Original article

Seedling bank dynamics in managed holm oak (*Quercus ilex*) forests

Marc Gracia[a,b], Javier Retana[b,*] and Francesc Xavier Picó[b]

[a] Departament de Producciò Vegetal i Ciència Forestal, Universitat de Lleida, Rovira Roure 177, 25006 Lleida, Spain
[b] Centre de Recerca Ecològica i Aplicacions Forestals i Unitat d'Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra (Barcelona), Spain

Abstract – The present study reports spatiotemporal variations in seedling bank dynamics during a 5-year period in thinned and unthinned holm oak (*Quercus ilex*) plots in the Montseny Massif (NE Spain). Large spatial and temporal variations in seedling density have been found in the three plots studied, while the spatial pattern has shown low temporal fluctuations. However, differences in recruitment and survival among thinned and unthinned plots were small, but both variables had large between-year variability. The monitoring of seedling growth over time demonstrated that holm oak seedlings hardly grew in height after five years. According to these results, holm oak seedlings persisted through time in the understory and remained suppressed while in the shade, but did not show any release after thinning. Thus, the seedling bank only represents a reserve of small individuals that do not have any evident role in holm oak forest dynamics under the present disturbance/management regime.

holm oak / seedling / recruitment / growth / survival

Résumé – Dynamique du banc de plantules dans des taillis coupés et non coupés de chêne vert (*Quercus ilex*). Cette étude analyse les variations spatiales et temporelles de la dynamique du banc de plantules de chêne vert (*Quercus ilex*) pendant cinq ans, dans des taillis coupés et non coupés dans le massif du Montseny (NE Espagne). Nous avons trouvé de grandes variations spatiales et temporelles de la densité de plantules dans les trois taillis étudiés. Cependant, les différences de recrutement et survivance des plantules entre les trois taillis sont minimes, mais les deux variables ont montré une grande différence interannuelle. L'échantillonnage de la croissance des plantules au fur et à mesure a montré qu'elles ne poussent pas après cinq ans. En accord avec ces résultats, les plantules de chêne vert survivent sans être altérées pendant des années dans le sous-bois, mais elles ne présentent aucune libération après la coupe. Pour cette raison, le banc de plantules de chêne vert peut être considéré comme une réserve de petits individus qui n'a aucun rôle évident dans la dynamique des chênaies sous le régime actuel de perturbation/gestion de ces forêts.

chêne vert / plantule / recrutement / croissance / survivance

* Correspondence and reprints
Tel. +34 93 581 20 28; Fax. +34 93 581 13 12; e-mail: retana@uab.es

1. INTRODUCTION

Seedling recruitment is one of the mechanisms of forest regeneration, which plays an important role for numerous tree species [9, 16, 21]. Nevertheless, recruitment patterns vary widely, and it is frequently difficult to appraise the role of seedlings in forest dynamics. This is especially true when seeds germinate under a closed canopy, which is usually unfavourable for rapid seedling growth. Under these environmental conditions, two different and even opposite strategies may be found. One strategy is that of plants whose seedlings have a limited ability to persist under a closed canopy, and that depend on an intense and continuous recruitment. At the other extreme we find some shade-tolerant species whose seedlings may survive in shady conditions for long periods of time with very reduced growth rates. These potential recruits can accumulate in a dormant state when conditions are unfavourable, but then resume growth toward maturity when conditions become favourable [20]. Grime [15] called such a population of persistent seedlings a "seedling bank". The presence of seedlings in the forest understory is insufficient to indicate whether a species maintains a persistent bank; only by monitoring individuals over time can it be demonstrated that tree seedlings are surviving more than a few years, and that they are not growing continuously upward [20].

Holm oak (*Quercus ilex* L.) is one of the most representative forest tree species in the western part of the Mediterranean Basin [25, 26]. It is one of the clear examples of the importance of resprouting as a regeneration mechanism, because most present-day holm oak forests in the west Mediterranean basin have originated through resprouting after disturbances such as fire, overgrazing, wood extraction or charcoal production [10, 13, 23]. Nowadays, postdisturbance regeneration of holm oak stands is still ensured by sprouting from the stool bud bank [13, 23]. Under the present management and disturbance conditions, the seedling bank probably plays only a minor role in the regeneration of holm oak stands at short or medium temporal scales, because seedlings are less competitive than stump sprouts [23, 24]. Nevertheless, the dynamics of the holm oak seedling populations may be viewed in relation to ecological phenomena such as the persistence of plant populations, genetic variability or potential forest decline [12, 24]. The dynamics of the seedling bank has been used to hypothesise about the past and the future of holm oak forests. Thus, different authors (Bacilieri et al. [1], Li and Romane [19]) suggest that the low seedling regeneration in holm oak stands in

southern France may lead to the replacement of holm oak by downy oak (*Quercus humilis = Q. pubescens*), while Espelta et al. [12] consider that the present seedling dynamics in holm oak forests in NE Spain prevents vigorous regeneration and, consequently, population renewal. Nevertheless, most of these studies on holm oak forests are based on data obtained from chronosequences, but not from monitoring the seedling bank over time. The present study reports the dynamics of the holm oak seedling bank during a 5-year period in thinned and in unthinned plots, in order to understand how seedlings contribute to holm oak forest dynamics. It would be expected that holm oak seedlings remain in the understory of holm oak stands until the canopy is opened by thinning and they can resume growth. Specific objectives are: (1) to determine the spatial (within and between plots) and temporal (between years) variability in the size and composition of the seedling bank; (2) to investigate the patterns of seedling recruitment, mortality growth and biomass allocation determining these dynamics.

2. METHODS

2.1. Study site

The study was conducted at Arbúcies (Montseny Massif, Catalonia, NE Spain). Mean annual temperature within the study area is 12 °C, with mean monthly temperatures for January and July averaging 1 °C and 28 °C, respectively, and mean annual precipitation is 750 mm (data were obtained from the meteorological station of Viladrau, located near the study area). As in other Mediterranean areas, the climate was highly unpredictable, with irregular periods of rainfall and drought throughout the year, not always related to seasonal variations. The geological substratum in the area was composed by siliceous rocks. The study site was located at an elevation of 800–820 m, and was occupied by a pure holm oak forest. The whole area has been traditionally exploited by selection thinning, which consists of a partial removal of standing trees and biomass [14]. Three adjacent 1600 m^2 plots, which differed in the time since the last thinning, were considered.

1) The first plot (not thinned, hereafter called NT) had a north-eastern slope and had not been thinned for more than 40 years. Shoot (i.e. stems with diameter at breast height higher than 5 cm) density was 1262 ha^{-1}, and basal area was 28.2 m^2 ha^{-1}. Holm oaks reached a height of 10–18 m.

2) The second plot (thinned in 1993, hereafter called T93) had a north-eastern slope and had been thinned one month before the beginning of the study. Shoot density before thinning was 1338 ha^{-1}, and basal area was 35.0 m^2 ha^{-1}. Holm oaks reached a height of 8–16 m. The percentage of basal area thinned was 42.8%.

3) The third plot (thinned in 1994, hereafter called T94) had not yet been thinned at the beginning of the study (March 1993), but was thinned the following winter. It had an eastern slope. Shoot density before thinning was 1465 ha^{-1}, and basal area was 40.4 m^2 ha^{-1}. Holm oaks reached a height of 8–18 m. The percentage of basal area thinned was 43.3%.

2.2. Sampling

A total of 36 permanent quadrats (2 × 2 m each) were set at each plot. Quadrats were contiguous and distributed among three transects, which were separated by a distance of 10 m between them. A seedling was defined as any individual smaller than 40 cm. In March 1993, all holm oak seedlings standing within each quadrat were tagged and mapped. At that time, recently-established seedlings (hereafter "1993 cohort") were separated from older seedlings ("pre-1993 seedlings", hereafter). From 1994 to 1997, cohorts of newly-established seedlings in each quadrat were also tagged and mapped. The fate of seedlings from the different cohorts was monitored over time to determine survival rates. Although different vertebrates (small rodents, birds, wild boars) may predate acorns and affect seedling emergence, no evidences of the destructive effects of large herbivores (wild boars, deers) on established seedlings were observed during the five years of study. Unfortunately, no data of acorn fall during these years were available. Total seedling height was recorded in March of each year, and the number of leaves was recorded in the last three years, from 1995 to 1997.

To measure light availability to seedlings, the gap light index (GLI) of Canham [6] was computed for each 2 × 2 m quadrat in the three plots. GLI specifies the percent of total PAR that is transmitted through a canopy gap to a specific point in the understory. To determine GLI, fisheye photographs were taken in each quadrat. Photographs were digitised to obtain canopy images that were analysed with the GLI/C software (Canham [7]).

To obtain a more precise measurement of annual growth rate in height, a random set of 100 seedlings per plot within the quadrats were marked in 1995 with a cotton thread just at the base of the terminal buds. Annual growth rate of each seedling was recorded in 1996 and in 1997. Since branching occurred in some seedlings, the number of new branches produced each year, as well as their length, were also recorded.

To determine biomass allocation patterns of the different seedling cohorts found in each plot, a random set of 15–25 seedlings per cohort and plot (1–5 seedlings per quadrat) were removed in the last sampling year of the study. Seedlings were separated into leaves, stem and roots. The number of leaves of each seedling was counted and the leaf area was measured with a Li-Cor LI-3100 area meter. Dry weight of roots, shoots, and leaves was determined for each seedling, after drying at 60 °C. From the primary data, the root-shoot ratio (R/S, root dry weight/shoot dry weight) of each seedling was calculated.

2.3. Analyses

The effect of plot and year on total seedling density, seedling establishment and survival of pre-1993 seedlings and those from the 1993 cohort was analysed using repeated-measures ANOVAs. Survival of the 1995 cohort after two years, and the 1996 cohort after one year, in the three plots was analysed using one-way ANOVA models. The effect of cohort and plot on size and resource allocation variables was analysed using two-way ANOVA models. All the relationships between establishment, total seedling density, seedling growth and GLI, were analysed using regression models. When necessary, analyses were run on log or arcsin-square root transformed data.

3. RESULTS

3.1. Spatiotemporal patterns of seedling density

The distribution of seedling density per quadrat differed among plots (*figure 1*). The variability was highest in the NT plot, with densities of up to 40 seedlings m^{-2}. In the T93 plot, many quadrats had few seedlings and few quadrats (almost none) had high seedling density. In the T94 plot, many quadrats had low seedling density.

In the two thinned plots, a high percentage of quadrats remained within the same density category four years after the first sampling, suggesting a low fluctuation rate in
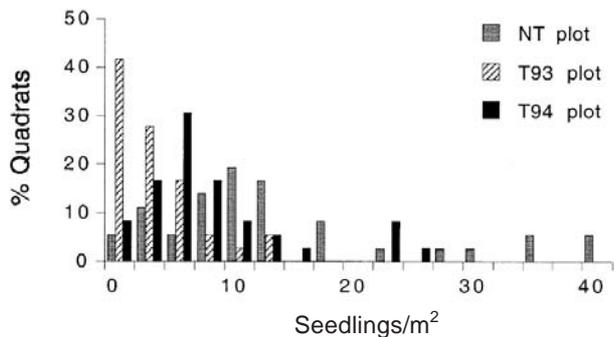
Figure 1. Distribution of quadrats according to seedling density in the three plots at the start of the study (March 1993). NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

seedling density within quadrats (*table I*). Nevertheless, in the NT plot, a relatively high percentage of quadrats changed to a lower-density category after four years (*table I*).

Total seedling density per quadrat varied between years (repeated measures ANOVA, $F = 39.5$, $p < 0.0001$). There were also significant differences among plots ($F = 13.2$, $p < 0.0001$), density being highest in the NT plot (together with the T94 plot in 1995, 1996 and 1997) and lowest in the T93 plot. The interaction plot × year was also significant, because seedling density showed higher between-year differences in NT than in the other two plots, with a very high decrease from 1993 to 1995 that was not observed in the other two plots (*figure 2*).
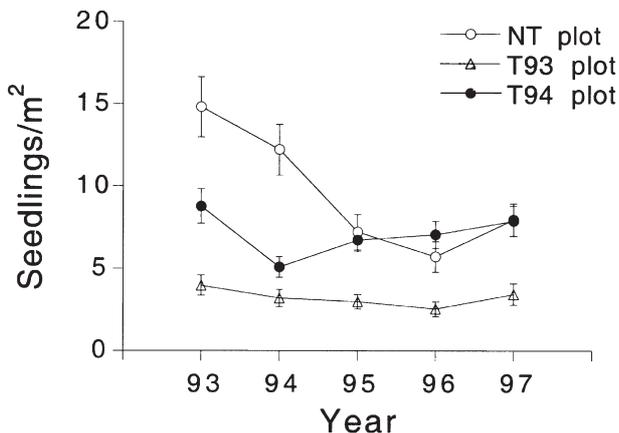

Figure 2. Total seedling density (mean ± *SE*) in the different plots and sampling years. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

Table I. Changes in seedling density from the first sampling period (year 1993, in rows) to the latest one (year 1997, in columns) in the three plots considered in this study. *N*, number of quadrats of each density category. In bold, percentage of quadrats that remain in the same density category after four years. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

Plot and seedling density in 1993	Seedling density 1997 ($N\,m^{-2}$)				
	N	< 5	5–9	10–19	20
- NT Plot					
< 5	7	**85.7**	14.3	0	0
5–9	6	66.6	**16.7**	16.7	0
10–19	16	25.0	56.3	**18.7**	0
20	7	0	0	71.4	**28.6**
- T93 Plot					
< 5	25	**96.0**	4.0	0	0
5–9	8	50.0	**37.5**	12.5	0
10–19	3	0	33.3	**66.6**	0
20	–	–	–	–	–
- T94 Plot					
< 5	9	**55.5**	44.5	0	0
5–9	17	41.2	**41.2**	17.6	0
10–19	6	0	33.3	**66.6**	0
20	4	0	25.0	50.0	**25.0**

3.2. Dynamics of the seedling bank

Establishment of new seedlings was highly significantly different between years (repeated-measures ANOVA, $F = 51.7$, $p < 0.0001$) and between plots ($F = 16.0$, $p < 0.0001$), and the plot × year interaction was also significant ($F = 19.6$, $p < 0.0001$) (*figure 3*). The highest recruitment was in the T94 plot, and the lowest in the T93 plot, although there were large between-year variations among plots (*figure 3*). The relationship between seedling establishment and seedling density the year before was analysed for each year and plot separately. This relationship was not significant for any of the years in the NT plot. Nevertheless, the number of new seedlings increased linearly with seedling density in 1996 and 1997 in the T94 plot, and in all years in the T93 plot (excepting 1994, when no new seedlings were established) (R^2 between 0.20 and 0.42, $p < 0.0001$ in all cases). Establishment of new seedlings in the last year
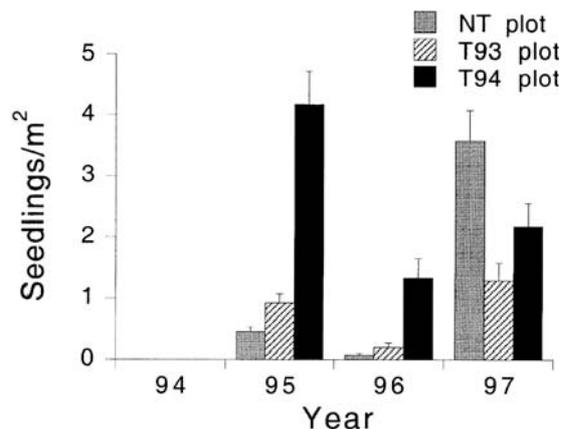
Figure 3. Establishment of new seedlings (mean ± *SE*) in the different plots and sampling years. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

did not depend on GLI in any of the three plots (linear regression, $p > 0.20$ in all cases).

Survival of the different seedling cohorts is represented in *figure 4*. There were differences between pre-1993 seedlings and 1993 cohort seedlings (repeated measures ANOVA, $F = 23.2$, $p < 0.0001$). On average for the three plots, only 15% of pre-1993 seedlings and 26% of the 1993 seedling cohort survived after four years. There were also differences in survival among plots ($F = 12.1$, $p < 0.0001$), but the pattern for pre-1993 seedlings and seedlings from the 1993 cohort differed (interaction cohort × plot: $F = 5.5$, $p = 0.0047$): seedlings from the 1993 cohort showed lower mortality than pre-1993 seedlings in the two thinned plots, but not in the NT plot (*figure 4*). Survival of the 1995 cohort after two years was lower in the T93 plot than in the other two plots (one way ANOVA, $F = 7.1$, $p = 0.0025$), while survival of the 1996 cohort did not differ among plots (one-way ANOVA, $F = 0.2$, $p = 0.79$). There were no significant differences in height between live and dead seedlings in any year or plot (ANOVA, $p > 0.15$ in all years and plots). Overall survival of seedlings in 1997 did not depend on GLI in any of the three plots (linear regression, $p > 0.10$ in all cases).

As a consequence of these survival and recruitment patterns, the composition of the seedling bank in the different plots varied from year to year (*figure 5*). Thus, in the NT plot, seedlings from the 1993 cohort represented more than 70% of all seedlings found from 1993 to 1996, but decreased in 1997, when there was major recruitment. In the two thinned plots the relative importance of
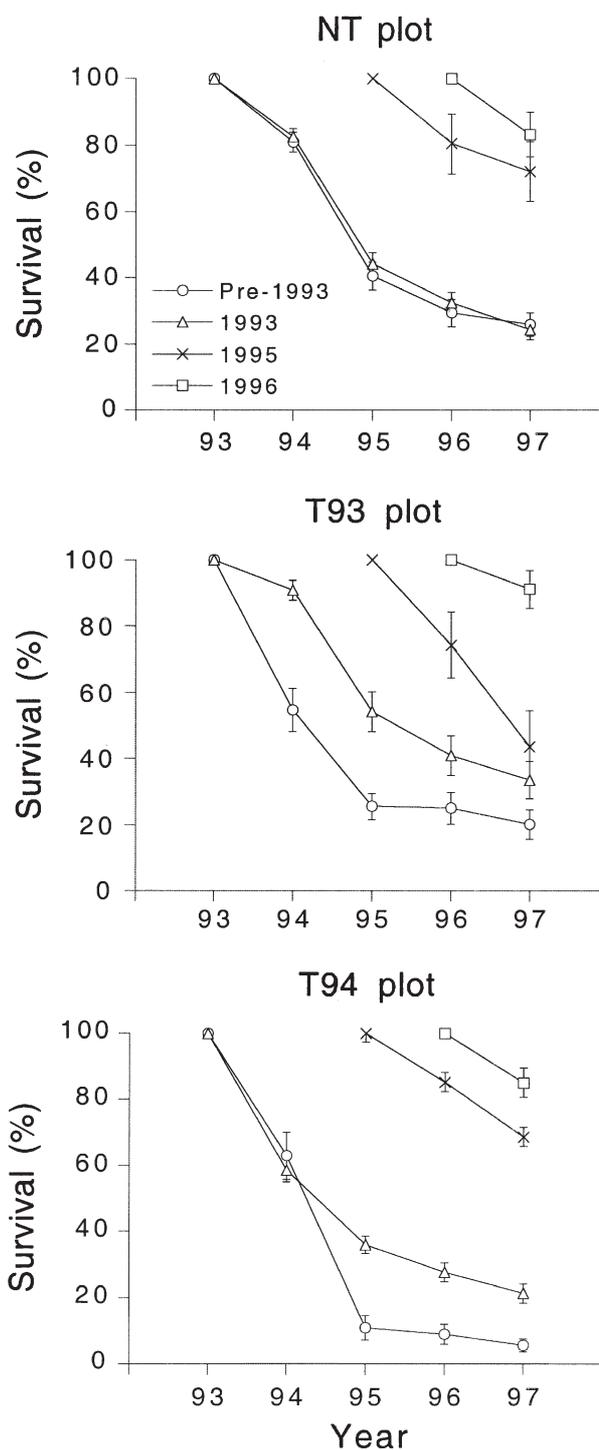

Figure 4. Survival (mean ± *SE*) of the different cohorts of seedlings in the different plots. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.
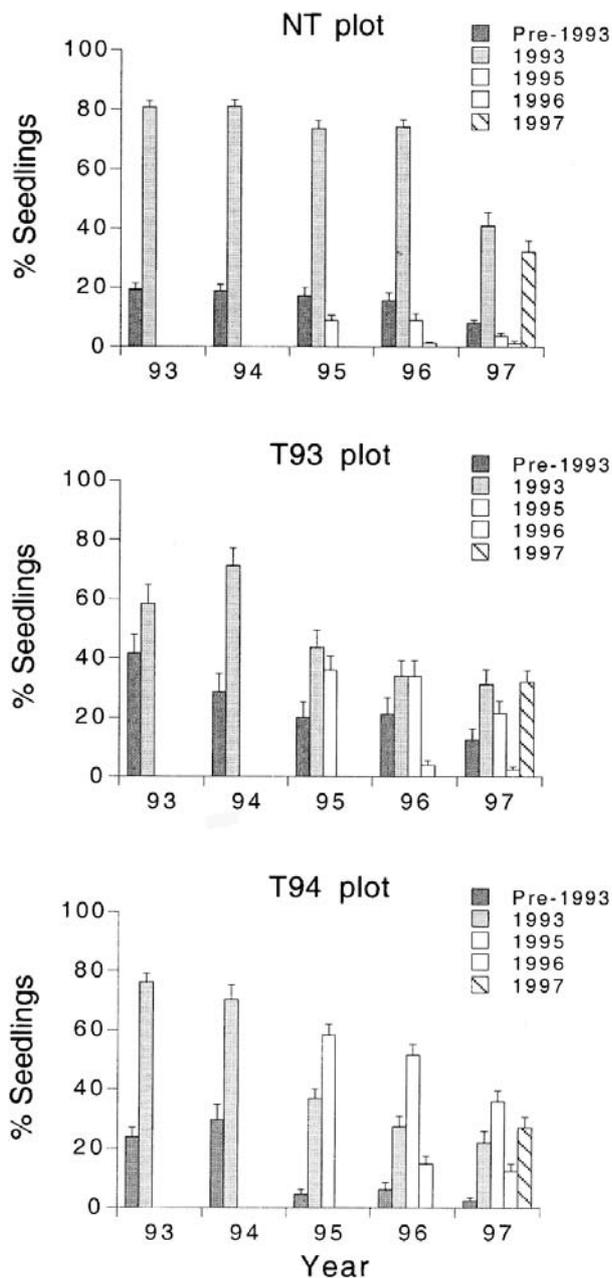
Figure 5. Composition of the seedling bank in the different plots and years of study. Mean (+ *SE*) is given for each value. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

seedlings from the 1993 cohort was lower than in NT, but still represented more than 40% of seedlings until 1996.

Height growth of surviving seedlings was very slow in the three plots. The height of both pre-1993 seedlings and

seedlings from the 1993 cohort increased by less than 1–2 cm during the five sampling years in the three plots. Direct measurements of seedling growth showed significant differences among plots in both 1996 and 1997 ($F = 21.6$ for 1996, $F = 17.4$ for 1997, $p = 0.0001$ in both cases): maximum length growth was highest in the T94 plot (Mean $\pm$ *SE*: 3.5 ± 0.3 cm), lower in the T93 plot (2.4 ± 0.2 cm) and lowest in the NT plot (1.7 ± 0.1 cm). This growth measurement was not related to GLI in any of the three plots (linear regression, $p > 0.55$ in all plots).

3.3. Variations in size and resource allocation of the different seedling cohorts

Significant differences among seedling cohorts were found for all analysed variables (*table II*). Thus, seedling height decreased progressively from the pre-1993 seedlings to the 1997 seedlings. For the remaining variables except R/S, pre-1993 seedlings and those from the 1993 cohort showed similar, and always higher values than the other three cohorts. Among these new cohorts, those from 1995 and 1996 showed similar, higher values than those of 1997 seedlings for all variables considered. A different pattern was found for *R/S*, which was highest in the 1997 cohort (although without showing significant differences with pre-1993 seedlings).

Significant differences among plots were also found for all variables except height (although for this variable there was a significant interaction between cohort and plot): in the NT plot, seedlings had fewer leaves, lower leaf area and lower root, aerial and overall weight than in either of the two thinned plots.

4. DISCUSSION

Seedling populations in holm oak forests show large variability across different spatial scales [12, 24]. The causes of this variability are various, and not always easy to explain. Thus, on a regional scale, no correlation has been found between density of holm oak seedlings and climatic features for a wide range of old holm oak stands distributed throughout Catalonia (NE Spain). On a smaller scale, the distribution of holm oak seedlings follows the topographical gradients more closely than on the regional one, and depends on water availability variations with elevation and aspect [24]. These patterns are important at the landscape scale, but understanding the role of the seedling bank in forest dynamics calls for a

Table II. Analysis of variance of cohort and plot for different morphological variables. *** $p < 0.001$; ** $p < 0.01$; ns: not significant. Mean ($\pm SE$) values of the different cohorts and plots are indicated. Within a column, significantly different means, based on Fisher LSD F-test (at $p = 0.05$), are indicated by different letters. All dependent variables except number of leaves and R/S were log-transformed. NT, plot not thinned; T93, plot thinned in 1993; T94, plot thinned in 1994.

Source	Height (cm)	N Leaves	Leaf area (cm^2)	Root weight (g)	Aerial weight (g)	Total weight (g)	R/S
Cohort	423.0 ***	10.3 ***	8.4 ***	13.3 ***	18.9 ***	17.5 ***	8.7 ***
Plot	2.0 ns	6.9 **	6.3 **	13.2 ***	7.4 ***	11.0 ***	5.4 ***
Cohort × Plot	6.6 ***	1.4 ns	1.4 ns	1.2 ns	1.9 ns	1.3 ns	2.2 ns
Mean ± SE for each cohort and plot	Height (cm)	N Leaves	Leaf area (cm^2)	Root weight (g)	Aerial weight (g)	Total weight (g)	R/S
- Cohorts							
Pre-1993	23.7 ± 0.8 e	8.1 ± 0.9 c	30.3 ± 6.1 c	0.91 ± 0.35 b	0.95 ± 0.20 c	1.86 ± 0.32 c	0.90 ± 0.15 ab
1993	16.0 ± 0.2 d	8.5 ± 0.7 c	29.9 ± 3.0 c	0.56 ± 0.05 b	0.77 ± 0.07 c	1.34 ± 0.15 c	0.78 ± 0.03 a
1995	12.6 ± 0.2 c	6.3 ± 0.6 b	19.5 ± 2.6 b	0.37 ± 0.04 a	0.48 ± 0.05 b	0.85 ± 0.10 b	0.82 ± 0.04 a
1996	11.4 ± 0.3 b	7.3 ± 0.7 b	23.3 ± 4.4 b	0.41 ± 0.05 a	0.53 ± 0.07 b	0.94 ± 0.11 b	0.87 ± 0.05 a
1997	8.6 ± 0.1 a	3.9 ± 0.1 a	13.4 ± 0.9 a	0.29 ± 0.02 a	0.33 ± 0.02 a	0.62 ± 0.07 a	1.08 ± 0.05 b
- Plots							
NT	13.4 ± 0.2 a	4.2 ± 0.2 a	14.0 ± 1.2 a	0.22 ± 0.02 a	0.36 ± 0.03 a	0.62 ± 0.08 a	0.90 ± 0.05 ab
T93	12.7 ± 0.2 a	6.6 ± 0.4 b	23.1 ± 2.6 b	0.32 ± 0.03 b	0.58 ± 0.05 b	1.04 ± 0.11 b	0.95 ± 0.04 b
T94	12.4 ± 0.2 a	8.1 ± 0.6 c	25.6 ± 2.5 b	0.35 ± 0.03 b	0.64 ± 0.05 b	1.14 ± 0.10 b	0.84 ± 0.03 a

deeper spatial and temporal analysis on smaller scales within the forest. In our study area, large spatial and temporal variations in seedling density occurred. Concerning spatial variation, seedling density was very different in the three adjacent plots studied (*figure 1*). In the plot with the lowest seedling density (T93 plot), the pattern of seedling distribution in the forest floor was characterised by small patches of medium seedling density distributed within a low density matrix (distribution of inverse J). In the plots with high seedling density (plots T94 and NT), there was great variability, with patches of different density distributed throughout the whole area. Results shown in *table I* suggest temporal fluctuations in seedling density are related to density, because quadrats with high seedling density showed higher temporal variations than those with low seedling density.

These spatiotemporal patterns can be only understood by analysing seedling inputs and outputs in the seedling bank. The temporal pattern of seedling recruitment shows large between-year variability (*figure 3*). This variability is consistent with the pattern of high and low acorn production found by Siscart et al. [28] for holm oak in a nearby area during these years, and has also been observed in other *Quercus* species [8, 17, 18, 29]. In fact, the lack of seedling recruitment found in this study in 1994 agrees with the very low acorn production found in 1994 by Siscart et al. [28], and could be related to the extreme drought of that year. Overall, seedling recruitment does not seem to be a problem for forest regeneration in the holm oak forests of this area, contrary to what has been suggested for French holm oak coppices, where different authors (Bran et al. [2], Li and Romane [19]) have proposed an inhibitory process during acorn germination, probably due to auto-allopathic factors, to explain the low recruitment rates of holm oak.

Different studies have shown that holm oak shows better recruitment rates under tree cover than in clearings or clear-cuts [2, 12], and experimental observations suggest that acorns have a short life span when exposed to full sunlight because they dry out very quickly [30], and that the percentage of holm oak acorn germination and survival at low light levels (8% *PAR*) is considerably greater than that at full sunlight [3]. Moreover, thinning usually causes high seedling mortality as a consequence of the dragging of tree trunks and, more importantly, to the presence of slash piles, which cover and finally kill large numbers of seedlings [24]. Nevertheless, in this study differences in recruitment among thinned and unthinned plots were very small, and no significant relationship was found between seedling recruitment and survival and GLI in any of the three plots. This lack of re-

sponse of seedling establishment to light increment is probably due to the low range of light conditions found in this study, where thinned plots were managed by selective cutting, which leads to a low percentage of PAR reaching the forest floor even just after thinning [14]. For this reason, differences at the plot level are more likely to be related to spatial patterns of seed germination caused by seed accumulation and favourable moisture conditions than to variations caused by thinning.

Together with seedling recruitment and survival, understanding seedling dynamics also requires knowledge of seedling growth. Our study demonstrated that holm oak seedlings hardly grew in height during five years. For the range of conditions considered, the time of development from young seedlings to old seedlings and, later, to saplings, is very difficult to determine. In the same Montseny massif, Espelta et al. [12] analysed 1- to 12-year-old seedlings, and found very limited growth during the first four years, and slightly faster growth thereafter. Nevertheless, it is quite difficult to extrapolate this information, based on the estimation of seedling age by counting the total number of terminal bud scars on the leading shoot. At least in our study area, it is difficult to determine seedling age from annual growth increments, because most holm oak seedlings hardly grew at all throughout the duration of this study, and exhibited frequent episodes of die-back of shoots.

Nevertheless, the comparison of seedlings from different cohorts shows a small but significant increment with age of all variables related to size (*table II*). These variables also depend on plot, being higher in the two thinned plots than in the unthinned one. Espelta et al. [12] also showed this negative effect of overstory development on holm oak seedling growth. The pattern of resource allocation obtained was less clear: among cohorts, the newest cohort showed the highest *R/S* values; among plots, the T93 plot had the highest *R/S* value, and the T94 plot, the lowest one. In general, all the *R/S* values obtained for the different cohorts and plots were around 1, a similar value to those given by different authors (Espelta et al. [13], Broncano et al. [3]) for holm oak seedlings under shade conditions. In these same studies, *R/S* values under full light conditions almost double those under shade but, in this study, seedlings from thinned plots did not significantly increase their *R/S* values after thinning. This suggests that, under these management conditions, root growth is probably more limited than shoot growth. In these managed holm oak forests of the Montseny massif, tree above-ground biomass is partially harvested at each thinning, and this temporarily allows a greater light availability [23], but holm oak trees develop massive

lignotubers in which below-ground biomass keeps accumulating [5]. In these cases, below-ground biomass can be even larger than above ground biomass [4], and below-ground competition between seedlings and old individuals could be very considerable.

According to the results obtained in this study, populations of holm oak seedlings fulfil two of the three key characteristics that Marks and Gardescu [20] propose for a seedling bank: holm oak seedlings persist through time in the understory, and remain suppressed within a restricted range of sizes while in the shade. Nevertheless, holm oak seedlings from this study did not show any release after thinning, which is another characteristic also proposed by the same authors for a seedling bank. In holm oak forests, and whatever the cutting management applied, vigorous resprouting ensures rapid canopy development [11, 23]. Under this intense resprout competition, holm oak seedlings must be of a sufficient size to overcome the changes which take place in the forest after thinning, and they usually are not large enough [12]. Under different management conditions, in old-growth forests where old individuals die and population renovation could be really important, holm oak seedlings neither respond to canopy gaps, and the only holm oak individuals growing in canopy gaps are trees already present before gap opening [22]. According to these authors, the natural gap dynamics of holm oak forests pass through a maquis phase before the new holm oak individuals are established. The eventual role of the seedling bank in holm oak forest regeneration would only be determined by means of long-term forest monitoring and experimental studies, which would enable us to evaluate whether some seedlings can grow to saplings, and some saplings can reach the canopy. Under the present conditions of high density of seedlings and low growth rates in both light and shade, the role of a few individuals might be decisive. Even if a very low percentage of individuals were able to grow and reach the forest canopy, this could be enough to insure forest regeneration. But until supplementary information is available, the seedling bank in holm oak forests only represents a reserve of "oskars" (sensu Silvertown and Doust [27]) or small individuals which do not grow and which do not have any evident role in forest dynamics.

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