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Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites

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Abstract

The extension of mixed evergreen (*Quercus ilex*) and winter deciduous (*Quercus cerrioides*) oak coppices is increasing in NE Spain as a consequence of large wildfires. The best alternative to manage these high-density and low production forests is their conversion into stored coppices (i.e. coppices with few stems per stool). However, in this process, functional differences arising from the contrasted leaf-habit of the two co-occurring oaks should be taken into account. In this study, we explore the resprouting patterns and the response to different intensities of stool cleaning and pruning of these co-occurring Mediterranean oak species in mixed extensive coppices which have appeared after large wildfires. According to our results, both species resprouted vigorously after fire in the different environmental conditions studied, with an important influence of the size of the stool. For a similar stool size, *Q. cerrioides* exhibited higher number of resprouts, height, basal diameter and crown cover, with specific differences increasing in high-quality sites. Cleaning of stools increased height and basal diameter growth, with low differences between the two cleaning intensities (i.e. one or three resprouts reserved per stool). Pruning did not modify height or diameter but enhanced crown expansion. As a consequence of cleaning, a new wave of basal resprouts appeared. The mean number of these new resprouts was higher in *Q. ilex* than in *Q. cerrioides*, while the height they reached increased with cleaning intensity. The reported benefits of cleaning on growth diminished earlier in *Q. ilex* in comparison with *Q. cerrioides*, probably due to the larger production of this new wave of basal resprouts in the former species. These results suggest that, despite the differences among evergreen and deciduous species, both oaks may operate successfully in a wide range of environmental conditions. In the two species, moderate cleaning (three reserved stems per stool) appears to be a more suitable practice than intense cleaning (one stem per stool), because these similar growth rates but moderate cleaning favours a lower development of new resprouts.

Keywords: Post-fire regeneration; Coppice management; Oak; *Q. ilex*; *Q. cerrioides*

1. Introduction

Resprouting is considered an efficient life-history trait by which woody plants can recover lost biomass after disturbance (Bellingham, 2000). This trait is

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widely observed in many taxa around the world, but it has been in Mediterranean-climate regions where it has received more attention, as one of the main regeneration mechanisms of plant communities subjected to fire (Keeley and Zedler, 1978; Malanson and O'Leary, 1982). Rapid recovery of vegetation through resprouting after fire plays a critical and positive role in preventing soil erosion (Calvo and Cerdà, 1994), preventing nutrient losses (Trabaud, 1994) and re-establishing suitable environmental conditions for the recovery of animal communities (Prodon et al., 1984). However, the fact that the actual fire regime in the Mediterranean Basin is characterised by more intense and large wildfires (Terradas, 1996; Moreno et al., 1998) questions the way to manage extensive new forest landscapes which have arisen through resprouting. Large wildfires destroy forest vegetation independent of its composition, age and density (Bessie and Johnson, 1995). This means that burned landscapes are more homogeneous than they were before. Thus, extensive burned Mediterranean forests regenerated through resprouting result in large coppices with a high homogeneity in their structure (Romane et al., 1988). These coppices are characterised by high-density stands of multi-stemmed stools with relatively small resprouts, slow vertical growth and low production rates (Cañellas et al., 1996; Terradas, 1999).

The spread of mixed evergreen and deciduous oak coppices has recently increased in NE Spain in areas affected by the large wildfires which occurred in 1994 and 1998 (ca. 40,420 forested hectare in Central Catalonia). This process has been favoured by the regeneration failure of the dominant pine species present in the area before the fire event (i.e. *Pinus nigra* Arnold), coupled with the resprouting of the *Quercus* species previously present in the forest understory (Retana et al., 2002). Transformation to mixed oak coppices has accounted for 40% (16,023 ha) of the surface burned in those wildfires. The two dominant *Quercus* species present in these burned areas are *Q. ilex* L. and *Q. cerrioides* Willk. et Costa, two co-occurring Mediterranean oaks in the West Mediterranean Basin. Both species share in common some life-history traits, such as resprouting ability, but they differ markedly in their leaf habit: *Q. cerrioides* is a winter deciduous oak, whereas *Q. ilex* is an evergreen species with smaller and thicker leaves. The evergreen habit has been considered an adaptation to poor environments, both in nutrient and water availability, due to its low resource-losses ratios (Aerts and van der Peijl, 1993; Berendse, 1994). Deciduousness, on the other hand, implies a higher cost of leaf production, and a shorter photosynthetically active period that should be compensated by a higher rate of light saturated assimilation (Eamus, 1999), requiring higher levels of nutrient and water availability. Thus, differences in leaf life-span of the two oaks may result in differences in the requirements of light, water, nutrients, and in the plant carbon allocation patterns (Cortés, 2001), which are important traits determining the success of the resprouting process (Mesléard and Lepart, 1989; Canadell and López Soria, 1998; Espelta et al., 1999). On the other hand, specific differences may also depend on the quality of the site: resprouting has been observed to increase in deep vs. shallow soils, and northern vs. southern slopes (López Soria and Castell, 1992), in favourable topographic positions, such as the bottom of the slope in contrast with the hilly top (Gracia, 2000) or with the increase in the total amount of precipitation (Riba, 1998).

The complexity of the resprouting process, influenced by both species characteristics and site quality (i.e. a compound of soil and climatic conditions), should be taken into account when planning management strategies to improve extensive mixed coppices. Several practices have been envisaged to accelerate the development of Mediterranean oak coppices towards more mature structures (Amorini et al., 1996; Carvalho and Loureiro, 1996). The best alternative appears to be their gradual conversion into either stored coppices (i.e. coppices in which there remains only one or two stems per stool) or, when possible, high forests (Serrada et al., 1996). This process involves the elimination and selection of resprouts (i.e. cleaning of the stools) in order to reduce competition among the reserved resprouts in the stool to raise the forest canopy (Ducrey and Toth, 1992). This practice has been argued to increase the potential of forest for wood production, livestock grazing and other alternative uses, while preserving their protective function and encouraging their sexual regeneration (Cañellas et al., 1996). Although the response of some Mediterranean oaks to cleaning has been thoroughly documented (Ducrey and Toth, 1992; Cutini and Benvenuti, 1996; Cutini and Mascia, 1996), there is a lack of information about possible differences in the resprouting patterns after fire and the response to cleaning of closely related coexisting species.

In this study, we explore the resprouting patterns and the response to different intensities of stool cleaning of two common co-occurring Mediterranean oak species in mixed extensive coppices after large wildfires. We have two main objectives. The first objective is to analyse the resprouting patterns of these two oak species in stands of different site quality. Because of the reported differences between evergreen and deciduous species (see above), we might expect a marked interaction between species and site quality in the resprouting process. The second objective is to evaluate in these species the effects of different treatments of stool cleaning on: (i) the growth of reserved shoots, and (ii) the appearance of new resprouts. Numerous studies have emphasised a positive relationship between intensity of stool cleaning and growth of reserved shoots (Ducrey and Turrel, 1992; Riba, 1998), but the high number and size of new resprouts appearing after cleaning could further decrease the performance of the selected shoots. Our expectation is that there is a trade-off between these two processes, because the increase in cleaning intensity might also increase resource availability and, consequently, the growth of the wave of new resprouts and vice versa.

2. Material and methods

2.1. Study area

This study was carried out in the regions of Bages and Berguedà (41°45′–42°6′N; 1°38′–2°1′E, Catalonia, NE Spain) in an area affected by a wildfire which occurred in July 1994 and which burned ca. 24,300 ha forested area. The burned forests were located at altitudes ranging from 350 to 950 m above sea level. Climatic conditions vary from dry-subhumid to subhumid Mediterranean (according to the Thornwaite index), with mean annual temperature of 10–13 °C and mean annual precipitation of 550–700 mm. According to the data provided by the Ecological Forest Inventory of Catalonia (IEFC) (Gracia et al., 2000), and the Spanish Second National Forest Inventory (IFN2) (ICONA, 1993), both carried out before the fire event (in 1993), most forested areas were occupied by black pine (*P. nigra*) forests (71% of the total surface), with *Q. ilex* and *Q. cerrioides*, extensively present in the understory. After the fire event, and due to the failure of *P. nigra* regeneration (see Habrouk et al., 1999; Retana et al., 2002), the resprouting of both *Quercus* species transformed most forested areas into mixed *Quercus* ssp. forests, with the typical structure of a coppice with numerous multi-stemmed stools (Retana et al., 2002).

2.2. Experimental design and sampling

The experiment was conducted from 1999 to 2001 in four mixed coppices of *Q. cerrioides* and *Q. ilex* located in the 1994 burned area, previously dominated by *P. nigra* forests. Two of those coppices were located in low-quality sites (hereafter, LOW) and two on higher quality sites (hereafter, HIGH). Choosing these two categories we did not try to establish an absolute site quality rank but to compare potential interactions in *Q. ilex* and *Q. cerrioides* resprouting in two contrasting situations. Site quality was defined as a compound of topography, climatic characteristics and forest structure and production before the fire event. Climatic information of each coppice was estimated through spatial interpolation of the nearest meteorological stations (Ninyerola et al., 2000). Topography and previous forest features of each coppice were assessed through inspection of the five nearest inventoried plots of the IEFC or the IFN2 inventories surrounding each coppice. Differences between coppices located in the two quality types were tested through a nested ANOVA. As shown in Table 1, low-quality coppices were located in higher and steep areas, with lower annual precipitation than high-quality ones. Before the fire event, low-quality sites had a significantly lower tree density, basal area and wood production than high-quality areas (Table 1). The distance between the two quality sites was 22 km.

Each sampling area was subdivided into five adjacent plots (ca. 30 m × 30 m), where the following experimental treatments of resprout selection and pruning were applied to all stools present in the plots: (i) selection of the tallest resprout (S1), (ii) selection of the tallest resprout and pruning of 40% of its height (S1P), (iii) selection of the three tallest resprouts (S3), (iv) selection of the three tallest resprouts and pruning of 40% of their height (S3P), and (v) control (C), with neither selection nor pruning. The treatments were

Table 1
Main topographical, climatic and structural characteristics of the low-quality and high-quality sites, according to the five nearest inventoried plots in the Ecological Forest Inventory of Catalonia (IEFC) (Gracia et al., 2000), and the Spanish Second National Forest Inventory (IFN2) (ICONA, 1993) surrounding each of the two coppices studied per site quality type

Site quality	Altitude (m)	Slope (°)	Precipitation ($l\ m^{-2}\ yr^{-1}$)	Density (trees ha^{-1})	Basal area ($m^2\ ha^{-1}$)	Wood production ($m^3\ ha^{-1}\ yr^{-1}$)
Low	632 ± 21	20.4 ± 2.9	724 ± 8.8	996 ± 185	14.1 ± 1.8	1.54 ± 0.26
High	568 ± 23	14.2 ± 2.3	743 ± 8.7	1591 ± 350	21.9 ± 1.9	2.77 ± 0.50

chosen to simulate a wide range of management practices, from a more conservative (S3 and S3P) to a more intense (S1 and S1P) strategy. Cutting and removal of non-selected resprouts and pruning were done by hand.

On each plot 20 *Q. cerrioides* and 20 *Q. ilex* stools were randomly chosen for the purpose of this study. Before applying their experimental treatments, the following variables were measured on these individuals to characterise the resprouting pattern: stool surface (as an estimator of the size of the individual before the fire event), total number of resprouts with basal diameter greater than 1 cm, basal diameter and height of the tallest resprout and crown cover of the stool (measuring two perpendicular diameters of the crown and computing the projection as an ellipse). Total biomass of each individual was estimated applying allometric equations that related resprout basal diameter and biomass for all the resprouts present in the stool. Allometric equations were constructed measuring the basal diameter and the dry weight (105 °C, 72 h) of a sub-sample (15 resprouts) of the removed resprouts during the cleaning process of *Q. ilex* ($y = 294.3x - 305.7$, $n = 15$, $p < 0.0001$, $r^2 = 0.89$) and *Q. cerrioides* ($y = 266.9x - 351.4$, $n = 15$, $p < 0.0001$, $r^2 = 0.84$).

Once the experimental treatments were performed (in winter 1999, year 0), reserved resprouts of S1, S1P, S3 and S3P stools, and the three tallest resprouts per stool of control (C) individuals were tagged and their basal diameter, total height and crown cover (except for control individuals) were measured. These variables were measured again at the end of the first (winter 2000) and second year (winter 2001) after the onset of the experiment. The response to the experimental treatments was analysed through changes in these variables. Growth was calculated both in absolute and relative terms. Relative growth rate (RGR) was calculated as $\mathrm{RGR} = (\ln X_i / \ln X_{i-1})$, where X_i was the value of the selected variable in year i, and X_{i-1} was its value in the previous year.

To evaluate the overall success of the treatments applied, the response to the experimental treatments was not only assessed in terms of the structural changes observed in the reserved resprouts, but also in the appearance of new resprouts after the onset of the experiment. In each stool, we recorded the number and mean height (five measures per stool) of the new resprouts at the stool basis, 1 and 2 years after the experimental treatment (winter 2000 and winter 2001, respectively).

2.3. Data analysis

At the onset of the experiment, a three-way ANCOVA was performed to analyse the effects of species (*Q. ilex*, *Q. cerrioides*), site quality (LOW, HIGH), plot (nested within site quality) and the assigned experimental treatment (S1, S1P, S3, S3P, C) on the number of resprouts, biomass, crown cover, and height and basal diameter of the dominant resprout of the stools. Stool surface was included as a covariate to check the influence of the previous size of individuals in these resprouting features (see Retana et al., 1992; Espelta et al., 1999). A preliminary three-way ANOVA on the stool surface variation due to species, site quality and assigned treatment pointed out the existence of an interaction between species and site quality ($F = 9.5$, $p = 0.0001$): *Q. ilex* stools were larger than *Q. cerrioides*, but size decreased in *Q. ilex* from low to high-quality sites (respectively, 3.71 ± 0.22 to $3.10 \pm 0.22\ m^2$) while it increased in *Q. cerrioides* (respectively, 0.81 ± 0.07 to $1.50 \pm 0.11\ m^2$).

Changes (growth) in the measured variables during the experiment, as well as the number and mean height of new basal resprouts, was analysed by a repeated-measures ANCOVA model, including the factors:

species, site quality, plot (nested within site quality), treatment, year (1999, 2000), and stool surface as a covariate. As the number of resprouts selected and measured was different in the five treatments applied (namely one in S1 and S1P and three in S3, S3P and C), two different types of analysis were run for height, basal diameter, and canopy cover: we compared the values obtained in S1 and S1P with: (1) the mean value of the three resprouts in S3, S3P and C, and (2) the value of the dominant (tallest) resprout in S3, S3P and C. As both analyses provided very similar results, we will only show those concerning the second one, in order to simplify Section 3. In fact, the tallest resprout of *Quercus* species has been reported to maintain its dominance with time and to be a good estimator of the vigour of the stool (Gracia, 2000).

In all cases, inspection of residuals was carried out to check for normality and homoscedasticity. When necessary, analyses were run on transformed data. For all statistical tests, the sequential Bonferroni method was employed to control the group-wide type I error rate (Rice, 1989). The individual values of the different levels of each variable were compared with a post-hoc test (Fisher's protected least significant difference).

3. Results

Five years after the fire event and before the onset of the experiment, *Q. cerrioides* and *Q. ilex* stools showed significant differences for all structural characteristics related with their resprouting pattern, with a strong influence of site quality (see interaction species × site quality in Table 2). *Q. cerrioides* individuals had a higher number of resprouts, crown cover and total biomass than *Q. ilex* in high-quality sites (HQ), while the opposite trend occurred in the low-quality (LQ) zones (Fig. 1A, B and E). On the other hand, basal diameter and height of the dominant resprout was higher in *Q. cerrioides* in both types of sites, although differences between species were much more contrasted in HQ than in LQ sites (Fig. 1C and D). The covariate stool size significantly influenced all the resprouting characteristics (Table 2), which increased with the size of the stool. However, the interaction species × stool size revealed a more pronounced increase in *Q. cerrioides* than in *Q. ilex*. At this stage, no significant differences were found in the resprouting patterns among groups of stools assigned to the various cleaning treatments (Table 2).

The effects of the experimental treatments on stool growth during the two consecutive years are summarised in Table 3. Resprout selection and pruning (treatment effect in Table 3) enhanced both absolute and relative growth rate in height and diameter of the dominant resprout: the highest growth was observed in stools with a single resprout and the lowest growth was found in control individuals (Fig. 2). Concerning the effects of pruning, both pruned and unpruned individuals showed a fairly similar response in terms of height and diameter growth (except that S1P had a

Table 2
F values from ANCOVA tests of effects of species (Sp), site quality (Q), plot (nested within site quality), experimental treatment (T) and stool surface (Ss) as a covariate on different structural variables related to the sprouting patterns of *Q. cerrioides* and *Q. ilex* stools 5 years after the fire event. Significant coefficients (at $p = 0.05$ after employing the sequential Bonferroni method) are indicated in bold. Non-significant interactions between the covariate and the other factors are not included

Source	Total height	Resprout basal diameter	Canopy cover	Biomass	Number of resprouts
Species (Sp)	**49.9**	**84.1**	**33.6**	0.4	0.8
Site quality (Q)	7.7	1.4	5.8	0.1	0.4
Treatment (T)	0.2	1.8	1.2	0.4	1.7
Plot (Q)	**8.7**	2.3	0.3	3.2	4.1
Sp × Q	**14.3**	**16.4**	**10.7**	**10.9**	**9.6**
Sp × T	1.2	0.8	1.4	1.4	1.3
Q × T	2.6	1.4	1.2	1.4	0.4
Sp × Q × T	2.0	2.6	1.0	0.7	0.5
Stump surface (Ss)	**18.8**	**16.0**	**68.9**	**34.2**	**94.2**
Sp × Ss	**9.8**	**10.8**	**20.6**	3.8	**17.9**

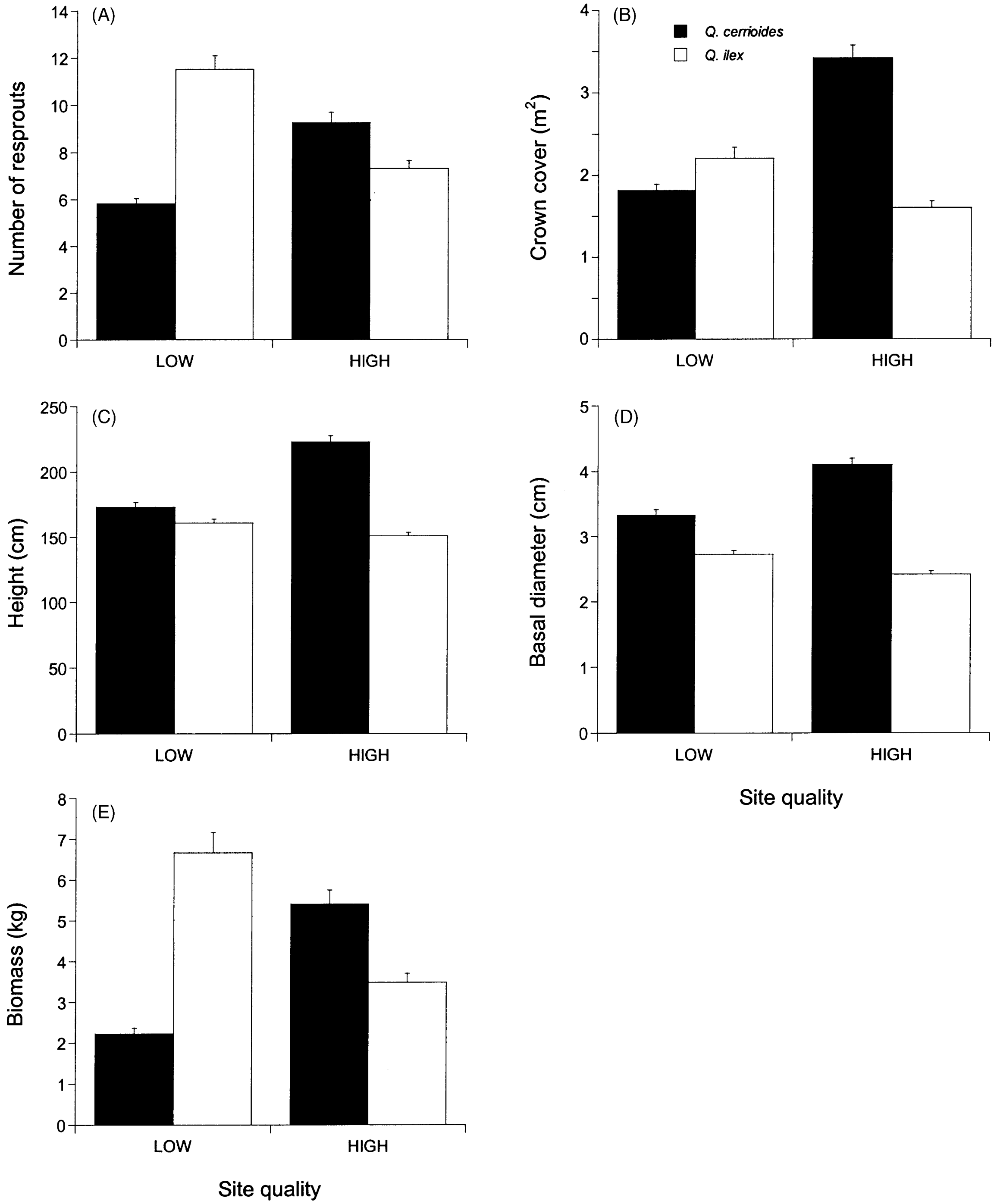

Fig. 1. Mean (+S.E.) of (A) total number of resprouts, (B) crown cover (m^2), (C) height of the dominant resprout (cm), (D) basal diameter of the dominant resprout (cm), and (E) total aerial biomass per stool (kg) of resprouting *Q. cerrioides* (solid bars) and *Q. ilex* (open bars) stools in high-quality (HQ) and low-quality (LQ) sites.

Table 3
F values from repeated-measures ANCOVA tests of effects of species (Sp), site quality (Q), plot (nested within site quality), experimental treatment (T), stump surface (Ss) as a covariate and time (Y) on the absolute and relative growth and production of new basal resprouts of *Q. cerrioides* and *Q. ilex* stools 2 years after the experiment onset. Significant coefficients (at $p = 0.05$ after employing the sequential Bonferroni method) are indicated in bold. Non-significant interactions between the covariate and the other factors are not included

Source	Height growth		Diameter growth		Canopy growth		Number of new resprouts	Height of new resprouts
	Absolute	Relative	Absolute	Relative	Absolute	Relative		
Species (Sp)	4.4	1.2	**14.6**	1.1	1.7	5.3	**41.9**	0.7
Site quality (Q)	2.8	7.0	**34.4**	**29.4**	9.6	**37.5**	1.6	7.0
Treatment (T)	**4.5**	**7.1**	**9.4**	**8.7**	**10.6**	**23.7**	1.2	**26.9**
Plot (Q)	**30.1**	**35.7**	**18.7**	**13.2**	**12.1**	**7.3**	5.3	7.1
Sp × Q	3.7	0.1	0.3	9.1	2.6	0.1	7.7	3.5
Sp × T	1.1	0.6	1.7	1.4	2.4	2.3	0.7	1.6
Q × T	1.6	1.9	0.2	0.2	1.2	2.4	0.3	1.8
Sp × Q × T	0.6	0.6	0.7	1.1	1.7	3.0	1.6	2.6
Stump surface (Ss)	7.8	2.2	0.7	1.4	**11.0**	1.6	**26.9**	**23.1**
Sp × Ss	6.4	2.5	0.1	2.0	7.9	1.5	0.1	**14.5**
Year (Y)	0.3	5.5	3.5	6.1	**115.2**	**434.3**	0.1	**75.9**
Sp × Y	**10.3**	**14.5**	**12.8**	**16.8**	1.7	7.2	0.1	1.2
Q × Y	**19.3**	**18.6**	**23.9**	**13.1**	7.7	0.5	2.0	0.2
T × Y	**6.6**	**4.9**	2.6	3.6	4.6	3.8	1.7	5.1
Y × Plot (Q)	5.5	6.1	3.4	5.6	0.8	1.0	0.6	**8.8**
Sp × Q × Y	7.3	6.9	1.5	0.3	**16.0**	7.9	1.7	0.4
Sp × T × Y	0.8	1.2	2.7	2.8	2.7	3.3	1.0	2.1
Q × T × Y	1.3	1.3	1.6	1.4	0.5	0.4	0.3	4.1
Sp × Q × T × Y	1.4	1.2	0.4	0.7	0.3	1.1	0.7	0.8

higher absolute height growth than S1). However, pruning clearly influenced the expansion of the canopy: pruned individuals showed higher canopy growth than unpruned individuals (Fig. 2E and F). The reported effects of the experimental treatments on height growth varied during the two consecutive years (treatment × year in Table 3): absolute and relative height growth of S1 and S1P individuals was higher in 1999, while that of S3, S3P and control was higher in 2000 (Fig. 3).

Concerning the response of the two species, *Q. cerriodes* exhibited higher growth rates than *Q. ilex* in height (24.0 ± 0.9 and 18.4 ± 0.6 cm, respectively), diameter (0.75 ± 0.02 and 0.61 ± 0.02 mm, respectively) and canopy cover (1.9 ± 0.2 and 1.1 ± 0.1 m^2, respectively). However, there were variations in the response of both species between the two years monitored (interaction species × year in Table 3). *Q. cerrioides* attained a similar absolute growth in height and diameter during the two consecutive years, while growth of *Q. ilex* decreased during the second year (Fig. 4A and C). In relative terms, height and diameter growth of *Q. cerrioides* increased with time while the opposite pattern was observed for *Q. ilex* (Fig. 4B and D). Height and diameter growth was also influenced by the quality of the site, showing different patterns depending on the year (interaction quality × year in Table 3): height and diameter growth (except in relative terms) increased from the first to the second year in low-quality sites, while growth in high-quality sites diminished with time (Fig. 5). Neither height, diameter nor canopy growth of the reserved sprouts were significantly influenced by the size of the stool (see the lack of covariate effects in Table 3).

After the experimental treatments, the appearance of a new wave of basal resprouts and the height they reached were significantly influenced by several factors (Table 3). The mean number of new resprouts was much higher in *Q. ilex* than in *Q. cerrioides* (35.0 ± 1.1 vs. 14.1 ± 0.4 new sprouts). In the two species, the intensity of stool cleaning increased the height of the new resprouts appeared (treatment effect in Table 3): sprouts were taller in S1 and S1P individuals (68.6 ± 2.3 and 71.5 ± 2.5 cm, respectively) than in S3 and S3P (48.9 ± 2.0 and 49.6 ± 2.1 cm,

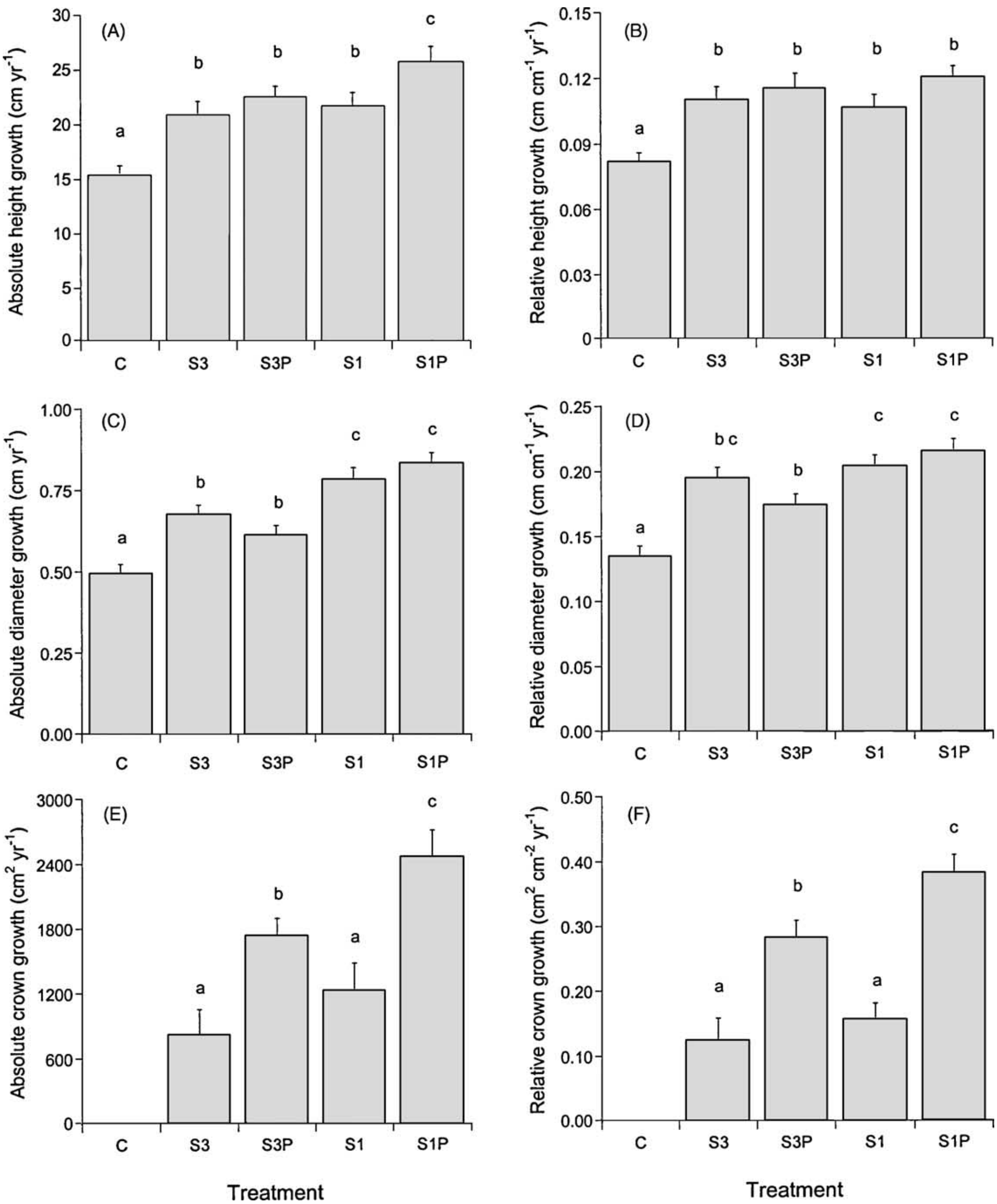

Fig. 2. Mean (+S.E.) of growth in height, basal diameter and crown cover of the dominant resprout in *Q. cerrioides* and *Q. ilex* stools subjected to different cleaning intensities: (A) absolute growth in height (cm yr^{-1}), (B) relative growth in height (cm cm^{-1} yr^{-1}), (C) absolute growth in diameter (cm yr^{-1}), (D) relative growth in diameter (cm cm^{-1} yr^{-1}), (E) absolute growth in crown cover (cm^2 yr^{-1}), and (F) relative growth in crown cover (cm^2 cm^{-2} yr^{-1}). Clearing intensities: control (C), selection of the three tallest resprouts (S3), selection of the three tallest resprouts and pruning of 40% of their height (S3P), selection of the single tallest resprout (S1) and selection of the single tallest resprout and pruning of 40% of its height (S1P). The control treatment has not been included in the crown cover analyses, because this variable was not measured in these individuals. Different letters indicate significant differences among treatments according to the Fisher PSLD post-hoc test.

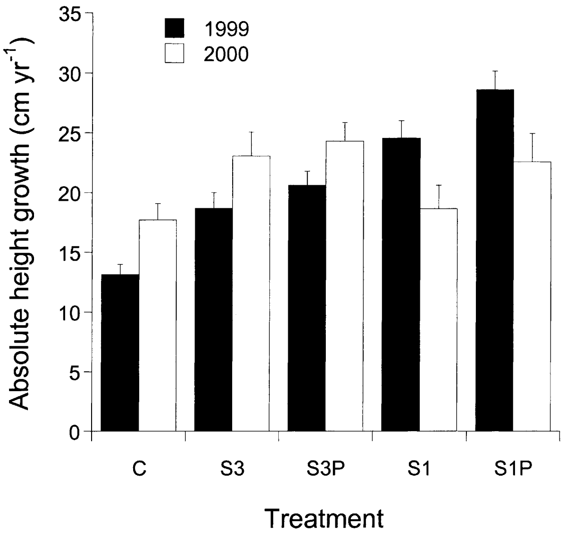

Fig. 3. Mean (+S.E.) of absolute growth in height (cm yr^{-1}) of the dominant resprout of *Q. cerrioides* and *Q. ilex* stools subjected to different cleaning intensities: control (C), selection of the three tallest resprouts (S3), selection of the three tallest resprouts and pruning of 40% of their height (S3P), selection of the single tallest resprout (S1) and selection of the single tallest resprout and pruning of 40% of its height (S1P) during 1999 (solid bars) and 2000 (open bars).

respectively). In *Q. ilex* and *Q. cerrioides* the number of new resprouts increased with stool size, and the interaction species × stool size revealed that, for a similar stool size, new resprouts of *Q. cerrioides* attained larger size than those of *Q. ilex*.

4. Discussion

Q. ilex and *Q. cerrioides* resprouted vigorously after fire, but showed significant differences in their architecture, with a strong influence of stool surface (an estimator of the previous size of individuals; see Table 2) and quality of the site (Fig. 1). In the two species, the number of resprouts, height, basal diameter and total biomass increased with stool size, in a similar way to results previously reported for other resprouter species (see Cañellas et al., 1996; Harrington, 1984). This positive effect of stool size has been argued to rely on a larger size of the bud bank (Riba, 1998; Vilà and Terradas, 1995) and on below-ground reserves present in individuals with larger stools (Canadell and López Soria, 1998; Canadell et al., 1999). However, in this study the interaction between species and stool size (Table 2) indicated that, for a similar size, *Q. cerrioides* showed a higher number of resprouts, and greater height, basal diameter and crown cover than *Q. ilex*. Inter-specific difference in the number of resprouts depends on differences in the bud-bank size (Sennerby-Forsse and Zsuffa, 1995), but could also be caused by different rates of self-thinning at the stool level, once competition among resprouts has started (Mesléard and Lepart, 1989). Moreover, the higher resprouting vigour of *Q. cerrioides* in terms of height, diameter and crown cover could be attributed to a different amount of below-ground resources in the two species (see Sakai et al., 1997) or to particular physiological and morphological traits of the resprouts. We lack information concerning the amount of below-ground resources of *Q. cerrioides* and *Q. ilex* stools, but previous studies have suggested that growth differences between deciduous and evergreen Mediterranean oaks could be based on architectural (e.g. LAI) rather than ecophysiological (e.g. net CO_2 assimilation rates or leaf construction costs) differences (Damesin et al., 1998; Joffre and Rambal, 1999). In that sense, measurements of the morphological characteristics of *Q. ilex* and *Q. cerriodes* resprouts in the coppices considered in this study have found a larger leaf area and specific leaf area per resprout in *Q. cerrioides* than in *Q. ilex* (Bascompta, 2001), features that could be responsible for the higher growth rates exhibited by the former species.

Although stools of *Q. ilex* were much larger than those of *Q. cerrioides* (approx. fivefold in LQ and twofold in HQ sites), the latter species attained similar height and diameter to *Q. ilex* in the low-quality areas and much higher values of height and basal diameter, crown cover and biomass in high-quality stands. These results suggest that, despite the predicted higher demands in resource availability of winter deciduous Mediterranean oaks (Cortés, 2001), *Q. cerrioides* may resprout successfully in a similar way to *Q. ilex* in the less favoured conditions encountered (namely, steep and lower precipitation sites) and clearly overtake the latter species in the higher quality sites. Since initial rapid growth has been considered to be a key factor in determining competitive advantages after disturbance (Oliver and Larson, 1990), these results suggest a clear advantage of *Q. cerrioides* over the evergreen *Q. ilex*.

In the two species, stool cleaning increased the absolute and relative growth in height, diameter and

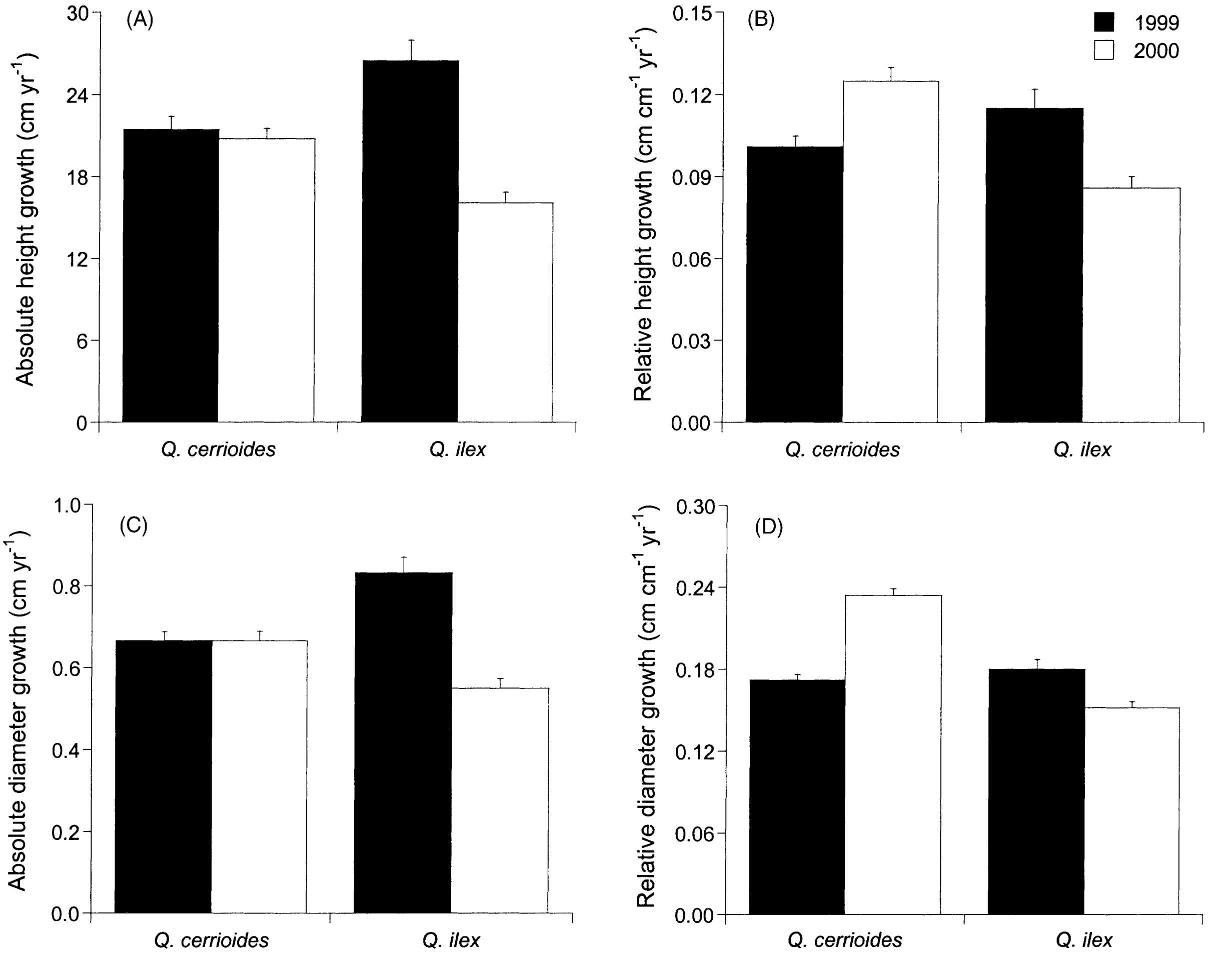

Fig. 4. Mean (+S.E.) of growth in height and basal diameter of the dominant resprout in *Q. cerrioides* and *Q. ilex* stools growing in low-quality (LQ) and high-quality (HQ) sites during the two consecutive years monitored: 1999 (solid bars) and 2000 (open bars). (A) Absolute growth in height (cm yr^{-1}), (B) relative growth in height (cm cm^{-1} yr^{-1}), (C) absolute growth in diameter (cm yr^{-1}) and (D) relative growth in diameter (cm cm^{-1} yr^{-1}).

canopy cover of the reserved resprouts. Elimination of resprouts has been demonstrated to drastically change the competitive relationships among the reserved resprouts in the stool (Ducrey and Boisserie, 1992). Growth enhancement of reserved resprouts has been stated to be positively correlated with cleaning intensity, with better results being obtained when cleaning affects more than 75% of shoots for young coppices (Ducrey and Turrel, 1992), or more than 50% of the basal area in more mature stands (Mayor and Rodà, 1993). These observations agree with our findings, as stools with a single resprout reserved (S1) showed higher basal diameter, height and canopy growth than individuals with three resprouts selected (S3), which in turn grew better than control stools. Nevertheless, differences among S3 and S1 treatments, although strictly significant, were moderate (or even nil in relative terms) compared to control individuals (Fig. 3). These results indicate that despite the number of resprouts reserved, competition among resprouts (either for underground resources—Riba, 1998—or for light availability—Castell and Terradas, 1994) was sufficiently diminished through stool cleaning to allow the two cleaning treatments to maintain similar growth rates. Coupled with the effects of stool cleaning, pruning had a major impact on increasing crown

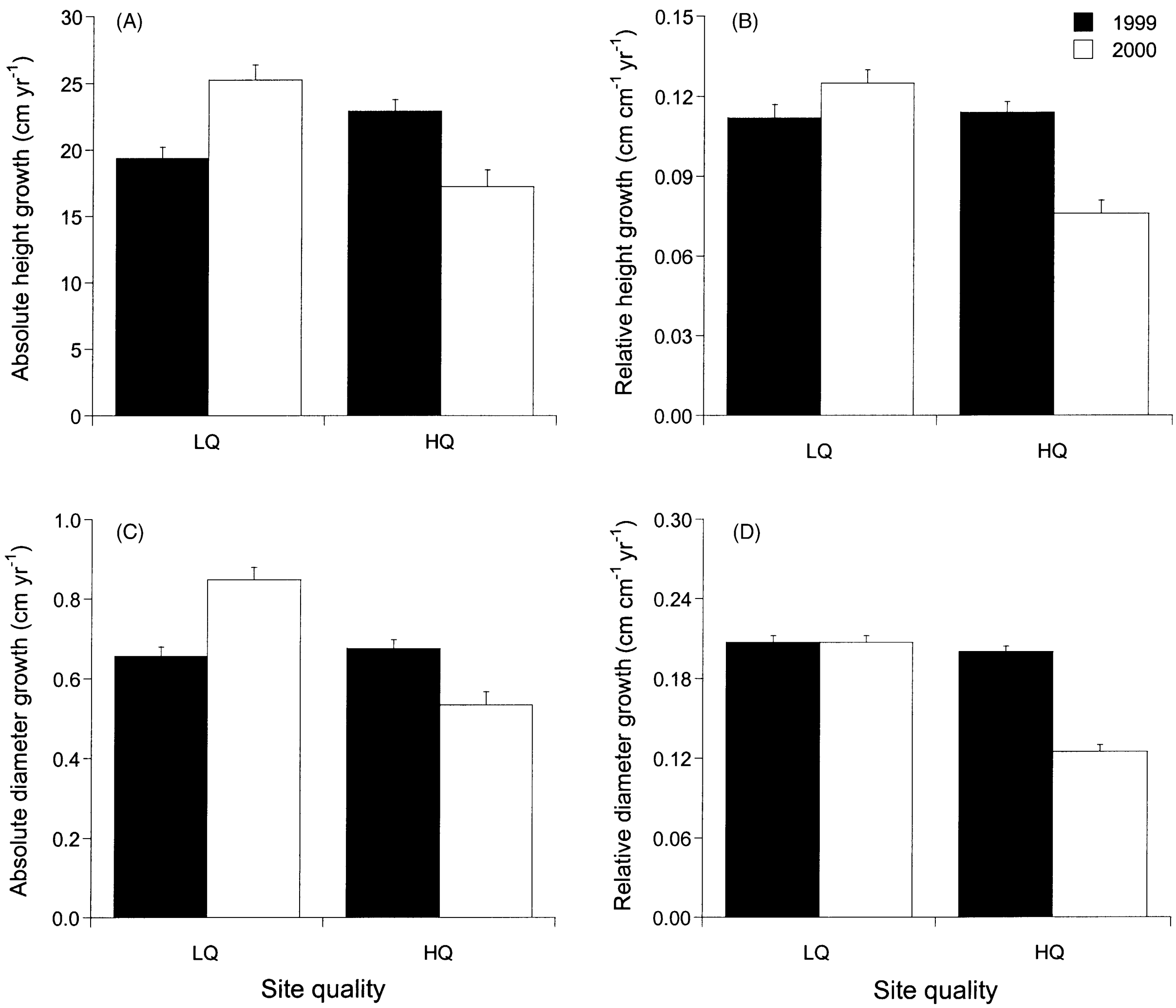

Fig. 5. Mean (+S.E.) of growth in height and basal diameter of the dominant resprout in *Q. cerrioides* and *Q. ilex* stools during the two consecutive years monitored: 1999 (solid bars) and 2000 (open bars). (A) Absolute growth in height (cm yr^{-1}), (B) relative growth in height (cm cm^{-1} yr^{-1}), (C) absolute growth in diameter (cm yr^{-1}) and (D) relative growth in diameter (cm cm^{-1} yr^{-1}).

cover, both in S3 and S1 individuals, but not in their height or diameter growth. Pruning of lower branches is a common practice to enhance the growth and shape of trees, but in young stems, as observed in our study, it may have a weak influence on basal diameter and height (Montoya, 1996). In these young stems, pruning may increase the growth in diameter in the upper part rather than in the basal diameter, leading to more "cylindrical" trunks, while usually having a nil effect on the height of those stems (such as oak resprouts) where apical dominance is not completely established (Montoya, 1996). However, as shown by our results, pruning may promote an increase in lateral growth and leafiness of the resprouts, probably due to the amelioration of resource availability in the reserved branches (Jackson et al., 2000). In our study, the number of new resprouts was not influenced by the intensity of cleaning or pruning, but new resprouts attained a larger size in the single-stemmed stools (S1) than in individuals with three resprouts selected (S3). Activation and growth of dormant buds in the stool leading to the new resprouts is controlled by a combined effect of increasing light availability, variation in temperature and changes in hormonal levels (Champagnat, 1989) that would be more intense in S1 individuals. Thus, the larger sizes attained by the new resprouts in S1 in comparison to S3 individuals (respectively, 33 and 22% of the height of the uncut dominant resprouts) casts some doubts on the appropriateness of the former treatment.

Q. ilex and *Q. cerrioides* stools showed a different growth pattern in basal diameter and height with time: growth of *Q. cerrioides* increased, while growth of *Q. ilex* decreased during the second year monitored. These specific differences in growth could be caused by the reported differences between the two species in shoot leafiness, but also by the differing number of new basal resprouts produced (Table 3). The larger number of new resprouts flushed from the root collar in *Q. ilex*, which is almost double than that of *Q. cerrioides*, might compete with the reserved shoots (Vigneron, 1988), and thus decrease potential growth during the second year. Production of a new flush of basal resprouts has been envisaged as one of the major problems after cleaning or thinning treatments, because it can lower the benefits of such management practices (Bergez et al., 1990). However, this high potential of resprouting observed in *Q. ilex* would be a trait of paramount importance in the case of a high recurrence of disturbances (Lloret and Lopez Soria, 1993; Espelta et al., 1999).

The conservation and amelioration of extensive Mediterranean oak coppices arisen after large fires requires knowledge about possible differences in the resprouting ability of the species involved. In spite of the above-mentioned functional differences between a deciduous and an evergreen species, our results show that both types of species may be able to resprout vigorously in different environmental situations. Furthermore, the greater resprouting vigour exhibited by the deciduous *Q. cerrioides* in comparison with the evergreen of *Q. ilex*, in terms of canopy, height and diameter growth, casts some doubts on the supposed advantages of evergreen Mediterranean oaks in response to disturbances (see Pons and Quezel, 1985; Romane et al., 1988). Nevertheless, the higher ability of *Q. ilex* to produce new waves of basal resprouts means that a possible dominance of *Q. cerrioides* in the area would require a low frequency of disturbances. Concerning the management practices tested, our results show that moderate stool cleaning is the most valuable practice to enhance growth of both deciduous and evergreen oaks in a wide array of Mediterranean coppices and environmental situations, because it provides similar growth rates to reserving a single resprout, but new and undesired resprouts reach lower development.

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