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Edible sporocarp production by age class in a Scots pine stand in Northern Spain

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Abstract With the aim of increasing knowledge of community structure, dynamics and production of ectomycorrhizal fungi, edible sporocarp yields were monitored between 1995 and 2004 in a *Pinus sylvestris* stand in the northeast zone of the Iberian Peninsula. A random sampling design was performed by stand age class according to the forest management plan: 0–15, 16–30, 31–50, 51–70 and over 71-years-old. Eighteen 150 m plots were established and sampled weekly every year from September to December. One hundred and nineteen taxa belonging to 51 genera were collected, 40 of which were edible and represented 74% of the total biomass. *Boletus edulis*, *Lactarius deliciosus*, *Cantharellus cibarius* and *Tricholoma portentosum* sporocarps, which are considered to be of high commercial value, represented 34% of the total production. *B. edulis* and *L. deliciosus* were the most remarkable and abundant species, and both were collected in more than 60% of the samplings. *B. edulis* fructified every year of the experiment; its mean production was 40 kg/ha and year and its maximum productivity was more than 94 kg/ha in 1998. The age class with the largest production of this taxa was the fourth (51–70 years), with 70 kg/ha. *L. deliciosus* only failed to fructify one autumn (2000); its mean production was almost 10 kg/ha and its maximum productivity close to 30 kg/ha in 1997. The maximum productivity of this species was found in the second (16–30 years) and fifth (71–90 years) stand age classes, with 18 and 16 kg/ha, respectively. Advances in this field can certainly offer new insights into factors affecting sporocarp production.

Keywords *Boletus edulis* · *Lactarius deliciosus* · *Pinus sylvestris* · Edible fungi production

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Introduction

Wild edible fungi are an important socioeconomic resource in many regions of the world. More than 2,000 fungi are known to produce edible sporocarps (Boa 2004). Over the last decade, the market value, consumer demand and interest in managing forests for non-timber products has increased (Díaz-Balteiro et al. 2003; Pilz et al. 1999). This resource is not only a food source but also could be an important income generator in rural forest areas if used properly (Barroetaveña et al. 2008; Boa 2004). In addition, edible mushrooms also represent the basis of multiple products made by manufacturers, including medicine, and are the source of a new wave of tourism resulting from recreational programmes linked to nature.

Nowadays, the commercial value of forest fungi may equal or even surpass that of timber, especially in the Mediterranean area (Alexander et al. 2002; Arnolds 1995; De Román and Boa 2006); therefore, fungi have become strategic in the conservation and management of forest systems. Where mushroom picking is a significant forest resource, it should be included in forest management and planning (Palahí et al. 2009). Paradoxically, only in the last 10 years has this resource begun to be integrated within forest planning, most of the time sporadically (Martínez de

Aragón et al. 2007). Lack of information and the low predictability of harvesting sporocarps may be partly the cause of this absence.

Edible ectomycorrhizal mushrooms comprise a specific group of edible fungal species that form symbiotic associations with their host plants. Among them, about 200 are common edible ectomycorrhizal mushroom species widely eaten in the Northern Hemisphere (Wang and Hall 2004). Cèpes or porcini (*Boletus edulis* species complex), chanterelles (*Cantharellus cibarius* Fr.), saffron milk caps (*Lactarius deliciosus* Fr.) and black truffles (*Tuber melanosporum* Vittad.) are the main edible wild mycorrhizal sporocarps traded and exported in Spain (De Román and Boa 2004). In an area of 4.5 million hectares in the autonomous community of Castilla and León (North Spain), the average gross annual production of edible wild mushrooms of social and economic interest has been estimated, excluding *Tuber* genus, at around 34,000 tonnes, being worth approximately 80 million euros (Martínez-Peña et al. 2006–2010).

This paper seeks to improve the still partial knowledge about the community structure, dynamics and production of edible ectomycorrhizal fungi in wild environments, which could serve to implement appropriate forest management plans. With this objective, we performed a random sampling design stratified by stand age in a Scots pine stand in northern Spain over ten consecutive years from 1995 to 2004. The aim of this study was to establish a relationship between stand age class and the production of edible ectomycorrhizal sporocarps, mainly *B. edulis* and *L. deliciosus*.

Material and methods

Study area

The study site is located in a homogeneous *Pinus sylvestris* L. stand known as "Pinar Grande". It is a 12,533 ha area situated in the Sistema Ibérico mountain range, in the inner northeast zone of the Iberian Peninsula. Altitude varies between 1,097 and 1,543 m a.s.l. dominating west and east orientations. Soils are acidic brown earths or illuvial, with marked acid pH (4–5), sandy loam to sandy texture, low holding capacity and low fertility. Medium annual rainfall is 865 mm/year, 69 mm/year falling in July and August and 132 mm/year in September and October. Medium annual temperature is 8.8°C, with July being the warmest month (17.4°C). The frost period begins in November and ends in April, with frequent frosts in late spring and early autumn. The forest management system is the periodic block method with a rotation of 100 years. The forests are silviculturally managed by clear cutting with soil movement and sowing.

Sampling design

A stratified random sampling design was performed by stand age. On a 1:20,000 scale map, a 1 ha grid was superimposed classifying every cell into one of this five age classes according to the forest management plan: 0–15, 16–30, 31–50, 51–70 and over 71-years-old. Every grid cell was numbered, and cells corresponding with every age class were selected randomly. Selected cells were located in the field and checked to confirm whether they met the strata assumptions; if they did not, another random cell was selected. Three plots per age class were installed, except for the last stand age class in which there are six, providing a total of 18 sampling plots. Each sampling plot covers a rectangular-shaped area of 150 m^2. Its size and form were established in accordance with previous studies by Fernández-Toirán (1994), Kalamees and Silver (1988) and Ohenoja (1989) that use rectangular plots with a minimum area of 100 m^2. Plots were fenced to prevent harvesting and trampling and were at least 500 m from stands corresponding to another age class. Sampling was performed on a weekly basis from weeks 35 to 50 every year from 1995 to 2004 as this period corresponds with most sporocarp emergence. The spring fruiting season was ignored because it is characteristically very short and almost insignificant in this area. All fully developed sporocarps were collected and identified to species level in the laboratory. Production study is focused on edible fungal species. The characteristic of edibility was determined by Breitenbach and Kränzlin (1981–2000), Boa (2004) and Cannon and Kirk (2007). Fresh weight (grams) and number of sporocarps collected for the species in each plot per week were recorded. Sporocarp identification was performed using morphological features with appropriate keys and monographs including Breitenbach and Kränzlin (1981–2000), Dennis (1968), Jülich (1989) and Moser (2003). Nomenclature follows Index Fungorum (http://www.indexfungorum.org). The names of authors were abbreviated according to Brummit and Powell (1992). Representative voucher specimens were deposited at the JCyL-FUNGI herbarium in the Centro de Investigación Forestal de Valonsadero (Soria, Spain), available in GBIF (http://data.gbif.org/datasets/resource/7925).

Data analyses

Autumnal sporocarp mean fresh weight production (kilograms per hectare) were analysed together with autumnal sporocarp stratified mean fresh weight production (kilograms per hectare). Statistical analyses were performed using STATGRAPHICS Plus 5.1 (Statistical Graphics Corp., Warrenton, VA, USA). The effect of stand age on sporocarp production was analysed using ANOVA. In order to normalise *L. deliciosus* data, variables were transformed as log (weight + 1). As data proved to be unbalanced, general linear model procedure was applied. Duncan's multiple rank test was used for the multiple mean comparison (Einot and Gabriel 1975).

Results

Between 1995 and 2004, a total of 140 samplings were performed and 29,273 sporocarps were recorded. All of them belonged to Basidiomycota, except *Fuligo septica* var. *septica* (L.) F.H. Wigg. (Amoebozoa, Myxogastria). One hundred and nineteen taxa were collected, belonging to 51 genera. The most abundant genera were *Russula*, *Cortinarius*, *Tricholoma*, *Amanita*, *Lactarius* and *Collybia*.

A total of 40 edible species belonging to 26 genera were recorded (Table 1), which represent 74% of the total of the collected biomass and almost 100 kg/ha. Distribution of species by trophic groups revealed a dominance of ectomycorrhizal species between the edible species, 75%, whilst saprotrophic were found to a lesser degree (Table 1). Species of socioeconomic interest represent 34% of the total of the collected biomass. Four of the edible species are considered to be of high commercial value: *B. edulis* Bull., *L. deliciosus*, *C. cibarius* and *Tricholoma portentosum* (Fr.) Quél.

Data analysis is focused on *B. edulis* and *L. deliciosus* due to the fact that both species were much more abundant on the plots than others. Although there is a high interannual variability in the fruiting, *B. edulis* and *L. deliciosus* could be considered as species that fructify frequently because both species were collected in more than 60% of the samplings. Sporocarps of *B. edulis* were collected in every year of the experiment, whilst sporocarps of *L. deliciosus* were collected in 90% of the sampled seasons. Only once did *L. deliciosus* not fructify, during the autumn of 2000.

B. edulis is the species with the maximum mean productivity per year, more than 40 kg/ha, representing 40.5% of the total of edible species (Table 1) and having a more or less regular productivity every year (Table 2). *L. deliciosus* has a mean productivity per year of close to 10 kg/ha, representing 10% of the total of edible species (Table 1). A sharp annual variability has been reported in sporocarp production of these species. *B. edulis* had its maximum productivity in 1998 with more than 94 kg/ha, whilst its minimum was 3 kg/ha in 2004 (Table 2). *L. deliciosus* had its maximum productivity in 1997 with almost 30 kg/ha, and almost 25 kg/ha in 1999, but in 2000, not a single sporocarp was collected in any plot (Table 3).

B. edulis sporocarp production is clearly different among the five stand age classes considered (p=0.1279). Sporocarp production appears for first time in the second stand age class, with almost 32 kg/ha and year. Maximum production is found in the fourth stand age class, with just over 70 kg/ha and year, and decreases in the fifth stand age class to 24 kg/ha and year (Table 2). *L. deliciosus* sporocarp production is also clearly different for the five stand age classes considered (p=0.0452). Sporocarp production begins in the first stand age class, reaching its maximum in the second and in the fifth stand age classes, 18 and 16 kg/ha and year, respectively (Table 3).

Sporocarp production began in September, just before week 39 in the majority of the sampled seasons, especially for *B. edulis*. Sporocarp production in this forest is usually higher during October, between weeks 40 and 44, and the sporocarp season has a mean of 12 weeks.

Discussion

The present study, conducted from 1995 to 2004, is a long-term monitoring of edible sporocarp production in a *P. sylvestris* forest. The only longer data series that exists is in a mixed forest in western Switzerland (Egli et al. 2006; Straatsma et al. 2001). Only long-term observation can address the uncertainty concerning the factors responsible for fungal fruiting, especially under the present climate change context (Dahlberg et al. 1997; Vogt et al. 1992).

Edible species represent 34% of the 119 taxa recorded, and only 3% are of commercial interest. These figures are similar to those found by Bonet et al. (2004), Martínez de Aragón et al. (2007) and Oria de Rueda et al. (2010).

With regard to biomass, nearly 74% of the fresh weight production, 99.70 kg/ha, are edible mushrooms, and the 34% are marketable edible mushrooms. Similar or higher fresh yields were reported by Kalamees and Silver (1988), Kardell and Eriksson (1987), Shubin (1988) and Väre et al. (1996). In *P. sylvestris* forests of the Pyrenees, Spain, Bonet et al. (2004) found 44.7 kg/ha of edible mushrooms and Martínez de Aragón et al. (2007) found 6.16 kg/ha of marketable edible mushrooms. Higher yields are reported in Central Spain by Oria de Rueda et al. (2010) who found that the fresh weight production of edible taxa in *P. pinaster* stands was 295 and 100 kg/ha in *P. sylvestris* stands. Similar results were found by Martín-Pinto et al. (2006) in *P. pinaster* stands.

Our highest yield for individual edible species was 40 kg/ha, obtained from *B. edulis*. Although there are some references about *B. edulis* sporocarp production in *P. sylvestris* stands (Hintikka 1988; Ohenoja 1984; Salo 1993), it is of lesser value than our study. It is surprising that this species has not been found in studies done in Pyrenees and north Finland (Bonet et al. 2004; Martínez de Aragón et al. 2007; Oria de Rueda et al. 2010; Väre et al. 1996).

Table 1 Edible species collected in Pinar Grande from 1995 to 2004 by stand class age

Sporocarp species	JCYL	TC	W	*Pinus sylvestris* stand age class										FT	FS	Total	
				Under 15		16–30		31–50		51–70		Over 71					
				P	S_P	P	S_P	P	S_P	P	S_P	P	S_P			P_E	S_{PE}
Agaricus silvaticus Schaeff.	1553	s		0.04	0.04									1	1		
Amanita rubescens var. *rubescens* Pers.	2761	m	22.9			0.53	0.53	0.45	0.45					2	2	0.19	0.14
Amanita spissa (Fr.) P. Kumm. var. *spissa.*	2774	m	38.9			0.22	0.22	3.55	2.00	2.30	1.72	2.58	1.83	6	9	2.14	0.88
Amanita vaginata (Bull.: Fr.) Vittad. var. *vaginata*	2442	m	20.4	0.22	0.22							0.05	0.05	4	2	0.02	0.02
Boletus badius (Fr.) Fr.	1798	m	36.7			0.31	0.31	0.57	0.57			6.34	5.41	9	14	2.20	1.75
Boletus edulis Bull.	2591	m	76.0			31.93	15.65	41.50	37.89	70.26	29.25	24.42	10.75	10	3	40.35	12.18
Cantharellus cibarius Fr. var. *cibarius*	2766	m	4.1			0.03	0.03			0.35	0.20	2.87	1.82	6	14	1.02	0.59
Chroogomphus rutilus (Schaeff.) O. K. Mill.	2522	m	10.6	0.18	0.18	1.01	0.68	0.14	0.14			0.36	0.35	9	8	0.35	0.21
Clitopilus prunulus (Scop.) P. Kumm.	2777	m	5.0			0.11	0.08	0.62	0.36	1.06	0.70	2.03	1.19	10	14	1.07	0.45
Cortinarius caperatus (Pers.) Fr.	2776	m	23.8									2.40	2.40	6	1	0.77	0.77
Cortinarius variicolor (Pers.) Fr.	665	m	35.9			0.03	0.03	1.28	1.03	0.21	0.21	0.45	0.39	4	6	0.45	0.31
Cystoderma terreyi (Berk. & Broome) Harmaja	1541	s				0.01	0.01							1	1		
Gomphidius roseus (Fr.) Fr.	2311	m	6.2	0.25	0.16	0.17	0.11	0.04	0.04	0.09	0.09	0.17	0.13	6	1	0.12	0.06
Gymnopus dryophilus (Bull.) Murrill	2514	s		0.02	0.02	0.03	0.03			0.03	0.03	0.01	0.01	4	1		
Hygrophorus hypothejus (Fr.) Fr.	2589	m	2.1	1.97	1.49	3.63	1.80	2.14	1.12	0.42	0.28	0.01	0.01	9	12	1.30	0.46
Laccaria bicolor (Maire) P.D. Orton	2662	m	1.9	0.80	0.76	1.71	0.95			0.08	0.08			8	7	0.39	0.20
Laccaria laccata (Scop.) Cooke	2285	m	2.0	0.98	0.65	0.35	0.14			0.15	0.15			6	7	0.14	0.06
Lactarius deliciosus (L.) Gray	2511	m	25.2	5.45	5.45	18.44	11.76	0.51	0.35	2.81	2.27	16.27	6.58	9	16	9.89	3.46
Lactarius vellereus (Fr.) Fr.	2788	m	81.3					2.21	2.21					3	1	0.42	0.42
Lepista nuda (Bull.) Cooke	2492	s	27.2			0.18	0.18							3	3	0.04	0.04
Lycoperdon perlatum Pers.	2547	s	6.7	0.13	0.13	1.38	1.20	0.40	0.28			0.34	0.32	9	1	0.46	0.32
Macrolepiota procera (Scop.) Singer	2798	s	53.7	0.22	0.22							1.03	1.03	6	9	0.33	0.33
Pluteus atromarginatus (Konrad) Kühner	2770	s		0.10	0.10									2	2		
Pseudoclitocybe cyathiformis (Bull.) Singer	2792	s	1.7			0.04	0.03	0.01	0.01					2	1	0.01	0.01
Ramaria aurea (Schaeff.) Quél.	2303	m	55.1									0.10	0.10	2	1	0.03	0.03
Rhizopogon luteolus Fr. & Nordholm	2544	m	13.3	0.13	0.13	0.49	0.43	0.01	0.01	0.53	0.20	0.23	0.19	8	1	0.32	0.15
Rhizopogon roseolus (Corda) Th. Fr.	2673	m	19.3			0.37	0.37			0.07	0.07	0.02	0.01	3	2	0.10	0.08
Rhodocollybia butyracea f. *butyracea* (Bull.) Lennox	2541	s	4.3					2.38	2.38					4	5	2.45	1.72
Russula albonigra (Krombh.) Fr.	1509	m										0.03	0.03	1	1	0.01	0.01
Russula amethystina Quél.	1517	m	9.9					0.11	0.09			0.03	0.02	2	1	0.03	0.02
Russula integra var. *integra* (L.) Fr.	1908	m	30.7			2.87	2.49	16.72	8.97	0.16	0.10	6.27	4.30	8	1	5.80	2.42

Russula xerampelina (Schaeff.) Fr.	2618	m	19.3			2.94	2.66	5.53	2.08	3.18	2.62	1.92	0.83	8	8	3.08	1.16
Sarcodon imbricatus (L.: Fr.) P. Karst.	2764	m	35.1			0.67	0.67	16.46	9.78	0.74	0.74	0.02	0.02	9	14	3.46	1.94
Suillus bovinus (Pers.) Roussel	1949	m	11.1	9.56	6.35	3.86	2.76	0.25	0.22	3.42	2.67	6.10	4.81	9	1	3.95	2.00
Suillus flavidus (Fr.) J. Presl	2780	m	9.9							0.25	0.25	1.34	0.93	4	16	0.49	0.31
Suillus luteus (L.) Roussel	2498	m	32.6	5.34	4.20	3.78	3.57	3.23	1.99	3.53	1.71	24.93	14.62	10	5	10.42	5.02
Suillus variegatus (Sw.) Kuntze	2506	m	33.7	0.96	0.96	1.08	1.00	2.95	2.88	17.85	12.51	6.95	4.95	9	17	7.67	3.75
Tapinella atrotomentosa (Batsch) Šutara	2588	s	32.4									0.04	0.04	1	12	0.01	0.01
Tricholoma portentosum (Fr.) Quél.	174	m	26.4			0.88	0.88	0.31	0.31					4	2	0.24	0.20
Tricholoma terreum (Schaeff.) P. Kumm.	2694	m				0.01	0.01							1	2		
Total				26.35	21.10	77.10	48.60	101.00	75.20	107.50	55.90	107.30	63.10			99.70	41.50

JCYL CYL-FUNGI herbarium voucher specimen number, *TC* trophic condition, *m* mycorrhizal, *s* saprotrophic, *W* mean sporocarp weight (grams), *P* autumnal mean fresh weight production (kilograms per hectare) by stand age class (years) and its standard error (S_P), *FT* number of years that each species has been recorded, *FS* number of plots in which each species has been recorded, P_E total autumnal stratified mean fresh weight production (kilograms per hectare) and its standard error (S_{PE})

L. deliciosus is the second species with significant commercial value in this stand, with 10 kg/ha. Bonet et al. (2004) reported a yield for this species of 1 kg/ha and year and Martínez de Aragón et al. (2007) of 0.3 kg/ha.

Edible mushrooms make a significant contribution to the local economy in terms of sales and tourism. In addition, there are some non-edible or edible forest fungi with important medicinal qualities, which may become commercially important in the future. In our region, one of the most productive *B. edulis* environments in Spain, their collection creates a net value added of over 2 million euros every year (Martínez-Peña and García-Cid 2003), whilst *L. deliciosus* creates a net value added of 1.7 million euros each year (Yagüe et al. 2006).

It is important to take into account the fact that sporocarp production varies considerably between different years in the same locality (Baptista et al. 2010; Fernández-Toirán et al. 2006; Smith et al. 2002; Straatsma et al. 2001), which may be due to a variation of weather conditions or the sporadic fruiting of some species (Ferris et al. 2000). In our study, the autumnal mean fresh weight production of *B. edulis* has a huge interannual variability, with over 94 kg/ha in 1998 yet only 3 kg/ha in 2004. *L. deliciosus* also has a huge interannual variability, with close to 30 kg/ha in 1997 and no production in 2000.

Ectomycorrhizal species present in any ecosystem depend on the host species and also on plant age (Dighton and Mason 1985; Mason et al. 1982). Some studies on the succession of ectomycorrhizal fungi reveal that there are fungi characteristic of early-seral stages and others of late-seral stages of stands (Arnolds 1995; Matsuda and Hijii 1998; Senn-Irlet and Bieri 1999; Smith et al. 2002); therefore, *Hebeloma* sp., *Laccaria* sp. and *Inocybe* sp. are considered as early-seral stage, and *Amanita* sp. and *Leccinum* sp. as late-seral stage symbionts (Dighton et al. 1986; Last et al. 1984).

B. edulis sporocarp production is highly influenced by the *P. sylvestris* stand class age. The higher production is in the fourth stand age class, between 51 and 70-years-old, which could be considered mature stands. Hintikka (1988) and Keizer and Arnolds (1994) also found this species typical of mature pine stands, but there are few references for high yields of this species in conifer forests. Arnolds (1995) reported higher sporocarp numbers in mature oak plots (20–50-years-old) than in young oak plots (10–20-years-old), although *B. edulis* is considered as early-stage fungi in deciduous forest by Buée et al. (2011).

L. deliciosus showed two peaks of sporocarp production: the first in the second age class stand of between 16 and 30-years-old and another in the fifth age class stand of over 71-years-old. Although this species is mainly found in young conifer stands of <40-years-old (Fernández-Toirán et al. 2006; Kranabetter et al. 2005), Bonet et al. (2004) indicate that this species shows no preference for a

Table 2 *B. edulis* autumnal sporocarp mean fresh weight production by *P. sylvestris* stand age class (years) between 1995 and 2004

Year	*Pinus sylvestris* L. stand age class										Total	
	Under 15		16–30		31–50		51–70		Over 71			
	P	S_P	*P*	S_P	*P*	S_P	*P*	S_P	*P*	S_P	P_E	S_{PE}
1995	0.00	0.00	0.00	0.00	5.10	5.10	12.57	12.14	10.09	6.07	7.47	3.83
1996	0.00	0.00	3.08	3.08	32.06	23.12	20.60	17.09	15.26	8.68	16.95	6.87
1997	0.00	0.00	16.18	9.54	70.64	45.42	129.45	53.95	37.00	12.29	62.15	17.04
1998	0.00	0.00	104.81	59.56	72.02	70.12	185.87	59.47	35.75	16.78	94.41	24.23
1999	0.00	0.00	48.90	37.15	35.13	35.13	96.23	44.96	23.45	10.76	48.98	15.76
2000	0.00	0.00	3.93	3.93	46.64	46.64	22.02	11.33	14.18	8.34	19.91	9.75
2001	0.00	0.00	7.53	3.83	67.91	67.91	38.53	28.83	34.30	20.00	35.40	16.26
2002	0.00	0.00	36.42	8.22	58.94	58.94	135.52	41.53	47.14	15.75	68.80	16.43
2003	0.00	0.00	98.41	31.21	24.74	24.74	51.56	12.89	27.06	8.84	46.45	8.96
2004	0.00	0.00	0.00	0.00	1.78	1.78	10.29	10.29	0.00	0.00	3.01	2.70
Mean	0.00	0.00	31.93	12.44	41.50	37.59	70.26	6.82	24.42	8.83	40.35	8.27

P autumnal mean fresh weight production (kilograms per hectare) by stand age class (years) and its standard error (S_P), P_E total autumnal stratified mean fresh weight production (kilograms per hectare) and its standard error (S_{PE})

particular stand age class in studies done in *P. sylvestris* stands of the Pyrenees (Spain). Zamora-Martínez and Nieto Pascual (1995) reported productions of almost 26 kg/ha of *L. deliciosus* from open-canopy conditions within mature stands.

B. edulis and *L. deliciosus* showed very different fruiting patterns with regard to the stand age class. *B. edulis* mainly grows in stands above and around canopy closure, whilst *L. deliciosus* grows in open stands, mainly in young stands without canopy closure, but also in old open stands. Silvicultural techniques could modify stand structure, creating the environmental conditions which could induce the fruiting of this species in mature stands.

Ectomycorrhizal sporocarp production seems to be coupled with the physiological status of the host, with stand age being a main factor in sporocarp formation, highly correlated with other environmental factors such as climate, soil and silvicultural management. Often, stand age class is associated with open or close canopy according to standard silvicultural treatments (Bonet et al. 2004; Senn-Irlet and Bieri 1999). Perhaps light is not a relevant factor for the survival of fungi as they do not depend on light for growth, but the resulting

Table 3 *L. deliciosus* autumnal sporocarp mean fresh weight production by *P. sylvestris* stand age class (years) between 1995 and 2004

Year	*Pinus sylvestris* L. stand age class										Total	
	Under 15		16–30		31–50		51–70		Over 71			
	P	S_P	*P*	S_P	*P*	S_P	*P*	S_P	*P*	S_P	P_E	S_{PE}
1995	0.00	0.00	0.57	0.57	0.00	0.00	0.00	0.00	1.06	0.50	0.45	0.20
1996	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.48	0.34	0.15	0.11
1997	2.58	2.58	53.57	29.62	3.73	2.17	4.43	1.05	52.52	13.31	29.46	7.31
1998	3.11	3.11	9.26	3.42	0.56	0.56	0.00	0.00	11.43	6.65	5.71	2.24
1999	4.57	4.57	39.02	19.39	0.16	0.16	5.84	5.84	47.86	22.09	24.81	8.21
2000	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2001	6.05	6.05	0.22	0.22	0.00	0.00	0.00	0.00	4.24	1.91	1.58	0.64
2002	19.58	19.58	31.78	19.07	0.00	0.00	11.47	11.47	29.37	13.28	19.32	6.47
2003	18.65	18.65	49.42	44.68	0.62	0.62	6.37	4.36	15.54	7.59	17.19	9.35
2004	0.00	0.00	0.60	0.60	0.00	0.00	0.00	0.00	0.23	0.15	0.19	0.13
Mean	5.45	5.45	18.44	10.62	0.51	0.25	2.81	2.23	16.27	5.43	9.89	2.81

P autumnal mean fresh weight production (kilograms per hectare) by stand age class (years) and its standard error (S_P), P_E total autumnal stratified mean fresh weight production (kilograms per hectare) and its standard error (S_{PE})

changes in soil temperature and moisture regimes are probably more relevant and are heavily influenced by canopy closure (Egli et al. 2010).

Reports of forest sporocarp production by stand age class are extremely variable across forests, but there are some species which are highly influenced by this factor. There are difficulties in generalising patterns of succession for sporocarps of ectomycorrhizal species in different forests and also in defining ecological traits common to all species within a genus. The concept of an old or young stand depends, amongst other factors, on the species, the altitude and also the latitude. Therefore, it would be helpful to describe successional patterns at levels higher than species for landscape-scale models of fungi occurrence (Dreisbach et al. 2002).

The data presented here highlight that changes in the ecosystems due to host ageing are one of the keys in its development, influencing the fruiting patterns of a fungal species.

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