Immediate effect of thinning on the yield of Lactarius group delicous in Pinus pinaster forests in Northeastern Spain

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ABSTRACT

Thinning forest stands is an increasingly valued leisure time activity in many regions of the world. In Northeastern Spain, edible mushrooms such as Lactarius delicous (saffron milk caps) are highly appreciated, stimulating interest in the multiple factors that influence their production. Topographic factors (altitude, slope and aspect), weather conditions and stand characteristics (tree species, stand density and stand age) are the main factors influencing mushroom production. Of these, only topographic factors can be modified by means of forest management. The objective of this study is to assess the effects of thinning on the production of Lactarius group spores in an uneven-aged Pinus pinaster forest in Northeastern Spain. A total of 30 plots with a basal area reduction ranging from 0% to 77% were established in 2008 and monitored during the autumn mushroom season of 2009 and 2010. Fifteen non-thinned plots were also surveyed in 2008. The results show a clear positive response of saffron milk cap production to forest thinning. Production was five times greater in plots in the first year after thinning and two times greater in the second year, as compared to the non-thinned plots. Thinning intensity and precipitation at the end of the year were the most significant factors explaining the annual yield of Lactarius group spores.

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1. Introduction

The market of wild edible fungi is growing fast worldwide favoured by the international free trade policies (De Roman and Boa, 2006). A large variety of mushrooms are edible (Boa, 2004) but only a few species are currently marketed. De Roman and Boa (2004) reported that 161 species of wild edible fungi are collected and consumed in Spain but differences vary greatly with region. Several outstanding species including Boletus spp., Cantharellus spp., Pleurotus ostreatus, Tricholoma terreum and Lactarius delicous are widely collected and eaten (De Roman and Boa, 2006).

Saffron milk caps (Lactarius delicous Fr.) have well-established markets in Europe, Asia and North Africa (Boa, 2004). They are sold together with other closely related species including Lactarius sanguiius, Lactarius semisanguiius, Lactarius salmonicolor and Lactarius vinosus. We will refer to this entire group as L. delicous in the present work. In Spain, this mushroom is probably the most abundantly marketed species (Cervera and Colinas, 1997; Voces et al., 2011). The price paid to collectors ranges from 1 to 12 € kg⁻¹ (De Roman and Boa, 2006), and is even higher when mushrooms are sold to wholesale markets and to retailers (Cervera and Colinas, 1997; De Roman and Boa, 2006).

L. delicous fruits from late fall to mid-winter in different continents (Europe, America, Oceania and Africa) and is found in a wide range of conditions in conifer forests. L. delicous has been described by Fernández-Torrijón et al. (2005) as an early colonizer of plantations (early-stage fungi), and found in greatest abundance in young stands. Bonet et al. (2004) observed that “marketed Lactarius sp.” are found in all age classes and on all aspects of Pinus sylvestris plantations in Northeast Spain. The apparent contradiction of these studies has been addressed by Bonet et al. (2004), observing that open forest conditions with relatively low basal areas typical to the early phase of natural forest succession (before canopy closure) were favorable for saffron milk cap production. These authors hypothesized that canopy closure was an important factor influencing their findings and proposed the use of silviculture treatments to reduce the density of older stands in order to enhance L. delicous production.

Martínez de Aragón et al. (2007) found a negative correlation between L. sanguiius yield and stand age, and a positive...
correlation between L. delicosa yield and altitude in stands of P. nigra, P. sylvestris and P. halepensis. This study showed a positive correlation between rainfall and L. delicosa. In central Spain, Martínez-Peña (2009) observed two peaks of production in Scots pine (P. sylvestris) forests of different age classes, the first peak occurring at the age of 20 years and the second one at the age of 70 years. Similar results have also been reported for American ecosystems. For instance, Zamora-Martínez and Nieto de Pascual-Pola (1995) collected L. delicosa sporocarps mostly in open-canopy conditions within mature stands of P. montezumae plantations. In Oregon, Smith et al. (2002) observed higher yields in 30–50-year-old Pseudotsuga menziesii forests and no yield at all in forests older than 400 years. In a recent study, Bonet et al. (2008) observed that the production of market-sized Lactarius was related to aspect, slope and stand basal area, with an optimal basal area of 15–20 m² ha⁻¹ for P. sylvestris forests. This basal area corresponds to the peak of growth efficiency for these stands.

The above studies suggest that higher saffron milk cap yields may be found in relatively open forest conditions and when the stand age is close to the period of the highest tree growth. By modifying forest structure using thinning treatments it may be possible to maintain high tree growth rates during the whole rotation period so as to provide suitable conditions for L. delicosa.

In Spain, saffron milk caps are most abundant in pine forests, many of which were planted during the second half of the twentieth century. These pine forests (both natural forests and plantations) have been traditionally managed for timber production using standard treatments like thinning, shelterwood cutting and clearfelling. However, the increasing interest in mushroom picking is directing the attention towards L. delicosa yield. This could create a conflict between the traditional aim of managing forests for maximal timber production and the growing interest in enhancing mushroom yield.

Both aims may be combined by promoting multifunctional forest management that supports both timber and mushroom production (Pilz et al., 1999). Palahi et al. (2009) analyzed the economic profitability and optimal management of the joint production of timber and mushrooms in Catalanian forests. These authors found that the maximal economic profit on sites with potentially high mushroom yield can be achieved by enhancing fungal yields by forest management.

Although factors affecting sporocarp production have been studied for many years (Vogt et al., 1992), many questions related to fungal ecology functioning are still open with regard to forest management practices to increase mushroom production. We are particularly interested in answering key questions on the effects of forest thinning on mushroom yield, which has been studied in the past, but with no singular trend in responses. Egli and Ayer (1997) observed that a 35% reduction of tree stems in a mixed forest of Switzerland had a positive effect on the yield of edible mushrooms. Similar results were obtained by Ayer et al. (2005) who found more mushroom production in forests with medium stand densities, and by Egli et al. (2010) who reported an increase in production and biodiversity after the thinning. In Russia, Shubin (1986) noted that fungal yields are higher in thinned forests than in denser stands but Kardell and Eriksson (1987) did not find any clear thinning effect on the edible mushroom yields. A positive reaction to thinning was reported by Shaw et al. (2003) but Kranabetter and Kroeger (2001) only report that forest thinning did not have a negative effect on ectomycorrhizal fungi. Shaw et al. (2003) described significant increases in some fungal species, while Buße et al. (2005) observed a positive effect on the ectomycorrhizal diversity. Kardell and Eriksson (1987) reported that some species such as Lactarius rufus are positively affected by thinning. On the contrary, Kropp and Albee (1996) found a negative effect of thinning on mushroom emergence in a Pinus contorta forest and Oehenoja (1988) found that many fungi species disappeared after forest thinning, mostly mycorrhizal species. A review of the literature shows different responses to forest thinning on mycorrhizal ecosystems, modifying fungal succession patterns, influencing fruit body productivity and providing favorable conditions for certain species in detriment to others.

Since results on the effect of silvicultural thinning treatments on mushroom yields are variable and even contradicting, we approach the question using an experimental approach. The purpose was to address the needs of forest managers faced with multifunctional management. A silvicultural thinning experiment was initiated in 2008 in a Pinus pinaster plantation in Northeast Spain to evaluate the short-term effects of thinning on the yield of the mushrooms included in the L. delicosa group. Based on sporocarp production from 2008–2010, this study analyzed the immediate effects of thinning on this ectomycorrhizal group.

2. Materials and methods

2.1. Establishment of the plots and associated treatments

In 2008 we established 15 mushroom inventory plots of 100 m² (10 m × 10 m) in a 50-year-old P. pinaster plantation located in the Natural Park of Poblet (Tarragona, Northeastern Spain), located at 41° 21′ 6.4726° latitude and 1° 2′ 25.7466° longitude. They were selected to include a range of aspects and altitudes (from 594 to 1013 m a.s.l.) and slope (3–23%) (Table 1) and are characterized by siliceous soils with franc-sandy textures. Although the original planting density was nearly the same for each forest stand where these plots were located, mortality and other biotic and abiotic hazards have caused a high between plot variation in stand density, which ranged from 446 to 2657 trees ha⁻¹ and with stand basal areas ranging from 20.9 to 81.7 m² ha⁻¹.

In 2009 we established a second set of 15 mushroom inventory plots in the same 50-year-old P. pinaster plantation but in places scheduled for thinning. These plots corresponded to the original mushroom inventory plots with respect to forest stand characteristics, and were centred on larger 1600-m² (40 m × 40 m) thinning plots. Establishing corresponding and similar treatment units separate from the original inventory plots allowed us to reduce the edge effects since a thinned plot was usually surrounded by another thinned plot on all sides. Thinning treatments were completed in 13 of the 15 plots in July and August 2009. Five different thinning intensities were randomly assigned to the thinning plots. However, the actual thinning intensities varied from the initially intended treatments, such that the actual basal area removed was uniformly distributed between 0% and 77% (Table 1). All the felled trees were removed from the plots. The shoots of Quercus spp. seedlings that appeared the following spring in some of the thinned plots were also removed, trying to maintain the same conditions as in the previous year.

Stand variables for all inventory plots were documented before and after the thinning treatments. All trees within both thinned and unthinned plots were inventoried and measured for diameter at 1.3 m breast height, and height for a minimum of 10 trees per plot was measured. Stump diameters of removed trees were measured and converted into dbh to obtain the thinning intensity and the removed basal area.

2.2. Monitoring of mushroom yield

Mushroom monitoring started in autumn 2008, with an inventory of the original 15 plots established in unthinned stands. After the thinning treatments in 2009, the mushroom inventory was expanded to include the 10 m × 10 m mushroom inventory plots...
within the larger (40 m x 40 m) thinned plots. In 2009 and 2010, 30 mushroom inventory plots were surveyed: 17 in unthinned stands and 13 in thinned stands (two thinning plots were not actually thinned). All the mushroom plots were enclosed by fences to prevent uncontrolled mushroom harvesting.

Autumn mushroom season usually begins in September and ends in December when cold temperatures stop the emergence of sporocarps. During the fruiting period, all the mushrooms (both ectomycorrhizal and saprophytic) with a cap diameter wider than 1 cm were collected weekly and taken to the laboratory for identification, fresh and dry weight measurements, and sporocarp counts. The collected mushrooms were classified by edibility and marketability. More information about the procedures is available in Martínez de Aragón et al. (2007). Although all mushrooms were collected, this paper focuses on the yield of the L. deliciousus group which, in our study includes L. deliciousus, L. sanguifluus and L. vinus, a group which represents 63.5% of the total yield of ectomycorrhizal mushrooms in the study area.

2.3. Statistical analysis

One-way analysis of variance was used to determine if the yield of L. deliciousus is significantly affected by thinning. The post-thinning yields of 2009 and 2010 from the thinned and unthinned plots were used in the analysis.

A regression model was developed to assess the impact of thinning intensity on the annual mushroom yield. The data set used for modeling (Table 1) included 75 observations. To avoid corrections due to transformed dependent variable (Baskerville, 1972; Snowden, 1991), a model for non-logarithmic Lactarius yield was fitted using non-linear regression analysis of the nls function of R software (R development core team, 2008). Variables representing thinning intensity (removed basal area) and weather conditions (temperature and precipitation) were considered as predictors. Different transformations of these variables were tested. Weather data from all 3 years, from 2008 to 2010, were included in the model fitting data in order to have more between year variation in rainfall. Weather data were recorded in a weather station near the Prades forest. The tested weather variables were annual rainfall, monthly rainfall of August-November, mean annual temperature and mean monthly temperatures in August-November. The measured variables for the different years were:

- Year 2009 (annual rainfall 705.1 mm; August + September + October + November rainfall 1169.5 mm; August + September rainfall 1153 mm; mean yearly temperature 10.7 °C; August + September + October + November mean temperature 13.7 °C)
- Year 2010 (annual rainfall 671.9 mm; August + September + October + November rainfall 244.1 mm; August + September rainfall 134.6 mm; mean yearly temperature 9.3 °C; August + September + October + November mean temperature 11.7 °C)

3. Results

3.1. Effect of thinning on the yield of Lactarius group deliciousus

Differences in the mean yield of Lactarius group in 2009 and 2010 between thinned and unthinned stands were clear (Fig. 1). Thinned stands were more productive. The analyst of variance showed that the difference was significant with Pr>F = 0.0106 and F = 6.9734. The difference in mean yield of L. deliciousus between thinned and unthinned stands was 90.6 kg ha⁻¹ year⁻¹ in 2009 and 53.6 kg ha⁻¹ year⁻¹ in 2010. The effect of thinning on the production of sporocarps was higher during the first productive season just after the thinning.

3.2. Model for the yield of Lactarius group deliciousus

Light thinning increased the Lactarius group yield, whereas very heavy thinning provoked a decrease in sporocarp production.
In addition, the amount of rainfall during late summer and early autumn had a strong positive effect on the production of sporocarps (Fig. 3). The model fitted for the annual yield of Lactarius group reflects these observations:

\[
\text{Lactarius} = \exp (0.4802 - 0.009318 \cdot G_{\text{thinned}} + 0.87365 \cdot \ln (G_{\text{thinned}}) + 0.02819 \cdot P_{\text{August-September}})
\]

where Lactarius is the annual yield of Lactarius group deliciousus (kg ha\(^{-1}\) year\(^{-1}\)), \(G_{\text{thinned}}\) is the removed basal area (m\(^2\) ha\(^{-1}\)) and \(P_{\text{August-September}}\) is the sum of the total rainfall in August and September. The residual standard error of the model was 87.65 and all predictors were significant (\(p\)-value < 0.05).

According to the model, light thinning is more beneficial for L. group deliciousus yield than heavy thinning (Fig. 4). Mushroom yield increased with removal basal area until a maximum benefit was reached when the removed basal area was about 10 m\(^2\) ha\(^{-1}\). Regardless of the basal area before thinning, the reduction in basal area was the most significant predictor, not the post-thinning basal area.

The amount of rainfall during late summer and early autumn had a strong positive effect on the production of sporocarps (Fig. 4). Under dry conditions of 2008 (67 mm of rainfall in August and September) the maximum yield in fresh weight was 30 kg ha\(^{-1}\) year\(^{-1}\) whereas in the two wet autumns (2009 and 2010 with 116.3 and 134.6 mm, respectively) the best yields were over 200 kg ha\(^{-1}\) year\(^{-1}\). Due to the multiplicative structure of the model, the results show that the higher the precipitation is in August and September, the stronger is the effect of thinning on the annual yield of L. deliciousus (Fig. 2).

4. Discussion

The most outstanding result of this study was that the effect of thinning on Lactarius group deliciousus yield was immediate. Only two months after thinning the yield increased sharply showing productions up to 440 kg ha\(^{-1}\) (Table 1). It seems that the new habitat conditions provided by the thinning treatment enhanced Lactarius group production, possibly at the cost of other species. As suggested by Kropp and Albee (1995), tree removal may alter fungal fruiting patterns without affecting below-ground populations. These authors based their conclusions on a three-year fungal inventory reporting a similar total number of fruiting bodies in thinned and undisturbed Pinus contorta forest 10 years after the silvicultural treatment, but L. deliciousus, and generally the Russulaceae family, were positively affected by the treatment, doubling in the number of sporocarps. Such a rapid reaction contradicts previous.

![Relationship between the removed basal area and the annual yield of Lactarius group deliciousus and between the current basal area and the annual yield of Lactarius group deliciousus. The solid black dots on the Y axis represent the (unthinned) plots in 2008. The empty circles represent year 2009 and the empty triangles represent 2010.](image-url)
studies in which the thinning reaction has normally been small or negative during the first years, after which production may be recovered. Egli et al. (2010) observed a recovery during the fourth year after thinning, with low production during the first 3 years after thinning. These authors suggested that the effect of the temporary site disturbance caused by the intervention could be a possible explanation for these dynamics. Similarly, Pilz et al. (2006) found an initial reduction of Cantharellus formosa sporocarps in heavily thinned stands with a 6-year period before the pre-thinning production of C. formosa was observed. Shaw et al. (2003) detected very minor variation in fungal productivity five years after thinning, except for a few species.

In our study, the increased yield of sporocarps in response to tree removal appears more relevant than the possible negative effects of thinning in the first year, but two years after thinning the differences in saffron milk caps yield between thinned and unthinned plots were smaller. However, this does not necessarily indicate decreased effect of thinning since long-term studies (Straatma et al., 2001; Straatma and Krisai-Greilhuber, 2003) show high inter-annual variability in mushroom production. A plausible hypothesis for future studies is that the temporal pattern of thinning effect on mushroom yield depends on the thinning intensity, light thinnings leading to immediate positive response, whereas intensive thinning may lead to short-term negative effects after which the mushroom yield may recover and increase.

The model obtained for L. deliciosus shows the combined effect of the removed basal area and late summer rain on the saffron milk cap yields. A close correspondence between tree growth and the yield of associated mycorrhizal fungi has been demonstrated by several studies (Saravieso et al., 2008; Nara et al., 2003; Kuikka et al., 2003; Egli et al., 2010; Egli, 2011). The immediate increased yield response by L. deliciosus – an ectomycorrhizal fungus which relies on the host tree for carbon allocation, requires a revision of the factors operating in our thinning experiment. Among these probable factors, increase in water availability for the residual trees, which is closely related to precipitation, seems the most evident. In the present study, the accumulated precipitation in August and September was the most significant variable explaining Lactarius group sporocarp biomass. This is especially important in the Mediterranean forests where water is the most limiting factor of tree growth. The results showed that considerable fluctuations in mushroom yield can be expected due to variation in precipitation,
as observed in the dry year of 2008 (10 kg ha \(^{-1}\) of Lactarius group deliciosus) and in the wet year of 2010 (200 kg ha \(^{-1}\) of Lactarius group deliciosus). Numerous studies emphasize the positive effect between rain and mushroom yields including Martínez de Aragón et al. (2007) and O’Fallon et al. (1999) who also observed an increase in species richness with higher precipitations. Similar results were obtained in a forest stand relatively near to our study area by Ogaya and Perellós (2005) who observed a 60% decrease in mushroom production when 30% of the rainfall was excluded. Straatsma and Knaap-Greilhuber (2003). Straatsma et al. (2001) or Krabbe and Kroeger (2001) also reported a positive relationship between mushroom biomass and annual precipitation although the latter authors noted that annual rainfall alone does not explain the variation in fruit-body emergence. In our study, positive effect of summer precipitation in terms of mushroom yields is probably favored by the thinning that opens the tree canopy and thereby decreasing the interception of rain by trees, and increasing the effective water to the below-ground ecosystem. In addition, a light thinning treatment (\(-10 \text{m}^2\text{ha}^{-1}\)) will also preserve the evaporation rates more effectively than a heavy thinning, conserving soil water content, and minimizing effects of higher temperatures. Negative effects of heavy thinning on mushroom production may be due to decreased soil water availability as a consequence of higher solar exposure, higher evaporation rates and higher soil temperatures.

Modification of forest structure by thinning treatments seems to enhance Lactarius group yield with a predicted maximum yields when basal area removed was near 10 m\(^2\text{ha}^{-1}\). It seems clear that saffron milk caps, which are present in the ectomycorrhizal community before thinning, was always clearly favored by these forest operations, but with the upper limit of around 35 m\(^2\text{ha}^{-1}\) of removed basal area, beyond which the model predicts a decrease of fungal yields, as compared with unthinned plots. After very heavy thinning, the new colonization of roots by Lactarius group deliciosus does not compensate the effect of removing trees. Luoma et al. (2004) examined the response of ectomycorrhizal sporecarps to four levels of basal area removal with two spatial patterns, either aggregated or dispersed, and found a sharp decline of mushroom yields under heavy thinning, especially when the thinning was aggregated. Ayer et al. (2006) obtained higher mushroom productivity with a medium thinning intensity.

Previous studies carried out in the same forested region by Ronet et al. (2008, 2010) proposed a standing basal area of 15 m\(^2\text{ha}^{-1}\) as optimal for forest fungi productivity. The results obtained in the present experiment showed no significant effect of before- or after-thinning basal area on Lactarius group yield when removed basal area was included in the model. The results suggest that the removed thinning intensity should be around 10 m\(^2\text{ha}^{-1}\) irrespective of the pre-thinning density of the forest with a maximum basal area removal of 35 m\(^2\text{ha}^{-1}\).

In conclusion, the results presented in this study, compiling a 3-year monitoring period of fungal productivity under different thinning intensities, shed new light on the early response of thinning on mushroom yields. The accumulated precipitation in late summer is important for Lactarius group deliciosus production in Northern Spain, confirming that the emergence of mushrooms is affected by both environmental conditions and stand characteristics. Analysis of long-term data series is needed to better understand such combined effects. Continued monitoring of these sites will help provide clearer results and better understanding of the factors important for good mushroom production.

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