

Empirical models for predicting the production of wild mushrooms in Scots pine (*Pinus sylvestris* L.) forests in the Central Pyrenees

José Antonio BONET^{1*}, Timo PUKKALA², Christine R. FISCHER¹, Marc PALAHÍ³, Juan Martínez de ARAGÓN¹, Carlos COLINAS¹

¹ Centre Tecnològic Forestal de Catalunya, Pujada del seminari s/n, Solsona, Spain

² University of Joensuu, Faculty of Forestry, PO Box 111, 80101 Joensuu, Finland

³ European Forest Institute, Mediterranean Regional Office, Passeig Lluís Companys, 23, 08010 Barcelona, Spain

(Received 5 February 2007; accepted 22 August 2007)

Abstract – Mushroom picking has become a widespread autumn recreational activity in the Central Pyrenees and other regions of Spain. Predictive models that relate mushroom production or fungal species richness with forest stand and site characteristics are not available. This study used mushroom production data from 24 Scots pine plots over 3 years to develop a predictive model that could facilitate forest management decisions when comparing silvicultural options in terms of mushroom production. Mixed modelling was used to model the dependence of mushroom production on stand and site factors. The results showed that productions were greatest when stand basal area was approximately 20 m² ha⁻¹. Increasing elevation and northern aspect increased total mushroom production as well as the production of edible and marketed mushrooms. Increasing slope decreased productions. Marketed *Lactarius* spp., the most important group collected in the region, showed similar relationships. The annual variation in mushroom production correlated with autumn rainfall. Mushroom species richness was highest when the total production was highest.

multiple-use forestry / forest management / non-wood forest products / mixed models / *Lactarius deliciosus*

Résumé – Modèles empiriques de prédiction de la production de champignons sauvages dans des peuplements de pin sylvestre (*Pinus sylvestris* L.) des Pyrénées centrales. La cueillette de champignons est devenue une activité de loisir très répandue dans les Pyrénées centrales ainsi que dans d'autres régions d'Espagne. Aucun modèle prédictif de production ou de richesse en espèces en fonction des caractéristiques des peuplements et des stations n'est disponible actuellement. La présente étude s'est basée sur des données de récolte de champignons de 24 placettes de pin sylvestre suivies pendant 3 ans pour développer un modèle prédictif pouvant servir de modèle d'aide à la décision pour des opérations de gestion forestière. Un modèle mixte a été mis en œuvre pour analyser les relations entre facteurs stationnels et de peuplement. Les résultats montrent que la production était maximale quand la surface terrière était de l'ordre de 20 m² ha⁻¹. La production totale ainsi que celle de champignons comestibles et commercialisables augmentaient avec l'altitude et dans les pentes orientées au nord. Le groupe des Lactaires (*Lactarius* spp.) le plus important champignon commercialisable de la région, présentait des réponses similaires. La variabilité interannuelle de production était étroitement corrélée à celle des pluies automnales. La richesse en espèce était étroitement corrélée à la production totale.

gestion multifonctionnelle des forêts / sylviculture / gestion forestière / produits non ligneux / *Lactarius deliciosus*

1. INTRODUCTION

Forests have always provided multiple resources for society in addition to wood and wood products, including animal and plant habitat, resins and oils, water cycling, soil development, hunting, and recreation. The concept of multiple-use forestry has been integrated into forest policy programs at regional, national and international levels during the past few decades due to losses in forest cover, threats to biodiversity, increasing demands from growing populations, concerns for carbon sequestration and ecological awareness [3]. Integration of multiple-use forestry in forest planning is a regional challenge because it depends on complicated socio-economic factors and the dynamics of forest and plant communities.

With the increasing exodus from rural areas and urbanization of society, the rising incomes and environmental awareness of society compounded with the lack of profitability of wood production, forest and land managers are seriously evaluating the importance of many non-wood forest products (NWFP) such as mushrooms, berries, medicinal plants, and floral greens [18]. In addition the importance of the ecological, recreational and landscape values of the forests is growing.

Wild edible and medicinal mushrooms represent an important NWFP world-wide [3] with international trade of many ectomycorrhizal genera including *Amanita*, *Boletus*, *Tuber*, *Tricholoma*, *Cantharellus* and *Lactarius* and saprophytic genera including *Morchella*, *Pleurotus* and *Agaricus*. The market demand has increased to the extent that the commercial value of forest fungi may equal or even surpass the value of timber [1, 2, 24]. Consequently, there is growing interest on the

* Corresponding author: jantonio.bonet@ctfc.es

part of forest owners and managers to inventory, predict, and develop the commercial mushroom production [26].

Commercial collections of forest fungi have become increasingly important in several regions of Spain as reflected in programs to promote research, education, sustainability, marketing, tourism and rural development associated with forest mushrooms. Annual mushroom productions vary considerably throughout Spain, but one of the most productive areas is the forested region of the Pyrenees and Prepyrenees. Recent inventories of wild mushrooms from *Pinus sylvestris* forests of the Prepyrenees of Catalonia report productions of approximately 60 kg ha⁻¹ fresh weight [16] of which 54% are edible species, 29% are marketed species and the other 25% are edible but not marketed species [4].

Within the marketed species from Central Pyrenees, the *Lactarius deliciosus* group that also includes *L. sanguifluus*, *L. semisanguifluus* and *L. vinosus* are highly valued species sold under the generic name of *rovelló*. Annual revenue from 478 metric tons of *L. deliciosus* sold in the central Barcelona market (Mercabarna) is estimated at 1.5–2 million €. This represents more than half of the total mushroom sales from this market. The marketed *Lactarius* group is highly profitable in other regions of Spain where it has been introduced with *P. sylvestris* reforestation [5].

Mushrooms are not only a source of income for the collectors and tourism businesses but may soon provide an economic incentive for the forest landowners. A recent survey demonstrated that Catalonians are willing to pay for the experience of picking wild mushrooms [17]. Consequently we could expect incentives for improved forest management. When mushrooms become a source of revenue for forest managers, management priorities shift and interventions such as thinning, pruning, and control of invasive plants are carried out on a more frequent basis with forests significantly less vulnerable to wildfire, and much more protected from overgrazing.

However, the mushroom production has only recently become a recognised management objective in forest planning [28]. To integrate mushrooms and other NWFP and services in forest planning, models based on empirical studies that can predict production or function and are applicable to planning parameters are needed. However, other than empirical models to predict the yield of wild berries in Finland [11–13], very few empirical models have been developed to predict productions of NWFP for use in forest planning. No models were found in the literature for predicting the production of wild mushrooms in forest planning.

Site and growing stock characteristics are the most reasonable predictors when developing an empirical mushroom production model for forest planning because the site and stand characteristics are known factors. In addition, stand characteristics can be altered through forest management. However, mushroom productions also depend on weather conditions such as timing and quantity of rainfall, which are not equally useful in forest planning because they cannot be accurately predicted beyond a few weeks.

The construction of reliable models for predicting mushroom productions requires collecting large quantities of empirical data over several years because there are multiple

factors responsible for high temporal variation in mushroom productions. These include variations in precipitation, temperature, frost, evapotranspiration, relative humidity, and water deficits [16, 21, 23, 31, 34].

P. sylvestris (Scots pine) is the most widespread of pine forests throughout Europe and hosts hundreds of forest fungi. Factors influencing fungal diversity associated with Scots pine include host specificity for ectomycorrhizal species [19], forest age [4, 9, 14, 15] and aspect [4]. Other influences include human intervention and forest management practices (timber harvesting, precommercial thinning or removal of competing under story vegetation, reforestation, controlled grazing, wildfire management) as well as soil properties, basal area, plant community macroclimate and microclimate characteristics [6, 8, 22, 32].

The aim of the study was to develop empirical models for predicting the production of wild mushrooms in Scots pine (*Pinus sylvestris* L.) forests in the Central Pyrenees based on mushroom production data from three consecutive years. The predictive parameters used include stand basal area, number of trees per hectare, mean age, mean diameter, mean height, standard deviation of diameter and height, site index, elevation, slope and aspect. A mixed model technique was used to account for random annual variation of mushroom productions. These models could allow the forest manager to optimize economic returns by predicting potential productions of mushrooms.

2. MATERIAL AND METHODS

2.1. Mushroom plots

In 1995, 36 plots of 10 × 10 m were established in *Pinus sylvestris* plantations of the Central Pyrenees in order to evaluate the productivity and diversity of ectomycorrhizal and edible fungi in this forest community. These plots were randomly selected from the total of 118 plantations established by the Forest Service during the 20th century. The plantations and the plots ranged from 5 to 84 years in age, with the 55–64 age-class missing due to the Spanish Civil War. The plots represent different Scots pine stand conditions with respect to site and density (see Tab. I), and management practices. The site index (dominant height at 100 years) ranged from 13 m to 27 m.

The plots were sampled at 1-week intervals from September through November during the 1995, 1996 and 1997 autumn seasons. Data from spring fruiting have not been included due to very low productions. The mushroom production data, for ectomycorrhizal and edible mushrooms, were obtained by species and are expressed as fresh weight, dry weight and number of sporocarps per hectare. All collections were classified by edibility and by marketability. We used the following groupings in the model: all species, the edible species, the marketed edible species, and the marketed edible *Lactarius* species. Additional information on the sampling sites, the fungal species list and inventory methodology can be found in Bonet et al. [4].

2.2. Forest plots

Of the total 36 plots established to determine mushroom productivity and diversity, 24 were evaluated in 2006 to measure relevant site

Table I. Summary of stand variables and mushroom productions for the 24 plots used for modelling the production of mushrooms. The stand variables are given for the first year of the mushroom production measurements (1995). The mushroom productions are the averages of the 3-year measurement period. The fungal species diversity indices (number of species, Shannon index, Simpson index) of are based on 3-year data. The Shannon and Simpson indices are calculated from fresh weight (kg/ha).

Variable	Mean	Standard deviation	Minimum	Maximum
Stand variables				
T (y)	27.9	12.4	10.4	55.3
H _{dom} (m)	12.3	4.4	3.3	20.0
G (m ² ha ⁻¹)	20.6	13.6	1.0	54.8
N _{trees} (trees ha ⁻¹)	1171.7	392.3	717.2	2196.3
D _m (cm)	17.2	7.0	4.9	34.2
SI (m)	22.3	2.9	13.3	27.5
Elevation (m)	1238.8	220.2	846.0	1528.0
Aspect (degrees)	179.9	130.4	4.0	356.0
Slope (%)	24.1	7.2	7.0	38.0
Mushroom productions and diversity indices				
Total (kg ha ⁻¹)	123.7	135.2	0.2	466.6
Edible (kg ha ⁻¹)	63.0	75.0	0.2	283.4
Marketed (kg ha ⁻¹)	25.6	39.1	0.2	153.4
<i>Lactarius</i> (kg ha ⁻¹)	7.9	21.6	0.0	104.5
Shannon index	1.34	0.45	0.00	2.13
Number of taxa	17.33	8.20	1.00	32.00
Simpson index	0.27	0.20	0.02	1.00

T: Stand age; H_{dom}: dominant height; G: stand basal area; N_{trees}: the number of trees per hectare; D_m: mean diameter; SI: site index at a reference age of 100 years.

and growing stock variables. The other plots had either been cut or significantly transformed through management actions. The plot area varied between 0.04 and 0.16 ha. The mean plot area was 0.057 ha. Plots were established so that at least 100 trees with dbh > 7.5 cm were within the plot. For each plot, tree diameter at 1.3 meters height (dbh) and the growth for the last ten years were measured for all trees. In addition, tree heights, tree age and bark thicknesses were recorded for a sample of at least 20 trees per plot.

2.3. Methods

2.3.1. Data preparation

The forest stand measurements taken in the winter 2006 correspond to the stand characteristics of these plots at the end of 2005 tree growing season. The mushroom production data were collected in the autumns of 1995, 1996 and 1997, also at the end of the tree-growing season (September through November). Before relating mushroom productions to forest stand characteristics (Tab. I), stand measurements for 1995, 1996 and 1997 were calculated as follows. The sample-tree data were utilised to fit the following tree age and tree height models separately for every plot:

$$t = a_0 + a_1 d \quad (1)$$

$$h = 1.3 + d^2 / (b_0 + b_1 d)^2 \quad (2)$$

where t is tree age (years), d is diameter (cm), h is height (m) and a_0 , a_1 , b_0 , b_1 are parameters. These models were used to estimate the age and height of trees other than sample trees. Bark measurements were used to fit the following model, which was common to all plots

$$b = -0.668 + 0.701d \quad (3)$$

where b is bark thickness (mm). The over-bark diameters of trees 10 years earlier were calculated by first subtracting the doubled bark thickness prediction (Eq. (3)) from the measured diameter. Subtracting the doubled measured radial growth from the under-bark diameter gave the under-bark diameter 10 years ago. This was converted to over-bark diameter by assuming that the ratio of under- and over-bark diameters 10 years ago was the same as at plot measurement (2006). Over-bark diameters 9 and 8 years ago (1996 and 1997) were obtained by assuming a constant diameter growth between 1995 and 2005. Tree heights 10, 9 and 8 years ago were obtained from the plot-wise height models (Eq. (2)) and tree ages by subtracting 10, 9 or 8 years from the tree age at plot measurement.

These tree variables were used to calculate the following stand level variables for the plots: stand basal area, number of trees per hectare, mean age, mean diameter, mean height, standard deviation of diameter and height, and site index calculated from the model of Palahi et al. [25]. In addition to growing stock variables, some topographical variables (elevation, slope and aspect) were included as potential predictors of the mushroom production models.

2.3.2. Diversity indices

Fungal species richness and diversity indices were determined for each plot as follows: number of taxa (N), Shannon index (H), and Simpson index (S). The indices of Shannon and Simpson were calculated from:

$$H = - \sum_{i=1}^N p_i \ln(p_i) \quad (4)$$

$$S = \sum_{i=1}^N p_i^2 \quad (5)$$

where p_i is proportion of species i (of fresh biomass in kg/ha). The mushroom measurements from 1995, 1996 and 1997 were pooled before calculating the indices. A high value of Shannon index and a low value of Simpson index imply high diversity.

2.3.3. Modelling

The predicted variable in the mushroom production model was the logarithmic transformation of the yearly production. This resulted in a linear relationship between the dependent and independent variables, and enabled development of multiplicative production models. The predictors were chosen from stand and site variables as well as their transformations. All predictors had to be significant at the 0.05 level, and the residuals had to indicate a nonbiased model in order to be included in the model. Due to the hierarchical structure of the data, mushroom measurements of the same year were correlated observations as were the measurements on the same plot. Therefore, the generalised least squares (GLS) technique was applied to fit mixed linear models. The linear models were estimated using the maximum likelihood procedure of the computer software SPSS [30]. The following random parameter model (also called mixed model) was the basic model:

$$y_{ij} = f(x_1, x_2, \dots, x_n) + \mu_i + \mu_j + \varepsilon_{ij} \quad (6)$$

where y_{ij} is the mushroom production of plot i in year j , $f(\cdot)$ is the fixed part of the model, x_1, \dots, x_n are predictors, μ_i is random plot factor, μ_j is a random year factor and ε_{ij} is residual (that part of the production which is not explained by the fixed part, plot factor and year factor). The model was fitted for the total production, production of edible species, production of marketed species, and productions on individual species or species groups.

When models for species diversity were developed, there were no correlated observations because the mushroom measurements of the three years were pooled before fitting the models. Therefore, the model was simply

$$z_i = f(x_1, x_2, \dots, x_n) + \varepsilon_i \quad (7)$$

where z_i is the diversity index for plot i and ε_i is residual.

3. RESULTS

3.1. Models for mushroom production

The regression analyses showed that stand basal area, elevation, aspect and slope were the most significant predictors of mushroom productions. No other variables had a significant contribution to the fitting statistics after these variables had been included in the models. The analyses also showed that, of the species-specific models, only the model for the marketed *Lactarius* group was statistically significant. Therefore, the model set prepared to describe the dependence of mushroom productions on stand and site variables was as follows:

Total production

$$\ln(y_{ij}) = 0.981 + 2.483\ln(G) - 0.128G + 0.934 \cos(Asp) - 0.0135Slo^{1.5} + u_i + u_j + e_{ij} \quad (8)$$

Table II. Variances of random factors, fitting statistics and the Snowdon correction factor for the mushroom production models. Low values of residual variance, $-2 \times \text{Log likelihood}$ and Akaike's information index (AIC) imply good fit.

	Total production	Edible mushrooms	Marketed mushrooms	Marketed <i>Lactarius</i>
Variance of plot factor (u_j)	0.216	0.466	1.929	0.527
year factor (u_j)	0.353	0.836	0.854	0.847
residual (e_{ij})	0.805	1.656	1.105	1.659
Total variance	1.374	2.958	3.888	3.033
$-2 \times \text{Log likelihood}$	223.6	275.5	294.0	273.8
AIC	229.6	281.9	300.0	279.8
Snowdon correction	1.511	2.093	3.011	12.472

Edible mushrooms

$$\ln(y_{ij}) = -4.329 + 1.966\ln(G) - 0.118G + 0.636 \cos(Asp) + 0.00331Alt + u_i + u_j + e_{ij} \quad (9)$$

Marketed mushrooms

$$\ln(y_{ij}) = -6.236 + 1.246\ln(G) - 0.0599G + 0.00459Alt + u_i + u_j + e_{ij} \quad (10)$$

Marketed *Lactarius*

$$\ln(y_{ij}) = -0.192 + 1.016\ln(G) - 0.106G + 1.489 \cos(Asp) - 0.0151Slo^{1.5} + u_i + u_j + e_{ij} \quad (11)$$

where y_{ij} is the production of plot i in year j , G is stand basal area (m^2ha^{-1}), Asp is aspect (rad), Slo is slope (%), i.e. 45° is equal to 100%), Alt is elevation (m above sea level), u_i is random plot factor, u_j is random year factor, and e_{ij} is residual. All random factors (u_i , u_j and e_{ij}) are assumed to be normally distributed with mean equal to zero. The variances of the random factors are given in Table II together with some fitting statistics. All the regression coefficients of predictors were significant ($p < 0.05$).

When only the fixed part of the model is used for predicting (as is usual), the Baskerville correction factor, which is half of the total residual variance $((u_i + u_j + e_{ij})/2)$, is commonly added to the prediction before exponentiation of the predicted logarithmic production. This is due to the logarithmic transformation of the predicted variable. If e.g. the year factor is known, only $(u_i + e_{ij})/2$ should be added. However, we propose the use of the Snowdon correction [29] because it has been found that using the Baskerville correction often leads to biased back-transformed predicted values if the degree of explained variance is low [33]. The exponentiations of the predictions of the fixed model part should be multiplied by the Snowdon factors shown in Table II rather than adding $(u_i + u_j + e_{ij})/2$ to the logarithmic production.

Even though plot and year factors are rarely used in prediction, it is interesting to note that the year factors of 1995, 1996 and 1997 correlate with the September–October rainfall of those years (Tab. III). This suggests that the year factor may be partly predicted from climatic data and in this way the

Table III. Year factors of the model for total mushroom production (Eq. (8)) and rainfall for September–November in the Central Pyrénées.

Year	Year factor	Rainfall (mm)
1995	0.0063	60.0
1996	0.5644	72.6
1997	-0.5707	33.2

mushroom production prediction of the current year could be improved (after knowing the amount of autumn rains). If the fixed model part predicts a total production of 100 kg, more accurate production predictions for 1995, 1996 and 1997 would be as follows:

- 1995: Production = $\exp(\ln(100) + 0.0063) = 101 \text{ kg ha}^{-1}$
- 1996: Production = $\exp(\ln(100) + 0.5644) = 176 \text{ kg ha}^{-1}$
- 1997: Production = $\exp(\ln(100) - 0.5707) = 57 \text{ kg ha}^{-1}$.

These calibrated predictions vary in the same way as the measured mean productions, which were 118, 177 and 77 kg ha^{-1} , respectively, in 1995, 1996 and 1997. If the production in 1995 is indicated by 100, the measured relative productions of 1996 and 1997 were 149 (1996) and 65 (1997).

According to the models, mushroom productions are the highest when stand basal area is 10–20 $\text{m}^2 \text{ha}^{-1}$ (Fig. 1A). Aspect is another factor which strongly affects the predicted production so that northern aspects have the highest productions and southern the lowest (Fig. 1B). Aspect has a similar effect also on the production of marketed mushroom (Eq. (10)) but in this model the effect of aspect was not statistically significant.

Increasing altitude improves the production of edible and marketed mushrooms and increasing the slope decreases the total production and the production of marketed *Lactarius* (Fig. 2). In fact, all the used predictors (basal area, altitude, aspect and slope) have a similar effect for all the production components (total, edible, marketed, and marketed *Lactarius*) but all predictors were not statistically significant in all models. Figure 2 depicts the effects of stand basal area, slope and aspect on total mushroom production.

The predictions have a rather good correlation with the measured productions, especially when the plot and year factors are used in prediction (Fig. 3). The correlations are better when the mean productions of the 3-year measurement period are compared (Fig. 4) indicating that the models fairly well predict the overall level of the mushroom production of Scots pine dominated stands in Central Pyrenees.

3.2. Models for mushroom diversity

The species diversity of mushrooms depended on stand basal area, altitude, slope and aspect in the same way as the production. If all predictors were forced in the models, increasing elevation and northern aspect always improved diversity, and increasing slope decreased it. Logarithm of stand basal area had a positive sign and untransformed basal area

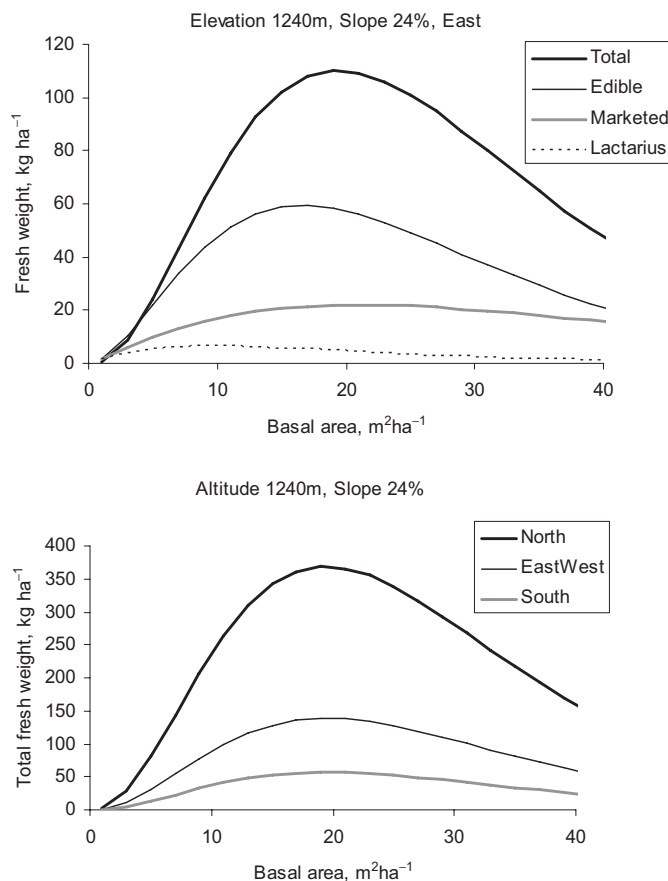


Figure 1. Mushroom production as a function of stand basal area according to Equations (8)–(11). Elevation and slope are equal to their mean values in the modelling data. The lower diagram shows the effect of aspect and stand basal area on total mushroom production (Eq. (8)).

a negative sign. However, only stand basal area was a statistically significant predictor on the models for Shannon and Simpson indices. The models for diversity indices were therefore

$$\ln(N) = 1.081 + 1.134\ln(G) - 0.051G + 0.292 \cos(Asp) - 0.005Slo^{1.5} \quad (12)$$

$$H = 0.417 + 0.590\ln(G) - 0.033G \quad (13)$$

$$S = -0.763 - 0.245\ln(G) + 0.009 \quad (14)$$

where N is the number of species, H is Shannon index, and S is Simpson index. The standard deviation of the residual was 0.341 for the model for $\ln(N)$, 0.333 for the model for H and 0.142 for the model for S . The R^2 statistics were 0.85, 0.52, and 0.58 for the models for $\ln(N)$, H and S , respectively. According to the models, species diversity is the highest when stand basal area is between 15 and 25 $\text{m}^2 \text{ha}^{-1}$ (Fig. 5).

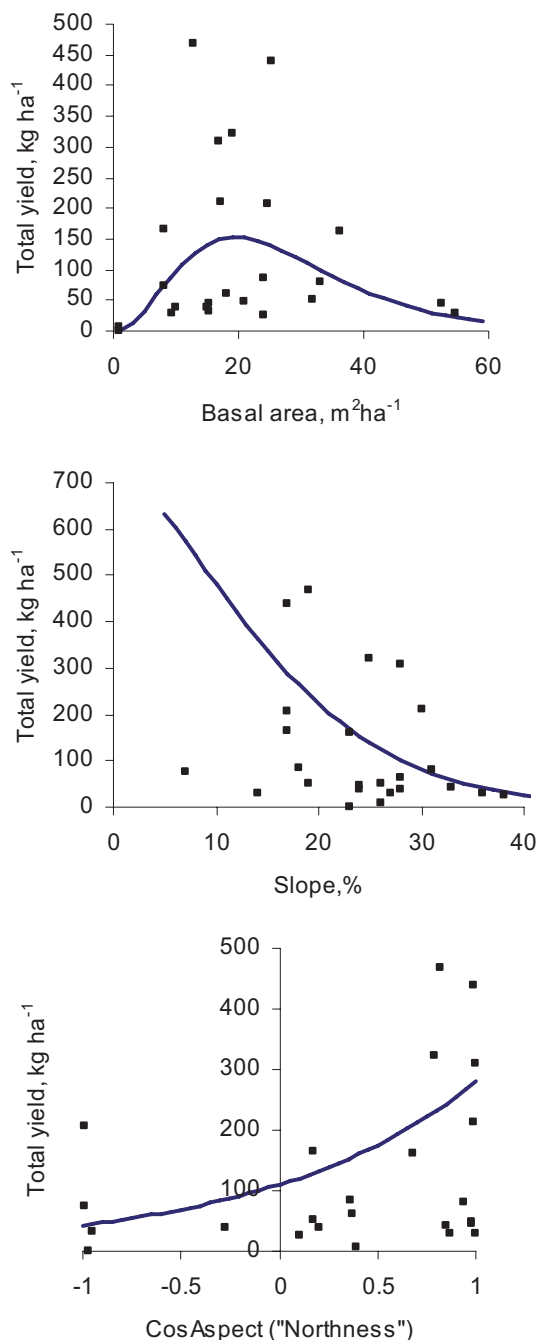


Figure 2. Dependence of total mushroom production (kg ha^{-1}) on stand basal area, slope and aspect. The dots indicate the means of the measured productions of the plots (3-year averages) and the curves are predictions of Equation (8).

4. DISCUSSION

Recreational and commercial mushroom hunters typically look for extended weather forecasts to predict when and where to search for wild mushrooms each year. For forest managers, who recognize the increasing value of this forest resource, predictions must go beyond annual weather conditions

to make it possible to develop management programs that can enhance mushroom production. Of the traditional forest stand variables we found that stand basal area, elevation, aspect and steepness of slope were important predictors of mushroom productions.

Stand basal area is correlated with site conditions such as soil quality, water availability, temperature and overall forest health. It is logical that this variable can predict mushroom production given that carbon allocation to all ectomycorrhizal fungi is derived from the live standing biomass. Approximately 90% of fungi in the 3-y inventory were fruitbodies of ectomycorrhizal species.

In our study, stand basal area was correlated with several other stand variables including site index, stand age, growing stock volume, and tree size. Estimation of the effects of other variables would require more plot measurements or a population in which stand variables are less correlated.

An important observation is that the highest mushroom production coincides with the stage of stand development where wood volume growth is the highest. These are forests at their peak of growth efficiency. As shown by Högberg et al. [10] the flux of current photosynthates is critical for soil respiration and ectomycorrhizal sporocarp production. Nara et al. [20] also demonstrated that formation of mycorrhizal sporocarps was strongly correlated with the growth and photosynthetic rate of the host trees.

Our observed relationship of lower mushroom production with lower stand basal area could be a reflection of the lower forest stand photosynthesis with lower carbon available for belowground allotments. These sites are usually warmer and dryer. In contrast, in our overstocked forests with high basal areas, mushroom production, as well as photosynthesis, may be limited by decreased water availability to support the high leaf area. In these stagnated stands, photosynthates are directed at maintenance rather than belowground assimilation and respiration. Stands near canopy closure with vigorous growth rates should be the optimal sites for mushroom production in Scots pine forests of the Spanish pre-Pyrenees.

Elevation, aspect and slope, in the Prepyrenees range, also reflect water availability, and soil quality. Elevations ranged from 900–1500 m, and forests located near 1200 m typically have higher rainfall and cooler temperatures than at 900 m. At the very highest elevations, temperatures may be too low for abundant mushroom production. Northern-facing slopes are characteristically more shaded and protected from the intense afternoon solar exposure that south-facing slopes experience in late summer and early autumn months. Increasing slope has been shown to have a negative impact on mushroom production, most likely due to increasingly thinner soils associated with steep grades and greater water runoff than in forests with a less steep gradient.

Species diversity of mushrooms was the highest when the total production was maximal. This supports findings of Bonet et al. [4] who found a strong correlation between production and species diversity. Two-thirds of the variation in total production can be explained by the sheer number of taxa.

The models presented in this study can be used to optimize stand management when the combined benefits from

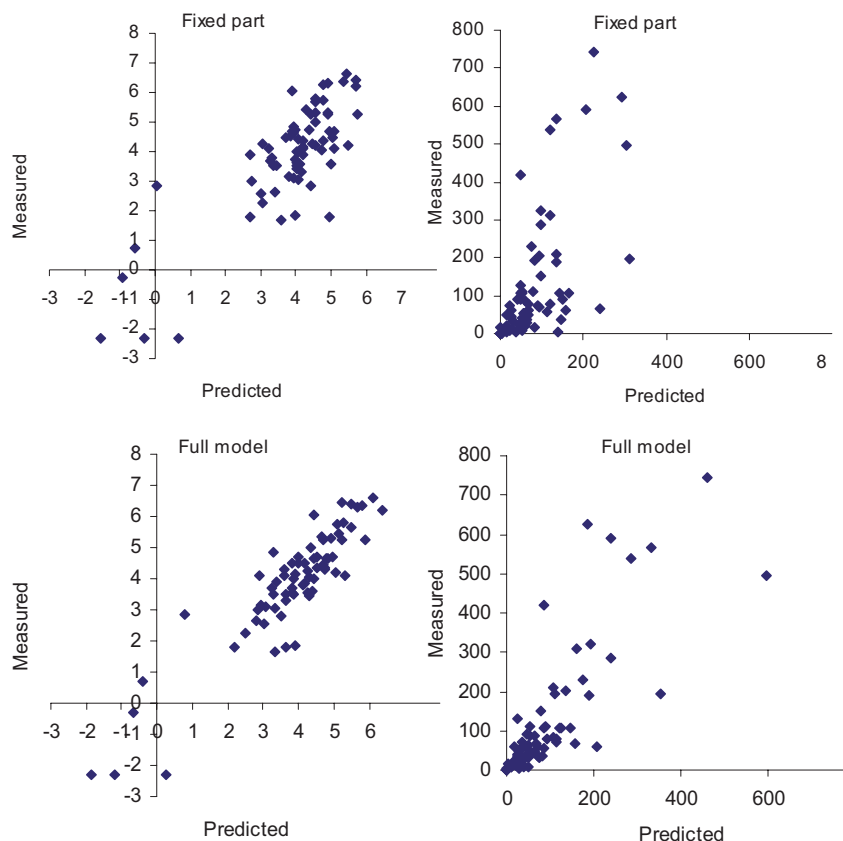


Figure 3. Correlation between the predicted and measured total annual production of mushrooms calculated with the fixed part on the model (top) or by using the plot and year factors in prediction (bottom). The diagrams on the left show logarithmic productions and the diagrams on the right show the productions in kg ha^{-1} .

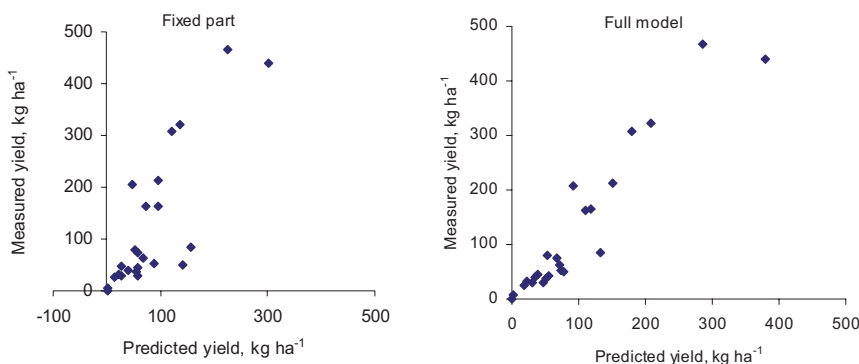


Figure 4. Correlation between predicted (Eq. (8)) and measured mean annual production of mushrooms calculated with the fixed part on the model (left) or by using the plot and year factors in prediction (right).

mushrooms and timber sales are of concern. The model prediction of species diversity can be used as a diversity index in forest planning. Our results suggest that timber and mushrooms production in these sites are not necessarily competing but rather have a complementary relationship.

The results of this study are encouraging because they demonstrate that mushroom productions are related to stand characteristics that can be influenced by silvicultural interventions. Similar models for other forest products and services

make it possible to analytically derive the optimal management plans for multiple-use forestry. However, our models were prepared specifically for even-aged Scots pine stands in Central Pyrénées. The logical next step would be to collect similar data from other species and stand types. A larger data set would also make it possible to model the dependence of mushroom production on stand variables other than basal area, for instance stand age, species composition, and vertical structure of the canopy.

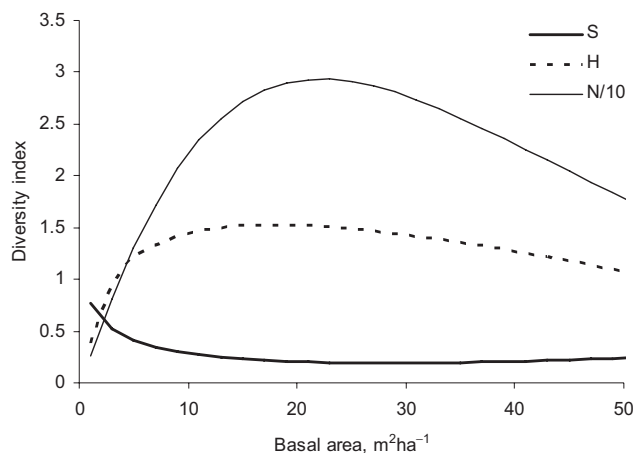


Figure 5. Dependence of the number of mushroom species (N , divided by 10), Shannon index (H) and Simpson index on stand basal area if elevation is 1240 m and slope is 24%.

In order to create the most accurate models possible, we incorporated all the data available into the model development. Currently, a new set of mushroom plots is being inventoried in order to expand the data set to other tree species and stand conditions. Such data set will allow the validation of the models developed in this study.

When evaluating the effects of silvicultural interventions on mushroom productions it is important to assess effects over several years. Pilz et al. [27] found that forest thinning significantly reduced fruitbody production of the economically important ectomycorrhizal fungus, chanterelle (*Cantharellus formosus*), in the first year after light and heavy thinning treatments, but that these differences disappeared within 2–6 years. Reduction of basal area in our overstocked forests could potentially result in decreased mushroom production immediately after thinning, with a potential for increased fruitbody production when tree density matches levels that promote vigorous growth.

Monitoring responses of fruitbody production to silvicultural interventions will be crucial for verifying the usefulness of our proposed models. We anticipate that with climate changes there will also be changes in mushroom production by species and by forest type. Gange et al. [7] demonstrated that the fruiting period of autumn fruiting forest fungi has increased over the last 50 years in Southern England and that these changes correlate with changing temperatures. They also observed that among the mycorrhizal species, a delay in the last fruiting date was observed in deciduous forests, but not in coniferous forests.

This is a first attempt to incorporate mushroom production into silvicultural models. Models will need further validation and adjustments for different forest types, for different biomes and for the expected alterations in weather patterns.

Acknowledgements: This study has been funded by the research project AGL2004-00382 (*Ministerio de Educación y Ciencia of Spain, Secretaria de Política Científica y Tecnológica*) and by the

Departament de Medi Ambient i Habitatge of the Generalitat de Catalunya. We are also grateful to the inventory group of the Forest Technology Centre of Catalonia for valuable assistance in the characterization of forest plots. We thank the anonymous reviewers for their helpful comments.

REFERENCES

- [1] Alexander S.J., Pilz D., Weber N.S., Brown E., Rockwell V.A., Mushrooms, trees, and money: Value estimates of commercial mushrooms and timber in the Pacific Northwest, *Environ. Manage.* 30 (2002) 129–141.
- [2] Arnolds E., Conservation and management of natural populations of edible fungi, *Can. J. Bot.* 73 (1995) 987–998.
- [3] Boa E., Wild edible fungi: A global overview of their use and importance to people, Food and Agriculture Organization of the United Nations, Rome, Italy, 2004.
- [4] Bonet J., Fischer C., Colinas C., The relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi in *Pinus sylvestris* forest of the central Pyrenees, *For. Ecol. Manage.* 203 (2004) 157–175.
- [5] De Román M., Boa E., The Marketing of *Lactarius deliciosus* in Northern Spain, *Econ. Bot.* 60 (2006) 284–290.
- [6] Egli S., Ayer F., Can wild edible mushroom production in forests be improved? The example of the La Chaneaz fungus reserve in Switzerland, *Champignons et mycorhizes en forêt*, *Rev. For. Fr.* 49 (1997) 235–243.
- [7] Gange A.C., Gange E.G., Sparks T.H., Boddy L., Rapid and recent changes in fungal fruiting patterns, *Science* 316 (2007) 71.
- [8] Hernández A., Fernández M., Los Hongos, un recurso más del bosque. Análisis de los principales hábitats de la provincia de Soria, *Montes.* 52 (1998) 99–114.
- [9] Hintikka V., On the macromycete flora in oligotrophic pine forests of different ages in South Finland, *Acta Bot. Fenn.* 136 (1988) 89–94.
- [10] Högberg P., Nordgren A., Buchmann N., Taylor A., Ekblad A., Högberg M., Nyberg G., Ottosson-Löfvenius M., Read D., Large-scale forest girdling shows that current photosynthesis drives soil respiration, *Nature* 411 (2001) 789–792.
- [11] Ihalainen M., Pukkala T., Modelling cowberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus*) yields from mineral soils and peatlands on the basis visual field estimates, *Silva Fenn.* 35 (2001) 329–340.
- [12] Ihalainen M., Alho J., Kolehmainen O., Pukkala T., Expert models for bilberry and cowberry yields in Finnish forests, *For. Ecol. Manage.* 157 (2002) 15–22.
- [13] Ihalainen M., Salo K., Pukkala T., Empirical prediction models for *Vaccinium myrtillus* and *V. vitis-idaea* berry yields in North Karelia, Finland, *Silva Fenn.* 37 (2003) 95–108.
- [14] Kalamees K., Silver S., Fungal productivity of pine heaths in North-West Estonia, *Acta Bot. Fenn.* 136 (1998) 95–98.
- [15] Keizer P.J., Arnolds E., Succession of ectomycorrhizal fungi in roadside verges planted with common oak (*Quercus robur* L.) in Drenthe, The Netherlands, *Mycorrhiza*, 4 (1994) 147–159.
- [16] Martínez de Aragón J., Bonet J.A., Fischer C.R., Colinas C., Productivity of ectomycorrhizal and selected edible saprotrophic fungi in pine forests of the pre-Pyrenees Montains, Spain: predictive equations for forest management of mycological resources, *For. Ecol. Manage.* 252 (2007) 239–256.
- [17] Mogas J., Riera P., Bennett J., Accounting for afforestation externalities: a comparison of contingent valuation and choice modelling, *European Environment* 15 (2005) 44–58.

- [18] Mogas J., Riera P., Bennett J., A comparison of contingent valuation and choice modelling with second-order interactions, *J. For. Econ.* 12 (2006) 5–30.
- [19] Molina R., Massicotte H.B., Trappe J.M., Ecological role of specificity phenomena in ectomycorrhizal plant communities: potentials for interplant linkages and guild development, in: Read D.J., Lewis D.H., Fitter A.H., Alexander I.J. (Eds.), *Mycorrhizas in Ecosystems*, CAB International, Wallingford, Oxon, UK, 1992, pp. 106–112.
- [20] Nara K., Nakaya H., Hogetsu T., Ectomycorrhizal sporocarp succession and production during early primary succession on Mount Fuji, *New Phytol.* 158 (2003) 193–206.
- [21] O'Dell T.E., Ammirati J.F., Schreiner E.G., Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone, *Can. J. Bot.* 77 (1999) 1699–1711.
- [22] Ohenoja E., Behaviour of mycorrhizal fungi in fertilized forest, *Karstenia*, 28 (1988) 27–30.
- [23] Ohenoja E., Effect of weather conditions on the larger fungi at different forest sites in Northern Finland in 1976–1988, *Scientiae Rerum Naturalium*, 243 (1993) 11–69.
- [24] Oriá-de-Rueda J.A., Martínez de Azagra A., Ecología y productividad de *Pleurotus eryngii* (Dc.:Fr.) Qué. y *Cantharellus cibarius* Fr. en España, *Boletín Sociedad Micológica de Madrid*, 15 (1991) 5–12.
- [25] Palahí M., Tomé M., Pukkala T., Trasobares A., Montero G., Site index model for *Pinus sylvestris* in north-east Spain, *For. Ecol. Manage.* 187 (2003) 35–47.
- [26] Pilz D., Molina R., Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: Issues, management, and monitoring for sustainability, *For. Ecol. Manage.* 155 (2002) 3–16.
- [27] Pilz D., Molina R., Mayo J., Effects of thinning young forests on chanterelle mushroom production, *J. For.* 104 (2006) 9–14.
- [28] Pilz D., Smith J., Amaranthus M.P., Molina R., Luoma D., Mushrooms and timber. Managing commercial harvesting in the Oregon Cascades, *J. For.* 97 (1999) 4–11.
- [29] Snowdon P., A ratio estimator for bias correction in logarithmic regressions, *Can. J. For. Res.* 21 (1991) 720–724.
- [30] SPSS Inc., *SPSS Base system syntax reference Guide*. Release 14.0., 2005.
- [31] Straatsma G., Ayer F., Egli, S., Species richness, abundance and phenology of fungal fruit bodies over 21 years in a Swiss forest plot, *Mycol. Res.* 105 (2001) 515–523.
- [32] Termorshuizen A.J., The influence of nitrogen fertilizers on ectomycorrhizas and their fungal carpophores in young stands of *Pinus sylvestris*, *For. Ecol. Manag.* 57 (1993) 179–189.
- [33] Trasobares A., Pukkala T., Miina J., Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain, *Ann. Forest Sci.* 61 (2004) 9–25.
- [34] Wilkins W.H., Harris G.C., The ecology of the larger fungi. V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and a pinewood, *Ann. Appl. Biol.* 33 (1946) 179–188.