 summarizes the correlations found between mean annual rainfall and temperature and total species, trophic groups, total carpophores, and carpophores per trophic group.

Temperature did not seem to have any general influence on fungal diversity or productivity, although a highly significant positive correlation was found between number of saprotrophic species on wood and maximum temperature. A less significant positive correlation was found between saprotrophic species on wood and mean temperature. Productivity was also correlated with maximum temperature ($r = 0.59$; $p \leq 0.05$), in line with the finding (Bohus, 1957) that a temperature between 5 and 30 °C is important for the growth and development of the mycelium of many saprotrophic species. Abundant rain was found to be essential for fruiting of the mycelium. A highly significant positive correlation was found between rainfall and species diversity, although the correlation with abundance of carpophores was less significant. This suggests that in oak woods, the rain necessary to induce fruiting is similar for all species, but the different species react differently in the number of carpophores they produce. Positive correlations emerged between total rainfall and number of species and carpophores of species saprotroph on humus and number of symbionts. This is readily explained by the direct relationship between these species and the soil, in which moisture presumably favors the metabolic activity of the mycelium.

Table 4 summarizes the correlations examined between seasonal values of rainfall and temperature and total number of species, trophic groups, total number of carpophores, and number of carpophores in the different trophic groups. Abundant rain and cool temperatures in spring and autumn favored species diversity. In summer, neither rainfall nor temperatures seemed to influence species number. Mycorrhizal species were positively correlated with spring and autumn rainfall and also with mean and minimum spring temperatures. The number of mycorrhizal species decreased, however, when summer temperatures were very high, as shown by the negative correlation between these two parameters. The fruiting of wood saprotrophs seemed to be closely linked to seasonal rainfall and temperature. The number of wood saprotrophs showed a positive correlation with spring ($r = 0.40$; $p \leq 0.1$) and especially summer rainfall. This may explain the finding of some lignicolous species of oak woods (*Marasmius, Mycena,* etc.) in early September when other species have not yet begun to fruit. Abundant production of carpophores did not seem to be related to seasonal weather conditions, as no highly significant correlations were found except for wood saprotrophs that appeared to fruit abundantly after high spring and winter rainfall. Not only rainfall but also temperatures were correlated with the abundance of carpophores produced by this group of species. For abundant production, temperatures need to have high maxima and low minima in spring, and remain high in summer, autumn, and winter.

To detect any influence of weather conditions in the main fruiting period, correlations between production (number of species, number of carpophores, trophic groups) in the 10 stations and climate parameters of the various weather stations in the 5-, 10-, 15-, and 30-day intervals before the respective sampling day were analyzed (Table 5). The time intervals used to study the correlations between environmental conditions and possible effects they could have on fungal fruiting were chosen based on the fact that most genera of macrofungi have carpophores that develop within this time range. It emerged that conditions 5 days earlier were irrelevant for fruiting, but those in the other intervals influenced this process. Rainfall seemed to have a considerable influence on fruiting, as shown by the highly significant correlations found. Abundant rain in the 30 days before fruiting favored species diversity and productivity and

Table 4

Correlations (r-value) between number of species and total number of carpophores and their division among the trophic groups (M = mycorrhizal species; P = parasites; Sh = humus saprotrophs; Sl = litter saprotrophs; Sw = wood saprotrophs) and seasonal rainfall and temperature (minimum, maximum, mean) during the study period. Statistical significance: NS: $p > 0.1$; * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.01$

		Spring				Summer				Autumn				Winter			
		R tot	T min	T max	T mean	R tot	T min	T max	T mean	R tot	T min	T max	T mean	R tot	T min	T max	T mean
No. Species	Tot	0.41**	0.38*	0.36*	0.56**	NS	NS	NS	NS	0.34*	NS	NS	.40*	NS	NS	NS	NS
	M	0.36*	0.49**	NS	0.46**	NS	NS	NS	–0.38*	0.36*	NS	NS	NS	NS	NS	NS	NS
	P	NS	NS	NS	NS	NS	0.47**	NS	NS	NS	NS	NS	NS	NS	0.60**	NS	NS
	Sh	NS	NS	NS	NS	NS	NS	NS	NS	0.40*	NS	NS	NS	NS	NS	NS	NS
	Sl	NS	0.41**	NS	NS	NS	NS	NS	NS	0.54***	0.41**	NS	NS	NS	NS	–0.46*	–0.48*
	Sw	0.40*	NS	0.69***	0.51**	0.55***	NS	0.50**	NS	NS	NS	0.65***	0.69***	NS	0.52*	0.80***	0.81***
No. carpophores	Tot	0.40	0.20	0.14	0.20	0.11	–0.13	NS	NS	NS	NS	NS	NS	NS	0.53**	NS	NS
	M	0.30	0.27	0.03	0.15	0.07	–0.12	NS	–0.39*	NS	NS	NS	NS	NS	0.54**	NS	NS
	P	–0.10	0.17	–0.11	0.04	–0.07	0.13	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Sh	0.40	0.28	0.18	0.32	0.19	–0.13	NS	–0.37*	NS	NS	NS	NS	NS	NS	NS	NS
	Sl	0.33	0.25	0.02	0.11	0.01	–0.10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Sw	0.44	–0.54	0.62	0.20	0.23	–0.06	0.80***	0.57***	NS	NS	0.61***	0.44**	0.62**	NS	0.62**	NS

Table 5

Correlations (r-value) between number of species and total number of carpophores and their division among the trophic groups (M = mycorrhizal species; P = parasites; Sh = humus saprotrophs; Sl = litter saprotrophs; Sw = wood saprotrophs) and rainfall and temperature (minimum, maximum, mean) in the 5-, 10-, 15-, and 30-day intervals before the mycological relevé. Statistical significance: NS: $p > 0.1$; * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.01$

		5 d				10 d				15 d				30 d			
		R tot	T min	T max	T mean	R tot	T min	T max	T mean	R tot	T min	T max	T mean	R tot	T min	T max	T mean
No. Species	Tot	0.16*	NS	NS	NS	0.79**	NS	NS	NS	0.34***	NS	NS	NS	0.50***	NS	NS	NS
	M	NS	NS	NS	NS	0.83***	NS	NS	NS	0.25***	NS	NS	NS	0.41***	NS	NS	NS
	P	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	–0.17*	NS	0.17*	NS	NS	NS
	Sh	0.16*	NS	NS	NS	NS	NS	NS	NS	0.32***	NS	NS	NS	0.41***	NS	NS	NS
	Sl	0.20**	NS	NS	NS	0.64*	NS	NS	NS	0.42***	NS	NS	NS	0.49***	NS	NS	NS
	Sw	NS	NS	–0.17**	–0.18**	0.67*	NS	NS	NS	0.20**	NS	–0.15*	–0.21**	0.36***	NS	NS	NS
No. carpophores	Tot	NS	NS	NS	NS	0.64*	NS	NS	NS	NS	NS	NS	NS	0.20**	NS	NS	NS
	M	NS	NS	NS	NS	0.78**	NS	NS	NS	NS	NS	NS	NS	0.16*	NS	NS	NS
	P	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.15*	NS	NS	NS
	Sh	NS	NS	NS	NS	NS	NS	NS	NS	0.17*	NS	NS	NS	0.30***	NS	NS	NS
	Sl	NS	NS	NS	NS	NS	NS	0.65*	0.69*	0.17**	NS	NS	NS	0.22**	NS	NS	NS
	Sw	NS	NS	NS	NS	0.69*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

in the 15 days before fruiting, only number of species but not number of carpophores. Rain in the 5 days before production only seemed to favor litter and humus species, presumably because their mycelium is closer to the surface than that of symbionts and is therefore influenced by changes in moisture. High temperatures recorded in the 5- and 15-day intervals before production seemed to inhibit fruiting of the mycelium of species saprotrophs on wood and parasites.

DISCUSSION

The aim of this study was to examine the influence of temperature and rainfall on fruiting of macrofungi in Mediterranean oak woods of central Italy. Although the various stations considered are spread over a relatively large geographical area, from the coast to the inland hills, late summer (September) and autumn were the period of greatest production in all cases. Perini et al. (1996) reached the same conclusion studying several types of forest communities (juniper thickets, evergreen oak woods, and chestnut woods). This suggests that in the Mediterranean area, the various types of vegetation have little influence on the mechanisms regulating fungal fruiting.

Some differences that could not always be attributed to weather were nevertheless found during the main production period and from year to year. The modest fruiting observed in spring (maximum 20 species in St. 10), when conditions are generally similar to those typical of autumn, is in line with the hypothesis of Hueck (1953) and Ellenberg (1986) that before fruiting, most fungal mycelia require a period of vegetative growth, the ideal conditions for which occur in spring. This hypothesis was demonstrated in the laboratory by Witkamp (1960) and Nagel-de Boois and Jansen (1971), who observed a peak of mycelial growth in spring.

Although the fruiting pattern was generally the same in all seasons, the number of species was not constant in months of major production nor in the various years of observation. For example, maximum diversity (35 species) was observed in St. 1 in October 1996 but the following year not a single species was found in the same month (Fig. 2a). On the other hand, in St. 2, which is likewise characterized by a Mediterranean evergreen vegetation, maximum production was in December both years (Fig. 2b). These differences could be due to many factors, but a determinant role is certainly played by the type, age, and management of the two forest ecosystems. The woods of St. 2 have been managed to promote tree height and are dominated by *Q. ilex*, whereas those of St. 1 are mixed with a predominance of *Q. ilex*, plus many broad-leaved species and some conifers. Analysis of the mycorrhizal status of the root tips (Torta et al., 2000) showed, moreover, that the *Q. ilex* trees in St. 1 are in better health than those of St. 2. The trees in St. 2 are older than those in St. 1, where the undergrowth is more varied and flourishing (Chiarucci et al., 1996). All these observations suggest that the differences observed are not a mere fluctuation of the fungal community, but rather the beginning of a succession, since according to Arnolds (1981), about ten years of observations are necessary to reveal true successions. The present observations may therefore be due not to random reversible factors such as heavy rain, prolonged drought, snowfalls, extreme temperatures, and high winds, but rather to irreversible changes such as different forest management and/or evolution of the plant community.

In Sts. 7–10 (Fig. 2d–e) the greatest differences were not between months but between different years of observation. In Sts. 7–9, the number of species observed in 1995 was much less than in 1994 and 1996 (Fig. 2d); in St. 7, for example, the number of species found in 1995 was nearly 50% less than in 1994. The difference observed in St. 10 (Fig. 2e) was even greater: Only 27 species were observed in the second year of research, against 181 the first year. These results confirm the observed alternation of "good and bad" years of fungal fruiting by Guminska (1962) and Thoen (1970, 1971). According to Thoen (1970, 1971), low carpophore production is associated with storage of reserves for the following year, when production is therefore greater.

Analysis of correlations between annual meteorological parameters and those of fungal production showed that rainfall has the greatest influence on fruiting, especially in the qualitative sense (number of species), whereas temperature does not seem to be determinant.

Analysis of correlations with seasonal meteorological parameters showed that abundant spring rainfall favored species diversity but not abundance. This result confirms a link between vegetative growth in spring and fruiting in autumn (Hueck, 1953; Ellenberg et al., 1986) but shows that vegetative development in spring and the factors that favor it do not determine productivity. This analysis also showed a close relationship between the fruiting process in wood saprotroph species and seasonal rainfall and temperature. This may be due to the fact that the mycelium of these species is more readily affected by atmospheric changes, being more superficial than that of symbionts, and humus and litter saprotrophs.

The time interval used (5, 10, 15, and 30 days) should assure the detection of species fruiting; in fact, not all macrofungi produce carpophores at the same time and with the same life span (Arnolds, 1981). Temperature and rainfall in the 5 days preceding fruiting seem to have little effect on the number of species fruiting, whereas this

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