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# Response of *Tuber melanosporum* fruiting to canopy opening in a *Pinus-Quercus* forest

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## Abstract

The wild production of the highly appreciated fungus *Tuber melanosporum* is negatively affected by canopy closure in the stand. Habitat improvement has been proposed as a tool to recover the production in close forests, but evaluations based on scientific monitoring are still lacking. This study analyses the short-term effect of a pilot project on improvement of *T. melanosporum* reproduction habitat. The results support the project hypothesis that the canopy closure was hampering truffle fruiting in the larger *brûlés*. The silvicultural treatment alone has not triggered a clear positive response in all the *truffières*, suggesting that complementary actions are necessary to ensure their sustainability. Weather conditions provoke a year-to-year variation in the fruiting and determine the responsiveness of the *truffières* to the treatment.

**Keywords:** *Tuber melanosporum*; non-wood forest products; canopy closure; *Quercus ilex*; silviculture

## 1. Introduction

Wild edible mushrooms are an important forest product worldwide (Boa, 2004). Communities of ectomycorrhizal fungi are frequently linked to particular forest types and structures (Pilz et al., 1996). Detailed studies about the habitat requirements of these fungi are crucial to developing ecosystem management criteria aimed to enhance fungal diversity and productivity, and ultimately supporting the sustainability of ecosystems.

The European black truffle (*Tuber melanosporum* Vitt.) is a commercially harvested mushroom responsible for a multi-million euro industry in France, Italy and Spain (Reyna and Garcia-Barreda, 2009). *T. melanosporum* is ectomycorrhizal and grows wild in open forests of *Quercus* (Olivier et al., 2002; Reyna et al., 2004). The ground where it fruits is affected by the phytotoxic activity of the fungus (Splivallo, 2008), and this causes the appearance of the so-called *brûlé* (truffle burn). Fruiting is typically associated to particular host trees and *brûlés* from year to year (the so-called *truffières*). The sporocarp production of a *truffière* has been found related to the characteristics of the *brûlé* and the host tree (Sourzat et al., 2004; Oliach et al., 2005; Garcia-Montero et al., 2007b), although highly variable from year to year. This variability has been found closely linked to weather conditions (Ricard et al., 2003).

In Spain, wild *T. melanosporum* production has suffered an important decline in the last decades, due to both natural and human causes (Reyna and Garcia-Barreda, 2009). This

occurs in the framework of Mediterranean forests, with low economic profitability (Domínguez-Torres and Plana, 2002) and the loss of involvement of the rural communities in the protection and management of forests. Some experts propose to improve *T. melanosporum* reproduction habitat by opening the canopy around the *truffière* (Reyna et al., 2004; [Diette and Lauriac, 2005](#)), with the ultimate aims of conserving local wild populations of the fungus (and their gene pool), and enhancing ecosystem provisioning services. But for the moment the application of this technique in wild *truffières* has not been evaluated with large-sample studies. The full development of rehabilitation techniques requires a periodic evaluation of the success and the eventual adjustment of the management criteria ([Vallauri et al., 2005](#)).

In one of these habitat enhancement projects, in El Toro (Spain), an evaluation programme involving the monitoring of the fruiting, the ectomycorrhizal community and the tree vegetation was designed (Reyna et al., 2004). This paper analyses the short-term (9 years) advances in the process of improvement of *T. melanosporum* reproduction habitat in El Toro pilot site. The effectiveness of the project is evaluated through two criteria: (1) the influence of the canopy cover on the response of the treated *truffières*, and (2) the time trend of fruiting after treatment. The former is used to test the project hypothesis that canopy closure hampered *T. melanosporum* fruiting. The latter is used as a criterion of self-sustainability: following Lugo (1992), it is considered that a *truffière* with a positive trend is approaching the recovery goal. A secondary aim is to analyse if the technique has succeeded in all the range of *truffière* attributes in which it has been applied, with the purpose of “fine-tuning” the technique.

## **2. Materials and methods**

### *2.1. Study site and habitat improvement strategy*

El Toro pilot site is located in the Valencian Community, eastern Spain (39° 58' to 40° 2' N, 0° 44' to 0° 47' W, 990-1110 m a.s.l.). The climate is Continental Mediterranean, with a mean annual rainfall of 500-550 mm and a mean annual temperature of 11.9-12.4°C. The soils are calcixerepts developed on a calcareous glaciis with less than 5% slope. Dominating texture is sandy clay loam, pH ranges from 7.7 to 8.3, and organic matter content ranges from 2 to 3%.

Until 1958, patches of *Q. ilex* L - *Quercus faginea* Lam. coppices and cereal cultures dominated the landscape. In the latter, isolated *Quercus* were also present in field boundaries. About 1955, the local population began to harvest truffles. Since then, *T. melanosporum* is intensively exploited as a common-pool resource and no management practices have been carried out. From 1958 to 1969, the forest administration reforested the site with *Pinus nigra*

Arnold. By the 1990s, the reforestation had formed a close canopy (density: 900-2500 trees ha<sup>-1</sup>, canopy cover: 60-95%) and the *Quercus* survived as suppressed trees.

In 1997 the forest administration initiated a programme to support the recovery of *T. melanosporum* reproduction habitat and the economic revenues provided by wild *truffières* to the local community. El Toro was selected as pilot site: with the aid of local harvesters, the *truffières* that still remained productive were located and measured. According to harvesters, *T. melanosporum* production had sharply decreased from the 1970s, and the major causes of degradation were the canopy closure around the *truffières* (mainly due to the pine plantation) and the intensive harvesting. Consequently, a silvicultural model that adapted the forest structure to the habitat requirements of *T. melanosporum* was developed and implemented from 2000 to 2001 (Reyna et al., 2004). The pines within a radius of 14-50 m from the *brûlé* (depending on the height of the host tree and the surrounding pines) were systematically cut down, since *Pinus* species do not encourage *T. melanosporum* fruiting (García-Montero et al., 2007a). All shrubs within the radius were removed, whereas *Quercus* were preserved and slightly pruned (less than 10% of the live crown was removed). This resulted in the opening of circular gaps with reduced canopy cover around the *brûlé* (Table 1). During the silvicultural operations, the *brûlés* were completely encircled with marking tape, in such a way that trampling, tractor passage and incorporation of logging residues were avoided.

## 2.2. Data collection and statistical analysis

The 74 treated *truffières* selected for the monitoring meet the following requirements: (1) they produced sporocarps of *T. melanosporum* until (at least) the fruiting season 1997-1998, (2) they do not produce sporocarps of other *Tuber* species, (3) before being treated, they were located inside the pine plantation, and (4) the canopy cover within a radius of 15 m from the *brûlé* was reduced below 50% by the treatment. Other eleven *brûlés* are located in non-reforested plots. They have not been considered treated *truffières* but reference areas, and they have also been intensively exploited. Ten *truffières* located inside the pine plantation were either not treated or the canopy cover (within the radius of 15 m) was not reduced below 50%; they have been considered as non-treated. Reference and non-treated areas have not been statistically compared to treated *truffières*, because they are scarce and the range of *truffière* attributes is narrower. Instead, the effect of *truffière* attributes on reference and non-treated areas has been analysed independently.

The exploitation as a common-pool resource has made it impossible to measure sporocarp number or biomass, which would be a direct measure of the provisioning services delivered

by the *truffières*. Although not ideal, we have measured instead the number of digs made by harvesters as an estimator of the occurrence of successful fruiting events. The occurrence of fruiting events is relevant in biophysical terms because it can reflect the annual suitability of environmental conditions for a species to reproduce sexually and therefore site functionality as a reproduction habitat. Thus, this approach focuses on the occurrence of successful fruiting events and not on sporocarp productivity, which could be influenced by variations in either the number of fruiting events or in sporocarp size.

In the study area raking the *brûlés* is forbidden, sporocarps must be located with trained dogs, which only mark mature sporocarps, and there were few reports of poaching, so that digs in which no sporocarp was extracted were likely very scarce. Truffle sporocarps are harvested with a small spade, and that makes the diggings clearly different from animal excavations.

In a previous fruiting season, sporocarp biomass was monitored in eight *truffières*, and a mean of 56 g per dig (standard deviation: 16) was obtained. In one of these *truffières*, sporocarp biomass was monitored during four fruiting seasons, with a mean of 55 g per dig (standard deviation: 30).

The abundance of harvester digs has been monitored from the fruiting season 2001-2002 to 2008-2009 (i. e. until 9 years after treatment) to evaluate the temporal trend. The *truffières* have been repeatedly visited during each fruiting season and the location of digs of the same year has been recorded to distinguish fresh digs from the old ones. The digs from previous seasons are easy to differentiate thanks to the soil texture in the study site and to the low rainfall and snowfall during the fruiting season.

A linear mixed model (LMM) is used to test the null hypothesis of no temporal trend in the number of harvester digs after treatment, and a Toeplitz covariance structure has been specified (SPSS, 2006). Data from the first season have been excluded because of the excessive number of zeros. Time from treatment is treated as repeated measures variable, and both linear and quadratic components have been tested. An estimate of the weather conditions has been included as a covariate, to deal with interannual variability.

Given that no meteorological station existed in the study site, the width of latewood rings in dominant *P. nigra* (calculated as the mean of 20 trees) has been chosen. [Lebourgeois \(2000\)](#) and [Martín-Benito et al. \(2008\)](#) found that the width of *P. nigra* latewood related to abundant rainfall and mild temperatures during late spring and summer, and this is the period with the greatest incidence on *T. melanosporum* fruiting (Ricard et al., 2003). In our study site, latewood width shows a positive correlation with august rainfall estimated through interpolation from the four nearest meteorological stations, located 5-12 km away (Pearson's

$r=0.66$ ,  $P=0.019$ ,  $n=12$ ), and a negative correlation with July mean temperature in the only nearby thermometric station, located 10 km away (Pearson's  $r=-0.64$ ,  $P=0.036$ ,  $n=12$ ).

The main attributes of the *truffière* (measured in 1998) are included as fixed predictors in the LMM: abundance of harvester digs in the season 1997-1998 (as an indicator of the frequency of fruiting events before treatment), surface of the *brûlé*, canopy surface of the host tree, and surface stoniness (percentage of the *brûlé* surface covered by stones). Truffle production in the season 1997-1998 was extraordinary both in the study site and nationwide (not repeated since), and therefore dig abundance in that season can be considered an indicator of the fruiting potential of the *truffières* before treatment. The LMM also includes the characteristics of the tree vegetation around the *brûlé* before (1997) and after (2005) treatment: canopy cover within a radius of 15 m from the *brûlé* centre, and distance from the *brûlé* center to the untouched dense pine plantation.

Model adequacy has been assessed using Akaike's information criterion, and non-significant factors and interactions have been removed from the final model. The response variable has been log transformed to more closely meet the assumptions of normal distribution and constant variance. The interaction effects are investigated using the "pick-a-point" approach for testing simple slopes ([Bauer and Curran, 2005](#)).

### 3. Results

The abundance of digs in the treated *truffières* is significantly related to several interactions involving time elapsed from treatment, width of latewood rings, *brûlé* surface, abundance of digs in season 1997-1998 and variation in canopy cover from 1997 to 2005 (Table 2). The quadratic component of time, the canopy surface of the host tree, the stoniness, the canopy cover in 2005 and the distance to the pine plantation have not been included in the final model because they do not show a significant effect and do not improve the adequacy of the model.

The post-treatment temporal trend of the dig abundance is significant but determined by the value of annual latewood growth (Table 2, Fig. 1). According to the test of simple slopes, the regression between dig abundance and time from treatment is negative and significant at values of latewood growth less than 1.1 (latewood growth is expressed as a ratio to the mean value in the period 1997-2008). Six of the eight years of monitoring showed lower scores. The simple slope is positive and significant at values of latewood growth more than 1.4 (two of the eight years showed a higher score). From the other point of view, when time is considered the moderating variable, the test of simple slopes shows that the regression

between dig abundance and annual latewood growth is significantly positive only from the fourth year ( $P < 0.001$ ), whereas it was not significant previously.

The interaction between annual latewood growth and dig abundance before treatment significantly affects post-treatment dig abundance (Table 2). According to the test of simple slopes, the regression between post-treatment dig abundance and latewood growth is significant and positive at values of pre-treatment dig abundance higher than 1 (71 of the *truffières* are above this threshold). The slope of this simple regression increases with increasing values of pre-treatment dig abundance (Fig. 2).

The interaction between pre-treatment dig abundance and *brûlé* surface significantly influences post-treatment dig abundance (Table 2). According to the test of simple slopes, the regression between post-treatment dig abundance and *brûlé* surface is significant and positive at values of pre-treatment dig abundance higher than 10 (38 of the *truffières* are above this threshold). The simple slope is significant and negative at values of pre-treatment dig abundance lower than 3 (4 of the *truffières* are below this threshold). The slope of this simple regression increases with increasing values of pre-treatment dig abundance (Fig. 3).

The interaction between *brûlé* surface and variation in canopy cover from 1997 to 2005 significantly influences post-treatment dig abundance (Table 2, Fig. 4). According to the test of simple slopes, the regression between post-treatment dig abundance and *brûlé* surface is significant and positive at values of canopy cover reduction higher than 42% (39 of the *truffières* are above this threshold). The simple slope is significant and negative at values of canopy cover reduction lower than 18% (7 of the *truffières* are below this threshold).

The observed number of digs in each *truffière* has been compared to the values inferred by the LMM for the case that canopy cover had not been reduced. The model predicts that in the larger *brûlés* (surface  $> 77 \text{ m}^2$ ) the mean number of digs would have decreased by 66% if no treatment had been applied, whereas in the smaller *brûlés* it would have increased by 58%.

In the non-treated *truffières*, the abundance of digs does not show a significant time trend, does not relate to latewood growth and is not significantly affected by any other of the variables evaluated. Its global mean is not significantly different from zero, and 50% of the *truffières* did not show any dig during the monitoring period.

In the reference areas, dig abundance shows a positive and significant relationship with latewood growth ( $P < 0.001$ ) and a positive and marginally significant relationship with canopy cover in 2005 ( $P = 0.06$ ). No significant time trend has been observed.



## 4. Discussion

### 4.1. Influence of the canopy cover

In large *brûlés* the intensity of canopy cover reduction shows a direct relationship with frequency of fruiting events after treatment (Fig. 4), indicating that the initial levels of canopy closure in the study site were able to influence fruiting success of the fungus. Truffle fruiting in large *brûlés* appears to have been suppressed before treatment and to be released by the treatment, and according to the LMM if the treatment had not been executed the frequency of fruiting events would have decreased in these *truffières* (the large *brûlés* account for 57% of the digs in season 1997-1998 and for 64% from 2002 to 2009).

The suppressed fruiting is supported by the fact that treated *truffières* have responded to propitious weather conditions only from the fourth year after the silvicultural treatment. The dependence of *T. melanosporum* fruiting on annual weather is widely accepted (Ricard et al., 2003). The effect of weather has been greater in the *truffières* showing more digs before treatment. Accordingly, the relationship between weather and dig abundance has been significant in the reference areas but not in the non-treated *truffières*. The *truffière* responsiveness to weather appears related to its productivity, and we therefore consider that the increase in responsiveness after treatment is an improvement in the functioning of the *truffières*.

Canopy opening eliminates pine roots, reduces leaf litter accumulation and increases the insolation of the soil surface. [López et al. \(2003\)](#) found that thinning a *Q. ilex* forest increased soil water and temperature. These environmental conditions have been associated with *T. melanosporum* reproduction habitats (Olivier et al., 2002; Reyna et al., 2004; [García-Montero et al., 2007a](#)). Ricard et al. (2003) found that coarse fraction organic matter decreases in *T. melanosporum brûlés*. [García-Montero et al. \(2007b\)](#) pointed that solubilisation of calcium carbonate is also characteristic in *T. melanosporum brûlés* and that it is related to aeration and water flow through the soil.

### 4.2. Time trend after treatment

The time trend of dig abundance in the treated *truffières* has not been clearly positive in the short term (years 2-9), suggesting that the occurrence of truffle fruiting events is not self-sustainable at mean weather conditions under the current management. Similarly, in the reference areas (which are also subject to intensive harvesting) no significant time trend has been found. However, in both cases the *truffières* are weather-responsive. Neither the canopy cover after treatment nor the distance to the pine plantation influence dig abundance in the

treated *truffières*, suggesting that the cutting has eliminated the influence of the surrounding tree layer. Consequently, some other limiting factor aside from canopy closure seems to be hampering self-sustainability. Stakeholders recognise that intensive harvesting has been another major cause of degradation, because truffle spores are completely encased in the sporocarp. Harvesting regulation and field inoculation (Ricard et al., 2003) could be worthy options for improving the fruiting performance of the *truffières*.

Although canopy closure before treatment hampered the occurrence of truffle sporocarps in large *brûlés*, the canopy opening by itself does not trigger a clear positive response in the short term. Weather conditions clearly determine the capacity of the treated *truffières* for positively evolving. As a result, cultural practices increasing soil water content during the summer, which is the period with the greatest incidence on *T. melanosporum* fruiting (Ricard et al., 2003), appear as worthy areas for further research.

In spite of the year-to-year variation due to the weather, our results suggest that the *truffières* show release from the fourth year. This agrees with the empirical experience of truffles harvesters in Soria (Spain), Umbria (Italy), Els Ports (Spain) and Hérault (France), which report that wild *truffières* require 2-3 years to respond to canopy opening (PROYNERSO, 2002; [Granetti, 2005](#); [Garcia-Barreda et al., 2006](#); [Sourzat et al., 2008](#)). Similar silvicultural treatments in wild stands of *Tuber magnatum* Pico (in Italy) and *Tricholoma matsutake* Singer (in Japan) have succeeded to recover sporocarp production in 2-3 years ([Ogawa in Hosford et al., 1997](#); [Gregori et al., 2001a](#)). On the other hand, habitat improvement projects immediately release sporocarp production in closed truffle plantations inoculated with *T. melanosporum* or *Tuber albidum* Pico ([Zambonelli et al., 2000](#); [Gregori et al., 2001b](#); [Sourzat et al., 2008](#)).

In cuttings that create gaps around adult trees, it is commonly accepted that the leaf mass and the stem growth of the retained trees will increase thanks to the higher availability of resources. However, in many cases this increase is not immediate. Jones and [Thomas \(2004\)](#) propose that the initial response will differ depending on the relative influence of resources flux and the shock provoked by the new microclimate. In a monitoring of eight treated *truffières*, the density of ectomycorrhizal tips increased only four years after canopy opening ([Garcia-Barreda and Reyna, 2012](#)), suggesting a lagged response of the fine roots of the host tree and the need for acclimation to the new conditions (e. g. irradiance, soil temperature). This could affect fungal fruiting: after a disturbance that decreased carbon allocation from the tree to the ectomycorrhizas, [Kuikka et al. \(2003\)](#) found a decrease in sporocarp production at the expense of the maintenance of fungal vegetative structures.

#### 4.3. Influence of truffière attributes

Our results demonstrate that the technique is not equally effective in all the studied truffières. The silvicultural treatment has led to a better response in large brûlés, whereas small brûlés have responded better to moderate cuttings. This should be considered in the design of future habitat improvement projects. [García-Montero et al. \(2007b\)](#) showed the close correlation between brûlé surface and sporocarp productivity in Spanish wild truffières. In our study site, large brûlés show a better response to the treatment, but the relationship between brûlé surface and dig abundance is influenced by pre-treatment fruiting potential. This relationship is significant only where pre-treatment potential was medium or high. This suggests that brûlé surface, when used as an indicator of truffière responsiveness, should be combined with previous fruiting state.

In our study site, the cuttings have effectively reduced canopy cover because the eliminated trees (*Pinus*) do not show resprouting ability. The decrease in above-ground competition is accompanied by a decrease in below-ground competition. This may not be the case if the trees cut had been resprouting *Quercus*. Inferences to these forests should be made with caution.

#### 4.4. Implications for management

In Mediterranean calcareous forests with low economic profitability *T. melanosporum* can play a role in promoting sustainable rural development. To enhance this, managers need clear and scientifically-based prescriptions for conserving the fungus in its habitat and integrating truffle production into multi-objective forest management. To our knowledge this is the first monitoring of a habitat improvement project in wild truffières with a large sample size ( $n > 30$ ).

Researchers had identified canopy closure as a key factor in the decline of wild truffières. Our results support that view: canopy closure suppressed *T. melanosporum* fruiting and this would have continued if the treatment had not been executed.

The study provides an insight into the dynamics of wild truffières and the influence of weather conditions on potential outcomes of the treatment, showing a simple way to integrate interannual climate variability into the evaluation. The canopy opening alone does not always allow that truffières achieve self-sustainability. An adaptive management approach should be adopted to deal with the uncertainty associated with weather and harvesting intensity. Soil water content during the summer could be increased through irrigation or mulching. The impact of harvesters walking on the brûlés could be mitigated by shallow soil tilling. These techniques need to be scientifically evaluated, although they are promising according to

PROYNERSO (2002), Ricard et al. (2003) and Sourzat and Ricard (2008). Assessing the impact of the intensive harvesting, which restricts the dispersal of *T. melanosporum* spores in the soil, would be also important and novel.

The study shows the importance of the heterogeneity in the characteristics of the *truffières* and their environment. This can help practitioners design treatments and predict if a habitat improvement treatment would be likely successful. In the case of small *brûlés* with low occurrence of fruiting events a fine-tuning of the technique is needed. The vegetation around them has been modified to fulfil *T. melanosporum* habitat requirements, but forest dynamics also implies the evolution of the root system and the ectomycorrhizal community (Sourzat et al., 2008). Assessing the influence of these factors on the response of the *truffières* could help improve their treatment.

The use of silviculture to improve the habitat for *T. melanosporum* involves deteriorating the habitat for other species. However, with the model used the cuttings affected only 2% of the study area (in which there is a density of about 7 *truffières* per 100 ha). The impact on the habitat of other species is therefore small, as well as the impact on other potential forest uses.

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Table 1 Attributes (mean and standard deviation) of the treated *truffières* (n=74), the non-treated *truffières* (n=10), and the reference areas (n=11). *Q. ilex* is the dominating host tree in 86% of the treated *truffières*, 100% of the reference areas and 70% of the non-treated *truffières*. In the rest, *Q. faginea* is the dominating host tree (sd: standard deviation).

	Treated <i>truffières</i>	Non-treated <i>truffières</i>	Reference areas
Dig abundance in 1997	15 (14)	8 (5)	10 (9)
<i>Brûlé</i> surface (m <sup>2</sup> )	73 (59)	23 (13)	52 (42)
Canopy surface of the host tree (m <sup>2</sup> )	49 (45)	24 (13)	45 (33)
Surface stoniness (%)	67 (27)	64 (28)	50 (36)
Canopy cover around the <i>brûlé</i> , in 1997 (%)	70 (18)	68 (15)	26 (15)
Canopy cover in 2005 (%)	27 (9)	57 (9)	24 (14) <sup>a</sup>
Distance from <i>brûlé</i> to pine plantation, in 1997 (m)	8 (3)	5 (2)	16 (20)
Distance to pine plantation, in 2005 (m)	27 (6)	18 (9)	37 (14)

<sup>a</sup> In the reference areas, these values are due solely to the canopy surface of the host trees

Table 2. ANOVA table for the effect of *truffières* attributes (between-subjects), time and annual latewood growth (within-subject) on post-treatment dig abundance. The response variable has been log transformed.

Category	Parameter estimate	Standard error	Type III, F	P
Between				
Dig abundance in 1997 (DI) <sup>a</sup>	-1.260	0.451	7.8	0.007
<i>Brûlé</i> surface (BR) <sup>a</sup>	-1.451	0.325	19.9	<0.001
Canopy cover in 1997 (CC)	0.748	0.442	2.9	0.095
Variation in canopy cover from 1997 to 2005 (VarCC)	3.083	0.969	10.1	0.002
DI×BR	0.889	0.239	13.8	<0.001
BR×VarCC	-1.635	0.480	11.6	0.001
Within				
Time from treatment (TI)	-0.104	0.022	22.9	<0.001
Latewood growth (LW)	-0.448	0.104	18.4	<0.001
DI×LW	0.194	0.062	9.6	0.002
TI×LW	0.0856	0.021	17.0	<0.001

<sup>a</sup> DI and BR have been log transformed

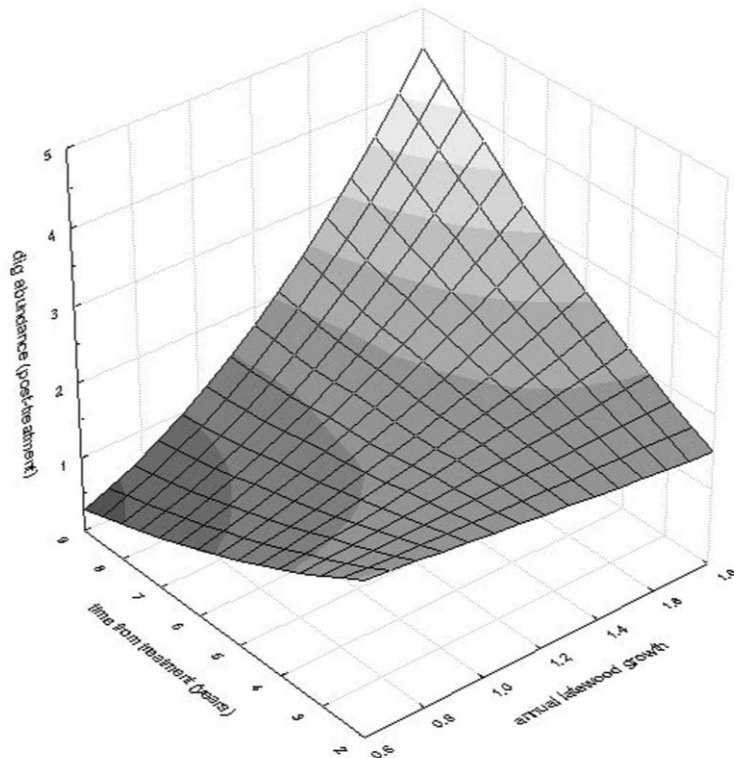


Fig. 1. Predicted effect of the interaction between time elapsed from treatment and annual latewood growth on annual mean dig abundance per *truffière*. Lighter colour indicates higher predicted values of the response variable. The between-subject variables are fixed at mean values. Annual latewood growth is expressed as a ratio to the mean value in the period 1997-2008.

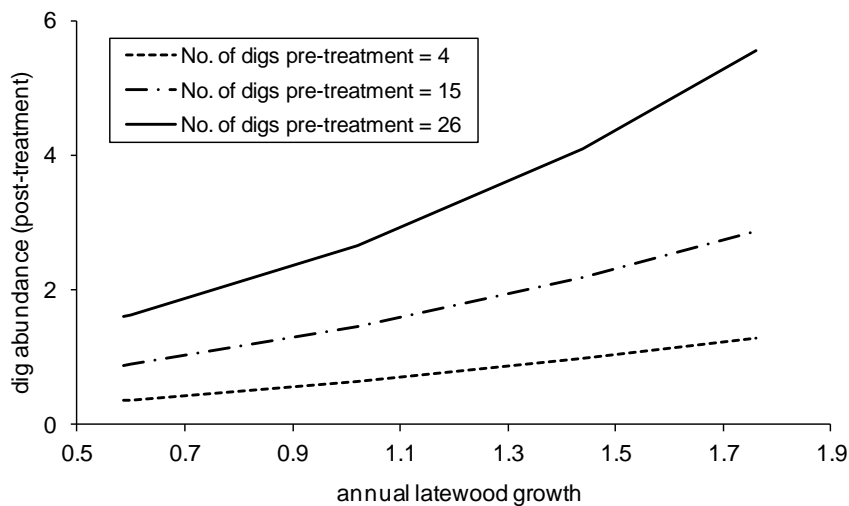


Fig. 2. Predicted effect of the interaction between annual latewood growth and pre-treatment dig abundance on post-treatment dig abundance. The values of pre-treatment dig abundance (in season 1997-1998) depicted are the mean in the treated *truffières* and the mean minus and plus one standard deviation. The remaining variables are fixed at mean values.

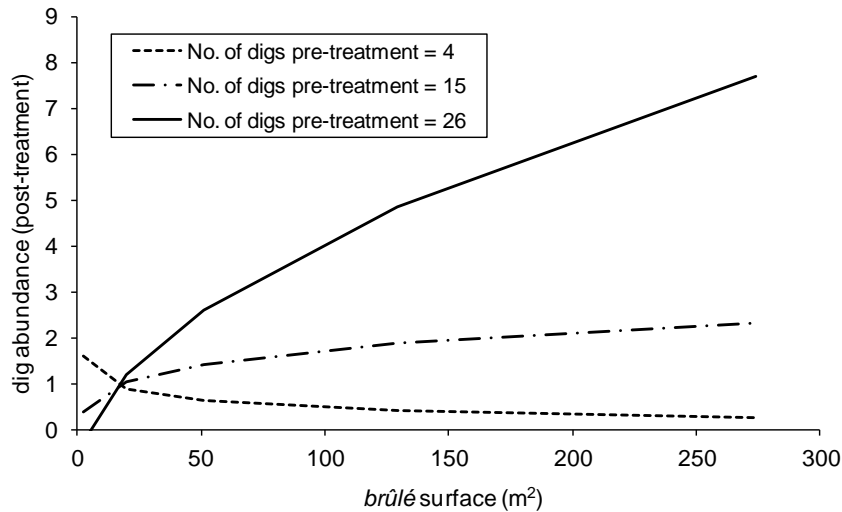


Fig. 3. Predicted effect of the interaction between *brûlé* surface and pre-treatment dig abundance on post-treatment dig abundance (mean annual abundance from year 2 to 9). The values of pre-treatment dig abundance (in season 1997-1998) depicted are the mean in the treated *truffières* and the mean minus and plus one standard deviation. The remaining variables are fixed at mean values.

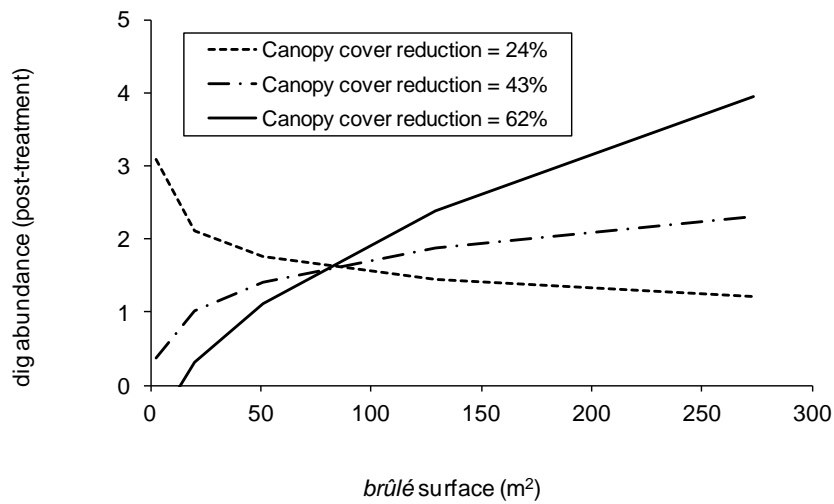


Fig. 4. Predicted effect of the interaction between *brûlé* surface and canopy cover reduction on post-treatment dig abundance (mean annual abundance from year 2 to 9). The values of canopy cover reduction (from 1997 to 2005) depicted are the mean in the treated *truffières* and the mean minus and plus one standard deviation. The remaining variables are fixed at mean values.