

### **Capítulo 3**

**Resprouting response to natural and simulated grazing of two Mediterranean oaks with contrasting leaf habit after a wildfire**



## Introduction

Grazing by domesticated animals remains one of the major human impacts on ecosystems throughout the world (National Research Council 1994, in Callaway et al. 2000). In the Mediterranean Basin, livestock grazing has been a common and traditional practice during the last 5000 years (Le Houerou 1981). Mediterranean landscapes bear testament to the negative ecological consequences of intensive grazing on a fragile landscape (Le Houerou 1981; Quinn 1986). In fact, overgrazing by domestic animals has been pointed out as one the major causes of forest degradation and desertification of Mediterranean-type ecosystems (Thirdwood 1981; Papanastasis 1998). Herbivores can severely constrain population regeneration of woody plants and alter the outcome of competition among plant species, thus modifying the composition and dynamics of plant communities (Quinn 1986; Noy-Meir et al. 1989; Putman 1996; Hodar et al. 1998).

Response of Mediterranean-type ecosystems to disturbances (e.g. wildfires, overgrazing) has been extensively studied (e.g. Naveh 1975; Le Houerou 1987; Trabaud 1987). However, despite a long history of fire and grazing coupling in ecosystems on the circum-Mediterranean fringe, less attention has been paid to the consequences of consecutive disturbances, such as the impact of grazing on post-fire succession. Overall, the effect of fire on populations of Mediterranean species has been reported to be usually small, because plants have different life-history characteristics that allow a very effective post-fire recovery, either by resprouting from fire-resistant structures or by germination of fire-protected seeds (Naveh 1975; Keeley & Zedler 1978; Trabaud 2000). Nevertheless, resilience of Mediterranean species and landscapes after a wildfire may be affected by the feeding activity of mammalian herbivores, which may lengthen the time required for the system to return to the pre-fire initial conditions (Quinn 1986). Grazing on resprouter species after a wildfire usually does not kill them but reduce their vigor, because resprouting involves a large mobilization and consumption of below-ground reserves (Canadell et al. 1991). If grazing is reiterated, it may deplete below-ground reserves and thus compromise the success of the regeneration process (Vilà & Terradas 1995a; Canadell & López-Soria 1998).

Mediterranean plants exhibit different avoidance and tolerance mechanisms in order to survive from continuous grazing. Avoidance, which reduces the probability and severity of grazing, is usually achieved through selection for morphological or chemical defensive traits (Bryant et al. 1983; Papanastasis 1998), while tolerance includes morphological and physiological mechanisms that promote growth after defoliation (Briske 1996). The development of a particular type of response to browsing depends on life-history traits of plants. Among them, the type of leaf life-span, i.e. evergreens, whose leaves remain throughout the year, versus deciduous, whose leaves are shed at least every year, is one of the most important ones. Comparison of functional differences among deciduous and evergreen

Mediterranean plants has shown that, according to their carbon balance and water and nutrient relationships, both groups may operate in the same habitat with different adaptive response to environmental constraints (Schulze 1982). Nevertheless, differences between evergreen and deciduous species in leaf texture and thickness (Rundel 1988; Damesin et al. 1998), content of nitrogen, indigestible substances (cutin, lignin) and secondary compounds (e.g. tannins) (Aerts 1995; Eamus 1999; but see Gallardo & Merino 1993; Gillon et al. 1994), have been used as arguments to explain a marked preference of herbivores for deciduous species instead of con-generic evergreens (Leouffre et al. 1989; Etienne et al. 1996).

Although in the northern rim of the Mediterranean basin grazing pressure has drastically decreased in the last century (Papanastasis 1998), recent UE policies have encouraged extensive livestock as a management strategy to take economic benefit of the low-wood productivity in Mediterranean forests and to prevent wildfires (Dubost 1998). Moreover, in Catalonia (NE Spain), extensive livestock has also increased because productive pine forests have been transformed, after large wildfires, into shrublands of evergreen and deciduous oaks, due to the regeneration failure of the dominant pine species (*Pinus nigra* (Arnold) and *P. sylvestris* L.) present before the fire (Retana et al. in press). The two dominant *Quercus* species in these burned areas are the evergreen *Q. ilex* L. and the deciduous *Q. cerrrioides* Willk. et Costa, two co-occurring Mediterranean species in many sites of NE Spain. *Q. ilex* is a widespread species, present over a large area extending 6000 km longitudinally from Portugal to Syria and 1500 km latitudinally from Morocco and Algeria to France (Terradas 1999), whereas the distribution of *Q. cerrrioides* is more restricted to lower elevation areas of NE Spain (Castroviejo et al. 1990). In the Mediterranean region, evergreen oaks are much more abundant than deciduous ones, and some authors support the idea that expansion of evergreens has been favored by the appearance of domestic herbivores (Cuartas and García González 1992).

In this study, we explore the response to grazing of these two co-occurring Mediterranean oak species in areas affected by large wildfires in central Catalonia (NE Spain). On the basis of the available information on plant response to grazing, we have tested three different hypotheses. The first one is that the evergreen species will be favored under a high grazing pressure because different authors have pointed out a marked bias among browsers towards deciduous instead of evergreen *Quercus* species (Leouffre et al. 1989; Etienne et al. 1996). The second hypothesis refers to the time-from-fire when grazing takes place: as deciduous species have higher growth rates than con-generic evergreens (Aerts 1995), *Q. cerrrioides* will be less affected than *Q. ilex* when grazing begins some years after disturbance, because it attains larger height and can partially escape browsing. Finally, in communities where species grow asynchronously, season of grazing may determine which species are grazed most severely during each grazing period (Briske 1996). Due to their different leaf habit, the two species studied differ in the phenology of leaf production (Blondel & Dias 1994; Blondel & Aronson 1999): *Q. cerrrioides* renews completely its foliar tissues in early spring (i.e. April),

while partial renewal of leaves and shoots of *Q. ilex* occurs one month later, in May, although in this species a second flush of shoot growth, carrying a smaller generation of leaves, can be produced in late summer or early autumn (De Lillis & Fontanella 1992; Terradas 1999). These distinct seasonal patterns of growth and carbon and nutrient allocation may have important implications for palatability and vulnerability to herbivores (Bryant et al. 1983; Kozłowski 1991). The third hypothesis is that the response to grazing of *Q. ilex* and *Q. cerrioides* will differ depending on the season of the year where grazing occurs. In particular, (i) grazing during the growing season will be more detrimental to plant performance than grazing during the dormant state, because plants are more vulnerable in this period (see Briske 1996), and (ii) the negative effects of grazing will be different for the two species: they will be higher in early spring for the deciduous than for the evergreen species, because the former renews completely its foliar tissues. To validate these hypothesis, we have undertaken the monitoring of the effects of grazing over evergreen and deciduous individuals on different times after fire, and we have carried out an experiment of simulated grazing on the two species in different seasons of the year.

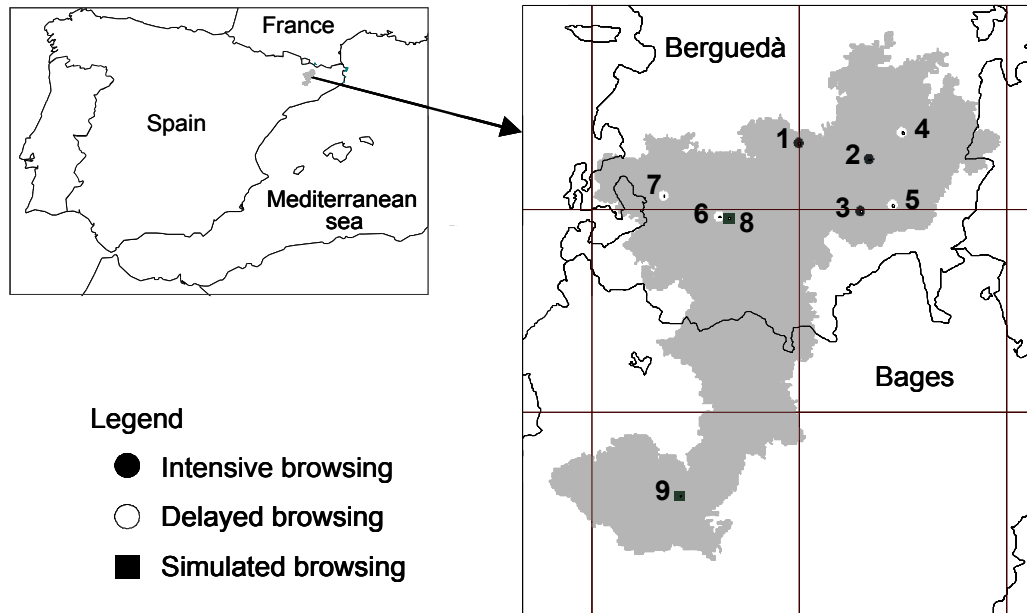
## Material and methods

### *Study area*

This study was carried out in the regions of Bages and Berguedà (central Catalonia, NE Spain; 41° 45' to 42° 6' N; 1° 38' to 2° 1' E; 350 to 950 m above sea level). This area was affected in July 1994 by the largest wildfire historically recorded in Catalonia, that burned ca. 24322 forested ha. Before the fire, forests (71% of the total surface burned) were dominated by *P. nigra* and, to a lesser extent, by *P. halepensis*, *P. sylvestris*, *Q. ilex* and *Q. cerrioides*. These two *Quercus* species were also very common in the understory of *P. nigra* forests and, due to the nil regeneration of this pine species after the fire, *P. nigra* forests changed to woodlands dominated by resprouted *Q. ilex* and *Q. cerrioides* stools (Retana et al. in press). The large extension of the burned area and the need to replace the traditional exploitation of wood in the pine forests, have promoted extensive land use changes involving the conversion of 2.365 ha of post-fire woodlands (9.7% of the total burned area) to rangelands. In that scenario, we have carried out three different studies to asses: i) the impact of intensive post-fire browsing, ii) the impact of delayed browsing and iii) the impact of intensity and the season of simulated grazing on *Q. ilex* and *Q. cerrioides* sprouting stools. Those experiments were carried out in different locations within the burned area (Figure 1).

### *Impact of intensive browsing on sprouting stools*

This study was carried out in three sites, Socarrada, Alzina Grossa and Cal Teixidor (Figure 1), in 1998, i.e., 4 years after the fire. In each site, an area intensively browsed by cows



**Figure 1.** Geographical location of the sites sampled in this study along the area of Bages and Berguedà regions affected by the large wildfire of 1994.

since the first year after fire was chosen, together with a nearby area protected from cow browsing during all this time. Browsing was estimated as intense (following Etienne et al. 1996) because of the consumption of all tips and more than 70% of the edge of *Q. ilex* and *Q. cerrrioides* stools and the heavy consumption of low palatable plants (e.g. *Rosmarinus officinalis*, *Cistus* spp.). Fifteen browsed stools and fifteen control (not browsed) stools of *Q. ilex* and *Q. cerrrioides* were sampled in each site. Stool surface was used as a measure of the size of the individual before sprouting, and no initial differences in this variable were found among sites or species before browsing (two-way ANOVA,  $p > 0.09$  in all cases).

The following variables were measured from each stool: number of stems, total height and crown projection (measuring two perpendicular diameters of the crown and computing the projection as an ellipse). The ratio total height/square root of crown projection was computed as a measure of stool shape. The effects of site, species and treatment (browsed, not browsed) on these variables were analyzed by ANOVA. All variables except the number of stems were normalized by a log transformation. The sequential Bonferroni method was employed to control the group-wide type I error rate (Rice 1989), considering together all statistical tests of this study. The Fisher's protected least significant difference post-hoc test was used to analyze differences among levels of each main factor.

*Impact of delayed browsing on sprouting stools*

This study was carried out in four sites: Cal Barraler, Seubota, Cererols and Can Armengol (Figure 1) in 1998, i.e. 4 years after the fire. These areas were not browsed during the first years after the fire, but cow browsing started in a part of the study just at the beginning of the study and continued until the end of the study. As in the previous section, this delayed browsing treatment could be classified as intense because of the consumption of all leaves in the *Q. ilex* and *Q. cerrrioides* resprouts (except the tallest ones), and the heavy consumption of low palatable shrubs (Etienne et al. 1996).

Initially, two 20x20 m plots were chosen in each site, one that was browsed and another that was protected from cow browsing. In each plot, fifteen *Q. ilex* and fifteen *Q. cerrrioides* stools were randomly chosen and numbered. Stool surface was used as a measure of stool size. There were initial differences in size between species (three-way ANOVA,  $F=27.7$ ,  $p<0.001$ , d.f.=1: *Q. ilex* stools were larger than *Q. cerrrioides* ones) and among sites ( $F=5.8$ ,  $p<0.001$ , d.f.=3: the Seubota individuals were larger than those of the other three sites), but not between individuals assigned to browsed and control treatments ( $F=2.5$ ,  $p=0.12$ , d.f.=1). Total number of sprouts larger than one cm of basal diameter, total height and crown projection (computed as in the former study) were measured from each stool at the beginning (1998) and the end (1999) of the study. Relative growth rate (RGR) of number of stems, height and crown projection was calculated as  $RGR = (\ln X_i / \ln X_{i-1})$ , where  $X_i$  was the value of the selected variable in 1999, and  $X_{i-1}$  was its value in 1998. The three largest sprouts per stool were marked, and the two last annual growths in height, and the length of the part of the stem completely defoliated were registered for each of them in 1999. Means per individual were calculated for these variables with three values per individual

The effects of site, species and treatment (browsed, not browsed) on the variables considered were analysed by ANOVA. When necessary, data were normalized by a log transformation. For all statistical tests of this part of the study, 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).

*Experiment of simulated browsing*

This experiment was carried out in two sites: L'Obaga d'Antius and Cal Barraler (Figure 1). In each site, two 0.25-ha plots were established. At the beginning of the experiment, 96 *Q. ilex* and 96 *Q. cerrrioides* stools were randomly chosen and numbered in each plot. These marked individuals were randomly assigned to one of the three clipping treatments applied. The treatments simulated browsing by cows by clipping a certain proportion of all annual shoots

from the previous season: 0% (control, stools were left untouched), 25% (low-intensity browsing) and 50% (high-intensity browsing). This experimental procedure was repeated with different individuals at the end of each season: spring (June), summer (September), autumn (December) and winter (April). For each combination of species, treatment and season, there were 8 sampling stools per plot. At the start of the study, there were significant differences in height between the two species (ANOVA,  $F=19.7$ ,  $p<0.0001$ ,  $d.f.=1$ ; *Q. ilex*:  $157\pm 2$  cm; *Q. cerrrioides*:  $171\pm 3$  cm) and the two sites ( $F=11.9$ ,  $p<0.001$ ,  $d.f.=1$ ; Cal Barraler:  $157\pm 3$  cm; Obaga d'Antius:  $172\pm 2$  cm), but not among browsing treatments or browsing seasons ( $p>0.10$  in both cases).

The experiment lasted one year, i.e., stools of each season were sampled again one year later, that is, in spring, summer, autumn and winter of the following year. In each stool, the following variables were measured at the beginning and at the end of the experiment: total number of sprouts larger than one cm of basal diameter, height and crown projection of the stool. Three shoots per stool were marked at the beginning of the experiment and were also monitored one year later to determine mean annual shoot growth per individual. Relative growth rate (RGR) of number of stems, height and crown projection was calculated as  $RGR = (\ln X_i / \ln X_{i-1})$ , where  $X_i$  was the value of the selected variable at the end of the experiment, and  $X_{i-1}$  was its value at the beginning of the experiment.

The effects of the simulated browsing treatment, season, site and plot (nested within site) on these variables were analyzed by ANOVA. In all cases, inspection of residuals was carried out to check for normality and homoscedasticity. Data of crown projection and RGR of crown projection were normalized by a log transformation. The sequential Bonferroni method was employed considering all ANOVA tests together, and the Fisher PLSD post-hoc test was used to compare the different levels of each variable.

## Results

### *Impact of intensive browsing on sprouting stools*

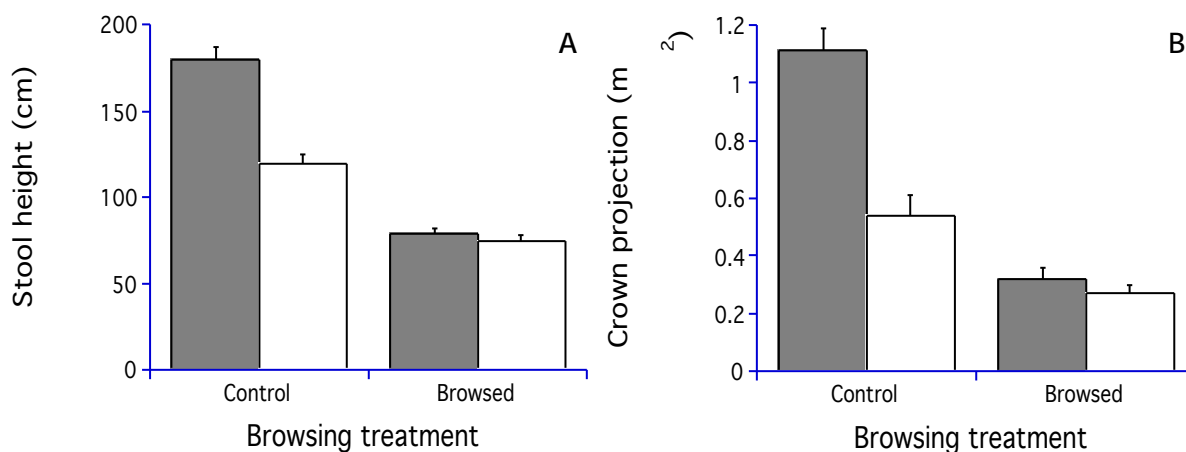
None of the factors or their interactions affected the number of stems per stool (Table 1). There was a significant effect of species and a very important effect of browsing treatment in total height and crown projection of the individual (Table 1). These variables attained higher values in *Q. cerrrioides* than in *Q. ilex* stools, and in control than in browsed stools. However, there was an interaction between both factors, so there were differences between species in the control treatment, but not in the browsed one (Figure 2). The effect of site not significant, while the interaction between site and browsing treatment was only significant for total height: values in the control treatment in Socarrada were lightly lower than in the other two sites, while they were similar in the browsing treatment. None of the factors affected the ratio total height/square root



of crown projection, with both species showing similar values (*Q. ilex*:  $1.82 \pm 0.08$ ; *Q. cerrroides*:  $1.97 \pm 0.12$ ).

**Table 1.** F values from ANOVA tests of effects of species, site and browsing treatment (browsed, not browsed) on different morphological variables of sprouting stools in the study of the effects of intensive browsing. Significant coefficients (at  $\alpha = 0.05$  when the sequential Bonferroni method is employed) are indicated in bold. All variables except number of stems were log-transformed.

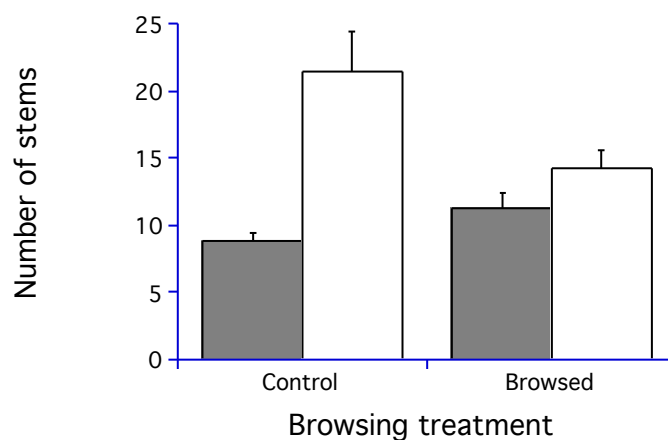
Source	df	Number of stems	Total height	Crown projection	Height/Crown projection
Species (SP)	1	0.4	<b>20.0</b>	<b>8.4</b>	1.3
Site (S)	2	0.9	0.1	0.4	0.2
Browsing treatment (B)	1	4.2	<b>138.1</b>	<b>91.1</b>	0.4
SP x S	2	0.4	2.3	1.9	4.1
SP x B	1	0.0	<b>8.7</b>	<b>19.6</b>	4.6
S x B	2	1.0	<b>8.0</b>	0.5	3.7
SP x S x B	2	1.0	0.3	1.9	2.3



**Figure 2.** Total height (A, in m) and crown projection (B, in m<sup>2</sup>) of sprouting *Q. cerrroides* (solid bars) and *Q. ilex* stools (open bars) in control and in browsed plots in the study of the effects of intensive browsing. Vertical bars extend over +1 SE of the mean.

*Impact of delayed browsing on sprouting stools*

All control and browsed individuals survived at the end of the study. There were significant differences in the number of stems per stool according to species (*Q. ilex*:  $2.5 \pm 0.1$  stems larger than one cm of basal diameter per stool; *Q. cerrroides*:  $2.1 \pm 0.1$  stems per stool), although the interaction Species x Browsing treatment was significant, with larger differences between species in the control treatment than in the browsed one (Figure 3). The interaction between Site and Browsing treatment was also significant, because the number of stems decreased from control to browsed plots in all sites except in Seubota.



**Figure 3.** Number of stems per stool of sprouting *Q. cerrroides* (solid bars) and *Q. ilex* stools (open bars) in control and in browsed plots in the study of the effects of delayed browsing. Vertical bars extend over +1 SE of the mean.

The different size variables of Table 2 showed a similar pattern, although not all factors reached significance after applying the Bonferroni correction. Thus, size of individuals was larger in control plots than in browsed ones in total height (control individuals:  $190 \pm 7$  cm; browsed individuals:  $167 \pm 5$  cm) and crown projection (control individuals:  $2.28 \pm 1.49$  m<sup>2</sup>; browsed individuals:  $1.40 \pm 1.0$  m<sup>2</sup>). The ratio total height/square root of crown projection was higher in browsed than in control individuals (browsed individuals:  $1.61 \pm 0.05$ ; control individuals:  $1.40 \pm 0.04$ ). This variable did not depend on species (*Q. ilex*:  $1.51 \pm 0.05$ ; *Q. cerrroides*:  $1.50 \pm 0.04$ ) but, for the other variables considered, *Q. cerrroides* showed higher values than *Q. ilex*. There were also significant differences among sites, because Cererols and Seubota showed lower values of total height than the other sites, while Seubota showed lower ratio total height/square root of crown projection.

**Table 2.** F values from ANOVA tests of effects of species, site and browsing treatment (browsed, not browsed) on different morphological variables of sprouting stools in the study of the effects of delayed browsing. Significant coefficients (at  $\alpha=0.05$  when the sequential Bonferroni method is employed) are indicated in bold. Data of number of stems, total height and crown projection were log-transformed.

Source	df	Number of stems	Total height	Crown projection	Height/Crown projection
Species (SP)	1	<b>20.5</b>	<b>86.4</b>	<b>37.3</b>	0.1
Site (S)	3	0.4	<b>9.4</b>	4.4	<b>6.7</b>
Browsing treatment (B)	1	0.2	<b>19.1</b>	<b>34.6</b>	<b>11.2</b>
SP x S	3	2.6	3.3	3.6	4.5
SP x B	1	<b>6.7</b>	0.3	3.0	1.7
S x B	3	<b>6.2</b>	0.9	0.3	0.2
SP x S x B	3	1.8	0.8	1.6	1.2

In the analyses of growth variables (Table 3), differences between species were only found for relative growth rate of crown projection: relative growth of *Q. ilex* was higher than that of *Q. cerrrioides*. This variable, together with annual shoot growth also showed significant differences for browsing treatment (Table 3): the effect of browsing was to decrease RGR of

**Table 3.** F values from ANOVA tests of effects of species, site and browsing treatment (browsed, not browsed) on different relative growth (RGR) variables of sprouting stools in the study of the effects of delayed browsing. Significant coefficients (at  $\alpha=0.05$  when the sequential Bonferroni method is employed) are indicated in bold. All variables were log-transformed.

Source	df	RGR of number of stems	RGR of total height	RGR of crown projection	Annual shoot growth
Species (SP)	1	3.8	4.1	<b>25.3</b>	1.4
Site (S)	3	<b>4.4</b>	2.7	<b>15.8</b>	1.1
Browsing treatment (B)	1	0.0	6.8	<b>10.3</b>	<b>185.0</b>
SP x S	3	1.5	0.9	2.2	3.1
SP x B	1	0.0	0.3	2.0	0.2
S x B	3	3.7	<b>4.4</b>	<b>9.4</b>	<b>21.1</b>
SP x S x B	3	1.4	0.3	0.8	2.0

crown projection (control stools:  $0.60 \pm 0.05$ ; browsed stools:  $0.50 \pm 0.07$ ) and, especially, annual shoot growth (control stools:  $9.0 \pm 1.1$  cm; browsed stools:  $1.3 \pm 0.2$  cm). Two variables, RGR of number of stems and RGR of crown projection showed differences between sites, with Seubota and Can Armengol having lower values than the other two sites. The interaction between site and browsing treatment was significant for RGR of total height, RGR of crown projection, and for annual shoot growth (Table 3): in all cases, relative growth was higher in control than in browsed stools, except in Cerarols, where the opposite pattern was attained.

The analysis of the effect of cattle on shoot defoliation showed that defoliated length varied between species (ANOVA,  $F=56.3$ ,  $p<0.0001$ ,  $d.f.=1$ ): it was considerably shorter for *Q. ilex* than that for *Q. cerrrioides* ( $13 \pm 2$  and  $27 \pm 4$  cm, respectively). Differences among sites were also significant (ANOVA,  $F=35.6$ ,  $p<0.0001$ ,  $d.f.=3$ ), but the interaction species x site was not significant (ANOVA  $F=1.0$ ,  $p=0.39$ ,  $d.f.=3$ ).

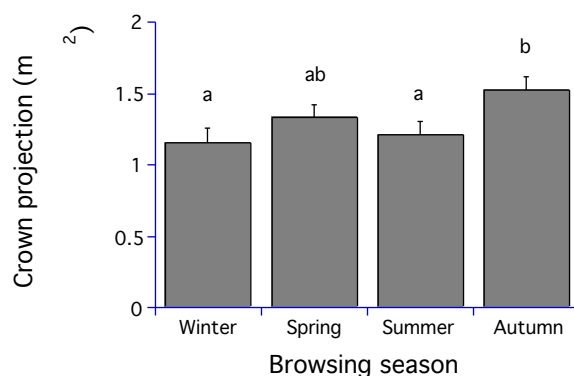
#### *Experiment of simulated browsing*

None of the individuals died as a result of the simulated browsing experiment. As table 4 shows, there were significant differences between species in number of stems (*Q. ilex*:  $7.5 \pm 0.3$  sprouts per stool; *Q. cerrrioides*:  $4.1 \pm 0.1$  sprouts per stool) and total height (*Q. ilex*:  $167 \pm 2$  cm; *Q. cerrrioides*:  $186 \pm 3$  cm). Differences among browsing periods were only found in crown projection (Figure 4), which also showed differences among browsing treatments (Figure 5). The ratio total height/square root of crown projection only varied with browsing intensity (control:  $1.65 \pm 0.03$ ; low-intensity browsing:  $1.85 \pm 0.04$ ; high-intensity browsing:  $1.98 \pm 0.05$ ). The two sites showed significant differences for all variables except number of stems (Table 4), with individuals of Obaga d'Antius being larger than those of Cal Barraler in all cases. None of the interactions were significant.

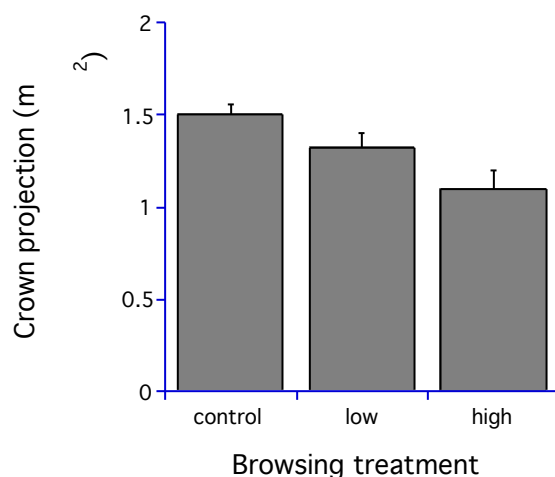
RGR of number of stems did not differ for any of the main factors or interactions tested. The other two variables showed significant differences among browsing periods (Table 5). In the two cases, stools browsed in winter showed lower relative growth rates than stools browsed in the other periods of the year (Figure 6). Concerning the browsing treatment, control stools grew less in crown projection than the two browsing treatments (control:  $0.39 \pm 0.04$ ; low-intensity browsing:  $0.68 \pm 0.7$ ; high-intensity browsing:  $0.82 \pm 0.09$ ). The interactions of species and site with period of the year were significant for RGR of crown projection (Table 5). Thus, *Q. ilex* showed higher RGR of crown projection than *Q. cerrrioides* when browsed in autumn and winter, while the opposite was obtained when stools were browsed in spring and summer. Concerning sites, the highest RGR value in spring was obtained in Obaga d'Antius, while in the other three seasons the highest value was obtained in Cal Barraler.

**Table 4.** F values from ANOVA tests of effects of species, period of the year, browsing treatment (not browsed, low- intensity and high-intensity browsing), site and plot (nested within site) on different morphological variables of sprouting stools in the experiment of simulated browsing. Significant coefficients (at  $\alpha=0.05$  after applying the sequential Bonferroni method) are indicated in bold. Crown projection data were log-transformed.

Source	df	Number of stems	Total height	Crown projection	Height / Crown projection
Species (SP)	1	<b>106.2</b>	<b>19.7</b>	0.0	6.3
Period of the year (P)	3	1.1	0.4	<b>4.5</b>	3.0
Browsing treatment (B)	2	1.5	0.1	<b>8.3</b>	<b>17.9</b>
Site (S)	1	0.1	<b>11.9</b>	<b>23.2</b>	6.8
Plot (Site)	2	4.1	2.9	0.4	2.7
SP x P	3	0.8	0.4	4.1	4.0
SP x B	6	0.5	0.1	1.6	4.1
SP x S	1	0.0	0.1	1.9	3.8
P x B	6	0.7	0.2	0.7	1.0
P x S	3	1.0	0.2	0.0	0.2
B x S	2	0.5	0.9	0.5	0.4
SP x P x B	6	0.5	0.4	0.6	1.0
SP x P x S	3	1.9	0.1	0.2	0.3
SP x B x S	2	3.3	0.1	0.4	0.8
P x B x S	6	0.6	0.1	0.6	0.6
SP x P x B x S	6	0.8	0.1	0.2	0.5



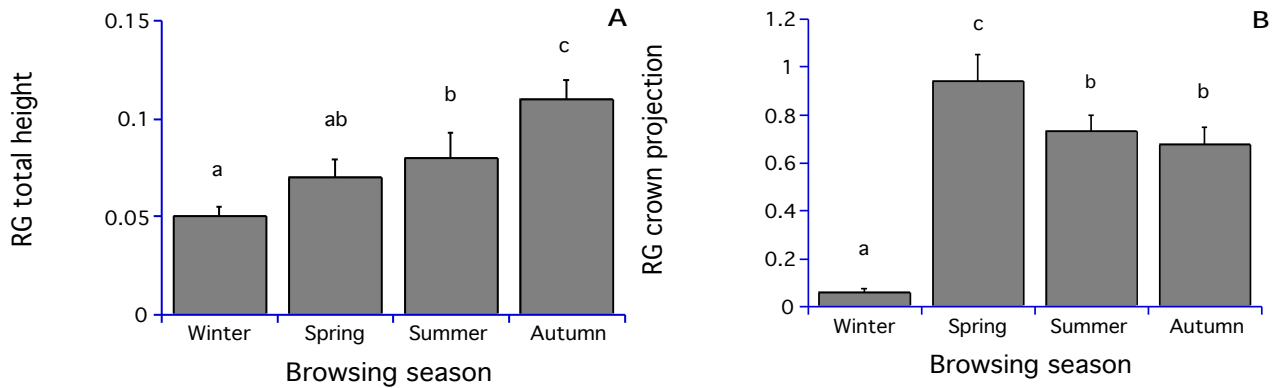
**Figure 4.** Crown projection of individuals browsed in the different periods of the year in the experiment of simulated browsing. Vertical bars extend over +1 SE of the mean. Different letters indicate significant differences among periods according to the Fisher PSLD post-hoc test.



**Figure 5.** Crown projection of individuals of the different experimental treatments in the experiment of simulated browsing. Vertical bars extend over +1 SE of the mean. Different letters indicate significant differences among periods according to the Fisher PSLD post-hoc test.

**Table 5.** F values from ANOVA tests of effects of species, period of the year, browsing treatment (not browsed, low- intensity and high-intensity browsing), site and plot (nested within site) on different relative growth (RGR) variables of sprouting stools in the experiment of simulated browsing. Significant coefficients (at  $\alpha=0.05$  after applying the sequential Bonferroni method) are indicated in bold. Data of RGR of crown projection were log-transformed.

Source	df	RGR of number of stems	RGR of total height	RGR of crown projection
Species (SP)	1	0.2	3.7	0.1
Period of the year (P)	3	2.7	<b>6.6</b>	<b>60.4</b>
Browsing treatment (B)	2	1.5	0.3	<b>11.4</b>
Site (S)	1	7.8	1.2	0.6
Plot (Site)	2	0.3	4.0	<b>14.1</b>
SP x P	3	0.3	1.6	<b>7.6</b>
SP x B	6	1.1	0.6	0.4
SP x S	1	0.1	0.1	0.2
P x B	6	1.8	1.2	3.5
P x S	3	0.2	0.1	<b>14.6</b>
B x S	2	1.9	0.1	0.2
SP x P x B	6	0.8	0.6	0.9
SP x P x S	3	1.3	0.2	3.7
SP x B x S	2	0.3	1.4	0.6
P x B x S	6	0.1	1.0	1.0
SP x P x B x S	6	1.2	0.1	1.0



**Figure 6.** RG of (A) total height and (B) crown projection of stools browsed in the different periods of the year in the experiment of simulated browsing. Vertical bars extend over +1 SE of the mean. Different letters indicate significant differences among periods according to the Fisher PSLD post-hoc test.

## Discussion

The first hypothesis discussed in this study, that the evergreen species will be favored under a high grazing pressure, is not confirmed in terms of mortality of individuals, because neither the effect of post-fire cattle grazing, both immediately or delayed, nor the different levels and seasons of simulated grazing led to stool mortality of the two *Quercus* species. Mortality as a result of defoliation has been argued to be virtually nonexistent among plants affected by intensive grazing (McNaughton 1983). However, in this study the fact that grazing was carried out on individuals recovering from a recent disturbance event (i.e. fire) points out a high ability of both *Quercus* species to withstand severe and repeated disturbances. The role of repeated disturbances on Mediterranean resprouting species has been extensively studied, and while major architectural changes are produced (in sprout number, height or nutrient content), there are few mortality effects (see, among others Canadell et al. 1991; Vila and Terradas 1995b). Initial mortality of resprouting species following a disturbance event has been observed in different species. For example, mortality of *Q. ilex* stools ranges from 12-15% after a wildfire episode (López-Soria & Castell 1992); 4-6% after a drought period (Lloret & Siscart 1995), or 3-5% after coppicing (Ducrey & Boisserie 1992; Retana et al. 1992). However, beyond those initial mortality rates, resprouters show a high resilience to disturbances and it is difficult to observe further mortality processes, even if stools suffer new disturbances (Espelta et al. 1999; Bellingham 2000).

The effect of herbivory on plant structure and growth has been more controversial (Belsky 1986), because different studies have shown that herbivory exerts negative effects on plant growth (e.g. Marquis 1984, 1992), while other authors have claimed that plants can compensate (nil effect of herbivory) or even overcompensate (beneficial effect of herbivory) for browsing (e.g. McNaughton 1983; Paige and Whitman 1987; Aguilar et al. 1996; Riba 1998). In this study, as has been described for other *Quercus* species (Gómez-Gutiérrez & Pérez-

Fernández 1996; Papatheodorou et al. 1998), the negative effects of grazing were evident. In the studies of intensive browsing and delayed browsing, no overcompensation nor compensation was observed but, on the contrary, a significant reduction in size and growth of browsed compared to control individuals was obtained. Moreover, in the study of simulated browsing, clipped stools did not recover one year after the experimental treatment application. Nevertheless, comparison of the response of the two species indicates that, under a high grazing pressure, the negative effect of grazing on *Q. cerrroides* stools is much more evident than on those of *Q. ilex*, because although the initial size of *Q. cerrroides* was considerably larger, the two species attained similar size and shape when grazed. It remains unclear whether this fact is caused by structural or chemical differences between species, (i.e. lower nitrogen content and higher sclerophylly of evergreen oaks compared to deciduous ones, Joffre and Rambal 1999), arguments used to explain why evergreen species may reduce grazing intensity (Bryant et al. 1983), or by the behavior of herbivores, in this case cattle. Some authors have noted that cattle are less selective than other domestic herbivores, and browse more of the larger (*Q. cerrroides* in our study) or dominant plants (Wilson and Harrington 1990). The fact that stools of the two species were browsed until they attained a similar size and shape seems to indicate that grazing activity proceeds until cattle can not easily consume them, because the branching pattern of those resprouted individuals, with numerous and lignified resprouts, protects a fraction of the leaves from browsing.

The second hypothesis tested was that, as dominant resprouts of deciduous species grow faster in height than con-generic evergreens, *Q. cerrroides* would be less affected than *Q. ilex* when grazing begins some years after disturbance. This asseveration was not confirmed by the results obtained in the study of delayed browsing. In fact, some observations even suggest the opposite: although the shape of grazed stools was similar, the defoliated length of *Q. cerrroides* shoots was larger than that of *Q. ilex* ones, and the later species showed larger growth increments in crown projection both in grazed and in control plots. The ability of plants to compensate for biomass loss (e.g. due to overgrazing) depends upon their capacity to increase the growth rates of the remaining tissues (Oosterheld 1992; Papatheodorou et al. 1998). Comparisons of ecophysiological traits among deciduous and evergreen Mediterranean oaks at the leaf level, have shown very similar net CO<sub>2</sub> assimilation and stomatal conductance rates in both groups, thus pointing out a very similar productivity, despite differences in their leaf morphology and composition (Damesin et al. 1998). In that sense, the higher LAI exhibited by evergreen oaks in comparison with deciduous ones (Joffre & Rambal 1999) and the possibility of photosynthesis during a larger period of time (Save et al. 1999) could even contribute to enhance growth in the former, as seems to be the case for *Q. ilex* stools in our study.

As Mediterranean plants have distinct seasonal patterns of growth and of carbon and nutrient allocation, in our third hypothesis we expected that the grazing season could affect the growth response of sprouting stools. However, in the experiment of simulated grazing, the



effect of grazing season on the final size of individuals was relatively small, as one year after the browsing treatment there were only differences in crown projection (Figure 4): stools grazed at the end of winter and at the end of summer were smaller than those grazed at the end of the two growing seasons (i.e. spring and autumn). On the other hand, differences in growth among seasons were much more evident, because stools grazed at the end of winter showed lower relative growth in height and crown projection (Figure 6). The negative impact of browsing at the end of winter, just prior to the onset of the growing period, could be caused by the loss of new formed buds. This same pattern observed at the end of summer could be linked to the interaction among grazing and the water stress suffered by stools during that period. Moreover, the expectancies at the beginning of the study were that the effects of grazing would be different in both species according to the browsing season because of they differ in the phenology of leaf production (Blondel & Dias 1994; Blondel & Aronson 1999). However, there were no differences between them in their final size and only slight differences appeared in crown growth depending on the grazing season.

The overall results presented in this study suggest that the impact of grazing on the two species and their response to this disturbance are quite similar. Survival of grazed individuals is almost granted and, concerning growth, *Q. cerrioides* has a larger size when ungrazed than *Q. ilex*, but a high grazing pressure matches the two species in most of the size variables considered. Holm oak has been considered a Mediterranean paradigm, partly because of its evergreen habit (Terradas 1999). It has been proposed that the expansion of *Q. ilex* in the north of the Mediterranean basin was not related to climatic changes, but to the settlement of human populations (Barbero and Loisel 1980). In fact, the area in which domestic Caprini have developed coincides partly with the distribution area of *Q. ilex* (Clutton-Brock 1987). Nevertheless, although it has been suggested that mammalian herbivory can alter the outcome of the regeneration process in Mediterranean areas (Quinn 1986), the results obtained in this study do not indicate that the greater dominance of *Q. ilex* versus *Q. cerrioides* might be determined by a marked difference in their response to herbivory, although its short duration does not allow to generate long-term implications of the effect of grazing on these species. It has been stated that deciduous oaks are more palatable than holm oak for domestic livestock (Leouffre et al. 1989; Cuartas and García-González 1992; Etienne et al. 1996) but, according to our results, the browsing effect of herbivores does not seem more damaging for the deciduous than for the evergreen *Quercus* species considered. Other studies dealing with the response of evergreen and deciduous Mediterranean oaks in front of disturbances (Consuelo Bonfil and Pilar Cortés; unpublished data) agree with this line of evidence, as they register only slight differences in the response of evergreen and deciduous oaks to repeated fires. Therefore, the different degree of dominance of *Q. ilex* and *Q. cerrioides* in large areas of the Mediterranean region does not seem related to a different response to disturbances.

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## **Capítulo 4**

**Patterns of resprouting after fire and response to stool cleaning of two Mediterranean oaks with contrasting leaf habits**



## Introduction

Resprouting is considered an efficient trait by which woody plants can recover lost biomass after disturbance (Bellingham 2000). This life-history trait is widely observed in many taxa around the world, but it has been in Mediterranean regions where it has received more attention, as one of the main regeneration mechanisms of plant communities subjected to fire (Keeley & Zedler 1978; Malanson & O'Leary 1982). In fact, the resprouting habit of many Mediterranean shrubs and trees has been one of the most important keystones to build up the paradigm of the high resilience (*sensu*, Westman 1986) of these communities in front of fire. Moreover, this rapid recovery of the vegetation after the fire has been emphasised to play a critical and positive role to prevent soil erosion (Calvo & Cerdà 1994), to avoid nutrient losses (Trabaud 1994) and to re-establish suitable environmental conditions which facilitate the recovery of animal communities (Prodon et al. 1987).

Despite the aforementioned benefits of the resprouting habit for the regeneration and maintenance of Mediterranean communities, 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) puts some threats about the different ways to manage extensive new forest landscapes arisen through resprouting. Large wildfires have a major effect on the landscape, because they may destroy forest vegetation independently of its composition, age and density (Christensen et al. 1989; Bessie & Johnson 1995). This results that burned landscapes are more homogeneous than they were before the fire event, as large wildfires turns the previous mosaic-like vegetation patterns, generated by the different succession pathways and management practices, to be synchronised in large areas (Huston 1994). Thus, extensive burned Mediterranean forests regenerated through resprouting turn on coppices with a high homogeneity on their structure (Romane et al. 1988). Coppices are characterised by high-density stands of multi-stemmed stools with relatively small sprouts, slow vertical growth and low production rates (Terradas 1999). This forest typology involves two negative consequences: it condemns coppices to be only profitable for small firewood or charcoal production, two management practices in trend to disappear nowadays, and it increases the risk of new fire events, owing to the accumulation of biomass, both horizontally and vertically (Cañellas et al. 1996).

Several management practices have been envisaged to accelerate the natural developmental trends of Mediterranean coppices towards more mature structures (Amorini et al. 1996). The best alternative appears to be their gradual conversion into either stored coppices (i.e. a coppices in which only one or two stems per stool remains) or, when possible, to 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 & 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).

Response of stools to cleaning has been analysed from different points of view, as the effects of intensity and season of cleaning on the stool (Harrington 1984; Johansson 1992), the changes in the forest environment (Cutini & Benvenuti 1996), and the growth, architecture and ecophysiological traits of the reserved shoots (Cutini & Mascia 1996). However, these studies have usually focused in more or less mature forests originated through old management practices, rather than young coppices created after wildfires, and have been carried out in mono-specific stands of similar site quality. However, resprouting is a biologically complex phenomenon that may be influenced by both species characteristics and site quality, i.e. a compound of soil and climatic conditions (Midgley 1996). For this reason, a successful amelioration of extensive coppices should take into account these two factors. On the one hand, Mediterranean species may differ in their ability to resprout and respond to stool cleaning due to differences on sprout architecture and ecophysiology, bud bank size, total amount of belowground reserves, and tolerance to stresses, such as drought (Mesleard & Lepart 1989; Canadell & López Soria 1998; Espelta et al. 1999). Moreover, the resprouting vigour and the effects of cleaning may also depend on the quality of the site, as resprouting increases in stands with higher water availability as deep vs. shallow soils, or northern vs. southern slopes (Lopez Soria & Castell, 1992) or in favourable topographic positions, as the bottom of the slope in contrast with the hilly top (Gracia 2000).

The extension of mixed evergreen and deciduous oak coppices has recently increased in NE Spain (Central Catalonia) in areas affected by the large wildfires occurred in 1994 and 1998 (40420 forested ha). This process has been favoured by the regeneration failure of the dominant pine species present in the area before the fire event (*Pinus nigra* Arnold), coupled with the vigorous resprouting of the *Quercus* species previously present in the forest understory (Retana et al., in press). Transformation to mixed oak coppices has accounted for 40% (16023 ha) of the surface burned in those wildfires. The two dominant *Quercus* species present in these burned areas are *Q. ilex* L. and *Q. cerrroides* Willk. et Costa, two co-occurring Mediterranean species in many sites of the West Mediterranean Basin (Castroviejo et al. 1990). Both species share in common several life history-traits, as their resprouting ability after disturbances, but they differ markedly in their leaf habit: *Q. cerrroides* is a deciduous oak, while *Q. ilex* is an evergreen species with smaller and thicker leaves.

In this study, we explore the resprouting patterns and the response to different intensities of stool cleaning of these two co-occurring Mediterranean oak species in mixed extensive coppices appeared after large wildfires. According to previous information available on the differences among deciduous and evergreen species and the response to thinning in

Mediterranean oaks, we have tried to achieve two objectives. The first objective is to analyse resprouting patterns after fire of these two oak species with different leaf habit, in stands of different site quality. We expected a marked interaction between species and site quality in the resprouting process, because 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 & van der Peijl 1993; Berendse 1994). Instead, deciduousness implies a shorter photosynthetically active period that should be compensated by a larger rate of light saturated assimilation (Eamus 1999), but that would require higher levels of nutrient and water availability. The second objective is to evaluate 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 & Turrel 1992; Riba 1998), but a high number and size of new resprouts appearing after cleaning could further decrease the performance of these selected shoots. Our expectation was that there was a trade-off between these two processes, because the increase in the intensity of stool cleaning might also increase resource availability and, consequently, the growth of a new resprouts wave.

## Material and Methods

### *Study area*

This study was carried out at the regions of Bages and Berguedà (41° 45' to 42° 6' N; 1° 38' to 2° 1' E, Catalonia, NE Spain), in an area affected by a wildfire occurred in July 1994 which burned ca. 24.300 forested ha. Climatic conditions varies from dry-subhumid to subhumid Mediterranean (according to the Thornwaite index), with mean annual temperature of 10-13 °C and mean annual precipitation of 550-900 mm. . According to the data provided by the Forest Ecological Inventory of Catalonia (IEFC), and the Spanish Second National Forest Inventory (IFN2), both of them 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 (Gracia et al. 2000). After the fire event, and due to the failure of *P. nigra* regeneration (see Habrouk et al. 1999, Retana et al. in press), the vigorous 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., in press).

### *Experimental design and sampling*

The experiment was conducted from 1999 to 2001. Four zones of mixed *Q. cerrioides* and *Q. ilex* coppices, differing markedly in their site quality characteristics, were chosen in the 1994 burned area. The quality of the site was assessed through inspection of the IEFC and

IFN2 forest inventories databank, analysing the main topographic and structural characteristics of the 10 inventoried plots surrounding each of our selected experimental areas. Those data pointed out that zones differed in their main topographic and structural characteristics (Table 1). They also significantly differed in wood production (ANOVA,  $F = 4.43$ ,  $p = 0.0100$ ,  $df = 3$ ), which was one of the main criterion to establish the two site quality categories: LOW (low productivity) and HIGH (high productivity). In choosing these two categories we did not attempt to establish the site quality of both zones in absolute terms but to compare them on a relative approach.

Each sampling area was subdivided into five adjacent plots (ca. 30 x 30 m), where the following experimental treatments of resprouts selection and pruning were applied: i) selection of the single tallest resprout (S1), ii) selection of the single tallest resprout and pruning of 40% of its height (S1P), iii) selection of the 3 tallest resprouts (S3), iv) selection of the 3 tallest resprouts and pruning of 40% of their height (S3P) and v) control (C), with neither selection nor pruning. Those treatments were 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, as well as pruning in the appropriate treatments, was done by hand.

On each plot, 20 *Q. cerrioides* and 20 *Q. ilex* stools were chosen. Before applying the experimental treatments, the following variables were measured on these individuals to characterise the resprouting pattern: stump surface (as an estimator of the size of the individual before the fire event), total number of resprouts, basal diameter of the tallest resprout, total height and crown cover of the stool (measuring two perpendicular diameters of the crown and computing the projection as an ellipse). Total biomass of each stool was also estimated applying allometric equations relating resprout basal diameter and biomass to 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) of the removed resprouts during the cleaning process of stools. We constructed a different equation for each species, *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 (growth) in these variables. Growth was calculated both in absolute and relative terms. Relative growth rate (RGR) was calculated as  $RGR = (\ln X_i / \ln X_{i-1})$ , where  $X_i$  was the value of the selected variable in year  $i$ , and  $X_{i-1}$  was its value in the previous year.

**Table 1.** Main topographic and structural characteristics of the 10 nearest inventoried plots in the IEFC and IFN2 surrounding each of the experimental plots established in the actual study in two different site quality areas.

Site Quality	Plot	Altitude	Slope	Tree density (i. ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> .ha <sup>-1</sup> )	Wood Production (m <sup>3</sup> .ha <sup>-1</sup> .year <sup>-1</sup> )
Low	1	435±29	23.6±3.9	857.2±187.0	10.1±1.8	1.54±0.26
	2	666±17	17.3±2.7	1333.8±121.8	16.8±2.0	2.09±0.31
High	1	572±11	14.2±2.3	1170.8±182.5	21.9±1.9	3.60±0.50
	2	580±24	12.4±2.7	1813.2±266.0	21.7±2.9	3.68±0.76

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 on the selected resprouts, but also on the appearance of new resprouts during the two years monitoring. In each stool, we recorded the number and mean height (five measures per stool) of the new resprouts appeared at the stool basis, one and two years after the experimental treatment (winter 2000 and winter 2001, respectively).

### *Data analysis*

As in the five applied treatments the number of resprouts measured was different (namely one in S1 and S1P and three in S3, S3P and C), two different types of analysis were carried out for height, basal diameter, and canopy cover: 1) comparing the single value in S1 and S3 with the mean value of the three resprouts in S3, S3P and C and 2) comparing the results of the single resprout of S1 and S1P and the value of the dominant (tallest) resprout in S3, S3P and C. As both analysis provided the same results, we have focused in the results section on the second alternative, because the tallest resprout usually maintains its dominance and reflects the vigour of the stool (Gracia 2000).

The effects of species (*Q. ilex*, *Q. cerrioides*), site quality (LOW, HIGH), plot (nested within site quality) and experimental treatment (S1, S1p, S3, S3p, C) on the structural variables of stools have been analysed by a three-way ANOVA model while their effect on changes (growth) in the measured variables has been analysed by a three-way repeated-measures ANOVA model including the time effect (1999, 2000). In those treatments with three resprouts measured (S3, S3P and C), we have also analysed the variability (asymmetry) among them using the coefficient of variation (CV) of the former variables. The effects of the species, site quality, experimental treatment and time on the CV of height and diameter growth were analyzed by a repeated-measures three-way ANOVAs. 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).

## **Results**

### *Patterns of resprouting of Q. ilex and Q. cerrioides after fire*

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 considered (Table

2). There was a strong influence of site quality in those differences (see interaction SPECIES x SITE QUALITY in Table 2). *Q. cerrrioides* individuals had higher number of resprouts, crown cover and total biomass than *Q. ilex* in the higher quality (HQ) sites, while the opposite trend occurred in the low-quality (LQ) zones (Figures 1 A, C and E). Differences in total height were less evident, but also showed the same pattern (Figure 1D). Stump surface was similar in both species at the HQ sites but much higher in *Q. ilex* than in *Q. cerrrioides* at the LQ stands (Figure 1 B). Finally, basal diameter of the dominant resprout was always higher in *Q. cerrrioides*, although differences between species were especially contrasted in HQ sites (Figure 1F). As expected, no significant differences were found among groups of stools assigned to the different cleaning treatments before the onset of the experiment (Table 2).

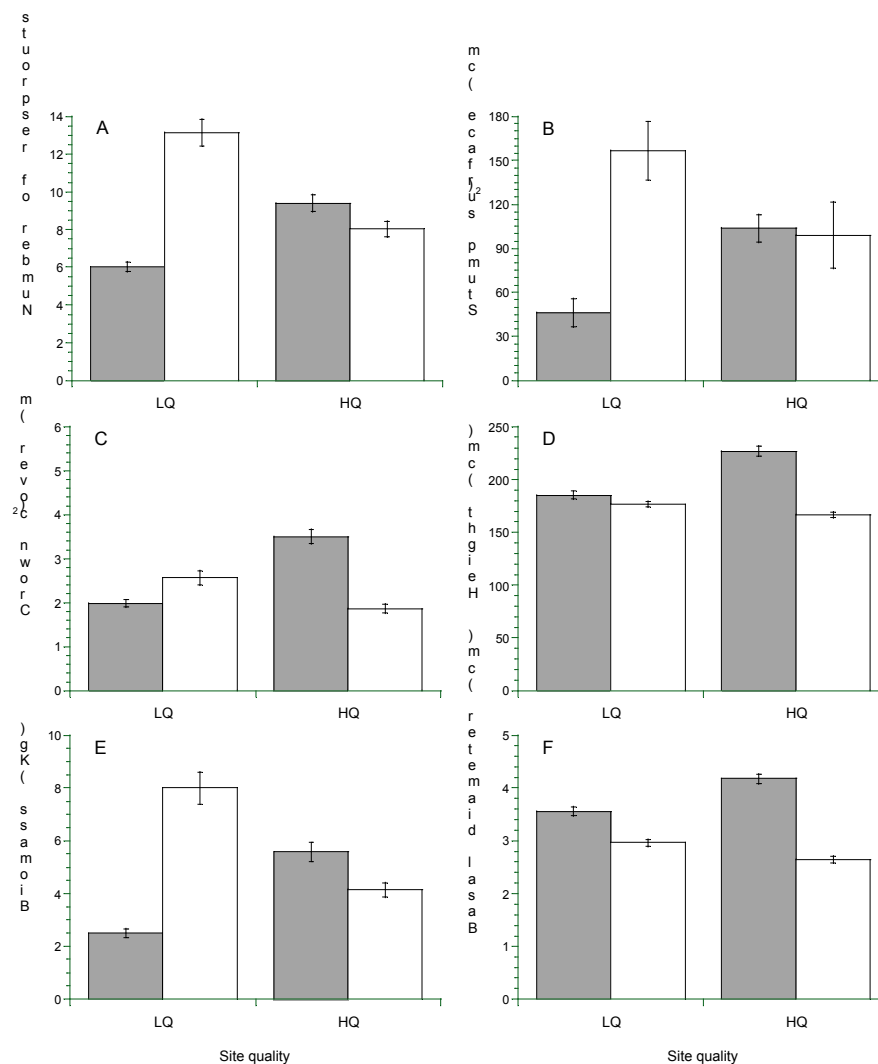
#### *Response of resprouted stools of Q. ilex and Q. cerrrioides after stool cleaning*

Results concerning the effects of the experimental treatments on the growth of *Q. cerrrioides* and *Q. ilex* stools during two consecutive years are summarised in table 3. Resprout selection and pruning (TREATMENT effect, in Table 3) enhanced both absolute and relative growth in height and diameter of the dominant resprout in both species (Figure 2 A,B,C,D). The highest growth was observed in stools with a single resprout and the lowest growth was found in control individuals. Concerning the effects of pruning, both pruned and not pruned individuals showed a fairly similar response except that individuals with a single resprout selected and pruned (S1P) had a higher absolute height growth than individuals with a single resprout selected but not pruned (S1) and that pruned individuals (both S3P and S1P) had higher canopy growth than pruned ones (Figure 2 E,F). The effects of the experimental treatments in height growth varied during the two consecutive years (TREATMENT x YEAR, in Table 3): absolute and relative height growth of S1 and S1P individuals was higher during the first year, while that of S3, S3P and control was higher in 2000 (Figure 3). *Q. cerrrioides* and *Q. ilex* differed in their growth in height ( $24.0 \pm 0.9$  and  $18.4 \pm 0.6$  cm, respectively), diameter ( $0.75 \pm 0.02$  and  $0.61 \pm 0.02$  mm, respectively) and canopy cover ( $1858 \pm 209$  and  $1123 \pm 105$  cm). Specific differences were observed along the two years monitored (interaction SPECIES x YEAR in Table 3): both species attained a similar absolute growth in height and diameter during 1999, which further increased for *Q. cerrrioides* but decreased in *Q. ilex* during 2000 (Figure 4 A,B). In relative terms, height and diameter growth of *Q. ilex* was higher than in *Q. cerrrioides* the first year after the experiment onset, but the opposite pattern was observed for the second growing season (Figure 4 C, D). Site quality influenced both height, diameter and canopy cover growth (only in absolute terms), with different patterns depending on the year (interaction QUALITY x YEAR, in Table 3). As shown in Figure 5, height, diameter and canopy cover growth was similar in HQ and LQ sites in 1999, but was higher in LQ compared to HQ sites in 2000. The three-order interaction SPECIES x QUALITY x YEAR revealed that the higher height growth observed in *Q. cerrrioides* in comparison to *Q. ilex* during 2000 was specially relevant in those LQ sites.

**Table 2.** F values from ANOVA tests of effects of species (Sp), site quality (Q), plot (nested within site quality) and experimental treatments (T) on different morphological variables related to the sprouting patterns of *Q. cerrroides* and *Q. ilex* stools 5 years after the fire event. Significant coefficients (at  $\alpha=0.05$  when the sequential Bonferroni method is employed) are indicated in bold.

Source	Total Height	Resprout basal diameter	Canopy cover	Biomass	Number of resprouts	Stump area
Species	<b>93.78</b>	<b>175.80</b>	<b>17.00</b>	<b>27.6</b>	<b>35.28</b>	<b>10.66</b>
Site Quality	<b>18.88</b>	0.01	2.92	1.81	3.76	2.09
Treatment	1.1	1.17	0.80	0.95	2.21	2.26
Plot (Q)	<b>20.31</b>	0.64	<b>8.67</b>	4.16	<b>7.62</b>	<b>8.57</b>
Sp x Q	<b>56.41</b>	<b>36.47</b>	<b>69.75</b>	<b>84.76</b>	<b>81.42</b>	<b>13.53</b>
Sp x T	1.56	1.72	0.50	0.72	0.64	1.76
Q x T	3.23	3.59	1.69	2.10	2.57	0.50
Sp x Q x T	2.28	0.73	1.47	2.85	1.92	0.95

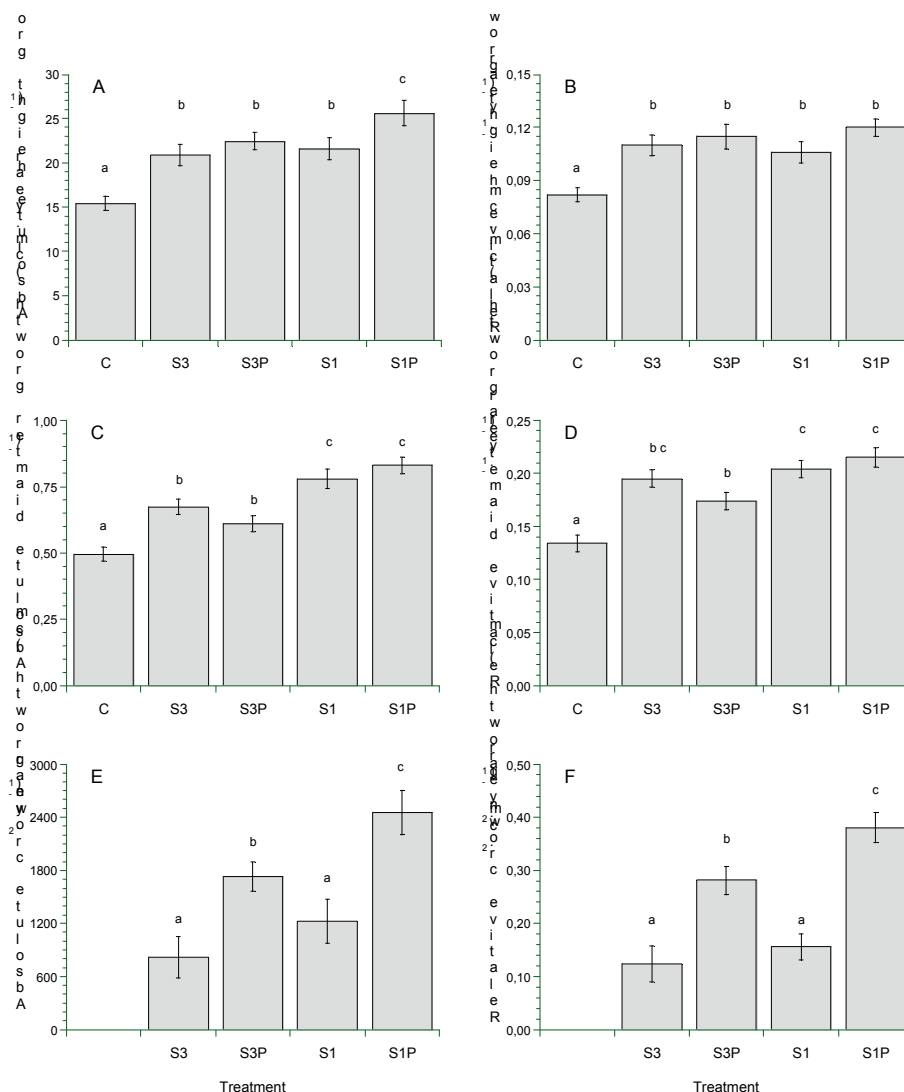
Some of these differences were also evident when analysing the influence of the same factors in the differences (asymmetry, measured as the coefficient of variation) in height and diameter growth among the three main resprouts, in those treatments where three resprouts were reserved (S3 and SP3) and controls (C). Asymmetry among resprouts was higher in *Q. cerrrioides* in comparison with *Q. ilex* for height (ANOVA,  $F=27.9$ ,  $p<0.001$ ,  $df=1$ ) and diameter (ANOVA,  $F=31.5$ ,  $p<0.001$ ,  $df=1$ ). The interaction SPECIES x QUALITY for height (ANOVA,  $F=8.41$ ,  $p=0.0039$ ,  $df=1$ ) revealed that asymmetry in resprout height did not vary according to site quality for *Q. cerrrioides* ( $0.16\pm 0.01$  in LQ and  $0.15\pm 0.01$  in HQ), but increased from LQ to HQ for *Q. ilex* ( $0.09\pm 0.01$  in LQ and  $0.13\pm 0.01$  in HQ). In the two species, the asymmetry in diameter growth diminished according to the treatments applied (ANOVA,  $F=8.9$ ,  $p=0.0034$ ,  $df=2$ ) from the control individuals ( $0.26\pm 0.01$ ) to S3 ( $0.22\pm 0.01$ ) and S3P ( $0.21\pm 0.01$ ).



**Figure 1.** Mean  $\pm$  standard error of (A) total number of resprouts, (B) stump surface ( $\text{cm}^2$ ), (C) crown cover ( $\text{m}^2$ ), (D) height (cm), (E) aerial biomass per stool (kg) and (F) basal diameter (cm) of the dominant resprout of resprouting *Q. cerrrioides* (solid bars) and *Q. ilex* (open bars) stools in high-quality (HQ) and low-quality (LW) stands



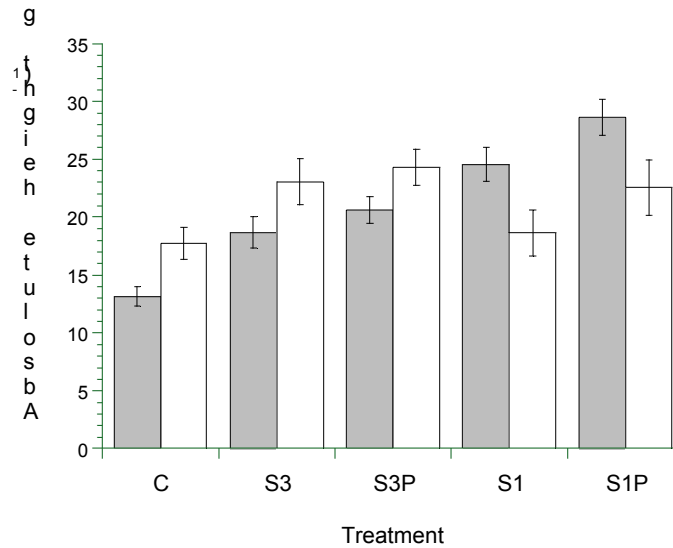
The number of new resprouts produced at the root collar during the experiment and the height they reached were significantly influenced by the interaction between species and site quality, while the later variable was also influenced by the treatment received (Table 3). As shown in Figure 6, the mean number of new resprouts was much higher in *Q. ilex* than in *Q. cerrrioides*, but differences between species were higher in LW than in HQ sites (Figure 6 A). No differences existed in the height of new resprouts among the two species in LQ, while new resprouts of *Q. cerrrioides* were taller than



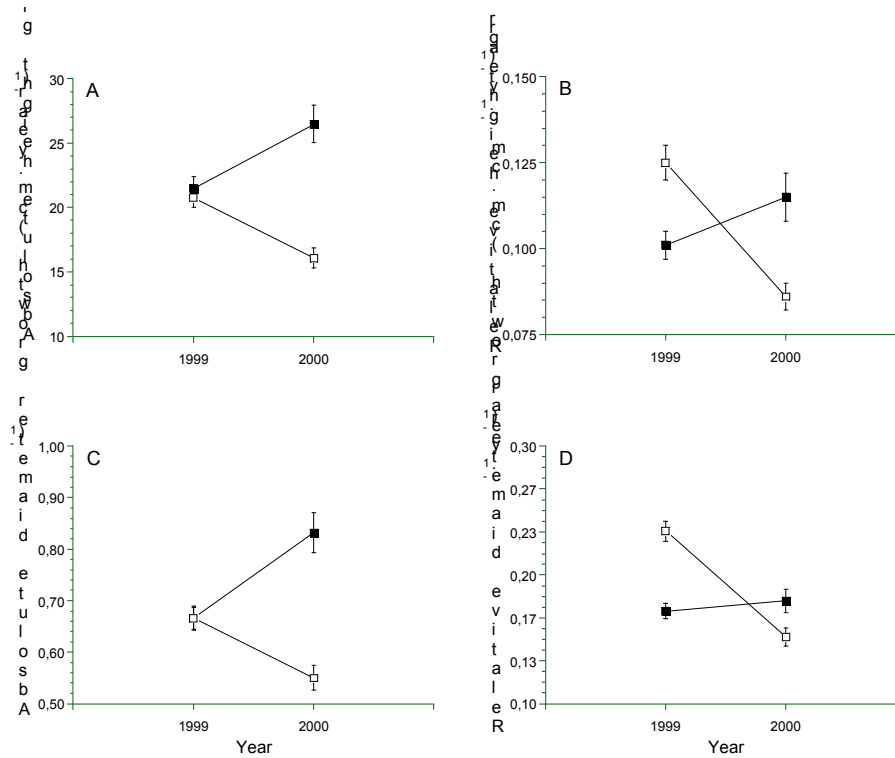
**Figure 2.** Mean  $\pm$  standard error of absolute and relative growth in height (A,B), diameter (C,D), and crown cover (E,F) of stools subjected to different cleaning intensities: control (C), selection of the 3 tallest resprouts (S3), selection of the 3 tallest resprouts and pruning of 40% of their 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.

those of *Q. ilex* in HQ (Figure 6 B). The intensity of stool cleaning increased the height of the new resprouts (TREATMENT effect, in Table 3), being taller in S1 and S1P individuals

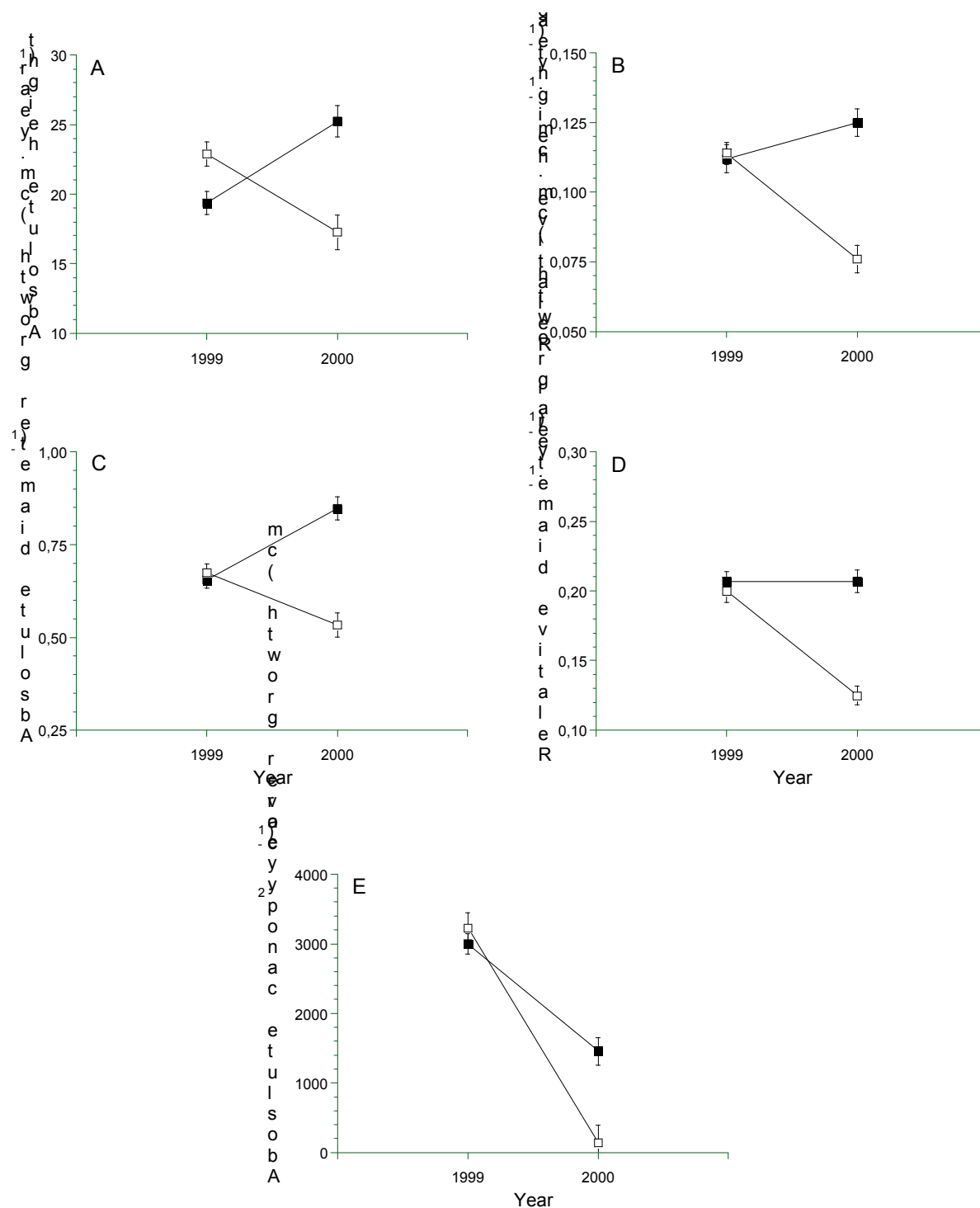
( $68.6 \pm 2.3$  cm and  $71.5 \pm 2.5$  cm, respectively) than S3 and S3P ( $48.9 \pm 2.0$  cm and  $49.6 \pm 2.1$  cm, respectively). New resprouts attained roughly 33% of the height of the uncut dominant resprouts in S1 and S1P, but only 22% in the S3 and S3P treatments at the end of the experiment.



**Figure 3.** Mean  $\pm$  standard error of absolute growth in height of stools subjected to different cleaning intensities: control (C), selection of the 3 tallest resprouts (S3), selection of the 3 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).



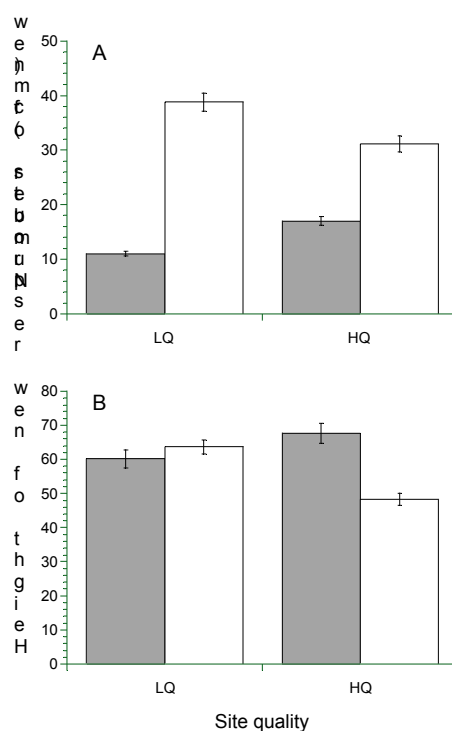
**Figure 4.** Mean  $\pm$  standard error of absolute and relative growth in height (A, B) and diameter (C, D) of *Q. cerrioides* (solid dots) and *Q. ilex* (open dots) stools during two consecutive years (1999, 2000).



**Figure 5.** Mean  $\pm$  standard error of absolute and relative growth in height (A, B), diameter (C, D) and crown cover (E) of stools growing in high quality (solid dots) and low quality (open dots) sites during the two consecutive years (1999, 2000).

**Table 3.** F values from ANOVA tests of effects of species (Sp), site quality (Q), plot (nested within site quality), experimental treatments (T) and time (Y) on different morphological variables related to the sprouting patterns of *Q. cerrroides* and *Q. ilex* individuals during 2 years after the experiment onset. Significant coefficients (at  $\alpha=0.05$  when the sequential Bonferroni method is employed) are indicated in bold.

Source	Height Growth		Basal diameter growth		Canopy cover growth		Number of new basal resprouts	Height of new basal resprouts
	Absolute	Relative	Absolute	Relative	Absolute	Relative		
Species (Sp)	<b>32.05</b>	0,17	<b>29.43</b>	5,89	<b>17.21</b>	3,52	<b>194,30</b>	10,03
Site Quality (Q)	5.10	<b>23,74</b>	<b>32.41</b>	<b>42,12</b>	9.44	<b>75,32</b>	0,28	10,33
Treatment (T)	<b>11.52</b>	<b>7,64</b>	<b>21.04</b>	<b>17,51</b>	<b>17.05</b>	<b>39,19</b>	4,83	<b>35,72</b>
Plot (Q)	<b>29.51</b>	<b>40,13</b>	<b>14.32</b>	<b>13,37</b>	<b>7.31</b>	6,01	6,95	3,75
Sp x Q	10.08	0,01	4.74	4,29	6.14	0,46	<b>202,04</b>	<b>16,76</b>
Sp x T	2.00	0,92	2.49	1,93	4.89	2,28	3,09	3,13
Q x T	1.89	1,61	0.13	0,49	0.46	2,72	3,54	1,32
Sp x Q x T	0.28	0,59	1.39	0,53	0.38	2,68	2,99	0,44
Year (Y)	0.02	7,87	0.89	<b>27,07</b>	<b>208.98</b>	<b>713,52</b>	1,08	<b>251,38</b>
Sp x Y	<b>26.07</b>	<b>33,19</b>	<b>28.93</b>	<b>37,75</b>	6.15	<b>12,46</b>	5,45	5,14
Q x Y	<b>35.73</b>	<b>30,48</b>	<b>41.25</b>	<b>27,03</b>	<b>10.96</b>	0,02	1,10	0,34
T x Y	<b>6.93</b>	<b>8,41</b>	2.32	2,61	<b>5.84</b>	5,04	0,41	4,10
Y x Plot (Q)	6.86	<b>7,91</b>	2.83	4,14	0.66	0,29	1,25	<b>11,44</b>
Sp x Q x Y	<b>18.65</b>	<b>18,39</b>	3.42	0,11	1.87	3,70	3,03	4,22
Sp x T x Y	2.16	2,14	<b>5.76</b>	<b>4,96</b>	1.22	2,73	0,64	1,46
Q x T x Y	1.13	1,29	2.03	1,50	0.72	2,39	4,42	3,30
Sp x Q x T x Y	1.82	1,36	2.50	2,88	0.50	1,44	2,33	0,27



**Figure 6.** Mean  $\pm$  standard error of the total number (A) and height (B) of new resprouts appeared in *Q. cerrroides* (solid bars) and *Q. ilex* (open bars) stools growing in high quality (HQ) and low quality (LQ) sites.

## Discussion

*Q. ilex* and *Q. cerrrioides* showed, 5 years after the fire event, significant differences in their architecture (s.e. number, height, diameter and biomass of resprouts) with a strong influence of site quality (Table 2 and Figure 2). Differences in the number of resprouts have been argued to depend on specific characteristics that determine the size of the bud bank (Canadell & López Soria 1998) thus, con-generic species sharing common life-history traits, such as *Q. ilex* and *Q. cerrrioides*, may differ in the number of buds located at the root collar which finally will determine the number of resprouts. Nevertheless, the number of resprouts may also depend on the previous size of stools before the disturbance event (Retana et al. 1992), because there is a positive relationship between stump surface, which is an estimator of stool size, and the abundance of buds (Djema 1995). On the basis of our results, we can not discard specific differences in the bud bank, but there was probably an important effect due to differences in stool sizes: i.e. *Q. ilex* showed higher number of resprouts than *Q. cerrrioides*, and consequently total biomass in the low quality zones because the former species had bigger stools, while in the high quality areas, where both species had a similar size, the number of resprouts and biomass was almost the same.

The vigour of the stool, which can be related with variables such as height and basal diameter of dominant sprouts (Carvalho & Loureiro 1996), has been suggested to be probably more dependent on other factors, not directly determined by the previous size of the individual, such as specific differences in below-ground reserves (Mesléard & Lepart 1989; Canadell & López Soria 1998) or site characteristics (Gracia 2000). In this study, *Q. cerrrioides* presented larger height, crown cover and basal diameter than *Q. ilex* in high quality stands, where stools of the two species were of similar size, while the two species reached similar height and basal diameter in low quality stands, where *Q. cerrrioides* stools were much smaller than *Q. ilex* ones (Figure 2). These differences in the resprouting vigour of *Q. ilex* and *Q. cerrrioides* stools have to be examined in light of possible differences in the two species in ecophysiological and morphological traits. Different studies have suggested that possible growth differences between deciduous and evergreen Mediterranean oaks would relay in architectural (e.g. LAI) rather than ecophysiological differences (Joffre & Rambal 1999). Thus, the comparisons of ecophysiological traits among deciduous and evergreen Mediterranean oaks have pointed out a similar response in terms of net CO<sub>2</sub> assimilation rates and stomatal conductance in both groups, and even a similar construction cost of leaves (Damesin et al. 1998). In that sense, an extensive survey carried out in our study areas has found larger leaf area per resprout in *Q. cerrrioides* stools than in *Q. ilex* (Bonfil et al., unpublished results), which could explain the higher resprouting vigour, in terms of height and diameter of shoots, exhibited by the former species. Since initial rapid height growth has been considered a key factor determining competitive advantages after disturbance (Oliver & Larson 1990), these results suggest an

advantage of the deciduous *Q. cerrrioides* over the evergreen *Q. ilex* in the range of site conditions analysed. However, the higher resprout production in *Q. ilex* stools could be a trait that would provide this species a better ability to resprout after repeated disturbances (Lloret & Lopez Soria 1993; Espelta et al. 1999).

Stool cleaning increased the absolute and relative growth in height, diameter and canopy cover of the reserved resprouts in the two species. Elimination of resprouts has been demonstrated to drastically change the competitive relationships among the reserved resprouts in the stool (Ducrey & Boisserie, 1992) with two major consequences. On the one hand, growth enhancement of reserved resprouts is positively correlated with cleaning intensity, with better results being obtained when cleaning affects more than 75% of shoots for young coppices (Ducrey & Turrel 1992), or more than 50% of the basal area in mature stands (Mayor & Rodà 1993). Besides, cleaning of stools equalises the growth of the reserved sprouts as it diminishes the asymmetry in their growth due to competition for limited below-ground resources and light, which would favour growth in dominant resprouts in detriment of the more suppressed ones (Weiner 1990; Riba 1997; Vilà & Terradas 1995). 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 (Figure 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 & Terradas 1994) was diminished enough through stool cleaning to allow the different treatments to maintain similar growth rates in both S1 and S3 treatments. Moreover, the three reserved resprouts in S3 had similar diameter growth rates in comparison with the hierarchy exhibited by the three resprouts monitored in the control treatment.

Coupled with the effects of the cleaning of stools, pruning had a major impact on increasing crown cover, both in S3 and S1 individuals. Pruning of lower branches is a common practice to enhance growth and shape of trees (Meson & Montoya, 1993) but, as observed in our study, it may have a weak influence on basal diameter and height. In young stems, pruning may increase the growth in diameter in the upper part, leading to more “cylindrical” trunks, but it usually has nil effect in the height of those stems (as oak resprouts) where apical dominance is not completely established (Montoya 1996). As stated by our results, instead of modifying height, pruning may promote an increase in lateral growth and leafiness of the resprout, probably due to the amelioration of resource disposal in the remaining branches (Montoya 1996; Jackson et al. 2000).

The different treatments of stool cleaning and pruning did not interact with site quality, suggesting a similar release of resources in stools of areas of different site quality after experimental treatments. However, individuals from the different site quality types showed a different growth pattern during the two years monitored: absolute and relative diameter and height growth decreased during the second year in high quality sites, but increased (or maintained for relative diameter growth) in the low quality stands. The importance of site quality in the resprouting process, has been previously reported, both in terms of stool survival (López Soria & Castell 1992) and growth of resprouts (De la Fuente et al. 1997). In *Q. ilex* coppices, differences in the resprouting dynamics between sites with contrasted site quality have been attributed to the rapid expansion of resprout canopies in the higher quality sites in comparison with the lower quality ones (Gracia 2000). In our study areas, the very large canopy growth occurred during the first year after cleaning drastically diminished in the second year, with very important differences in HQ compared to LQ sites. The large canopy growth in the HQ zones could probably promote interference competition among resprouts, causing lower height and diameter growth during the second year, while the moderate canopy expansion in the LQ areas during the first year could produce larger canopy, height and diameter growth during the second year. This interference among resprouts has been the main cause evoked to explain the low growth rates exhibited by Mediterranean oak coppices (see Gracia & Retana 1996; Espelta et al. 1999) and the progressive reduction on the growth of adult trees in mature stands several years after thinning (Mayor & Rodà 1993).

*Q. ilex* and *Q. cerrroides* stools manifested a similar response to the different cleaning intensities, but the two species showed a different growth pattern in basal diameter, height and canopy cover (only in relative terms) with time: growth of *Q. cerrroides* increased while that of *Q. ilex* decreased during the second year monitored. This specific differences in growth could be caused by the reported differences among the two species in shoot leafiness, but also by the different ability of the two species to produce new basal resprouts (Table 3). The larger number of new resprouts flushed from the root collar in *Q. ilex*, four times higher than that of *Q. cerrroides* in LQ sites and almost double in HQ sites, reflected large differences in the size of the bud bank in both species (see, a comparative study of the bud-bank in con-generic species in : Sennerby-Forse & Zsugga 1995). This second wave of resprouts might compete with the reserved shoots (Vigneron 1988), and thus decrease the potential growth of *Q. ilex* during the second year. In that sense, production of epicormic shoots and 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). In our study, the number of new resprouts was not influenced by the intensity of cleaning, but 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. On the other hand, asymmetrical competition among reserved shoots and new resprouts would be more intense in S3 than in S1 stools, thus reducing the future chances of this new wave of resprouts in the former treatment.

Conservation and amelioration of extensive Mediterranean oak coppices developed after fires requires comprehension about different management alternatives involving various species under heterogeneous environmental conditions. In that sense, both *Q. cerrroides* and *Q. ilex* resprout vigorously after fire although they exhibit different trends: higher vertical growth in *Q. cerrroides* resprouts, but higher potential of resprouting in *Q. ilex* stools. Those trends may be of paramount importance according to the disturbance regime, with both species favoured under a different frequency of disturbances (lower for *Q. cerrroides* and higher for *Q. ilex*). Concerning the management practices experimented, the results obtained in this study point out that the more conservative strategy assayed (the reservation of three resprouts per stool) should be recommended, because it provides similar growth rates than the more intense one, but the new, undesired resprouts reach lower development. Cleaning of stools in both species seems to be a reasonable management strategy under a wide range of environmental situations, at least those reflected in our areas of different site quality. Nevertheless, although this practice has proven to ameliorate the growth of both *Q. ilex* and *Q. cerrroides*, it would be preferably carried out in *Q. cerrroides* stools, due to the higher growth rates and the lower appearance of resprouts observed in this species.

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