Short-term dynamics of *Quercus ilex* advance regeneration in a *Pinus nigra* plantation after the creation of small canopy gaps

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Abstract

Aim of the study: The aim of the research is to analyse the role of *Quercus ilex* advance regeneration in the stand regeneration of pine plantations after small-sized canopy openings, and to assess the influence of the forest stand and the canopy opening. The performance of the advance regeneration under the pine plantation is also examined.

Area of study: A *Pinus nigra* plantation in dry Continental Mediterranean climate in eastern Spain.

Material and methods: The tree regeneration of ten canopy openings of 0.17-0.43 ha was monitored during five years after treatment. It was also sampled in 0.12 ha-plots in the non-treated pine plantation surrounding the openings.

Main results: An important increase in the height of *Q. ilex* regeneration was observed in the openings, unlike what was found in the intact pine plantation. In the pine plantation, stand density showed a moderate positive influence on the density of *Q. ilex* regeneration, whereas in the canopy gaps *Q. ilex* height was negatively influenced by stand density before the opening.

Research highlights: The canopy opening triggered a response in *Q. ilex* advance regeneration, although height growth rates seemed to reduce over time. The results support the view that promoting *Q. ilex* in pine plantations may require different management strategies depending on the characteristics of the pine overstorey and on the density and size of the advance regeneration.

Key words: Mediterranean forest; stand initiation; seedling resprout; group selection cutting; truffle.

Introduction

The evergreen holm oak (*Quercus ilex* L) forests represent the potential vegetation in more than half of Mediterranean Spain (Maldonado *et al.*, 2002). Their extension is nowadays much more limited, due to the historical spread of agriculture, abusive logging and overgrazing. In the second half of the 20th century the overexploitation was reduced and many of the degraded lands were recolonised or reforested with pines (Ortuño, 1990). In recent decades the decrease in the economic profitability of timber and traditional forest products has led to abandonment of forest management (Domínguez-Torres and Plana, 2002). Several alternative uses have been proposed to promote forest management, like hunting and mushrooms. In lands suitable for the growing of the prized black truffle (*Tuber melanosporum* Vitt.) the experts propose to convert pine plantations and shrublands to understocked oak stands in order to improve the habitat for *T. melanosporum* and promote forest profitability (Reyna *et al.*, 2004; Diette and Lauriac, 2005).

The plantations of Mediterranean pines are frequently invaded by seedlings of *Q. ilex* (Gómez, 2003). Many oak species regenerate through the accumulation of advance regeneration below overstorey (Johnson *et al.*, 2002). The shoot growth of these seedlings is suppressed by adult trees and they often dieback and resprout. Some of these seedlings show a rapid shoot growth when the overstorey is disturbed (Johnson *et al.*, 2002). Retana *et al.* (1999) studied the behaviour of *Q. ilex* seedling under forest canopies and concluded that shade favours seedling emergence and survival during the first year; however, light deficit li-

This work has two Supplemenary Tables that do not appear in the printed article but that accompany the papel online.

mits seedling growth and often interacts with water deficit.

The role of the advance regeneration of *Q. ilex* in the stand regeneration after canopy disturbance is controversial. In *Q. ilex* coppice forests, Retana *et al.* (1999) and Gracia *et al.* (2001) concluded that its role is minor in the short term, since the advance regeneration did not show release after thinning the overstorey. The stumps resprout vigorously, rapidly outcompeting seedlings (Espelta *et al.*, 1999). By contrast, its role in Mediterranean pines stands, which do not resprout, has not been thoroughly examined.

In this study, we analyse tree regeneration in a *P. nigra* plantation with *Q. ilex* advance regeneration during the five years after experimental small-sized canopy openings aimed to improve the habitat for *T. melanosporum,* and we focus on the role of the advance regeneration. The influence of the characteristics of the forest stand and the canopy opening on tree regeneration is also assessed, as well as the influence of forest stand characteristics on the advance regeneration under the intact pine plantation.

Material and methods

Study site

The study was conducted in El Toro, Valencian Community, eastern Spain (39° 59' to 40° 1' N; 0° 44' to 0° 46' W, 990-1,050 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 quaternary calcareous glacis with less than 5% slope.

The area was reforested between 1958 and 1969 with a mixture of the non-native *Pinus nigra* Arnold subsp. *nigra* and the native *P. nigra* subsp. *salzmannii* Franco. Formerly, it was cultivated with cereal crops. Scattered adult *Q. ilex* and *Quercus faginea* Lam. form a lower tree layer. These oaks already existed before the plantation, in the field boundaries.

In March 2000, an experimental silvicultural treatment was executed with the aim of improving the habitat for *T. melanosporum* fruiting (Reyna *et al.*, 2004). Circular canopy openings were created around the truffle-producing grounds by systematically cutting down all the pines and removing the shrubs. Woody coarse debris were chipped and spread throughout the opening. Adult oaks were retained and slightly pruned.

Table 1. Summary statistics for the canopy openings monitored and the control pine stand

	Mean (SD)	Range
Canopy openings		
Site index (Assman top height of *P. nigra* at age 60, in m)	16.4 (1.8)	13.6-19.6
Pre-treatment canopy cover (%)	88 (11)	69-99
Size of canopy opening (m²)	2,330 (829)	1,700-4,300
Basal area of residual *Quercus* (m² ha⁻¹)	1.55 (0.62)	0.44-2.49
Canopy cover of residual *Quercus* (%)	12 (5)	5-20
Shrub cover (%)	4 (2)	1-5
Herb cover (%)	8 (8)	2-30
Relative abundance of *P. nigra* subsp. *nigra* in the pine stand adjacent to opening (%)	57.8 (25.9)	5.2-100
Control pine stand (in 2001)		
Canopy cover (%)	78 (9)	58-92
Pinus nigra basal area (m² ha⁻¹)	40 (6)	28-51
Quercus basal area (m² ha⁻¹)	0.88 (0.74)	0.01-2.19
Shrub cover (%)	2 (4)	0.3-12
Herb cover (%)	8 (5)	1-17

SD: standard deviation.

When the treatment was executed, the density of adult pines ranged from 1,000 to 2,450 trees ha⁻¹, with Assman top height from 9 to 12 m; the density of adult *Quercus* ranged from 29 to 259 trees ha⁻¹, with 62% *Q. ilex* and 38% *Q. faginea;* and the understorey shrubs (*Juniperus* sp. pl., *Prunus spinosa* L, *Quercus coccifera* L and *Genista* sp. pl.) and herbs cover was low (Table 1).

Data collection

Tree regeneration (height < 130 cm) was measured in ten canopy openings created in 2000 in the matrix of the pine plantation. The opening was settled as an expanded gap, with its borderline delimited by the trunks of the trees bordering the gap. The openings were sampled one year after the treatment execution, and again the second year, the fourth and the fifth.

The height and crown surface area were recorded for all the tree regeneration in the opening. The regeneration of *Q. ilex* and *Q. faginea* was classified as recent acorn seedlings (with the acorn or cotyledon scatters still attached) or seedling resprouts (individuals subject to recurrent cycles of shoot dieback and resprouting). The

origin of the latter (root sprout or acorn) was not discerned, as the seedlings were not dug up. The oak regeneration coming from stump resprouts of adult trees was excluded from data analysis; they accounted for less than 0.4% of all the sampled individuals. In young *P. nigra* seedlings, subspecies were not distinguished.

The density of regeneration of *Q. ilex, Q. faginea* and *P. nigra* was computed. For *Q. ilex,* the percent soil covered by the regeneration was also calculated, as well as the median height of the individuals. The median was preferred instead of the mean because the height of *Q. ilex* shoots followed a lognormal distribution and a logarithmic transformation was performed. The median height of *Q. faginea* and *P. nigra* was not calculated, because in most plots there were less than 30 individuals.

The following characteristics of the forest stand and the canopy openings were determined from fieldwork and aerial photographs (Table 1): site index (Assman top height of *P. nigra* subsp. *salzmannii* at the age of 60 was estimated using site index curves from Gómez-Loranca, 1996), pre-treatment canopy cover, residual BA in the opening (in which *Q. ilex* and *Q. faginea* were the only trees) as an estimate of shading and competition from residual adult trees, the size of the canopy opening (edge effect is higher in smaller-sized gaps) and the relative abundance of the allochthonous *P. nigra* subsp. *nigra* in the dominant tree layer around the openings (in which *P. nigra* and *P. salzmannii* accounted for 95% of the trees).

A control plot was sampled in the matrix of pine plantation surrounding each canopy opening. Each control consisted of three square subplots of 400 m^2, randomly located around the opening, at a distance of 5-10 m from the borderline. The plots were sampled in 2001 and again in 2007.

Statistical analysis

An information-theoretic approach (Burnham and Anderson, 2002) was used to assess the time trend of tree regeneration after the opening and the influence of forest stand characteristics. For the analysis of *Q. ilex* and *Q. faginea* regeneration, a set of 32 models was developed that included all the combinations of the following predictor variables: time from treatment, site index, pre-treatment canopy cover, post-treatment BA and opening size. Since *P. nigra* does not regenerate through advance regeneration, in the analysis of *P. nigra* regeneration pre-treatment canopy cover was

excluded; the relative abundance of *P. nigra* subsp. *nigra* was included instead to assess regeneration differences between the two subspecies.

These a priori models were constructed with linear mixed models (LMM) in which time was included as a repeated measures variable, stand characteristics were included as fixed predictors and an unstructured covariance matrix was specified (SPSS, 2006). The response variables were log transformed when the model assumptions were violated, as well as time from treatment.

In the various analyses performed, none of the competing models was strongly supported as the best (w$_i$ > 0.9), so model averaging was employed to account for model selection uncertainty (Burnham and Anderson, 2002). The following statistics are provided for inference: the model-averaged parameter estimate, which shows the direction of a predictor effect on the response; its 90% confidence interval (CI); and the sum of the Akaike weights (Σw$_i$), which indicates the relative importance of a predictor. Predictor variables were considered important in explaining variation in the response when the CI did not overlap zero and Σw$_i$ approached one. The best models from each set (with the lower Kullback-Liebler distance to the observed data) are also provided (Supplementary Tables S1, S2).

The characteristics of *Q. ilex* and *Q. faginea* seedling bank in the control pine stand were also assessed with an information-theoretic approach. The following predictors were tested: time (sampling of 2001 *vs.* 2007), site index, canopy cover, and BA of adult *Quercus* (which grow in the lower tree layer).

A post-hoc analysis was conducted to explore the time trend of *Q. faginea* regeneration density. The width of the rings of dominant *P. nigra* subsp. *salzmannii* (20 trees distributed throughout the study site) was used as a proxy for the effect of weather on trees (Martín-Benito *et al.*, 2008).

Results

Density of *Q. ilex* regeneration

In the canopy openings, model averaging indicated that time from treatment was the only predictor whose effect on the density of *Q. ilex* regeneration was clearly supported by the data (the 90% CI did not overlap zero) while showing a high relative importance (Σw$_i$). The relation was positive (Table 2) and resulted in a rather

Table 2. Statistics used for inference on the characteristics of *Quercus* regeneration in the openings: model-averaged parameter estimates and their 90% confidence intervals (CI), and relative importance of each predictor (Σwi)

	Time[1]	SI	CCpre	BApost	Size
Quercus ilex density[2]					
Parameter estimate	0.0060	−0.059	0.0157	0.29	0.55
90% CI-lower	0.0053	−0.139	0.0060	0.10	−0.79
90% CI-upper	0.0067	0.022	0.0254	0.48	1.89
Σwi	1.00	0.05	0.01	0.17	0.38
Quercus faginea density[2]					
Parameter estimate	0.0085	0.33	0.0088	−1.07	1.13
90% CI-lower	0.0070	0.14	−0.0186	−1.85	−3.27
90% C- upper	0.0100	0.52	0.0363	−0.29	5.53
Σwi	0.45	0.36	0.01	0.44	0.73
Quercus ilex height					
Parameter estimate	19.9	1.67	−0.61	−2.04	5.6
90% CI-lower	17.8	1.10	−0.70	−3.40	−6.4
90% CI-upper	21.9	2.25	−0.51	-0.68	17.6
Σwi	1.00	0.90	0.90	0.83	0.54
Soil cover by *Quercus ilex*[2]					
Parameter estimate	0.95	0.138	0.0157	0.191	1.59
90% CI-lower	0.79	0.071	0.0032	−0.079	−0.18
90% CI-upper	1.11	0.205	0.0282	0.462	3.36
Σwi	1.00	0.27	0.01	0.19	0.57

[1] Time was log-transformed for the analysis of *Q. ilex* height and soil cover. [2] Variable log transformed. SI: site index. BApost: post-treatment basal area. CCpre: pre-treatment canopy cover. Size: size of the opening.

linear increase during the five years after treatment (Fig. 1a).

In the control pine stand, model averaging of *Q. ilex* regeneration density indicated that time was the only predictor with both a 90% CI not overlapping zero and a high Σw_i (Tables 3, 4). Canopy cover showed a moderate positive influence on the density (Table 4).

Seedling resprouts were the only regeneration type present in the openings one year after treatment, whereas in the fifth year they were 14 times more abun-
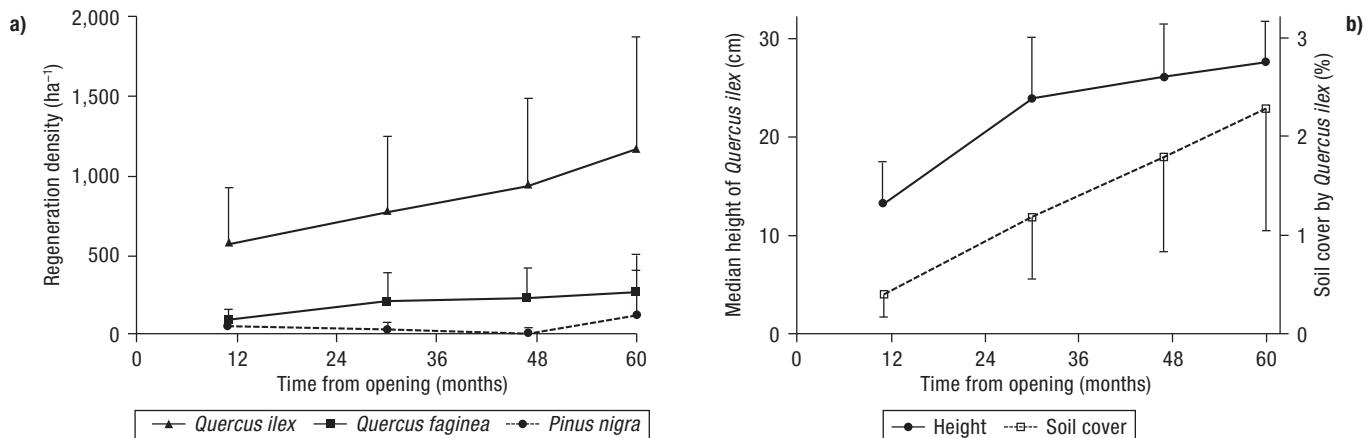

Figure 1. Mean density of tree regeneration (a), median height of *Quercus ilex* regeneration and soil covered by *Quercus ilex* regeneration (b). Error bars represent standard deviation (n = 10).

Table 3. Summary statistics for the tree regeneration in the control pine stand

	Sampling 2001		Sampling 2007	
	Mean (SD)	Range	Mean (SD)	Range
Quercus ilex density (ha^{-1})	1,609 (673)	683-2425	2,979 (1170)	1,333-5,125
Quercus ilex height (cm)	15 (3)	10-20	14 (2)	10-18
Quercus ilex soil cover (%)	0.67 (0.39)	0.03-1.23	1.92 (1.39)	0.22-5.05
Quercus faginea density (ha^{-1})	216 (120)	75-492	651 (310)	158-1,067
Pinus nigra density (ha^{-1})	0	0	361 (410)	8-925

SD: standard deviation.

Table 4. Statistics used for inference on the characteristics of the *Quercus* seedling bank in the control pine stand: model-averaged parameter estimates and their 90% confidence intervals (CI), and relative importance of each predictor (Σwi)

	Time[1]	SI	CC	BA-Qu
Quercus ilex density[2]				
Parameter estimate	0.0036	−0.0122	0.0111	−0.0072
90% CI-lower	0.0031	−0.0457	0.0059	−0.0549
90% CI-upper	0.0041	0.0213	0.0163	0.0405
Σwi	1.00	0.04	0.56	0.04
Quercus faginea density[2]				
Parameter estimate	0.0068	0.059	0.0055	0.083
90% CI-lower	0.0057	0.005	−0.0045	0.003
90% CI-upper	0.0078	0.112	0.0156	0.164
Σwi	1.00	0.21	0.01	0.26
Quercus ilex height				
Parameter estimate	−1.40	0.59	0.043	0.49
90% CI-lower	−2.23	−0.01	−0.069	−0.42
90% CI-upper	−0.57	1.19	0.155	1.40
Σwi	0.97	0.68	0.11	0.56
Soil cover by *Quercus ilex*[2]				
Parameter estimate	0.0073	0.075	0.0165	0.114
90% CI-lower	0.0061	−0.009	0.0017	−0.010
90% CI-upper	0.0086	0.160	0.0312	0.238
Σwi	1.00	0.19	0.07	0.27

[1] Time was log-transformed for the analysis of *Q. ilex* height and soil cover. [2] Variable log transformed. SI: site index. CC: canopy cover. BA-Qu: basal area of adult *Quercus* (which grow in the lower tree layer).

dant than recent acorn seedlings. In the control pine stand, seedling resprouts of *Q. ilex* accounted for almost all the individuals in 2001, and they were 6 times more abundant than recent acorn seedlings in 2007.

Density of *Q. faginea* regeneration

In the openings, none of the predictors used in the model averaging showed both a 90% CI not overlapping zero and a high Σwi. However, time from treatment and site index showed a moderate positive influence on the density of *Q. faginea* regeneration, and post-treatment BA showed a moderate negative influence (Table 2, Fig. 1a).

Since time did not show a strong and straightforward effect on *Q. faginea* regeneration density (Fig. 1a), a post-hoc analysis was conducted to compare three different time patterns: linear, quadratic and related to *P. nigra* ring width. Ring width reached a much lower

value of Akaike's information criterion (AIC = 14.6) than the linear (32.0) and the quadratic (41.3) time trends, indicating a better fit.

In the pine plantation, model averaging of *Q. faginea* regeneration density indicated that time was the only predictor with both a 90% CI not overlapping zero and a high Σw_i (Tables 3, 4).

Seedling resprouts were the only regeneration type found in the openings one year after treatment, whereas in the fifth year they were 15 times more abundant than recent acorn seedlings. In the pine stand, seedling resprouts of *Q. faginea* accounted for almost all the individuals in 2001, and they were 31 times more abundant than recent acorn seedlings in 2007.

Density of *P. nigra* regeneration

Model averaging of *P. nigra* seedling density in the openings revealed that relative abundance of adult *P. nigra* subsp *nigra* around the opening, opening size and site index showed a 90% CI not overlapping zero while having a high Σw_i. The effect of the two former on the density of *P. nigra* regeneration was negative, while the effect of the latter was positive (Table 5).

Five years after the opening only 9% of the seedlings were two or three years old and the rest were one year old. In the pine plantation, none of the seedlings found (Table 3) was more than three years old.

Height of *Q. ilex* regeneration

Model averaging of *Q. ilex* median height in the openings revealed that time from treatment, site index, pre-treatment canopy cover and post-treatment BA

Table 5. Statistics used for inference on the density of *Pinus nigra* regeneration (log transformed for the analysis) in the openings: model-averaged parameter estimates and their 90% confidence intervals (CI), and relative importance of each predictor variable

	Time	SI	PNN	BApost	Size
Parameter estimate	0.0155	0.34	–3.21	–0.20	–2.206
90% CI-lower	0.0073	0.20	–4.60	–0.81	–4.403
90% CI-upper	0.0238	0.48	–1.82	0.41	–0.009
Σw_i	0.02	0.77	0.97	0.16	0.77

SI: site index. PNN: relative abundance of *Pinus nigra* subsp. *nigra* in the adjacent pine stand. BApost: post-treatment basal area. Size: size of the opening.

presented both a 90% CI not overlapping zero and a high Σw_i (Table 2). Time showed a positive relation with the median height of *Q. ilex* regeneration, with an apparent curvilinear pattern reflecting an increase that levelled off with time (Fig. 1b). Site index showed a positive effect, whereas the effect of pre-treatment canopy cover and post-treatment BA was negative. The increase in height from the fourth to the fifth year after treatment did not show a negative correlation with the density of *Q. ilex* regeneration in the fourth year (Pearson's r = 0.59; 90% CI: 0.06, 0.86).

Model averaging of *Q. ilex* median height in the pine stand indicated that time was the only predictor with both a 90% CI not overlapping zero and a high Σw_i, with median height being lower in 2007 than in 2001 (Tables 3, 4).

On average 8.3 individuals ha^{-1} recruited into the adult stratum (height > 130 cm) between the first and the fifth year after the canopy opening, which account for 1.5% of the seedling resprouts found in the first year. In the pine stand, only one individual of *Q. ilex* regeneration recruited into the adult stratum in the ten plots between 2001 and 2007, whereas five individuals reduced their height from above to below 130 cm.

Soil cover by *Q. ilex* regeneration

In the openings, model averaging indicated that time from treatment was the only predictor with both a 90% CI not overlapping zero and a high Σw_i (Table 2). Its relation with the percent soil cover by *Q. ilex* regeneration was positive, and resulted in an apparently linear increase during the five years after treatment (Fig. 1b).

In the pine stand, model averaging of the soil cover by *Q. ilex* regeneration indicated that time was the only predictor with both a 90% CI not overlapping zero and a high Σw_i (Tables 3, 4).

Discussion

Canopy disturbance usually triggers a period of rapid change in the vegetation. During this stand initiation stage it is usually difficult to accurately predict changes, although of high interest because future stand characteristics are highly influenced by the initial stage (Johnson *et al.*, 2002).

In our study site the canopy openings were created in the matrix of a 31-42 year-old *P. nigra* plantation

with high density and a sparse lower tree layer of oaks. No established *P. nigra* regeneration was found under this canopy. Lucas-Borja *et al.* (2011) found that BA ranging 25-40 m² ha⁻¹ (similar to those in our study site, Table 1) are optimum for the emergence of *P. nigra* subsp. *salzmannii* seedlings in Central Spain, although Gómez-Aparicio *et al.* (2006) showed the negative effect of shade on seedling biomass. Tíscar-Oliver (2007) found that seedling survival is highly dependent on the first summer drought.

By contrast, *Q. ilex* regeneration was relatively abundant under the pine canopy, and its density was of the same order of magnitude than that found by Ruiz-Benito *et al.* (2012) in Spanish *P. nigra* plantations and by Gómez-Aparicio *et al.* (2009) in pine plantations in southern Spain, although much lower than the density found by Gracia *et al.* (2001) in *Q. ilex* coppice stands of northeastern Spain. In southern Spain, Urbieta *et al.* (2011) found that *Q. ilex* regeneration was much more abundant in oak than in pine forests, although the maximum was obtained in mixed stands.

European jays abundantly disperse *Quercus* acorns in pine stands (Gómez, 2003). However, seedling resprouts were much more frequent than young acorn seedlings. *Q. ilex* regeneration was small-sized and no evidences of a clear positive time trend in height growth were found. These are characteristic features of oak species that form seedling banks and perpetuate through repeated shoot dieback and resprout (Johnson *et al.*, 2002).

After the canopy opening *Q. ilex* was also the most abundant tree regeneration. The scarcity of recent acorn seedlings indicates the dominant role that the advance regeneration played in forest dynamics during the first years after the opening. Recruitment of new acorn seedling was also observed, but the survival of young *Q. ilex* seedlings in full sunlight is usually low (Marañón *et al.*, 2004; Prévosto *et al.*, 2011b) and therefore it is difficult to predict if they will increase the density of *Q. ilex* meaningfully.

Q. ilex is considered as intermediate in shade tolerance (Valladares and Niinemets, 2008), with seedling recruitment and early survival being higher under full canopy than in full sunlight. In our pine stands, the canopy cover positively related to the density of *Q. ilex* regeneration. The harvesting operations and the sudden exposition to full sunlight may have hampered the survival of some young seedlings and seedling resprouts with low root reserves (Dillaway *et al.*, 2007). However, after the opening the density of *Q. ilex* re-

generation increased linearly with time, indicating the vigour of the advance regeneration to resprout and survive in full light.

Retana *et al.* (1999) and Marañon *et al.* (2004) pointed out that, despite its shade tolerance, *Q. ilex* seedlings are unlikely to grow into saplings with low light levels. Gómez-Aparicio *et al.* (2009) found that in southern Spain the recruitment of *Q. ilex* seedlings was at maximum at pine densities similar to those in our study site, whereas the density of saplings was maximum at lower densities. In a *Pinus halepensis* Mill. shelterwood in southern France, Prévosto *et al.* (2011a) found that the growth of sown *Q. ilex* was higher in the stands with lower BA (10 m² ha⁻¹). We observed an important increase in the height of *Q. ilex* regeneration in the years immediately after the canopy opening, whereas in the pine plantation no evidences of a clear height increase were found during the same period of time. This indicates that under the pine canopy there were *Q. ilex* seedling resprouts that retained the ability to grow rapidly after release, in contrast to the lack of response reported by Gracia *et al.* (2001) in thinned coppice forests. This tends to support the view that at least part of the seedling resprouts is able to recruit into the adult stratum when they are released.

However, the evolution of *Q. ilex* median height suggests a reduction in the growth rate of the regeneration over time. This reduction is not apparently related to intraspecific competition among seedling resprouts, since the density of regeneration was low and the correlation between density and height increase was not negative. Another factor which could influence height growth in small openings is the edge effect; however in our openings the size did not appear to be as important as the other predictors. This could be an effect of the narrow range of this variable (Table 1): York *et al.* (2003) studied group selection cuttings with a larger range of sizes (0.1-1 ha) in California and found that opening size was positively related to seedling height growth.

Another factor frequently affecting the behaviour of oak advance regeneration is the competition of the understorey shrubs (Johnson *et al.*, 2002). However, in our study site the development of the understorey was moderate (Table 1). This is probably related to the former agricultural use and to the high stand density of the pine stand, although under the Continental-Mediterranean climate of central Spain the density of the woody understorey is usually low (Costa *et al.*, 1996).

On the other hand, the canopy cover before treatment and the residual (post-treatment) BA of adult oaks negatively related to the height of *Q. ilex* regeneration. The residual BA of adult oaks showed a negative effect despite being always lower than 2.5 m² ha⁻¹. Gracia *et al.* (2001) found that in thinned *Q. ilex* coppice forests with BA 15-17.5 m² ha⁻¹ the growth of *Q. ilex* seedlings was suppressed. This suppressive effect could be caused by shading, root competition or topsoil properties (Puerta-Piñero *et al.*, 2006). The negative influence of the canopy cover before treatment agrees with the results of Dillaway *et al.* (2007), where the light levels under close canopy positively related to the root diameter and reserves of *Quercus alba* L advance regeneration, the latter being related to the vigour of advance regeneration. This suggests that a previous thinning of the pines could have improved the growth of seedling resprouts after opening.

In the case of *Q. faginea* the advance regeneration also played an important role in the openings. In contrast with *Q. ilex,* the increase in *Q. faginea* density was not as steady, and it was moderately influenced by site index and by the residual adult oaks. This suggests a less vigorous resprouting and survival of seedling resprouts in full sunlight. *Q. faginea* is a semi-deiciduous species that exhibits biological features similar to those of *Q. ilex,* but it is considered more sensitive to drought (Sanz-Pérez *et al.*, 2007). The fact that the increase in the density of *Q. faginea* regeneration in the openings was better explained by annual weather conditions than by time from treatment supports this view.

The regeneration of *P. nigra* did not establish for the moment in the openings, and the emergence of seedlings was influenced by site index. This limitation in the effective recruitment is similar to the difficulties in regeneration after wildfire and clearcutting encountered for *P. nigra* subsp. *salzmannii* in Spain, where this taxon is considered quite shade-tolerant compared to other native Spanish pines (Ordóñez *et al.*, 2004; Tíscar-Oliver, 2007).

On the other hand, *P. nigra* subsp. *nigra* has been traditionally considered as shade-intolerant, although Chauchard *et al.* (2006) found that it did not behaved as such in southeastern France. In Spain we know of no study about its shade tolerance. Due to the high mortality of young *P. nigra* seedlings, we could not determine which taxon they belonged to. However, the negative relation of seedling density in the openings with the abundance of adult *P. nigra* subsp. *nigra*

around the openings suggests that the emerging seedlings were mostly *P. nigra* subsp. *salzmannii.*

The current lack of effective regeneration of *P. nigra* in the openings does not necessarily involve the loss of pines in the medium term. In burned Mediterranean pine forests, Gracia *et al.* (2002) observed that *P. nigra* subsp. *salzmannii* regenerated abundantly only after the resprouting *Q. faginea* covered the soil (from the 4ᵗʰ to the 15ᵗʰ year), and in the 37ᵗʰ year pines dominated the tree layer, pointing to a nurse effect. In our study site, the soil cover by *Q. ilex* is low five years after the opening (Fig. 1b), so a long-term monitoring would be necessary to discern if *P. nigra* establishment is restricted by site conditions or by the scarce canopy cover.

Our results show that the canopy opening triggered a response in *Q. ilex* advance regeneration. However, since the monitoring suggests a reduction in median height growth over time, the effective recruitment of *Q. ilex* into the dominant tree layer will depend on the proportion of seedling resprouts capable of maintaining a competitive height growth in the new conditions. Our results also suggest that the stand density before treatment and the stand density of oaks after treatment are detrimental to the height growth of this regeneration.

The management objective in the study site was to achieve an open oak-dominated stand around the truffle-producing grounds in order to improve the habitat for *T. melanosporum* fructification. The size of the openings was kept to the minimum necessary in order to enhance the compatible management of truffle and other forest uses (Reyna *et al.*, 2004). In canopy openings with sizes ranging 0.17-0.43 ha we did not find clear evidences that the opening size hindered the release of *Q. ilex* seedling resprouts; and *Q. ilex* regeneration enjoyed a competitive advantage over *P. nigra*. The statistical models predict that soil cover by *Q. ilex* regeneration will be on average 4% in the 10th year and 8% in the 20ᵗʰ year. This will add to the canopy cover of residual adult oaks, which was on average 12% one year after the opening and 13% in the fourth year. Soil cover by *Q. ilex* will likely remain below 30% in the short term, thus suitable for *T. melanosporum* production (Reyna *et al.*, 2004) without additional silvicultural operations.

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