# The role of disturbance in the co-existence of the evergreen *Quercus ilex* and the deciduous *Quercus cerrioides*

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#### Abstract.

Question: Which is the response of the evergreen *Quercus ilex* and the deciduous *Q. cerrioides* to repeated disturbances?

**Location:** central Catalonia (northeastern Spain), in the areas affected by two of the largest historically recorded wildfires in NE Spain: the Bages-Berguedà fire (24 300 ha forested area burned in July 1994), and the Solsonès fire (14 300 ha burned in 1998).

**Methods:** Survival and growth of individuals of *Quercus ilex* and *Q. cerrioides* were evaluated in plants subjected to different fire histories and experimental disturbances (burning, cutting or clipping) applied either before or after summer.

**Results:** Survival was high (>99%), with both species showing a similar high resistance to disturbances. Growth after experimental disturbance was positively related to the size of the individual before the latest forest fire occurred. Fire history had a large effect on resprout growth, as the repeated incidence of disturbances lowered the capacity of individuals to grow. The type and season of experimental disturbance experienced by plants had a large effect. Individuals that experienced total above-ground loss had lower growth rates than those with partial loss. A similar pattern was observed in individuals disturbed after the summer in relation to those disturbed before summer.

**Conclusions:** The larger growth rates recorded in Q. *cerrioides* across all fire histories and experimental treatments, and the higher vulnerability of Q. *ilex* to increased fire frequency, intensity of experimental disturbance, and disturbance season, provide evidence for the relatively high susceptibility of the latter to repeated disturbances. This view disagrees with the larger resilience of this species compared to co-existing deciduous oaks, as reported.

**Keywords:** Burning; Clipping; Fire; Survival; Growth; Resilience; Resprouting; Mediterranean region; *Quercus*.

## Introduction

In mediterranean-type climates, both vegetation structures and individual species show a wide array of responses to disturbances such as forest fires, clear cutting or browsing (Naveh & Liberman 1984; Blondel & Aronson 1999). Resprouting is one of the main regeneration mechanisms of woody plants here (Keeley & Zedler 1978; Espelta et al. 1999). It is a life-history trait allowing plants to recover from biomass loss (Bellingham & Sparrow 2000; Pausas 2001), and a complex process dependent on disturbance frequency (Riba 1998), site characteristics (Cruz et al. 2002; Gracia & Retana in press), and species attributes (Lopez Soria & Castell 1992; Espelta et al. 2003). The interaction between disturbance regime and specific differences in the response to resource availability (e.g. water availability) could play a crucial role in driving the distribution patterns of many plant species in a mediterranean-type climate (Zavala et al. 2000).

It has been assumed that disturbance would favour Mediterranean evergreen sclerophyllous Quercus over deciduous broad-leaved species (see Mazzoleni & Spada 1992; Mason 2000; Quézel & Médail 2003). Evergreen species may be better adapted to harsh environments than deciduous species due to the lower resource-loss ratios of the former (Aerts 1995). Thus, critical conditions during post-disturbance regeneration (e.g. water stress or high temperatures) would have a more negative impact on deciduous broad-leaved than on evergreen sclerophyllous oaks (Mazzoleni & Spada 1992). This view has been confirmed by palynological records showing that similar proportions of deciduous and evergreen oaks were present in the Mediterranean Basin around 5000 yr B.P., while evergreens expanded in more recent times (Riera-Mora & Esteban-Amat 1994), as a presumed consequence of human activity leading to a progressive increase in the disturbance regime (García-Latorre & García-Latorre 1996; Quézel & Médail 2003). These studies suggest that the co-existence of evergreen and deciduous Mediterranean oaks may be disturbance-mediated, although no

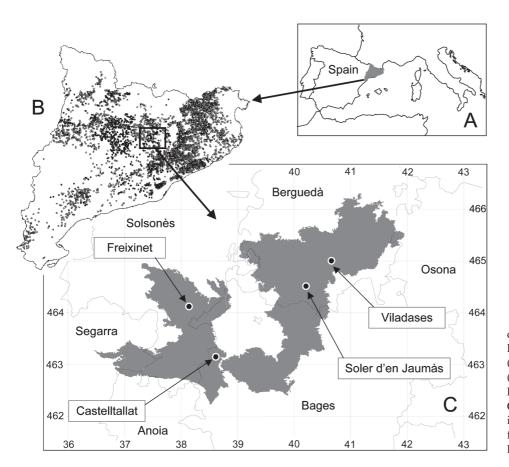
experimental evidence of the comparative response of these species to different types, frequencies and seasons of disturbance has been provided.

We analyse the response to different frequencies, types and seasons of disturbance of two contrasting species: Quercus ilex, a typically Mediterranean evergreen oak (Terradas 1999), and the deciduous Q. cerrioides from the Quercus humilis group with several probable introgressions form other deciduous Quercus species. According to the presumed differences between deciduous and evergreen oaks, our first hypothesis is that the evergreen Q. ilex will show higher resistance to repeated disturbances than the deciduous Q. cerrioides. A second hypothesis states that differences between the two species will increase with disturbance severity and when disturbance occurs after the summer, the drought season of the year. We evaluate survival and growth of Q. ilex and Q. cerrioides in response to different fire histories, and different experimental disturbances varying in their increasing intensity (clipping, cutting and burning), and the season of the year they occurred: at the onset and the end of the summer - this because the summer is a critical season regarding water shortage and high temperatures in Mediterranean regions.

#### Methods

#### Study site

The study was carried out in central Catalonia (northeastern Spain), a region affected by two of the largest historically recorded wildfires: the Bages-Berguedà fire, which burned ca. 24 300 ha of forested land in July 1994, and the Solsonès fire, which burned ca. 14 300 ha in 1998 (Fig. 1). Prior to these fires, theses areas had not burned for at least 70 yr. The climate of the region is drysubhumid Mediterranean (according to the Thornwaite index). According to the data provided by the Ecological Forest Inventory of Catalonia (IEFC) carried out in 1993 (Gracia et al. 2000), natural Pinus nigra ssp. salzmanii forests were dominant before the fires occurred (78% of the burned surface), with Q. ilex and Q. cerrioides being extensively present in their understorey. After the fires, P. nigra did not regenerate (Retana et al. 2002), and resprouting of Quercus transformed most forested areas into mixed Quercus forest, which show the typical structure of a coppice woodland, with numerous multi-stemmed individuals (Espelta et al. 2003).



**Fig. 1.** Geographical location of: **A.** Catalonia in the Iberian Peninsula; **B.** *Quercus ilex* (black dots) and *Q. cerrioides* (white dots) in plots of the Ecological Forest Inventory of Catalonia; **C.** Sites sampled in this study in the areas affected by the 1994 and 1998 large wildfires (shaded).

#### Experimental design

To analyse the response of Q. *ilex* and Q. *cerrioides* to repeated disturbances, the experimental design included three factors: (1) recent fire history, (2) site, and (3) type of experimental disturbance.

## Fire history

All the areas selected for this study had experienced at least one forest fire and, consequently, the above-ground parts of all *Q. ilex* and *Q. cerrioides* individuals originated from resprouting. Three different plot types were selected according to the time since the last fire or the recurrence of fire: plots that had experienced a forest fire in 1994: 'older burned area', hereafter F94, plots that had suffered a forest fire in 1998: 'recently burned area', F98, and plots that had experienced a natural forest fire in 1994 and a controlled fire in 1998: 'recurrently burned area', F94+98. In this case the severity of the second fire was probably lower, both because this fire occurred in winter and because the biomass that burned was considerably less than in a typical forest fire.

## Site

Two experimental sites, ca.  $30 \text{ m} \times 30 \text{ m}$  each, were chosen for each type of fire history plot (Fig. 1). Distance between sites of the same fire history area ranged between 4.5 and 14 km. According to data provided by the Ecological Forest Inventory of Catalonia (IEFC) (Gracia et al. 2000) from the five plots nearest to each study site, the sites were dominated by mixed and homogeneous *Q*. *ilex* and *Q*. *cerrioides* coppices but differed in some of their environmental characteristics (Table 1).

#### Experimental disturbance

In each site, seven disturbance treatments were applied to Q. *ilex* and Q. *cerrioides* individuals. Treatments consisted in applying three different types of disturbance of increasing intensity: clipping (half of the aerial biomass of each plant), cutting or burning, on two different dates (at the beginning and end of the summer, late June and early September 1999, respectively), and a

control treatment (not disturbed). The treatments are: (1) burning before summer (late June 1999): B1; (2) burning after summer (early September 1999): B2; (3) cutting before summer: C1; (4) cutting after summer: C2; (5) clipping before summer: P1; (6) clipping after summer: P2; (7) control: CT.

The experiment started in June 1999. In each site, 16 individuals per species were randomly assigned to each of the seven experimental treatments described below (112 individuals per species and site and a total of 1344 individuals studied). The previous size of the individual was measured before applying the experimental treatments. In the cutting and burning experiments, all living resprouts of each individual were cut down at their base and their fresh biomass was assessed with a field scale. The burning treatment consisted in applying the flame of a propane torch (at a mean temperature of 300 °C) directed to the base of the individual during three minutes (see Lloret & López-Soria 1993). This temperature was controlled through measurements with thermocouple sensors placed at the base of the individual, taken every 15 sec. In the clipping treatment the fresh biomass of cut resprouts was weighed and those resprouts remaining were tagged and their basal diameter was measured. In the control individuals every resprout was tagged and its basal diameter recorded. To estimate the standing biomass of cut and burned individuals before the experimental treatments were applied, dry biomass was estimated from a subsample of resprouts removed and weighed in the field, brought to the laboratory, and dried at 80 °C during 48 hr. In the clipped individuals, the same method was used to estimate the biomass of the resprouts removed (half of the total). To calculate the biomass of control individuals (not disturbed) and that of the remaining resprouts in clipped individuals, we used specific allometric equations between dry biomass and diameter of a sample of sprouts. Before the start of the experiment, individuals burned five years earlier (F94) had more biomass and more sprouts than individuals burned a year before the start of the experiment (either in F98 or F94+98). Q. cerrioides attained more biomass in F94 and F94+98, while differ-

**Table 1.** Main topographical, climatic and structural characteristics of the different sampling sites. Climatic information of each site was estimated through spatial interpolation of the nearest meteorological stations (Ninyerola et al. 2000). The proportion of the two species in the site is indicated in the last column.

	Fire history	Altitude (m)	Slope (°)	Aspect	Annual precipitation (mm·yr <sup>-1</sup> )	Mean annual temperature (°C)	Density before the fire (ind.ha <sup>-1</sup> )	Basal area before the fire $(m^2.ha^{-1})$	Q.ilex/ Q.cerrioides
Castelltallat	F98	$800 \pm 18$	$20 \pm 2$	S-SW	$721 \pm 19$	$11.4 \pm 0.7$	$945 \pm 128$	$19 \pm 2$	53/47
Freixinet	F98	$755 \pm 22$	$9 \pm 4$	N-NE	$699 \pm 21$	$11.8 \pm 0.8$	$1763 \pm 128$	$27 \pm 5$	59/41
Soler d'en Jaumas	F94, F94+98	$513 \pm 18$	$14 \pm 2$	S-SW	$709 \pm 18$	$12.7 \pm 1.0$	$960 \pm 152$	$18 \pm 2$	39/61
Viladasses	F94, F94+98	$596 \pm 26$	$13 \pm 3$	N-NW	$750 \pm 17$	$12.2 \pm 1.3$	$1433\pm240$	$18 \pm 3$	43/57

ences between species were less clear in F98. The number of resprouts was higher in *Q*. *ilex* than in *Q*. *cerrioides* in all fire history plots.

The responses to the treatments applied were recorded in July 2000, one year after the start of the experiment. Above-ground biomass was estimated using a procedure similar to that applied at the start of the experiment, i.e. the diameter of each resprout was measured and the total biomass of each individual was estimated by adding up the biomass obtained by the above-mentioned allometric regressions. In the cutting and burning treatments all resprouts observed in July 2000 were produced after the experimental treatments. In the clipped and control individuals we distinguished between not clipped resprouts and newly produced ones. Changes in biomass were expressed as net biomass increment (standing biomass of each individual at the end of the experiment minus biomass left after the application of the experimental treatments). Additionally, in order to analyse the main features of the resprouts that appeared after the experimental disturbances, the longest resprout of a subsample of cut, burned and clipped individuals was collected at the end of the study period, and its height, diameter and fresh weight recorded. They were brought to the laboratory to obtain their leaf area (using a LI-COR Model 3100, USA) and dry biomass (after drying at 80 °C).

## Statistical analyses

To analyse variations in survival according to the different factors tested, log-linear models were applied to the multiway contingency table obtained by indicating separately the number of living and dead individuals in each combination of the factors considered. The best model was considered to be the most acceptable one (goodness-of-fit P > 0.05).

The effects of the factors considered in net increment in biomass and number of resprouts produced were analysed by ANOVA tests. In these analyses, the residuals of the regressions of these variables against surface of the burned stumps were employed instead of their original values, in order to remove the effect of the size of individuals before the occurrence of the forest fires. Data of net increment in biomass were logtransformed. Inspection of residuals was carried out to check for normality and homoscedasticity. The sequential Bonferroni method was employed to control the group-wide type I error rate (Rice 1989). The same analyses were carried out to analyse biomass, length and leaf area of the largest resprout of burned, cut and clipped individuals.

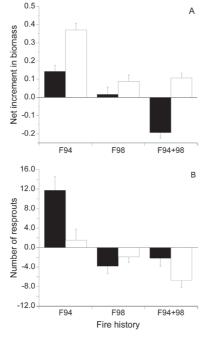
## Results

Survival of *Q. ilex* and *Q. cerrioides* was not significantly affected by the different experimental factors tested (log-linear model, goodness-of-fit P > 0.05). Survival of the two species was over 99%, with only 14 individuals (seven of each species) not resprouting from the 1344 considered in the study. All dead individuals were from the treatments that involved a complete loss of aerial biomass i.e., burned (10) or cut (4). Most (12) deaths occurred in the recently burned plots (F98).

In the two species, total biomass growth and number of resprouts produced after the experimental treatments increased significantly with individual size (linear regression;  $R^2 = 0.37$ , p < 0.001 for net increment in biomass;  $R^2 = 0.21, p < 0.001$  for the number of resprouts). The effects of the factors tested on these variables are summarized in Table 2. Both net biomass increment and number of resprouts produced were highest in F94 and lowest in F94-98 (Fig. 2). With respect to the interaction species  $\times$ fire history, net biomass increment was higher in Q. cerrioides than in Q. ilex individuals, and differences between species were higher in F94 and F94+98 than in F98 (Fig. 2). However, Q. ilex produced more resprouts than Q. cerrioides  $(23.7 \pm 1.2 \text{ and } 17.7 \pm 0.9 \text{ resprouts per})$ individual for Q. ilex and Q. cerrioides, respectively). The effect of site was also significant for the two variables analysed (Table 2), indicating spatial variability in the response of individuals to experimental treatments. Additionally, the experimental treatments significantly affected all the variables studied (Table 2). Net biomass increment was highest in control individuals, lower in clipped individuals and lowest in burned and cut ones (Fig. 3A). In all cases, individuals disturbed prior to the beginning of summer showed higher biomass increment than those disturbed at the end of the summer, although

**Table 2.** *F*-values from ANOVA tests of the effects of fire history, species, experimental disturbance and site (nested in fire history), applied on net biomass increment and number of resprouts produced. To remove the effect of individual size, the residuals of the regressions of the two variables against individual size were used instead of the original values. Significant coefficients (at  $p \le 0.05$  using the sequential Bonferroni method) are indicated in bold.

Source	df	Net increment in biomass	Number of sprouts 17.9	
Fire history (F)	2	44.2		
Species (Sp)	1	57.5	9.9	
Experimental disturbance (D)	6	10.3	22.3	
Site (Fire history)	3	14.8	5.9	
F×Sp	2	5.1	4.2	
$F \times D$	12	5.8	3.6	
$Sp \times D$	6	3.8	0.3	
$\mathbf{F} \times \mathbf{Sp} \times \mathbf{D}$	12	0.6	0.6	
Residual	1098			

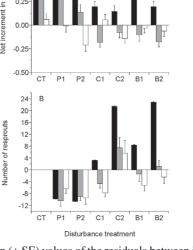


**Fig. 2.** Mean (+ SE) values of the residuals between individual size and (**A**) net biomass increment, and (**B**) number of sprouts, of Q. *ilex* (black bars) and Q. *cerrioides* (white bars) in plots of the three fire-history types. The analyses used the residuals after linear regression of the original variables against stump surface.

both types of individuals started resprouting in autumn. Conversely, the number of resprouts was higher in cut and burned individuals, with the maximum values obtained in those disturbed after the summer (Fig. 3B).

The interaction fire history × experimental disturbance was also significant for the two variables tested (Table 2). Control individuals showed a higher growth rate in F98 than in the other two fire history categories, and also compared to individuals in the different disturbance treatments (Fig. 3A). In the experimental treatments, the net biomass increment was higher in F94 than in the other two fire history categories. Individuals burned or cut after the summer showed a higher production of new resprouts in F94 compared to the plots with the other fire histories (Fig. 3B). The interaction species × experimental disturbance was also significant for net biomass increment (Table 2): the biomass increment of control and pre-summer clipped individuals was similar in both species, but attained higher values in Q. cerrioides than in Q. ilex in the other experimental treatments applied (Fig. 4), especially when burned after summer.

Biomass and length of the largest resprout produced after the experimental treatments increased significantly with individual size (linear regression;  $R^2 = 0.15$ , p < 0.001 for resprout biomass;  $R^2 = 0.16$ , p < 0.001 for



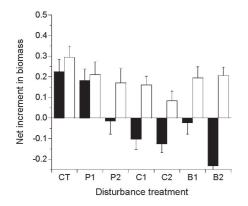
F94 F98 F94+98

**Fig.3.** Mean (+ SE) values of the residuals between individual size and net biomass increment (**A**), and number of sprouts produced (**B**) by individuals in plots of three fire-history types in the different experimental treatments. The analyses used the residuals after linear regression of the original variables against stump surface. Treatments: CT = Control; P1 = Clipping before summer; P2 = Clipping after summer; C1 = Cutting before summer; C2 = Cutting after summer; B1 = Burning before summer; B2 = Burning after summer.

resprout length), while leaf area did not (linear regression; p > 0.10). The effects of the factors tested on these variables, after removal of the effect of individual size, are summarized in Table 3. Biomass and length of this

**Table 3.** F-values from ANOVA tests of the effects of fire history, species, experimental disturbance and site (nested in fire history), applied on total biomass, length and leaf area of the largest resprout of individuals experimentally disturbed. To remove the effect of individual size, the residuals of the regressions of the two variables against individual size were used instead of the original values. Data of total biomass and length were log-transformed. Significant coefficients (at  $p \le 0.05$  using the sequential Bonferroni method) are indicated in bold.

Source	df	Total biomass	Length	Leaf area
Fire history (F)	2	5.9	9.9	0.7
Species (Sp)	1	39.3	138.9	20.9
Experimental disturbance (D)	5	54.4	33.0	6.9
Site (Fire history)	3	14.6	21.5	1.0
F×Sp	2	0.9	0.1	1.3
F×D	10	1.4	1.4	0.2
Sp ×x D	5	5.2	4.7	1.9
$\mathbf{F} \times \mathbf{Sp} \times \mathbf{D}$	10	1.1	1.4	0.4
Residual	378			

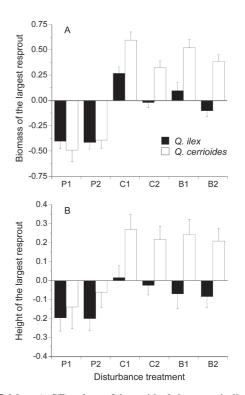


**Fig. 4.** Mean (+ SE) values of the residuals between individual size and net biomass increment of *Q. ilex* (black bar) and *Q. cerrioides* (white bar) in the different experimental treatments. The analysis used the residuals after linear regression of the original variables against stump surface. CT = Control; P1 = Clipping before summer; P2 = Clipping after summer; C1 = Cutting before summer; C2 = Cutting after summer; B1 = Burning before summer; B2 = Burning after summer.

resprout responded to fire history in a similar way to the whole individual: they showed the highest values in older burned areas and the lowest in the recurrently burned areas. With respect to the disturbance treatments, the length, biomass and leaf area of this resprout were higher in burned and cut individuals than in clipped ones, probably due to a dominance effect from the uncut resprouts in the latter. The three variables analysed showed significant differences between species (Table 3), with Q. cerrioides showing higher values than Q. ilex (length: 78  $\pm$  3 and 48  $\pm$  2 cm; biomass: 47  $\pm$  5 and 22  $\pm$  2 g; and leaf area:  $856 \pm 108$  and  $343 \pm 29$  cm<sup>2</sup>, respectively). Differences between species were lowest in the clipping treatments (Fig. 5), but increased in the other treatments, with Q. cerrioides attaining higher biomass and length than Q. ilex.

## Discussion

The high survival rates observed in the two species in relation to all fire histories and experimental disturbances applied, contradict our hypothesis and suggest that both the evergreen *Quercus ilex* and the deciduous *Q. cerrioides* show a similarly high resistance to repeated disturbances. These results agree with the reported resistance of evergreen Mediterranean oaks to fire (Trabaud 1991; Gracia & Retana in press), and provide experimental evidence of a similar performance of a Mediterranean deciduous oak (see also Espelta et al. 2003). Although the reiteration of disturbances had only a small effect on the survival of individuals, their growth was largely affected



**Fig. 5.** Mean (+ SE) values of the residuals between individual size and total biomass (**A**) and length of the largest resprout (**B**) produced by *Q. ilex* (black bar) and *Q. cerrioides* (white bar) individuals in the different experimental treatments. The analyses used the residuals after linear regression of the original variables against stump surface. P1 = Clipping before summer; P2 = Clipping after summer; C1 = Cutting before summer; C2 = Cutting after summer; B1 = Burning before summer; B2 = Burning after summer.

by the disturbance regime (fire history, experimental disturbances and season). In all cases, growth after experimental disturbance was positively related to the size of the individual present before the latest forest fire occurred (indicated by the size of the stump). Larger individuals are likely to have both more reserves and a larger bud bank, which can result in a better ability to produce new resprouts (Ducrey & Turrel 1992; Lloret & López Soria 1993). Q. ilex has been reported to allocate as much as half of its total biomass to the root system (Canadell & Rodá 1991), and the same pattern is expected for Q. cerrioides, as has been shown in other deciduous oak species (Reich et al. 1980; Rundel 1980). Notwithstanding this, the ability to resprout in response to disturbances was largely affected by site (site effect in Table 2), pointing out variations in edaphic and/or climatic conditions (see López Soria & Castell 1992; Riba 1998).

Concerning the different fire histories considered, the size of individuals in the F98 and F94+98 plots at the beginning of the experiment was similar. This suggests that two successive fires in an interval of four years do not

limit the resprouting ability of these oaks, either because below-ground reserves are still considerable after a single fire, or because this time period of four years is enough to replenish their reserves (similar results were obtained by Canadell & Lopez Soria 1998 for other Mediterranean resprouters). However, it should be taken into account that the second fire was of lower intensity. After the experimental treatments had been applied, the importance of the fire histories became more evident, and biomass and number of resprouts produced were higher in F98 than in F94+98 plots (Fig. 2), suggesting that increasing the incidence of disturbances in short time intervals would have a negative effect on the capacity of individuals to resume growth (see Canadell & Lopez Soria 1998).

Besides the effects of previous individual size and fire history, the intensity of the experimental disturbance experienced by individuals brought about large differences in their growth response, with a higher decrease in biomass increment in individuals that suffered total aboveground loss (burning or cutting) compared to those that experienced a partial loss (clipping). The fact that individuals that were cut and burned showed a similar growth response, indicates that the experimental fire did not cause a major reduction in the bud bank, probably due to the fact that the root collar is frequently located an inch or more below the soil surface, where fire temperatures are lower (De Bano et al. 1976). Conversely, the time of the disturbance (at the beginning or at the end of the summer) had great consequences in all experimental treatments (Fig. 3). Overall biomass growth decreased in individuals disturbed after summer, probably due to the stress that individuals face during this season in Mediterranean-type climates, involving the exhaustion of below-ground reserves. These results provide experimental evidence to support the major role attributed to lower water availability in reducing the resprouting response of Mediterranean species (see Ducrey & Turrel 1992; Cruz et al. 2002). Differences between individuals disturbed before and after summer also stress the importance that the season of disturbance may have in determining space recovery, and thus, dominance in the individual community, one of the supposed advantages of the resprouting process (Bellingham & Sparrow 2000).

Differences in growth between species were evident, but they refuted a better performance of the evergreen Q. *ilex. Q. cerrioides* showed larger growth rates across all fire histories and experimental treatments, whereas Q. *ilex* growth proved to be more vulnerable to increased fire frequency (Fig. 2), intensity of experimental disturbance, and season of disturbance (either before or after summer) (Fig. 4). Previous studies have suggested that deciduous and evergreen Mediterranean oaks exhibit similar ecophysiological traits (e.g. net CO<sub>2</sub> assimilation rates and stomatal conductance), and that growth differences between them may be related to morphological differences (e.g. leaf area) (see Damesin et al. 1998; Joffre & Rambal 1999). The higher capacity of this deciduous oak to recover after disturbances could be related to a more rapid foliage recovery, and a consequently higher carbohydrate synthesis than in *Q. ilex*, as shown by the higher leaf area recorded for the largest resprout. Moreover, growth in *Q. ilex* could be constrained by a higher investment in longer lasting, sclerophyllous leaves (Aerts 1995). Notwithstanding the lower growth rate of *Q. ilex*, it is important to point out that this species was able to produce more resprouts than *Q. cerrioides* in all fire histories analysed.

The results obtained in this study provide evidence for the relatively high susceptibility of Q. ilex to repeated disturbances, a view that disagrees with the previously suggested larger resilience of this species compared with co-existing deciduous oaks (Tatoni & Roche 1994). Moreover, based on this experimental study, it may be hypothesized that a moderate disturbance regime would favour Q. cerrioides over Q. ilex, and promote, in the long run, the withdrawal of the latter in areas where they currently co-exist. This trend could help to explain the recent increase in dominance of deciduous oaks in areas where previously intense human pressure has decreased during the last century (Bacilieri et al. 1993; Bonin & Romane 1996). However, attention should be paid to the high production of resprouts observed in Q. ilex in all fire histories studied. This observation suggests a larger budbank in this species that should be taken into account as a potential positive mechanism to overcome a higher frequency and intensity of the disturbance regime than the one applied in this study. On the other hand, the interaction between disturbance regimes and future scenarios of increasing temperatures and water stress as a result of climate change, stands out as crucial to understand potential changes in the dominance between co-existing deciduous broad-leaved and evergreen sclerophyllous Mediterranean oaks.

Acknowledgements. We thank T. Valverde, J. Meave and F. Lloret for their careful revision of the original manuscript. M. Bascompte made the analysis of the dominant resprouts. X. Cebolla, J. Prieto, I. Gimeno, R. Almeida and J.L. Ordóñez helped with fieldwork. This research was partly funded by INTERREG II (EU) project 'Reconstruction of forest land-scapes affected by large wildfires events' and the Department of Environment (Generalitat de Catalunya). The first author is grateful for the support received through a post-doctoral studentship from DGAPA, Universidad Nacional Autónoma de México.

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Received 11 June 2003; Accepted 26 January 2004. Co-ordinating Editor: A. Chiarucci.