Yield models for ectomycorrhizal mushrooms in *Pinus sylvestris* forests with special focus on *Boletus edulis* and *Lactarius* group *deliciosus*

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ABSTRACT

Mushrooms in general, and *Boletus edulis* and *Lactarius deliciosus* in particular, are important non-wood forest products worldwide. Despite their economic and ecological importance, models that describe the influence of different factors on mushroom yield are few. These models would support multi-objective forest management and planning that takes into account mushroom production. This study aims at providing models for predicting the total yield of wild ectomycorrhizal mushrooms and, especially, of *L.* group *deliciosus* and *B. edulis*. Mushroom data were collected in 18 permanent plots in pure even-aged *Pinus sylvestris* stands during fifteen consecutive years. Variables describing weather conditions, stand structure and local site characteristics were used as predictors in the modeling process. Rainfall and temperature were significant predictors in all the fitted models. In addition, the total yield of ectomycorrhizal fungi was significantly affected by dominant height and stand age. The production of *L.* group *deliciosus* was influenced by dominant height and stand basal area. The equation fitted for *B. edulis*, to our knowledge, is the first model for this species. It shows that stand basal area is a strong factor influencing the yield. The equations presented in this study enable predictions of mushroom yield under different forest management schedules and climatic scenarios.

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1. Introduction

Wild edible fungi are valuable non-wood forest products throughout the world and have a clear potential for commercial use (Boa, 2004). Some fungi such as boletes (*Boletus edulis*) or saffron milk caps (*Lactarius* group *deliciosus*) are specially valued in many countries, and their trade has become an important complementary economic activity in many regions (Voces et al., 2011; Cai et al., 2011; Martínez de Aragón et al., 2011). The socioeconomic relevance of non-wood resources coupled with the low profitability of timber production in many areas is driving a change in forest management paradigms and practices, switching from traditional forest planning focused on timber production to more complex multifunctional silvicultural schemes. One of these new schemes is the so-called mycosilviculture, which attempts to integrate timber and mushroom production (Martínez-Peña et al., 2011).

Sound forest planning for the joint production of wood and mushrooms requires predictions of both mushroom and wood production (Palahí et al., 2009). For that, detailed information on the main variables affecting mushroom yield is needed. However, predicting mushroom yields is not an easy task. In addition to the difficulty associated with mushroom inventories (Calama et al., 2010), a wide range of factors have been recognized as influencing fruit-body emergence. These factors can be classified into three main groups: (a) local site characteristics (e.g. altitude, slope, aspect); (b) stand structure (e.g. tree species, stand density, stand age); and (c) weather variables (e.g. precipitation, temperature). Since most of the collected mushroom species establish mycorrhizal symbioses with trees, it may be expected that stand structure, which can be modified through forest management, as well as soil properties, affect mushroom production. Moreover, it is well known that weather, together with other environmental factors, also affect mushroom dynamics. In addition, the local site characteristics have been repeatedly mentioned in the literature to have an impact on mushroom yield (Egli, 2011). The large amount of potential variables related to mushroom productivity and their interdependence makes it difficult to give clear recommendations for managing mushroom yields. Systematic quantitative analyses on the effect of different variables are required.

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Modeling techniques are a valuable tool that allows to identify factors most relevant for predicting mushroom yield. Forest management oriented models based on long historical data series of annual measurements in many locations can be used to model mushroom yield as a function of different types of predictors. These kinds of studies are rather recent, and only a few models for mushroom yield have been published so far. Bonet et al. (2008) developed a model for predicting the total, edible and marketable mushroom yield and species richness as a function of site and forest stand variables based on a three-year mushroom inventory in 24 Scots pine plots in north-eastern Spain. They showed that basal area was the most important growing stock characteristic for mushroom production with maximum mushroom yields at stand basal areas of approximately 20 m^2 ha $^{-1}$. Additional studies based on 21 plots established in *Pinus sylvestris*, *Pinus nigra* and *Pinus halepensis* forests in the same region also found that the maximum mushroom productivity corresponded to stands where the basal area ranged from 15 to 20 m^2 ha $^{-1}$. Site variables such as aspect, slope and elevation also had an important influence on annual mushroom yield (Bonet et al., 2010).

Between-region differences in site characteristics, weather and forest structure prevent a straightforward application of the above-mentioned results for north-eastern Spain in other regions. The ecological conditions in north-central Spain differ from those in the other parts of Spain. North-central Spain, where mushroom collection is an important activity, has a more continental climate, larger average tree size, higher stand volumes, different soil types and, partly, different mushroom species.

The aim of this study was to develop empirical models for predicting the total annual yield (fresh mass of sporocarps) of wild ectomycorrhizal mushrooms with a special focus on the most valuable species (*L.* group *deliciosus* and *B. edulis*) in Scots pine forests in north-central Spain.

2. Material and methods

2.1. Permanent plots for mushroom inventory

Eighteen permanent plots were established in pure even-aged stands of *P. sylvestris* L. forests, located within the "Pinar Grande" area, in the Iberian System Mountains of the province of Soria. The plots were randomly established in different locations so as to capture high variation in stand age (from 7 to 122-year-old *P. sylvestris* stands). Site variables (altitude, slope and orientation) were measured in every plot. Detailed soil analyses considering physical and chemical properties were carried out for every plot. Soils were acid (pH between 4 and 5) with a sandy-loam to sandy texture. The understory was mainly composed of *Erica vagans* and *Nardus stricta*. The mean monthly temperature and total monthly precipitation were also recorded during the inventory period.

Each of the 18 mushroom plots, 175 m^2 in size, was subdivided into 6 sub-plots of 5 m × 5 m for mushroom measurement, which resulted in a total sampled area of 150 m^2 per plot. All the plots were fenced in order to prevent uncontrolled mushroom harvesting. The inventory was carried out annually since 1995 until 2009. In every plot, all the sporocarps of ectomycorrhizal species having a diameter larger than 1 cm were collected at 1-week intervals during weeks 35–50.

The collected mushrooms were identified and classified in the laboratory according to their edibility and marketability. Afterwards, fresh weight was calculated for all the sampled mushrooms. This study focused on the total yield of ectomycorrhizal mushrooms (72 species, see Martínez-Peña et al. (2012)), *L.* group *deliciosus* and *B. edulis. Lactarius* yield refers to *L.* group *deliciosus*, which comprises three species (*L. deliciosus, L. quieticolor* and

L. sanguifluus) all of which are commonly sold together in the markets. Additional information concerning the study area and the permanent plots can be found in Martínez-Peña (2009).

2.2. Temporary plots for forest inventory

Eighteen temporary forest inventory plots, each centered on one permanent mushroom inventory plot, were also measured to characterize the forest stands. The forest stand plots were measured only once; plots 4–18 in the beginning of the mushroom inventories, and plots 1–3, which were young seedling stands in 1995, at the end of the mushroom inventories (in 2010). In order to reduce the sampling error of the stand variables, the forest inventory plots were larger, 800 m^2 (20 m × 40 m). In each plot, every tree was measured for diameter at 1.3 m. In addition, tree height was measured for a minimum of 10 trees. Table 1 summarizes the forest inventory data. Plot number 4 was thinned in 2006 according to the established management plan of the forest. The other plots were not treated during the period of mushroom measurements (1995–2009).

The site index of every plot was calculated on the basis of stand age and dominant height (mean height of 100 largest trees per hectare) using the model of Palahí et al. (2003). Site index is equal to dominant height at 100 yr. The stand characteristics of plots 4–18 were updated for each mushroom inventory year by simulating the stand development using the above-mentioned dominant height model and the individual tree models of Pukkala (2008) for diameter increment, tree height, and tree survival. The stand characteristics of plots 1–3 were back-tracked to years 1995–2009 using the dominant height model to obtain the stand dominant height for different years. The measured stand characteristics of all plots were used to fit a model that gives the quadratic mean diameter as a function of dominant height, stand age, and number of trees per hectare. The stand basal area for different years was then calculated from the quadratic mean diameter and the number of trees per hectare. It was assumed that the number of trees per hectare remained unchanged during 1995–2010, which is a reasonable assumption taking into account the still low basal area of plots 1–3 in 2010 (Table 1).

2.3. Model fitting

The dataset contained variables describing mushroom yield, monthly and annual weather conditions (temperature and rainfall), forest stand (age, basal area, dominant height, etc.) in different years and site characteristics (altitude, aspect, slope), as well as physical and chemical soil properties of each stand. Different transformations of these variables were tested when modeling the annual yield of ectomycorrhizal mushrooms, *L.* group *deliciosus* and *B. edulis*. The models were fitted using nonlinear regression analysis and fixed-effects modeling approach. A correlation analysis was used to find out whether mushroom yield was related to soil characteristics.

Based on the fitted equations, predictions were calculated using alternative weather scenarios typical to the region in order to show the model behavior and to facilitate a graphical comparison among the predictions of the different models. Based on the recorded data of a central meteorological station, dry and wet autumn conditions were calculated as the mean inter-annual autumn precipitation ± 30% (115 mm and 215 mm to simulate dry and wet autumns, respectively).

The following criteria were considered in model evaluation: (a) agreement with current biological knowledge, (b) logical behavior of the model set in extrapolations, (c) simplicity and robustness, (d) statistical significance (p-value < 0.05), (e) non-biasness, and (f) homocedasticity and normal distribution of residuals.

Table 1
Main characteristics and mushroom yield of the inventoried plots.

Plot number	Altitude (m)	Slope (%)	Orientation	Stand density (trees ha^{-1})[a]	Dominant height (m)[b]	Basal area (m^2 ha^{-1})[a]	Forest age (years)[b]	Ectomycorrhizal yield (kg ha^{-1} yr^{-1})[c]	L group deliciosus yield (kg ha^{-1} yr^{-1})[c]	B. edulis yield (kg ha^{-1} yr^{-1})[c]
1	1119	1	N	3675	8.4	24.5	7	47.8 (48.8)	13.2 (19.6)	1.0 (4.0)
2	1119	5	NW	2113	6.9	24.5	10	89.5 (116.1)	2.1 (7.0)	0.4 (1.7)
3	1139	4	SE	2513	5.0	10.8	5	56.3 (111.1)	0.5 (2.0)	1.1 (4.3)
4	1159	2	NW	3037	11.6	42.3	24	143.9 (153.9)	6.6 (13.7)	51.1 (67.5)
5	1109	5	NE	2212	9.4	29.0	21	76.9 (75.8)	8.5 (13.5)	9.4 (27.9)
6	1149	1	NE	587	7.5	9.5	19	133.2 (156.9)	45.1 (79.8)	26.9 (28.7)
7	1129	2	SE	2012	15.1	44.3	38	89.9 (101.3)	0.6 (2.1)	0.0 (0.0)
8	1089	3	NE	962	17.5	49.8	41	115.1 (111.2)	0.1 (0.3)	5.3 (15.0)
9	1149	1	NE	1825	15.5	45.6	37	136.3 (100.0)	0.4 (0.8)	71.2 (66.2)
10	1149	4	NE	1350	17.6	51.8	54	213.1 (186.0)	0.7 (1.7)	55.0 (58.7)
11	1149	1	SE	812	20.0	53.9	78	78.0 (95.3)	6.4 (12.0)	41.1 (60.4)
12	1119	4	NE	1162	17.2	39.2	58	161.7 (179.6)	0.4 (0.9)	59.3 (82.8)
13	1149	1	NE	312	20.8	40.0	85	154.3 (165.0)	18.3 (32.9)	39.0 (33.4)
14	1149	1	NW	450	22.8	44.5	96	69.6 (117.9)	14.2 (24.6)	2.1 (4.6)
15	1129	1	NE	487	26.4	51.5	78	152.3 (137.1)	8.2 (13.8)	29.8 (24.8)
16	1159	4	NE	712	25.2	70.9	117	185.1 (174.9)	32.8 (41.4)	19.9 (21.8)
17	1089	1	N	525	23.1	84.9	122	72.9 (85.8)	3.5 (8.8)	5.0 (12.3)
18	1129	2	SE	512	24.1	75.3	97	113.0 (135.0)	0.9 (2.7)	11.9 (23.5)

[a] Data refer to year 1997 in plots 5, 7, 8, 10, 12, 15, 17 and 18; year 1998 in plots 4, 6, 9, 11, 13, 14, and 16; and 2010 in plots 1, 2, and 3.
[b] Data refer to year 1995.
[c] Mean (Std. Deviation).

3. Results

3.1. Model for all ectomycorrhizal mushrooms

The model for annual yield of total ectomycorrhizal mushrooms was as follows:

$$Ectomyco = \exp(-2.389 + 0.008 P_{autumn} + 0.164 T_{autumn} + 0.664 \ln(Hdom) - 0.005 Age)$$

where *Ectomyco* is the annual yield of ectomycorrhizal mushrooms (kg ha^{-1} yr^{-1}), P_{autumn} is the sum of the total precipitation in August, September and October, T_{autumn} is the sum of the mean temperature in September, October and November, *Hdom* is the stand dominant height and *Age* is the stand age. The root mean square error (RMSE) was 106.0 kg ha^{-1} yr^{-1} and the R-squared was 0.417.
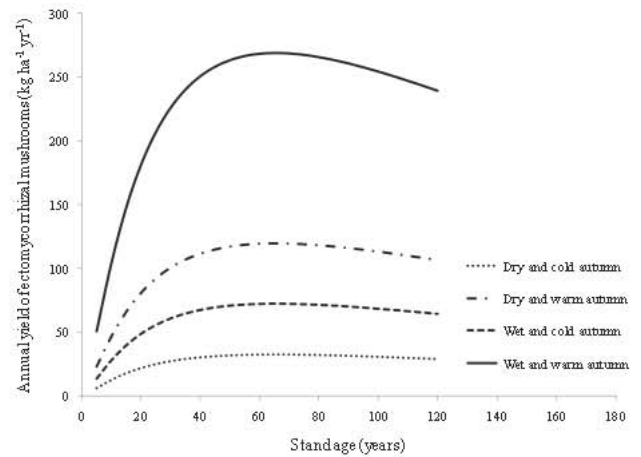
The annual yield of ectomycorrhizal mushrooms depends on both weather and stand-level variables. The annual yield of ecto-mycorrhizal mushrooms was, on average, around 120 kg ha^{-1} yr^{-1}. In a very good year it can reach more than 700 kg ha^{-1} yr^{-1} (Figs. 1–3).

Dry and cold autumns are predicted to be less productive, whereas it is likely that, in wet and warm autumns, the yield of ectomycorrhizal mushrooms will be much higher. The youngest stands are less productive and the maximum yield of ecto-mycorrhizal mushrooms seems to be in stands between 60 and 70 yr old (Fig. 1). Scatterplots showing the yield observations for different amounts of rainfall and temperatures are shown in Fig. 2. Fig. 3 shows a scatterplot between observed yield and stand age.

3.2. Model for L. group deliciosus

L. group *deliciosus* sporocarps emergence seems to be affected by the weather conditions (precipitation and temperature) and stand variables (stand dominant height and basal area). The model fitted for L. group *deliciosus* yield was as follows:

$$Lactarius = \exp(-3.309 + 0.008 P_{autumn} + 0.106 T_{autumn} + 0.653 \times \ln(Hdom) - 0.018 G)$$

Fig. 1. Relationship between the annual yield of ectomycorrhizal mushrooms and stand age according to the model. When constructing the curves, dominant height depended on stand age according to the used site index model.
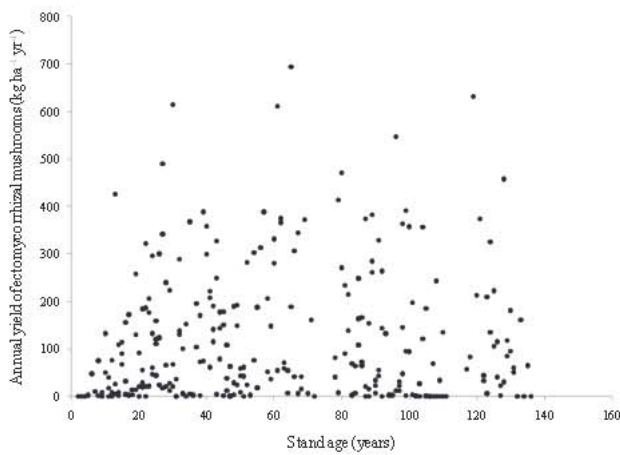
where *Lactarius* is the annual yield of L. group *deliciosus* (kg ha^{-1} yr^{-1}), P_{autumn} is the sum of the total precipitation in August, September and October, T_{autumn} is the sum of the mean temperature in September, October and November, *Hdom* is the stand dominant height and *G* is the stand basal area. The R-squared of the model was 0.261 and the RMSE was 25.75 kg ha^{-1} yr^{-1}.

As for the total ectomycorrhizal mushrooms, the annual yield of L. group *deliciosus* depends on both weather and growing stock variables. The average annual yield of *Lactarius* was around 9 kg ha^{-1} yr^{-1} (Fig. 4). In very good years and productive sites, the yield can go beyond 100 kg ha^{-1} yr^{-1} and, exceptionally, even exceed 200 kg ha^{-1} yr^{-1}.

Dry and cold autumns are predicted to be less productive whereas in wet and warm autumns the yield of *Lactarius* is much higher. Stands with low dominant height are less productive whereas the optimal dominant height for *Lactarius* production seems to be 13–14 m (Fig. 4). In an average *P. sylvestris* site from the study area (site index = 23 m), such a dominant height is reached when the stand is about 45 yr old.
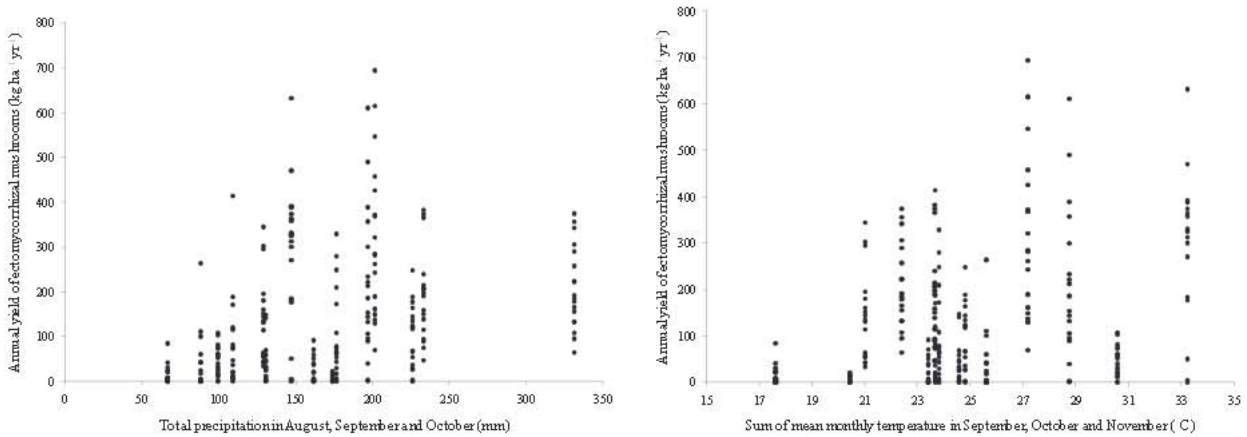
Fig. 2. Scatter plots between autumn precipitation (sum of precipitation in August, September and October) (left) or autumn temperature (sum of the mean temperatures in September, October and November) (right), and the measured annual yield of ectomycorrhizal mushrooms.

Fig. 3. Scatter plot between stand age and the measured annual yield of ectomycorrhizal mushrooms.
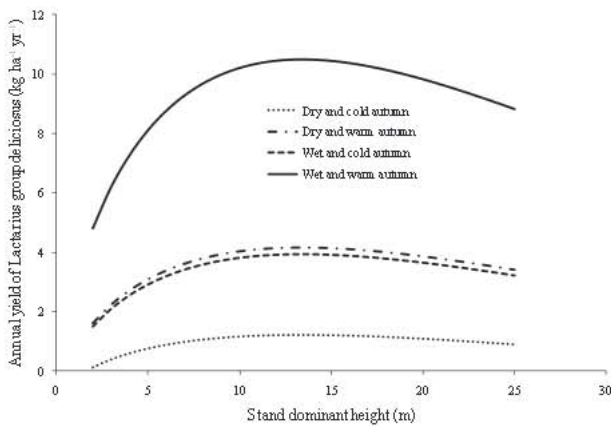
Fig. 4. Relationship between the annual yield of *L.* group *deliciosus* and stand dominant height.

3.3. Model for B. edulis

The model obtained for annual yield of *B. edulis* was as follows:

$$Boletus = \exp(-14.706 + 0.007\,P_{autumn} + 0.129\,T_{autumn} + 5.049 \\ \times \ln(G) - 0.121\,G)$$

where *Boletus* is the annual yield of *B. edulis* (kg ha^{-1} yr^{-1}), P_{autumn} is the sum of the total precipitation in August, September and October, T_{autumn} is the sum of the mean temperature in September, October and November, and *G* is the stand basal area. The *R*-squared of the model was 0.222 and RMSE was 43.2 kg ha^{-1} yr^{-1}.

As in the previous models, the annual yield of *B. edulis* depends on both weather and stand-level variables. The average annual yield of *B. edulis* was around 26 kg ha^{-1} yr^{-1} (Fig. 5). In very good years, the yield can go beyond 200 kg ha^{-1} yr^{-1} (Fig. 6).

According to the model, dry and cold autumns are less productive whereas wet and warm autumns are associated with high yield of *B. edulis*. Stands with low or high basal area are the less productive, the optimal stand basal area for *B. edulis* production being around 40 m^2 ha^{-1} (Fig. 5).

3.4. Correlation of mushroom yield with soil properties

Although many physical and chemical soil properties were considered during the modeling process, soil characteristics were not significant predictors of the annual yield of ectomycorrhizal mushrooms, *Lactarius* and *B. edulis*. However, since soil properties may affect mushroom dynamics; a correlation analysis was done in order to see if there are any statistical linear relationships between mushroom yield and soil characteristics (Table 2).

Water retention capacity, pH and soil texture showed significant and logical correlations with mushroom yields (ectomycorrhizal mushrooms, *L.* group *deliciosus* and *B. edulis*). Sand content
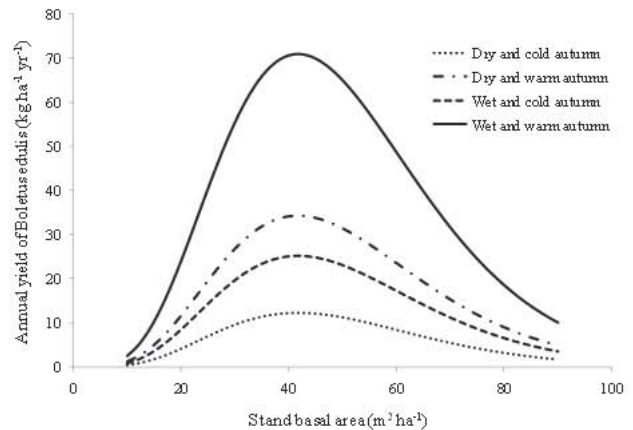
Fig. 5. Relationship between the annual yield of *B. edulis* and stand basal area.
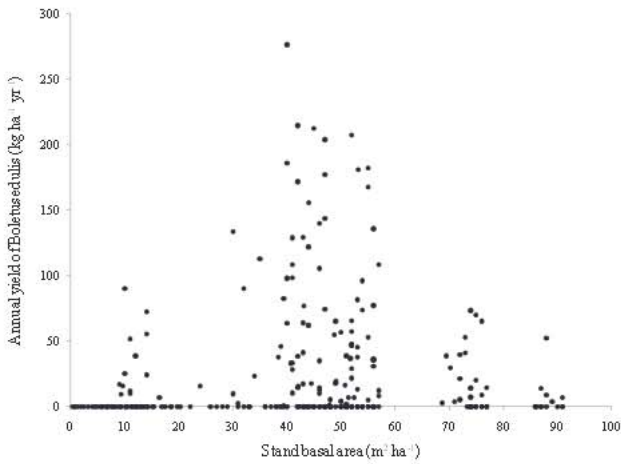
Fig. 6. Scatter plot between stand basal area and the measured annual yield of *B. edulis*.

Table 2

Significant correlations observed between measured soil parameters of the study plots and ectomycorrhizal mushroom yields.

Variable	All ectomycorrhizal fungi	*Lactarius* group *deliciosus*	*Boletus edulis*
Soil depth (cm)	−.136[*]		
Sand content (%)		−.240[**]	.124[*]
Silt content (%)		.221[**]	−.155[*]
Clay content (%)		.216[**]	
pH			−.182[**]
Water retention capacity (mm)	.128[*]	.186[**]	
K (ppm)	.137[*]		
Mg (ppm)		.131[*]	−.177[**]
Fe (ppm)			−.175[**]
P (ppm)		−.146[*]	
C/N			.171[**]

[*] Represents significance at 0.05 level.
[**] Represents significance at 0.01 level.

correlated negatively with *Lactarius* yield but positively with *B. edulis*. Silt content showed a negative correlation with *B. edulis* yield whereas silt and clay contents were positively correlated with *Lactarius* yield. Water retention capacity of the soil was positively correlated with the total yield of ectomycorrhizal mushrooms and also with *Lactarius* yield, whereas pH correlated negatively with *B. edulis* yield (Table 2).

4. Discussion

The main weather variables, rainfall and temperature, had a significant effect on the yield of all the mushroom species analyzed in this study. Weather has been mentioned in the literature as the most critical factor affecting the emergence of sporocarps. Studies based on long-term mushroom inventories such as those conducted by Straatsma et al. (2001) in Switzerland (21-year data series), by Straatsma and Krisai-Greilhuber (2003) in Austria (7-year data series) and by Krebs et al. (2008) in Canada (15-year data series) have also shown a strong positive correlation between the amount of rainfall and mushroom yields, leading to a general increase of the productivity of all fungal species. The fungal yields registered in Pinar Grande seem to be higher than those reported in the literature, which may be partly explained by the fact that the mushroom plots of this study were fenced preventing losses caused by mushrooms pickers and livestock.

In the above-mentioned studies, temperature was a key factor interacting with moisture, which is in line with the general empirical knowledge provided by mushroom pickers who associate mild temperatures in rainy autumns with maximum productivity. Nevertheless, it is worth mentioning that the models presented in this study show a one-month delay between the autumn rainfall (expressed as the sum of August, September and October monthly rainfall) and temperature (expressed as the sum of mean temperature in September, October and November), suggesting that mushroom emergence needs first a minimum amount of rainfall and, afterwards, appropriate temperatures (Martínez de Aragón et al., 2007). The study region is characterized by a continentalized Mediterranean climate with low minimum temperatures in autumn. Therefore, temperature seems to be more crucial than rainfall for explaining fungal yields, as shown in Figs. 1, 4 and 5.

By contrast, variables related to site characteristics (i.e. slope, aspect, altitude) did not explain differences in mushroom yield, probably due to the homogeneous conditions of the plots, as shown in Table 1. On the other hand, variables describing the stand structure (i.e. stand basal area, stand age, dominant height) had a significant influence on mushroom production. Dominant height and stand age had a significant effect on the total annual yield of ectomycorrhizal mushrooms (Fig. 1). The maximum fungal productivity was found in stands with ages ranging from 60 to 70 yr. This peak of production matches with the maximum current annual volume increment of *P. sylvestris* (Montero et al., 2008). In fact, the link between the presence of ectomycorrhizal (ECM) fungi and the photosynthetic activity of the trees is well known (Nehls, 2008). ECM fungi play an important role in mobilizing nutrients from the soil that enhance tree nutrition (Smith and Read, 2008). ECM fungi, in turn, retrieve carbon photosynthates from their host plants (Nehls, 2008), which suggests a relationship between the vigor of the trees and the associated fungal community (Rudawska et al., 2011). Recent research supports the hypothesis that carbohydrate metabolism plays and essential role in the development of ectomycorrhizal fungi (Ceccaroli et al., 2011). Other authors have also found less sporocarp biomass in old-growth stands than in younger stands (Dahlberg and Stenlid, 1994; Smith et al., 2002: Bonet et al., 2010) with logical differences between the maximum peaks of production and forest age according to the site quality of the forest stand. These results depend on the forest management schedule in such a way that, if the stands follow analogous silvicultural practices, the expected maximum mushroom yield will be found within a similar range of stand age. On the contrary, if different forest management schedules were applied to different stands, the effect of stand age would probably be obscured by the between-stand differences in stand structure (i.e. stand density and basal area) (Bonet et al., 2004).

The observed pattern of occurrence of the total ECM fungi in a forest stand may not necessarily be the same as the pattern found for every individual species. Fungal species have adopted their own ecological strategies to survive and face interspecies competition in the complex soil ecosystems. The models provided in this study for different mushroom taxa also reflect the ecology of different mushroom species. Dominant height and stand basal area had a significant effect on the yield of *L.* group *deliciosus*. The influence of stand age on the emergence of saffron milk caps has been tackled in previous research. Bonet et al. (2004) did not find a significant relationship between *Lactarius* yield and stand age in even-aged Scots pine forests of north-eastern Spain, whereas Fernández-Toirán et al. (2006) observed higher yields of *Lactarius* in 11- to 20-year-old *P. pinaster* forests even if this mushroom species appeared in all the range of stand ages. Similar trends were also described by Martínez-Peña et al. (2012) who observed fructifications covering the whole range of stand age classes in *P. sylvestris* forests. Smith et al. (2002) observed a peak of *Lactarius*

production in 30- to 50-year-old *Pseudotsuga menziesii* forests (coinciding with the period of maximum tree growth) and an absence of production in old-growth forests in Oregon (USA). Ortega-Martínez et al. (2010), in a specific study about the influence of *P. sylvestris* stand age on the development of ECM fungi sporocarps, observed that *L. deliciosus* fruitbodies were usually collected in young stands coinciding with the maximum annual basal area increment, noting that this species is characteristic of the early successional stages. In our study, stand age did not have an equally significant influence on the yield of saffron milk caps as dominant height. Since stand age and dominant height are correlated, only dominant height was selected as model predictor. The peak of *Lactarius* production occurs with 13–14 m of dominant height, which corresponds to an approximate stand age of 45 yr, which is in line with the findings reported in the literature.

Although stand basal area was a significant factor explaining the yield of saffron milk caps, high yields of this species can be found over a wide range of stand basal areas. This is in accordance with the results obtained by Bonet et al. (2012) who found an increase of *L. group delicious* yields when the removed basal area ranged from 10 to 35 m^2 ha^{-1} in a thinning experiment in *Pinus pinaster* forests. This suggests that *L. group deliciosus* had a high adaptive ability to different stand structures. Nevertheless, the three species included under the name *L. group deliciosus* could have particular habitat preferences and different production patterns such that they may exploit different niches.

The influence of stand basal area on the yield of *B. edulis* was more evident. The expected maximum production for this species (70 kg ha^{-1} yr^{-1} in wet and warm autumns) was reached when the stand basal area was 40–45 m^2 ha^{-1}. Although *B. edulis* occurs in whole Europe, the range of suitable ecological conditions for the emergence of its fruit bodies has remained so far unknown since it has not been the subject of detailed research (Alonso et al., 2011). The model presented in this study is, to our knowledge, the first one for *B. edulis*. The results of this study may be of high interest for forest managers who aim at directing forest management towards the production of this species. Stand structure can be modified by means of thinning treatments in order to achieve such a stand basal area which maximizes mushroom production according to the mushroom yield models. However, it is important to remember that this study considered only homogeneous even-aged stands in a restricted geographical region. Therefore, further experimental research on the influence of stand basal area on the yield of *B. edulis* based on plots with higher variability in terms of stand structure would be valuable to better understand the relationship between boletes yields and stand structure.

Although the sample plots were rather homogeneous in terms of soil properties, some interesting and significant correlations between mushroom yield and physical and chemical soil characteristics were found (Table 2). The influence of soil properties on ECM fungal community in both taxonomic and functional structure has been reported in the literature (Courty et al., 2010). However, there is a considerable lack of information regarding the soil requirements of many mushroom species, except for *Tuber melanosporum* (see Bonet et al., 2009).

According to our results, the yield of *B. edulis* was significantly and positively correlated with the sand content, acidity and C/N ratio of forest soils. On the other hand, *L. group deliciosus* production was significantly and positively correlated with the percentage of silt and clay in the soil as well as with water retention capacity. Several previous studies are in accordance with these findings. Hall et al. (1998) described *B. edulis* as a species that can be found within a wide range of habitats and soil conditions. As a general pattern, high C/N ratios seem to be a common positive factor explaining the emergence of *B. edulis* in most of the studied sites, which is in line with our results. Other variables found significant in our study,

such as the affinity of *B. edulis* for acid soils as well as the preference for permeable soils with sandy textures have also been reported by other authors (Muñoz, 2005; Alonso et al., 2011). Furthermore, the presence of boletes in sandy and well-drained soils is consistent with the empirical observations made by mushroom pickers. By contrast, the presence of *Lactarius quieticolor* in wet sites (Heilmann-Clausen et al., 2000) may explain the positive correlation between *L. group deliciosus* yield and soils with higher content of silt and clay, having higher water retention capacities.

This study highlights and confirms the crucial influence of rainfall and temperature as driving factors explaining mushroom production. On the other hand, stand characteristics were shown to also have a significant effect on the yield of different ectomycorrhizal fungi. The models provided in this study constitute a valuable tool to estimate the total yield of ectomycorrhizal mushrooms as well as the yields of two species of high economic interest (*L. deliciosus* and *B. edulis*) in *P. sylvestris* forests in north-central Spain. Although further research on both empirical and mechanistic modeling is needed for a better understanding of the relationship between stand characteristics, carbon allocation and mushroom productivity, some tentative recommendations can be already drawn for forest managers in order to improve mycological productions. In combination with forest growth and yield models, these equations enable predictions of mushroom yield under different forest management schedules and climatic scenarios.

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