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The relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi in *Pinus sylvestris* forests of the central Pyrenees

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Abstract

Due to increasing economic interest in forest fungi as important non-wood forest products, autumn mushrooms from *Pinus sylvestris* forests of the Spanish Pyrenees were collected for three consecutive years to examine the relationships between forest age and aspect on the sporocarp production of epigeous edible and ectomycorrhizal fungi. Fresh weight, dry weight and number of sporocarps were recorded from thirty-six 100 m^2 forest plots with a range of seven age classes and four aspects. The 9073 sporocarps collected represent 164 taxa and 34 genera. Age class was observed to be an influential factor for 21 taxa and aspect for 7 taxa. We gave special attention to edible and marketed mushrooms, particularly *Lactarius deliciosus*, which is the most widely collected species from these forests. Edible marketed-species comprise 20% of the total fresh weight yield. Species richness and distribution are presented, providing a baseline inventory for this forest community. There is a positive relationship between sporocarp yield (fresh weight, dry weight or number of sporocarps) and species richness for individual plots.

Keywords: Forest fungi; *Lactarius deliciosus*; Fungal succession; Fungal species richness

1. Introduction

Forestry production has historically focused on timber and wood products but declining timber revenues in rural communities have increased the importance of income from non-wood forest products such as floral greens, medicinal plants, and wild mushrooms (Molina et al., 1993; Liegel et al., 1998). In the Spanish Pyrenees, as well as in many Central European countries, the economic decline from timber production has created regional crises leading to abandonment of rural areas, and subsequent decreases in forest land management (Marraco and Rubio, 1992).

Mushroom harvests constitute a largely untapped economic resource in temperate forests (Sisak, 1998;

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Pilz et al., 1998). The commercial value of forests may be enhanced through mushroom harvest programs which include well-planned timber removals that may improve edible mushroom habitat as well as provide wood and employment Pilz et al. (1999). Forest managers concerned with this resource are creating new management models that integrate this ephemeral production with timber management (Díaz Balteiro et al., 2003).

There is continued interest in evaluating the response of forest fungi to forest management practices including clear-cutting (Kardell and Eriksson, 1987), thinning Kranabetter and Kroeger (2001) exotic tree plantations, road building, herbicide application (Ohenoja, 1988), nitrogen fertilizers (Shubin, 1988; Wiklund et al., 1995; Ohenoja, 1994) and logging wastes (Wästerlund and Ingelög, 1981). Egli and Ayer (1997) demonstrated that a partial clearing of 35% reduction of stems in a mixed forest of Switzerland increased up to six-fold the edible mushroom production. Researchers in the Pacific Northwest USA are monitoring long-term effects of commercial thinning of young forests on the economically important species *Cantharellus formosus* and *C. subalbidus* (Pilz et al., 2003) But in general there is not sufficient site-specific or species-specific information available as a basis for forest managers who wish to optimize forest conditions for mushroom production.

Sustainability or enhanced production of edible fungi cannot be evaluated without a knowledge base of the existing fungal populations. Inventories and productivity studies of forest fungi that include ecological parameters help provide a baseline for monitoring responses to management and harvesting activities (Pilz and Molina, 2002). A list of fungal yield studies according to forest tree species conducted in North and Central Europe since 1930 has been compiled by Ohenoja (1993), but does not include research from southern European forests.

Mushroom productivity research in Spain began fairly recently. Fernández et al. (1993) characterized *P. sylvestris* forests where *Boletus edulis* productivity is greatest. Rodríguez and Fernández de Ana (1997) measured fungal yields in chestnut forests (*Castanea sativa*). Fernández de Ana et al. (1989a, 1989b) quantified individual sporocarps by species in chestnut forests with different silvicultural treatments. Hernández and Fernández (1998) quantified mushroom productions under various silvicultural treatments in *Pinus pinaster* forests. Oria (1989) reported productivity of 6 commercial edible mushrooms of Soria from pine stands with a range of slope and moisture conditions.

The greatest production of large fleshy fungi in the Spanish Pyrenees occurs in *P. sylvestris* forests (Martínez de Aragón et al., 1998), with increasingly important economic potential (Cervera and Colinas, 1997). Every autumn thousands of mushroom pickers harvest commercial edible fungi from both private and public forests, contributing significantly to the regional economy. Mushroom yields vary greatly from 1 year to the next and, within the same season, from one site to another.

Variations in fungal yields and species distribution among different forest sites have been repeatedly observed (Mehus, 1986) and may be attributed to microclimatic (Egli and Ayer, 1997) and macroclimatic factors (Ohenoja, 1993). Differences in species distribution and number of sporocarps may be associated with soil properties and vegetation parameters such as quality of the humus layer or shrub community (Tyler, 1989a, 1989b). And since the majority of large fleshy edible forest fungi are ectomycorrhizal, host specificity may also play an important role (Molina et al., 1992).

Forest age has been observed to be a key factor determining the composition of fruiting fungi. Research on fungal succession (Frankland, 1981; Deacon et al., 1983; Shaw and Lankey, 1994; Keizer and Arnolds, 1994) demonstrates that the dynamics of population composition of forest fungi is influenced by the age of the associated host trees. Classifications of early and late-stage fungi are broad distinctions, primarily applicable to ectomycorrhizal fungal succession on previously unforested sites (Mason et al., 1987) and reflect the physiological and nutritional characteristics of the fungi (Dighton and Mason, 1985).

Aspect may be an important ecological factor influencing the fruiting of certain mushroom species. Forest landowners in the Pyrenees report that north-facing slopes favor the productions of *Tricholoma terreum*, while *Lactarius deliciosus* is more commonly found on dry southwest slopes. These are valuable observations but data on the differences in the yields of different fungi based on aspect are not available.

Given that wild mushroom production is becoming increasingly important as a non-wood forest product, there is a need for more site-specific data on the ecology of forest fungi and factors that affect their productivity. The aim of the present research is to examine the extent to which forest age and aspect can serve to explain variations in species distribution, biomass and numbers of fruiting bodies of autumn-fruiting fungi in the *Pinus sylvestris* forests of the central Pyrenees, and to provide a baseline inventory of ectomycorrhizal and edible fungi in this forest community.

2. Materials and methods

2.1. Forest sites studied

We chose to study the *P. sylvestris* plantations established during the early 20th century by the Spanish Forest Services in the counties of Ribagorça, Alta Ribagorça, Pallars Sobirà and Pallars Jussà in the central Pyrenees. There is no documentation of plantations before 1900 and, due to the Spanish civil war, reforestations were interrupted in the years 1935–1945. These plantations are fairly homogeneous ranging in altitude from 900 to 1500 m. The shrub layer is predominantly *Buxus sempervirens*, with occasional *Quercus* sp. understory. From the records we identified 118 plantations and classified them into seven age classes and four aspect classes with a total of 28 age-by-aspect classes. When a single plantation was large enough to clearly span two aspects, it was considered as two plantations. We randomly chose three plantations per age-by-aspect class when available. Unfortunately *P. sylvestris* was mainly planted on northern slopes and there were not always three plantations available for each class, so the design is unbalanced with a total of 36 plantations (Tables 1 and 2).

2.2. Establishment of the plots

We randomly established one 10 m × 10 m study plot (Vogt et al., 1983; Dahlberg and Stenlid, 1994; Kalamees and Silver, 1988) per selected plantation. These plots excluded a 10 m-wide strip along roads and a one tree-height band around the perimeter to reduce edge effects (Termoshuizen, 1990).

Table 1
Classification of the 36 study plots according to age class (age class VI is absent due to lack of plantation establishment from 1935–1945)

Age class	Forest age (years)	Number of plots
I	5–14	5
II	15–24	6
III	25–34	6
IV	35–44	6
V	45–54	7
VII	65–74	3
VIII	75–84	3

2.3. Sampling methods

Plots were sampled at 1-week intervals from September through November of 1995–1997. In order to reduce errors due to mushroom removals by recreational weekend pickers, the sampling day was always Thursday or Friday. The spring fruitings have not been included due to very low yields.

Criteria for samples collected were as follows: all sporocarps of epigeous ectomycorrhizal fungi (Trappe, 1962; Brundett et al., 1996) and/or edible fungi, in good condition and with a minimum cap diameter of 2 cm. We included all species in the genus *Clitocybe* because the mycorrhizal status of individual species in this genus is not clearly established in the literature and many are edible.

All fungi meeting these criteria were collected and brought to the laboratory for identification and fresh weight measurements. These fungi represented a mixture of young, mature and old fruit bodies.

The sporocarps were identified at the species level whenever possible according to the following keys: Phillips (1981), Moser (1983), Bon (1984, 1987),

Table 2
Classification of the 36 study plots according to aspect

Aspect	Compass degrees	Number of plots
N	340–20	18
S	160–200	5
E	70–110	7
W	250–290	6

Alessio (1985), Chaumeton (1985), Moreno et al. (1986), Bertea et al. (1989), García Bona (1989), Andrés-Rodríguez et al. (1990), Llimona et al. (1990) and Breitenbach and Kränzlin (1991). Some samples could only be identified to genus, subgenus, section or subsection, particularly in the genus *Cortinarius*. Samples that could only be identified to the genus level were grouped into a genus taxon.

Sporocarps were dried in air-vented ovens at 35–40 °C, and weighed to the nearest 0.01 g at room temperature in order to obtain comparable biomass data. The production of the 3 years of each taxon in all plots was added and divided by three as an estimate of the yearly production. Data are given in kilograms of fresh weight per hectare per year (kg fw/ha/year), kilograms of dry weight per hectare per year (kg dw/ha/year) and number of sporocarps per hectare per year (ns/ha/year) unless otherwise stated.

2.4. Data analysis

Taxa were grouped into three categories: marketed edibles (those sold in the local markets), non-marketed edibles (all other edibles) and non-edibles (Table 3).

The edibility status of many fungi varies according to country or region (Ohenoja, 1984). Because tradition, culture, and gastronomic trends influence these categories, we adopted the following criteria:

- If the taxon is described in the literature as both non-edible and edible, we classified it as a non-edible.
- If the taxon is described in the literature as having doubtful edibility, we classified it as a non-edible.
- *Lycoperdon perlatum* is considered in the literature an edible fungus when collected young, but non-edible when collected in the late phase. In the present work, we classified this fungus as a non-edible.

The effects of the variables were analyzed by ANOVA, with type III sums of squares due to the unbalanced design. The dependent variables were *fresh weight*, *dry weight*, or *number* of sporocarps and the factors were *forest age* and *aspect*. The data were transformed as necessary to meet ANOVA assumptions (Steel and Torrie, 1984). Taxa occurring in less than four plots were excluded from the analysis due to heterocedasticity and are reported as present/absent. All calculations were performed with DataDesk 6.1.1 (Data Description, Inc., Ithaca, NY, USA).

3. Results

3.1. General data

A total of 9073 sporocarps were collected in the three study years. The length of the autumn seasons varied from 9 to 11 weeks. Harvest period always started in September and finished in November. Fungi were classified into 164 different taxa, 144 of which are ectomycorrhizal, belonging to 34 genera (Table 3). There are 11 generic level taxa for which further identification was not possible and generally include more than a sinlge species: *Clitocybe* sp., *Cortinarius* sp., *Hebeloma* sp., *Hydnellum* sp., *Hygrocybe* sp., *Hygrophorus* sp., *Inocybe* sp., *Lactarius* sp., *Ramaria* sp., *Russula* sp., and *Tricholoma* sp.

Four genera comprised 62% and seven species 47% of the total number of sporocarps collected. The genus *Tricholoma* comprised 26% of the total, and the most frequent species were *Tricholoma imbricatum* (12% of the total) and *Hebeloma edurum* (11% of the total) (Fig. 1).

Taxa are classified according to edibility as well as commercial status (Table 3). Sixty percentage of total taxa are non-edibles, 30% are edible non-marketed, and 10% are edible marketed taxa (Fig. 2).

3.2. Yields

The non-edible fungi represent only 26% of total yield in fresh weight. Edible-marketed fungi represent 20% and the edible non-marketed fungi represent 54% of total yield, more than twice the biomass of non-edibles (Fig. 2).

Mushrooms were found in all the study plots but not every year of collection (Table 3). The greatest production from a single plot over the 3 years was 743.5 kg fw/ha. One plot was non-productive for two of the three sampling years.

Mushroom yields differed among plots and by year. The best season was 1996 with an average plot yield of 149.4 kg fw/ha (15.2 kg dw/ha and 11,861 sporocarps/ha). The poorest was 1997 with an average

Table 3
Species list for ectomycorrhizal and edible epigeous fungi collected for three study years in the Spanish Pyrenees with mycorrhizal status, frequency among plots, yearly presence and yields

Species	Mycorrhizal status	Number of plots	Presence			Edibility	Mean (95% CI) significance		
			1995	1996	1997		Fresh weight (kg/ha/year)	Dry weight (kg/ha/year)	Number of sporocarps/ha/year
Agaricus haemorrhoidarius Schulz. sp. Kalchbr.	No	1	0	0	1	E			
Aleuria aurantia (Fr.) Fuck.	No?	1	1	1	0	E			
Astraeus hygrometricus (Pers.) Morg.	Yes	1	1	0	0	NE			
Boletus fragrans Vitt.	Yes	1	1	0	0	E			
Cantharellus cibarius Fr.	Yes	1	1	0	0	EM			
Cantharellus lutescens (Pers.) Fr.	Yes	1	0	0	1	EM			
Chroogomphus helveticus (Sing.) Mos.	Yes	14	1	0	1	E	0.14 (0.05, 0.23)	0.01 (0.01, 0.02)	4.70 (1.61, 11.30)
C. rutilus (Sch.) Miller	Yes	29	1	1	1	EM	0.82 (0.54, 1.27)	0.14 (0.09, 0.22)	76.5 (32.8, 176.7)
Clavulina cinerea (Bull.) Schroet.	Yes	1	0	1	0	E			
Clitocybe brumalis (Fr.) Quél.	No?	1	0	1	0	NE			
Clitocybe cerussata (Fr.) Kumm.	No?	1	0	0	1	NE			
Clitocybe costata Kuehn. & Romagn.	No?	6	1	0	1	E	0.07 (0.00, 0.15)	0.005 (<0.001, 0.009)	1.01 (0.16, 2.49)
Clitocybe cyanolens Metr.	No?	1	0	1	0	NE			
Clitocybe dealbata (Sow.) Kumm.	No?	1	0	0	1	NE			
Clitocybe diatreta (Fr.) Kumm.	No?	2	0	1	1	NE			
Clitocybe gibba (Pers.) Kumm.	No?	5	1	1	1	E	0.05 (0.00, 0.11)	0.004 (0.000, 0.008)	0.80 (0.08, 2.00)
Clitocybe nebularis (Batsch) Kumm.	No?	2	1	1	0	E			
Clitocybe odora (Bull.) Kumm.	No?	2	1	1	0	E			
Clitocybe sinopica (Fr. ex Fr.) Kumm.	No?	1	1	0	0	E			
Clitocybe sinopicoides Peck.	No?	1	1	0	0	E			
Clitocybe sp.	No?	9	0	1	0	NE	0.09 (<0.01, 0.17)	0.004 (0.002, 0.014)	2.06 (0.55, 5.05)
Clitopilus prunulus (Scop.) Kumm.	Yes	4	1	1	0	E	0.07 (0.00, 0.18)	0.003 (0.000, 0.007)	0.68 (0.00, 1.83)
Collybia butyracea (Bull.) Kumm.	No?	2	0	0	1	E			
Cortinarius allutus (Secr.) Fr.	Yes	1	0	1	0	E			
Cortinarius amoenolens R. Hry.	Yes	4	0	1	0	NE	0.12 (0.00, 0.24)	0.005 (0.000, 0.012)	0.48 (0.01, 1.16)
Cortinarius bivelus Fr.	Yes	1	0	0	1	NE			
Cortinarius camurus (Bull. ex Fr.) Fr.	Yes	2	0	1	0	NE			
Cortinarius fulvoochrascens Mos.	Yes	2	0	1	0	NE			
Cortinarius guttatus R. Hry.	Yes	1	0	0	1	NE			
Cortinarius herbarum R. Hry.	Yes	1	0	0	1	E			
Cortinarius lilacinopes Britz.	Yes	1	0	1	0	NE			
Cortinarius multiformis (Fr.) Fr.	Yes	4	0	1	1	E	0.73 (0.00, 1.84)	0.01 (0.00, 0.02)	0.73 (0.00, 2.00) Ag
Cortinarius parherpeticus R.Hry.	Yes	1	0	0	1	NE			
Cortinarius saniosus (Fr.) Fr.	Yes	3	1	0	1	NE			
Cortinarius tenebricus Favre	Yes	1	0	1	0	NE			
Cortinarius variegatus Bres.	Yes	1	0	1	0	NE			
Cortinarius vibratilis (Fr.) Fr.	Yes	1	0	1	0	NE			

Table 3 (*Continued*)

Species	Mycorrhizal status	Number of plots	Presence			Edibility	Mean (95% CI) significance		
			1995	1996	1997		Fresh weight (kg/ha/year)	Dry weight (kg/ha/year)	Number of sporocarps/ha/year
Cortinarius sp. Subgen. *Leprocybe* Mos.	Yes	1	1	1	0	NE			
Cortinarius sp. Subgen. *Myxacium* sec. *Ochroleuci* (Fr.) Laud.	Yes	1	1	0	0	NE			
Cortinarius sp. Subgen. *Phlegmacium* sec. *Scauri* Fr. subsec. *Orichalcei*	Yes	1	0	0	1	NE			
Cortinarius sp. Subgen. *Phlegmacium* sec. *Scauri* Fr. subsec. *Purpurascents*	Yes	1	1	0	0	NE			
Cortinarius sp. Subgen. *Phlegmacium* sec. *Scauri* Fr.	Yes	6	1	1	1	NE	0.18 (0.01, 0.35)	0.007 (0.000, 0.014)	0.90 (0.15, 2.13) Ag
Cortinarius sp. Subgen. *Phlegmacium* Fr.	Yes	8	1	1	0	NE	0.60 (0.04, 1.16)	0.02 (0.01, 0.04)	1.65 (0.40, 4.01) Ag
Cortinarius sp. Subgen. *Sericeocybe* P.D. Orton sec. *Anomali*	Yes	1	1	0	0	NE			
Cortinarius sp. Subgen. *Sericeocybe* P.D. Orton sec. *Opimi*	Yes	7	1	0	0	NE	0.04 (0.01, 0.08) Ag, As	0.003 (0.001, 0.007) Ag, As	14.5 (4.0, 24.8) Ag, As
Cortinarius sp. Subgen. *Sericeocybe* P.D. Orton	Yes	5	1	1	0	NE	0.27 (0.00, 0.66)	0.02 (0.00, 0.04)	0.93 (0.08, 2.46) Ag
Cortinarius sp. Subgen. *Telamonia* (Fr.) Loudon	Yes	4	1	1	0	NE	0.13 (0.00, 0.29)	0.01 (0.00, 0.03)	0.72 (0.00, 2.00)
Cortinarius sp.	Yes	22	1	1	1	NE	0.58 (0.32, 0.89)	0.05 (0.03, 0.08) Ag	65.0 (29.0, 115.2) Ag
C. amianthinum (Scop. ex Fr.) Fay.	Yes	13	1	1	1	NE	0.09 (0.04, 0.16) Ag	0.010 (0.004, 0.017) Ag	6.15 (1.86, 16.9) Ag
Cystoderma carcharias (Pers. ex Secr.) Fay.	Yes	12	1	1	1	NE	0.10 (0.03, 0.18)	0.01 (0.00, 0.02)	4.51 (1.29, 12.3) Ag
Cystoderma cinnabarinum (A. & S. ex Secr.) Fay.	Yes	1	0	0	1	NE			
Cystoderma fallax Smith & Sing.	Yes	1	0	0	1	NE			
Cystoderma terrei (Bk. & Br) Harmaja	Yes	1	0	0	1	NE			
Hebeloma anthracophilum R. Mre.	Yes	1	1	0	0	NE			
Hebeloma crustuliniforme (Bull. ex Fr.) Quél.	Yes	10	1	1	0	NE	1.28 (0.00, 2.68)	0.02 (0.01, 0.04)	3.35 (0.86, 9.28)
Hebeloma cylindosporum Romagn.	Yes	1	1	0	0	NE			
H. edurum Metr.	Yes	15	1	1	1	NE	0.27 (0.13, 0.47) As	0.03 (0.01, 0.05) As	1.65 (0.68, 3.80) As
Hebeloma mesophaeum (Pers. ex Fr.) Quél.	Yes	1	1	0	0	NE			
Hebeloma pallidum Mal.	Yes	1	1	0	0	NE			
Hebeloma sacchariolens Quél.	Yes	1	0	0	1	NE			
Hebeloma sinapizans (Paulet ex Fr.) Gill.	Yes	10	1	0	1	NE	0.38 (0.13, 0.73)	0.04 (0.01, 0.08) As	4.25 (1.05, 12.4) As
Hebeloma subsaponaceum Karst.	Yes	2	1	0	0	NE			
Hebeloma truncatum (Schff. ex Fr.) Kumm.	Yes	1	1	0	0	NE			
Hebeloma sp.	Yes	10	1	1	1	NE	0.08 (0.03, 0.15)	0.010 (0.003, 0.018)	2.82 (0.75, 7.33)
Hydnellum aurantiacum (Batsch ex Fr.) Karst.	Yes	6	1	1	1	NE	0.09 (0.00, 0.20) Ag	0.006 (0.001, 0.013) Ag	1.10 (0.17, 2.71) Ag

Hydnellum caeruleum (Hornem. ex Pers.) Karst.	Yes	3	1	1	1	NE			
Hydnellum concrescens (Pers. ex Schw.) Banker	Yes	1	0	0	1	NE			
Hydnellum ferrugineum (Fr. ex Fr.) Karst.	Yes	1	0	0	1	NE			
Hydnellum scrobiculatum (Fr.) Karst.	Yes	2	0	0	1	NE			
Hydnellum spongiosipes (Peck) Pouz.	Yes	2	0	0	1	NE			
Hydnellum sp.	Yes	1	0	1	0	NE			
Hydnum repandum L.	Yes	1	1	0	0	EM			
Hydnum repandum var. *rufescens* Fr.	Yes	1	1	0	0	NE			
Hygrophoropsis aurantiaca (Wulf.) R. Mre.	Yes	1	1	0	0	E			
Hygrophorus agathosmus (Fr.) Fr.	Yes	11	1	1	0	EM	0.19 (0.06, 0.33)	0.02 (0.01, 0.04)	3.51 (0.97, 9.28)
Hygrophorus chrysodon (Batsch) Fr.	Yes	2	1	0	0	E			
Hygrophorus eburneus (Bull.) Fr.	Yes	10	1	1	1	EM	0.35 (0.11, 0.67)	0.02 (0.01, 0.03)	4.31 (1.03, 13.0)
Hygrophorus gliocyclus Fr.	Yes	2	0	0	1	E			
Hygrophorus hypothejus (Fr.) Fr.	Yes	1	1	0	0	E			
Hygrophorus latitabundus Britz.	Yes	1	0	0	1	EM			
Hygrophorus persicolor Ricek.	Yes	1	0	0	1	E			
Hygrophorus sp.	Yes	1	1	1	0	NE			
Hygrocybe quieta (Kühn.) Sing.	Yes	1	1	0	0	NE			
Hygrocybe reae (R. Mre.) Lange	Yes	1	1	0	0	NE			
Hygrocybe sp.	Yes	5	1	0	0	NE	0.05 (0.00, 0.11)	0.004 (0.000, 0.008)	0.77 (0.07, 1.94)
Inocybe fastigiata (Schff. ex Fr.) Quél.	Yes	1	1	0	0	NE			
Inocybe geophyllum (Bull.) Karst.	Yes	1	1	0	0	NE			
Inocybe maculata Boud.	Yes	1	1	0	0	NE			
I. nitidiuscula (Britz.) Sacc.	Yes	7	1	1	0	NE	0.07 (<0.01, 0.15) Ag	0.013 (0.001, 0.026) Ag, As	1.56 (0.31, 3.99) Ag, As
Inocybe perlata (Cke.) Sacc.	Yes	1	1	0	0	NE			
Inocybe pyriodora (Pers. ex Fr.) Quél.	Yes	1	0	0	1	NE			
Inocybe terrigena (Fr.) Kühn.	Yes	1	0	1	1	NE			
Inocybe sec. Depauperateae Lge.	Yes	1	1	0	0	NE			
Inocybe sp.	Yes	19	1	1	1	NE	0.16 (0.08, 0.26) Ag	0.02 (0.01, 0.03) Ag	66.3 (26.1, 124.5) Ag
L. amethystina (Balt. ex Hooker) Murr.	Yes	5	1	0	0	E	0.02 (<0.01, 0.04) Ag	0.0004 (0.000, 0.0008) Ag	0.79 (0.08, 1.92) Ag
Laccaria bicolor (R. Mre.) Orton	Yes	1	1	0	0	E			
Laccaria laccata (Scop.) Bk. & Br.	Yes	3	1	1	1	E			
Laccaria laccata var. *moelleri* Sing.	Yes	1	1	0	0	E			
Lactarius aurantiofulvus Blum ex Bon.	Yes	3	1	1	1	E			
L. deliciosus (L.) S.F. Gray.	Yes	17	1	1	1	EM	1.36 (0.54, 2.63)	0.15 (0.06, 0.29)	10.4 (3.44, 27.8)
Lactarius piperatus (Scop.) S. F. Gray.	Yes	1	1	0	1	E			
L. sanguifluus (Paul.) Fr.	Yes	4	0	0	1	EM	0.05 (0.00, 0.11)	0.01 (0.00, 0.02)	0.54 (0.01, 1.34)
Lactarius scrobiculatus (Scop.) Fr.	Yes	1	0	0	1	NE			
L. semisanguifluus Heim. & Lecl.	Yes	6	1	1	0	EM	0.64 (0.02, 1.26) Ag	0.01 (0.00, 0.03) Ag	1.44 (0.22, 3.85)
Lactarius sp.	Yes	1	0	1	0	NE			
Lepista nuda (Bull.) Cke.	Yes	4	1	1	0	E	0.23 (0.00, 0.54)	0.01 (0.00, 0.02)	0.63 (0.01, 1.64)

Table 3 (*Continued*)

Species	Mycorrhizal status	Number of plots	Presence			Edibility	Mean (95% CI) significance		
			1995	1996	1997		Fresh weight (kg/ha/year)	Dry weight (kg/ha/year)	Number of sporocarps/ha/year
Lepista sp. (Fr.) W.G. Smith	Yes	1	0	1	0	NE			
L. perlatum Pers.	Yes	9	1	1	0	E	0.09 (0.03, 0.15)	0.014 (0.005, 0.026)	0.69 (0.22, 1.52)
Lycoperdon pyriforme Sch.	Yes	6	1	0	1	NE	0.07 (0.00, 0.17)	0.005 (0.000, 0.011)	1.14 (0.17, 2.94)
Lycoperdon sp.	Yes	1	0	0	1	NE			
Lyophyllum crassifolium (Bk.) Sing.	No?	1	0	1	0	E			
Macrolepiota mastoidea (Fr.) Sing.	No?	1	1	0	0	EM			
Macrolepiota procera (Scop.) Sing.	No?	3	1	1	0	EM			
Paxillus atrotomentosus (Batsch) Fr.	Yes	2	0	0	1	NE			
Peziza badia Pers.	No?	1	0	0	1	E			
Phellodon confluens (Pers.) Pouz.	Yes	2	0	0	1	NE			
Phellodon niger (Fr.) Karst.	Yes	10	1	1	1	NE	0.27 (0.07, 0.54) Ag	0.02 (0.01, 0.03)	3.71 (0.87, 10.86)
Phellodon tomentosus (L.) Banker	Yes	4	1	0	1	NE	0.37 (0.00, 0.98)	0.13 (0.00, 0.36)	0.67 (0.00, 1.77)
Pleurotus ostreatus (Jacq.) Kumm.	No	1	1	0	0	EM			
Ramaria flavescens (Schaeff.) ex Petersen	Yes	1	0	0	1	NE			
Ramaria gracilis (Fr.) Quél.	Yes	7	0	0	1	NE	0.18 (0.01, 0.35)	0.01 (0.00, 0.02) Ag	0.99 (0.23, 2.22) Ag, As
Ramaria sp.	Yes	5	0	1	1	NE	0.14 (0.00, 0.34)	0.02 (0.00, 0.05)	1.01 (0.08, 2.82) Ag
Ramaria stricta (Pers.) Quél.	Yes	4	0	0	1	NE	0.01 (0.00, 0.02)	0.003 (0.000, 0.006)	0.54 (0.01, 1.34)
Russula acrifolia Romagn.	Yes	2	0	1	0	E			
Russula adulterina Fr.	Yes	1	0	0	1	NE			
Russula albonigra (Krombh.) Fr.	Yes	1	0	0	1	E			
Russula alutacea (Pers.) Fr.	Yes	1	0	1	0	NE			
Russula amarissima Romagn. & Gilb.	Yes	1	0	0	1	NE			
Russula densifolia Gill.	Yes	2	0	0	1	E			
Russula integra (L.) Fr.	Yes	2	0	1	0	E			
Russula luteotacta Rea.	Yes	5	0	1	1	NE	0.29 (0.02, 0.55) Ag, As	0.04 (0.00, 0.06) Ag, As	0.95 (0.09, 2.49) Ag, As
Russula odorata Romangn.	Yes	3	0	1	0	NE			
R. torulosa Bres.	Yes	11	0	1	1	NE	0.24 (0.09, 0.43) Ag	0.02 (0.01, 0.04) Ag	3.85 (1.06, 10.39) Ag
Russula turci Bres.	Yes	3	0	1	1	E			
Russula sp. sec. *Decolorantes* (R. Mre.) Sing.	Yes	1	0	0	1	NE			
Russula sp.	Yes	15	1	1	1	NE	0.47 (0.19, 0.87)	0.03 (0.01, 0.04) Ag	1.56 (0.65, 3.48) Ag
Sarcodon imbricatum (L.) Karst.	Yes	2	1	1	0	E			
Sarcodon joeides (Pass.) Pat.	Yes	2	0	0	1	NE			
Suillus bovinus (L.) Kuntze.	Yes	10	1	0	1	E	0.35 (0.11, 0.69) Ag	0.02 (0.01, 0.03)	2.90 (0.77, 7.0)
S. collinitus (Fr.) Kuntze.	Yes	19	1	1	1	E	0.98 (0.46, 1.68) Ag	0.04 (0.02, 0.07) Ag	51.3 (19.4, 98.0) Ag
Suillus granulatus (L.) Kuntze.	Yes	21	1	1	1	E	0.78 (0.42, 1.30)	0.05 (0.03, 0.07)	15.0 (5.8, 36.7)
S. luteus (L.) S.F. Gray.	Yes	25	1	1	1	E	2.19 (1.03, 3.95)	0.12 (0.07, 0.21)	118 (49, 216)
S. variegatus (Swartz) Kuntze.	Yes	15	1	1	1	EM	1.65 (0.64, 3.27) Ag	0.09 (0.04, 0.16) Ag	10.4 (3.1, 30.9) Ag

Tricholoma albobrunneum (Pers. ex Fr.) Kumm.	Yes	19	1	1	0	E	0.89 (0.43, 1.62)	0.16 (0.07, 0.31) As	15.2 (5.17, 41.5)
Tricholoma angulatum (Fr.) Quél.	Yes	1	1	0	0	NE			
Tricholoma argyraceum (Bull.) Gill.	Yes	1	1	0	0	E			
Tricholoma bufonium (Pers.) Gill.	Yes	2	0	1	1	NE			
Tricholoma equestre (L.) Quél.	Yes	1	0	0	1	EM			
Tricholoma fracticum (Britz.) Kreis	Yes	10	1	0	1	NE	0.23 (0.08, 0.43)	0.02 (0.01, 0.04)	0.78 (0.27, 1.67)
Tricholoma gausapatum (Fr.) Quél.	Yes	1	1	0	0	E			
T. imbricatum (Fr.) Kumm.	Yes	15	1	1	1	NE	2.39 (0.90, 5.05)	0.11 (0.05, 0.21)	16.6 (4.26, 58.2)
Tricholoma inoncybeoides Pears.	Yes	1	0	0	1	NE			
Tricholoma luridum Lasch ex Fries	Yes	2	1	0	0	NE			
Tricholoma portentosum (Fr.) Quél.	Yes	1	1	0	0	E			
Tricholoma robustum (A. & S.) Ricken	Yes	7	0	1	0	E	1.21 (0.00, 2.74)	0.01 (0.00, 0.02)	1.75 (0.34, 4.64)
Tricholoma saponaceum (Fr.) Kumm.	Yes	1	0	0	1	NE			
Tricholoma scalpturatum (Fr.) Quél.	Yes	2	1	0	0	E			
Tricholoma sejunctum (Soe.) Quél.	Yes	2	1	0	0	E			
Tricholoma stans (Fr.) Sacc.	Yes	1	1	0	0	NE			
Tricholoma sulphureum Kumm.	Yes	2	1	1	1	NE			
T. terreum (Sch.) Kumm.	Yes	22	1	1	1	EM	0.49 (0.27, 0.82)	0.04 (0.02, 0.07)	32.45 (10.70, 95.54)
Tricholoma ustaloides Romagn.	Yes	1	1	0	0	NE			
Tricholoma vaccinum (Sch.) Kumm.	Yes	1	1	0	0	E			
Tricholoma sp.	Yes	2	0	0	1	NE			
Total yield							60.6 (40.3, 91.8)	6.93 (4.61, 10.50)	5013 (3261, 7554)
Edible yield							44.7 (29.3, 63.4)	3.53 (2.38, 5.27)	2079 (1393, 3102)
Marketed yield							11.9 (7.4, 18.7)	1.41 (0.89, 2.19)	811 (528, 1248)
Marketed *Lactarius* sp.							1.79 (0.81, 3.30)	0.20 (0.09, 0.37)	20.6 (7.3, 54.9)

Taxa whose mycorrhizal status could not be confirmed are listed as "No?". The column "number of plots" indicates the number of plots from which each taxa was collected. "Presence" refers to the occurrence of the taxa during 1995, 1996 and 1997 (1 = collected, 0 = non-collected). In the column "edibility" taxa are grouped by three categories: E = edible non-marketed; EM = edible marketed; NE = non-edible. Mean yield and 95% confidence interval (CI) expressed in fresh weight, dry weight and number of sporocarps/ha are reported for taxa which occurred in four or more plots, as well as for the groups "total", "edible", "marketed" and "marketed *Lactarius* sp.". "Ag" and "As" indicate a significant ($P < 0.10$) relationship between the variable and forest age and aspect, respectively.

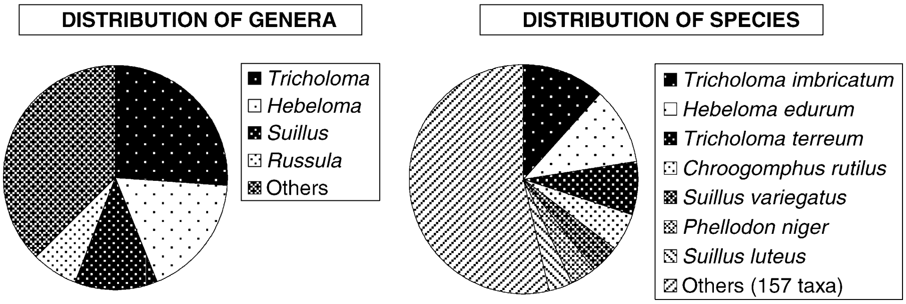

Fig. 1. Distribution of the total 9073 sporocarps collected by genus and by species. Of the 34 genera observed, 4 genera comprise 62% of the total, and 7 species comprise 47% of the total 164 taxa observed.

plot yield of 27.5 kg fw/ha (4.2 kg dw/ha and 1685 sporocarps/ha). The average plot yield over the 3 years was 60.6 kg fw/ha/year (6.93 kg dw/ha/year and 5013 sporocarps/ha/year) (Fig. 3).

Chroogomphus rutilus was the most widely distributed taxon, collected in 29 of the 36 plots. *Suillus luteus* was collected in 25 plots and *T. terreum* in 22 plots. Approximately 50% of the total, 82 taxa, were collected from single plots. Only 25 taxa were collected in 10 or more plots, 5 of which are genus level taxa which include several unidentified species (Table 3).

In order to focus on the more frequently occurring fungi, only taxa that were collected in four or more plots were included in our analyses of the effects of age class and aspect. The yields (fresh weight, dry weight and number of sporocarps) of the analyzed taxa are given in Table 3. In our analysis we grouped the

Fig. 2. Distribution according to edibility and commercial status of the total sporocarp collection by number of taxa and by yield of taxa in fresh weight.

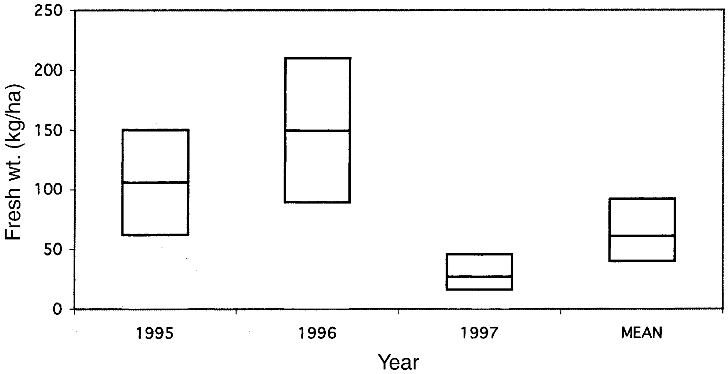

Fig. 3. Median and 95% confidence interval of total mushroom yield in fresh weight kg/ha for each of the 3 years of the study and the 3-year mean.

data of the three species *L. deliciosus*, *Lactarius sanguifluus* and *Lactarius semisanguifluus* under the single name "marketed *Lactarius* sp." because all three are sold together (under the name "rovelló") in the markets of the central Pyrenees.

3.3. Effect of stand age and aspect

We found that the level of significance of differences for age class and aspect for a given taxon in fresh weight, dry weight, or number of sporocarps is not always the same although the patterns are consistent for all three measurements. The 21 and 7 taxa for which a significant difference ($P < 0.10$) was observed for age class and/or aspect respectively are indicated in Table 3.

Significant influences ($P < 0.05$) of age class were observed for five individual taxa as shown in Fig. 4, demonstrating the patterns of distribution among of different forest age classes for dry weight and number of sporocarps. We found *Suillus variegatus* more frequently in older forests while *Suillus collinitus* was found with higher frequency in plots of younger age-class. *Cystoderma amianthinum* was collected in forests of age classes III, IV, V, VII and VIII and no sporocarps of this species were collected from the forests of younger age classes. *Russula torulosa* was present in almost all age class, but was most abundant in the intermediate and older age-classes. *Laccaria amethystina* was collected more abundantly in 25–34-year-old forests.

Significant influences ($P < 0.05$) of aspect were observed for two individual species as shown in Fig. 5. *H. edurum* was most productive on eastern slopes. *Inocybe nitidiuscula* was collected more frequently on western and southern slopes.

Sporocarps of the group "marketed *Lactarius* sp." were found in all age classes and were present on all aspects in these forests. However one of the three species making up this group, *L. semisanguifluus* was found most frequently in forests of age class VII. The distribution of this species and the group "marketed *Lactarius* sp." across age classes are shown in Fig. 6.

3.4. Species richness

We calculated the number of taxa per plot and the Shannon's index (*H*), utilizing fruitbody biomass as an indicator of total biomass, for each taxon. We did not observe significant differences in age class or aspect with respect to species richness. Mean number of taxa/plot was 19.5 (95% confidence interval (CI): 16.6–22.4) and mean H was 1.84 (95% CI: 1.66–2.02).

The greatest diversity observed in an individual plot for a single year was 21 identified taxa ($H = 2.16$) and the highest for the study as a whole was 36 taxa in one plot over 3 years ($H = 2.76$).

Species richness varied from 1 year to the next, but this variation is not as remarkable as the variation in productivity. Total yield of 1996 was higher (Fig. 3), but as shown in Fig. 7, the number of identified taxa was lower.

How does species richness relate to yield? It seems that the more diverse plots were also the more productive. This positive relationship was reflected not only in total yields (fw, dw and number of sporocarps) but also in yields of edible, marketed-edible and marketed *Lactarius* sp. (Table 4).

4. Discussion

4.1. General data

Thousands of individual sporocarps (9073) were collected from the 36 study plots (3600 m^2 total) over 3 years. The 144 ectomycorrhizal fungi represent the highest number reported for ectomycorrhizal taxa in *P. sylvestris* forest stands. In other studies of fungal sporocarp production in *P. sylvestris* forests, Hintikka (1988), in southern Finland, found 80 species in 25 stands of 0.3–0.5 ha, although he collected more individual sporocarps (11,542). Väre et al. (1996) reported 152 species associated with *P. sylvestris* in Finnish Lapland, 90 of them ectomycorrhizal and Salo (1979) in 18 plots of 150 m^2 each, observed 107 species on fertilized and drained peat lands where *P. sylvestris* was the dominant tree species.

Species of the genera *Tricholoma*, *Hebeloma*, *Suillus* and *Russula* comprised 62% of total sporocarps in the present study. Hernández and Fernández (1998) observed that fungi from the genera *Tricholoma* were also the most abundant in *P. pinaster* forests of central Spain.

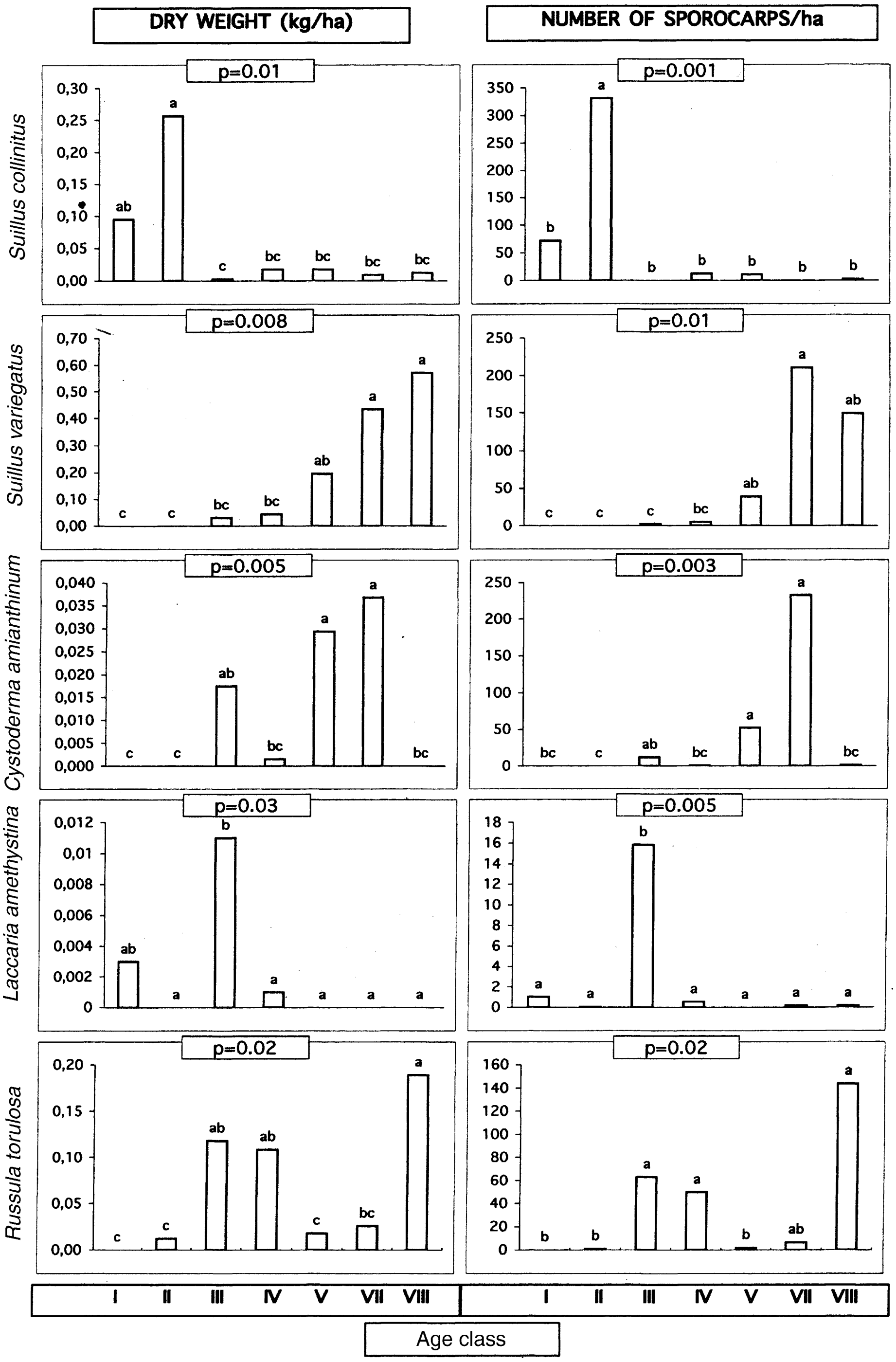

Fig. 4. Mean dry weight (kg/ha/year) and mean number of sporocarps/ha/year collected over 3 years for *S. collinitus*, *S. variegatus*, *C. amianthinum*, *L. amethystina* and *R. torulosa* by forest age class in the 36 study plots. Different letters indicate significant differences between age classes at $P \leq 0.05$.

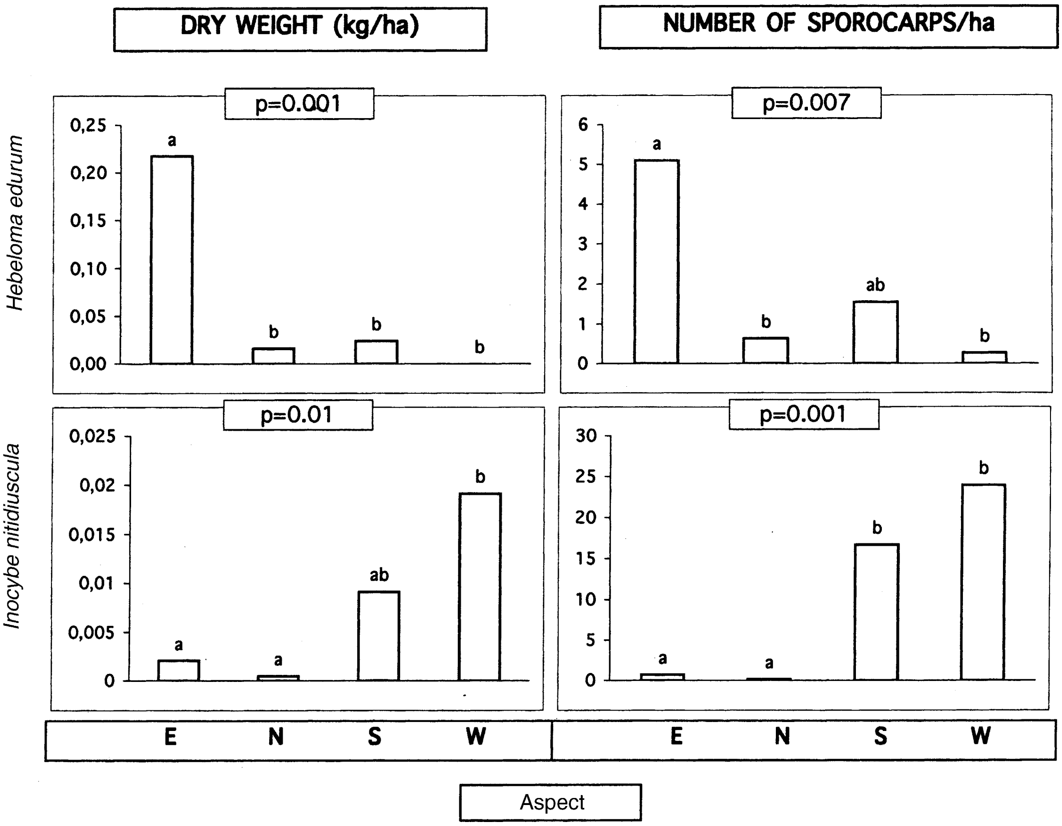

Fig. 5. Mean dry weight (kg/ha/year) and mean number of sporocarps/ha/year collected over 3 years for *H. edurum* and *I. nitidiuscula* by aspect in the 36 study plots. E = East, N = North, S = South and W = West. Different letters indicate significant differences between aspects at $P \leq 0.05$.

Fig. 6. Mean fresh weight (kg/ha/year) collected over 3 years for *L. semisanguifluus* and "Marketed *Lactarius* sp." by forest age class in the 36 study plots. Different letters indicate significant differences between age classes at $P \leq 0.05$.

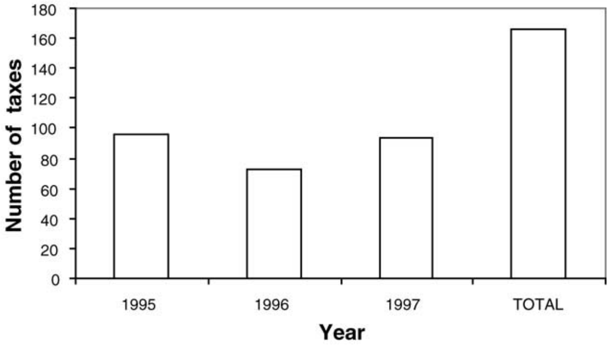

Fig. 7. Total number of taxa collected for each of the three study years and the 3-year total.

4.2. Variability in sporocarp production and distribution

The highest sporocarp production on a single plot was 743.5 kg fw/ha/year. Although no sporocarps were found on three plots during a single autumn of the study, all inventoried plots were productive at least once during the three collection seasons. Variations in annual mushroom production reported reveal yields of 0–940 kg fw/ha in mixed pine plots (Mehus, 1986), and of 1.12 kg dw/ha in the poorest season and of 9.69 kg dw/ha in the best (Väre et al., 1996). Sporocarp production not only varies considerably between different years in the same locality (Ohenoja, 1993), but also between different plots of the same aspect or age class in the same year, emphasizing the necessity of collecting samples for several years to adequately characterize the sporocarp composition and production of fruiting fungi in a given site.

Half of the total taxa were collected only once in our study. This phenomenon has been observed also by Hintikka (1988) and Tyler (1989b), who reported that the majority of the 302 fungi observed in deciduous forests of Sweden were found in less than 10–15% of sites and Väre et al. (1996) who found that 72 of the total 167 stipitate fungi were collected from single sites. O'Dell et al. (1999) in eight mixed *Tsuga heterophylla–Pseudotsuga menziesii* stands of the Pacific Northwest, USA also found the majority of fungal species in single stands, fruiting only one of two sampled autumns. The abundance of rare or single fruitings of some fungi is congruent with recent molecular studies which reveal that the majority of ectomycorrhizal species present in forest soils rarely or never produce obvious fruit bodies (Dahlberg, 2001).

4.3. Edible production

Edible taxa represented 40% of our total taxa but comprised 74% of fresh weight production. This can be explained by the larger individual sporocarps of edible fungi. Similarly, Väre et al. (1996) found that

Table 4
Positive relationship observed between number of taxa/plot and total yield (fresh weight (FW), dry weight(DW) and number of sporocarps (NS)) edible yield (fresh weight), marketed yield (fresh weight) and marketed *Lactarius* sp. (fresh weight)

Dependent variable	P	R^2 (%)	Model
Total yield (FW)	<0.0001	65.70	$\log(y) = -0.14(\text{S.E.: } 0.24) + 1.56(\text{S.E.: } 0.19)\log(x)$
Total yield (DW)	<0.0001	64.0	$\log(y) = -1.03(\text{S.E.: } 0.24) + 1.52(\text{S.E.: } 0.19)\log(x)$
Total yield (NS)	<0.0001	71.0	$\log(y) = 1.93(\text{S.E.: } 0.19) + 1.45(\text{S.E.: } 0.16)\log(x)$
Edible yield (FW)	<0.0001	53.5	$\log(y) = -0.17(\text{S.E.: } 0.27) + 1.36(\text{S.E.: } 0.22)\log(x)$
Marketed yield (FW)	<0.0001	44.2	$\log(y) = -0.71(\text{S.E.: } 0.34) + 1.42(\text{S.E.: } 0.27)\log(x)$
Marketed *Lactarius* sp. (FW)	0.0109	17.6	$\log(y + 0.1) = -1.62(\text{S.E.: } 0.34) + 1.27(\text{S.E.: } 0.27)\log(x)$

average annual production of edible species was nearly 70% of the total.

Our average, total fresh yield per plot/year was 60.6 kg/ha with 44.7 kg/ha of edible yield. Fernández et al. (1993) in *P. sylvestris* forests of central Spain reported 36 kg/ha of edible mushrooms.

Similar or higher fresh yields were reported by Kardell and Eriksson (1987) from Sweden with 43.2 kg/ha of edible fungi, and by Shubin (1988) who collected 153 kg/ha of edible mushrooms from *P. sylvestris* stands in Russia. From Estonian pine heaths Kalamees and Silver (1988) reported yields of 188–504 kg/ha of which 143–409 kg/ha were edible. Among our 164 fungal taxa, 65 are edible, but only 16 are marketed, a situation common in many countries.

Our highest yields for individual edibles were obtained from *T. imbricatum* (2.39 kg fw/ha), *S. luteus* (2.19 kg fw/ha) and *S. variegatus* (1.65 kg fw/ha). *S. variegatus* is one of the most common and heavily fruiting commercial edible mushroom species reported in the literature from European forests. In two studies from Finnish *P. sylvestris* forests, Ohenoja and Koistinen (1984) found it to be the most productive commercial species (7.9 kg fw/ha) and Salo (1993) reported average collections of 11.4 kg fw/ha of *S. variegatus*.

4.4. *Influence of age class and aspect*

In our study we were particularly interested in results obtained for *L. deliciosus* due to its high commercial importance in northeastern Spain. Our results for marketed *Lactarius* sp. indicate that these fungi are present in *P. sylvestris* forests of all age classes represented in this study and show no preference for aspect. These results have important implications for local pickers and forest managers. In an Oregon, USA *Pseudotsuga menzesii* forest study of fungi by age class, researchers observed *L. deliciosus* fruiting in forests of 30–50 years, the most rapid growth period for these forests, but absent in the Old Growth forests of 400+ years (Smith et al., 2002). In a study of edible mushroom production in 2-year-old *Pinus montezumae* plantations of Mexico, Zamora-Martínez and Nieto de Pascual (1995) reported collections of 25.9 kg/ha of *L. deliciosus* from open-canopy conditions within mature stands. If, by modifying forest structure, we could create within mature stands key environmental or microclimate conditions of younger forests that support the requirements of *L. deliciosus*, this species may proliferate in the new habitat.

Forest age is a more influential factor than aspect in this study although we did not observe differences in total production by age class. Reports of forest mushroom yield by age class are extremely variable across forest types. Chibisov and Demidova (1998) observed that young stands of 15–35 years have the highest mushroom production in the northern taiga mixed-coniferous forests of Russia, and Keizer and Arnolds (1994) reported higher sporocarp numbers in mature oak plots (20–50-year-old) than in young oak plots (10–20-year-old). In Finland, where Hintikka (1988) compared mushroom yields in pine forests of different age-classes, 20–30-year-old stands produced the most fruitbodies. Kalamees and Silver (1988) found that total and edible mushroom yields were greatest in 25-year-old *P. sylvestris*-dominated heath stands.

Our observations are not totally consistent with the concept of early and late-stage fungi (Dighton and Mason, 1985). The successional fruiting theories of ectomycorrhizal forest fungi (Mason et al., 1982; Last et al., 1983; Fleming et al., 1986; Dighton et al., 1986) describe a sequence which characterizes the species of *Hebeloma*, *Laccaria* and *Inocybe* as early stage, *Cortinarius* and *Tricholoma* as intermediate-stage and *Russula*, *Amanita* and *Leccinum* as late-stage symbionts. We found no significant relationships between the age class and the presence of *Hebeloma* sp. or *Inocybe* sp., genera which are described as early stage. We did find a significantly higher number of *R. torulosa* sporocarps in medium-to-older forest stands.

Keizer and Arnolds (1994) proposed a schematic classification of ectomycorrhizal species based on their appearance during forest development and general changes in forest architecture. Forest age is a principal factor, but highly interactive with other environmental factors such as land-use history, soil organic matter, silvicultural treatments and climate conditions. Termoshuizen (1990) and Baar and De Vries (1995) concluded that the aging of the forest soil rather than the trees determines ectomycorrhizal species composition in developing forests.

Often age class is associated with open or closed canopy according to standard silvicultural treatments, but in our research plots, canopy closure was not associated with age class of the trees. We found closed canopy conditions in some plots of every age class in our study due to different silvicultural treatments. If we repeat the study using percent canopy cover as a factor, we may be able to observe the effects of a combination of environmental factors such as light and wind penetration, ambient and soil temperatures and humidity, which are altered by this architectural characteristic, and thus influence decomposition rates, nutrient quality and moisture availability, which in turn influence conditions favorable for specific ectomycorrhizal and forest fungi.

There are some species for which age class seems to be a principal factor. *S. collinitus* is clearly more common in young stands, while *S. variegatus* is more abundant in older stands (Hintikka, 1988; Kalamees and Silver, 1988). According to Ohenoja (1989), this mushroom usually occurs in conditions of closed vegetation.

In the present study aspect has not been shown to be an important factor determining forest fungi distribution, although aspect may be an important factor for fruiting conditions for individual species in specific habitats. North-facing slopes are favored for production *T. magnivelare* in the Cascade Range of USA, but the dry southwest slopes are preferred in Japan and Korea (Amaranthus et al., 1998). Ohenoja and Koistinen (1984), in one of the few references available in the literature on the influence of aspect, did not find significant differences between southern and northern aspects with respect to commercial wild fungi.

4.5. Species richness

Greater sporocarp yield (fresh weight, dry weight or number of sporocarps) was positively correlated to species richness for individual plots. This relationship was also reported by Ohenoja (1978) and by O'Dell et al. (1999), who found sporocarp number and species richness correlated to annual precipitation. However, Brandrud (1987) in *Picea abies* forests found that the most productive plot had the lowest number of species.

We did not observe a significant relationship between age-class and species richness of ectomycorrhizal fungi, unlike Keizer and Arnolds (1994) who reported that ectomycorrhizal diversity increases with increasing tree age. They generalized that the most common process is a fairly rapid increase in fungal diversity during the first 30–40 years of forest development, with a gradual decrease afterwards to an intermediate, rather constant level. Smith et al. (2002) reported no differences in species richness but significant differences in abundance and species composition among *P. menziesii* forests of different age classes where canopy closure existed in all three age classes: young, rotation-age and old-growth forests.

Senn-Irlet and Bieri (1999) in a comparative study of young and mature *P. abies* stands found an almost doubled sporocarp production in younger open stands, but a greater species richness in mature closed-canopy forest. Dighton et al. (1986) in *Pinus contorta* forests reported that diversity peaked around canopy closure. These observations seem to confirm the important role of canopy cover within the forest age and fungal succession models. The influence of ambient conditions (temperature, moisture, light, soil conditions, wind) that are encompassed in the modification of canopy closure suggests that this factor could partially explain productivity, population composition and dynamics of forest fungi.

The *P. sylvestris* forests of the Pyrenees are highly productive in edible and ectomycorrhizal fungi, a forest resource deserving of conscientious management. The important commercial species *L. deliciosus* proliferates across young, medium and mature forests with no preference for aspect.

Sporocarp production was higher in areas with greater species richness, an observation that needs to be further examined for its implications in belowground forest dynamics. Results from this study may provide information to forest managers on a local scale until causal relationships can be better understood.

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