

Is selective thinning an adequate practice for adapting *Quercus ilex* coppices to climate change?

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Abstract

• **Introduction** Future climatic scenarios demand an increasing involvement of management for forest preservation, but little is known on how forestry practices will benefit stands in facing variation of climatic components.

• **Objectives** We investigated how selective thinning affected the response of an old *Quercus ilex* coppice to 6 years of throughfall reduction. Plots thinned from below ($\approx 30\%$ basal area removal) and unthinned plots were subject to either throughfall exclusion (TE; $\approx 33\%$ throughfall reduction) or normal rainfall. Stem diameter growth, stem survival, and seed and sprout production were measured.

• **Results** TE did not have a significant effect on stem growth but it reduced the production of viable acorns. Also, in the absence of thinning, TE accelerated the mortality of small stems and stimulated the emergence of new sprouts. Thinning reduced stem mortality, enhanced growth of residual stems, and caused a profuse emission of resprouts. Thinning also increased total seed production, but the crop had a large proportion of aborted seeds, especially in those areas subject to TE.

• **Conclusion** The mere elimination of suppressed and diseased stems in abandoned *Q. ilex* coppice stands helps remaining trees to cope with current and future (probably longer and more intense) droughts. Potentially drier con-

ditions might attenuate the success of thinning in producing a viable seed crop.

Keywords Stem growth · Seed production · Sprouting · Drought · Forest adaptation strategy

1 Introduction

It is predicted that temperatures will raise and rainfall will decline during the twenty-first century in Mediterranean-type climate regions (Giorgi 2006). Summer water shortage is already a primary limiting factor for tree growth, seed production, and seedling recruitment in these regions (Carevic et al. 2010; Castro et al. 2005; Espelta et al. 2008). Therefore, future increases in aridity will likely cause profound changes in the structure and composition of Mediterranean-type forests, especially where the water demand of the dominant species is already marginally met (Bréda et al. 2006; Breshears et al. 2009). Silvicultural management must be oriented to attenuate future drought impacts, but more research is still needed for anticipating the extent of such impacts and testing potential mitigation practices.

Thinning has a positive effect on dense forests stands by tempering water stress in seasonally dry environments (Bréda et al. 1995; Cañellas et al. 2004; Dwyer et al. 2007). Alleviation of competition by selective felling improves the vigor of residual trees as they benefit from the water, nutrient, and light resources no longer exploited by felled trees (Aussenac 2000; Corcuera et al. 2006; Gracia et al. 1999; Misson et al. 2003). More vigorous trees, with better water status and larger carbon pools, are more likely to resist to and/or recover from water- and carbon-limiting conditions (Breshears et al. 2009; Kohler et

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al. 2010; McDowell et al. 2008). This underlies the expectation that thinned stands may be better prepared to cope with an intensification of stresses in the near future, as what occurs after natural events of drought-induced thinning (Millar et al. 2007). Moreover, thinning often promotes seed production (Healy et al. 1999), which in a longer term can make stands with low genetic diversity more resilient to drought (and other potential hazards) if a more genetically diverse bank of seedlings eventually establishes (see Espelta et al. 1999).

Nonetheless, it is important to investigate whether reductions in precipitation interact on silvicultural practices aimed at improving stand health. Long-term studies (e.g., comprising exceptional climatic years) in stands submitted to different intensities of thinning can help us decide an optimal structure of forests to meet drier future conditions (Gea-Izquierdo et al. 2009; Kohler et al. 2010; Misson et al. 2003). Also, the application of silvicultural practices in stands where rainfall is experimentally reduced offers a good opportunity to examine the effectiveness of drought mitigation measures. Previous studies have evaluated the effects of partial rainfall exclusion on diverse functional processes (Borghetti et al. 1998; Brando et al. 2008; Hanson et al. 2003; Limousin et al. 2009, 2010a; Ogaya and Peñuelas 2007a, b), but there are very few studies addressing whether stand structure manipulation affects tree responses to rainfall reduction. Cotillas et al. (2009) observed a transient positive effect of thinning on tree growth in a Mediterranean mixed oak forest subject to a 15% reduction in rainfall. New experiments focusing on the vegetative and reproductive output of trees are needed.

Quercus ilex L. is an evergreen broadleaf tree covering more than 65,500 km² in the Mediterranean basin (Quézel and Médail 2003). Intense forest exploitation through millennia has favored its expansion and persistence in detriment of other tree species unable to resprout, such as *Pinus* sp., or less tolerant of nutrient and water scarcity, such as deciduous trees (Quézel and Médail 2003). As a consequence of past intensive coppicing and a lately decreasing demand for forest products (e.g., wood, charcoal, and acorns), dense abandoned *Q. ilex* coppice stands spread out nowadays over nutrient- and water-poor skeletal soils where trees grow very slowly (Gracia et al. 1999). These systems are viewed as notably resilient to perturbations and climatic fluctuations, a belief based on a “perpetual” capacity of trees to resprout and a presumed buffering effect of the root system from environmental fluctuations (Bond and Midgley 2001; Lloret et al. 2004). However, crowded over-aged forests are particularly susceptible to a potential increase in drought intensity. Ogaya and Peñuelas (2007a) observed that an experimental augmentation of drought reduced growth and exacerbated mortality of trees within a dense *Q. ilex* coppice stand in the Iberian Peninsula.

The abandonment of short rotation coppice management along the twentieth century has been a widespread phenomenon. As stated above, thinning is likely to mitigate the impact of a potential increase of drought severity in these systems. This work reports on how a sustained reduction in rainfall over 6 years—imposed by a throughfall exclusion system—affected the vegetative and reproductive output of *Q. ilex* trees in previously thinned and unthinned areas of an old coppice stand. We applied a selective thinning from below expecting some improvements for residual stems (i.e., increments in diameter growth and seed production and a reduction in mortality) both in throughfall exclusion and control areas. However, we hypothesized that throughfall reduction would particularly exacerbate competition for water in the unthinned areas and hence would enhance mortality and reduce growth and seed production with respect to control areas with natural rainfall; that is, we expected that the benefits of thinning would be more apparent under experimentally drier than current conditions.

2 Materials and methods

2.1 Site, experimental design, and study period

This study was conducted in a *Q. ilex* stand in southern France (Puéchabon State Forest; 43°44'29" N, 3°35'45" E; 270 m a.s.l.). The stand has been coppiced for centuries and the last clear-cut took place in 1942. No wildfire has occurred or any silvicultural treatment has been applied ever since. *Q. ilex* dominates the overstory (with a mean canopy height ≈5.5 m), while shrubs and saplings of *Buxus sempervirens*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Pistacia terebinthus*, and *Phyllirea latifolia* are abundant in the understory. The bedrock is Jurassic limestone and the soil is very stony (75% of stones by volume for the top 0–50 cm and 90% below). The climate is Mediterranean, with cold and wet winters alternating with warm and dry summers. Mean annual rainfall is 914 mm and mean annual air temperature is 13.1°C. A more detailed description of the study area is reported by Allard et al. (2008).

At the study site, three 20×20-m size plots were selected along a 400-m transect within flat areas of fairly homogeneous vegetation. A selective thinning from below (sensu Assmann 1970; hereafter thinning) was applied to half of each plot, leaving the other half untouched. In turn, half of each thinned and unthinned subplots were submitted to partial throughfall exclusion, while the other two halves were left as controls. Thus, each plot represented a complete block with the following four treatments: no thinning and no throughfall exclusion (UC), thinning and no throughfall exclusion (TC), no thinning and throughfall

exclusion (UE), and thinning and throughfall exclusion (TE). Structural characteristics of subplots (10×10 m size) were similar before application of treatments (Supplementary Table 1).

The thinning was made in March 2003 by removing 30% of total basal area (i.e., 29% of *Q. ilex* basal area and 27% excluding standing dead stems, see Supplementary Table 1). Dead, diseased, and suppressed stems were felled. Plant area index estimated at 0.5-m height with optical methods declined from 2.66 to 1.48 m² m⁻² after thinning. This large decline relative to that in basal area was due to the removal of individuals of *B. sempervirens* and other shrubs of dense foliage and intricate branching, which however account for a small proportion of total basal area; the decline in leaf area index of *Q. ilex* was probably lower. We distinguished two types of stems: those clumped together at the base and those separated from its nearest neighbor. Both types are probably resprouts from the last cutting in 1942. Within the clumps, one to five stems were cut leaving typically the two larger ones. The ratio of clumped to single stems after thinning was similar among treatments—1.5 for UE and UC, 1.3 for TE, and 1.2 TC—to control for a potential effect of stem type on the response to treatments.

The throughfall exclusion system was set up immediately after thinning. A system of PVC rain gutters was installed below the tree canopy at a variable height of 1.5–0.5 m to make water runoff (Supplementary Fig. S1). Gutters covered 33% of the ground area, reducing 27% and 29% of net precipitation in the unthinned and thinned subplots, respectively, due to canopy interception. Taking into account stemflow, interception by the canopy, and by gutters in the case of throughfall exclusion subplots, yearly averaged net precipitation at the soil level was 69.1% of incident rainfall for treatment UC, 79.8% for TC, 50.4% for UE, and 56.5% for TE (see Limousin et al. 2008 for more details). On the control subplots, the same area was covered by gutters (upside down) in order to homogenize whole canopy albedo and understory microclimate conditions in both subplots.

Meteorological conditions during the study period (2003 to 2008) are shown in Table 1. We highlight that all growing seasons during this period were warmer than last 25-years' average, particularly that of 2003. We also underline the severe drought that occurred during the growing season of 2006, with 61% lower rainfall than

average, and the exceptionally wet 2008 year, with 55% higher rainfall than average during the same growth period (April–August).

2.2 Field measurements

Stem growth was calculated from diameters measured at breast height (dbh) every winter from 2002 to 2008 (with a diameter tape) in all stems larger than 1 cm dbh. We used an allometric relationship between dbh and total above-ground biomass (AB) to estimate mass accumulation in the four treatments (AB=209.3 dbh^{2.157}, R²=0.945, n=22). Survival of stems was also monitored annually during the study period.

Annual seed production was estimated by means of seed traps systematically distributed beneath the canopy. In each plot, 12 circular traps per treatment (0.35 m of diameter) were placed at ≈1.5 m above the ground to avoid post-dispersal seed removal by mammals. Small holes were drilled at the bottom of each trap to facilitate draining of water. Trap content was collected monthly, and once at the laboratory, all acorns were further classified into three different categories: (1) aborted (incompletely or mal-developed seeds, with length <13 mm or diameter <7 mm), (2) infested by insects (having signs of larvae predation, such as gnaw marks or holes), and (3) sound (attaining mature seed size). For each fraction, all seeds were counted and the entire sample was oven-dried at 60°C for 48 h and weighed to the nearest 10⁻⁴ g.

In March 2009, i.e., 6 years after thinning, we counted and measured the diameter of all stump resprouts in the thinned subplots. Neither dead nor pre-thinning resprouts were included into data analyses. Pre-thinning resprouts were identified by having hardly noticeable bud scars on the main axis, rough bark, and typically more than 15 growth units. We noted whether resprouts were from a thinned clump (Supplementary Fig. S2) or a single stem (119 vs. 91, respectively). The diameter of the stumps was similar in the control and throughfall exclusion subplots (7.2±0.3 vs 7.0±0.2 cm, respectively) to control for a potential effect of stump size on resprouting (Espelta et al. 1999). We also counted and measured the diameter of all sprouts emerging at the base of a sample of stems (88 clumped vs. 73 single) in the unthinned subplots. Sampled stems had similar diameter in the control and throughfall exclusion subplots (8.0±0.3 vs 7.9±0.2 cm at breast height, respectively).

Table 1 Cumulated rainfall (millimeter) and mean temperature (°C) for the six study years

Data are from a meteorological station located in the study area. The average is from 1984 to 2008

	2003	2004	2005	2006	2007	2008	Average
Annual rainfall	1,311	990	832	952	682	1,231	914
April–August rainfall	225	340	200	97	311	387	250
Mean annual temperature	13.8	13.0	13.0	14.1	13.8	13.6	13.1
Mean April–August temperature	20.6	17.9	19.0	19.6	18.9	18.6	17.7

During the first 4 years of the study, leaf water potential (Ψ_{pd}) was measured before dawn with a pressure chamber (PMS Instrument Co. 7000, Albany, USA) to estimate plant water status. Two/three leaves from four replicate trees per treatment were periodically measured in one of the blocks during spring and summer. Leaves were taken from the top of the canopy and were measured within the following minute.

2.3 Data analyses

We considered individual stems to be the experimental unit for analyses of predawn leaf water potential, mortality, growth, and sprouting (presence, abundance, and diameter of the dominant sprout). We considered block, thinning, throughfall exclusion, and stem type (single vs. clumped) as independent factors for models of annual mortality, growth, and sprouting; second order interactions among factors (except for block) were included in the models. Because the interactions of stem type with the other factors were not significant, we present data means pooled for single and clumped stems. Initial stem diameter was used as a covariate to account for potential unnoticed differences in stem size before application of treatments. Data of Ψ_{pd} , seed production, and diameter of the dominant sprout were transformed to fulfill assumptions of normality and homoscedasticity. All analyses were carried out with Statistica (v. 6, Statsoft Inc. 2001), using generalized linear models (GLMs) with different link functions depending on the distribution of the response variable.

Stem survival was tested using two complementary approaches. On one hand, Kaplan–Meier analyses were performed to test whether stem survival rate differed by effect of thinning and throughfall exclusion over the 6-year study period. On the other hand, differences in annual mortality were analyzed by using GLMs assuming a binomial distribution for the dependent variable and a logit link function between predictor and response.

Absolute and relative annual stem diameter increments through the 6-year study period were analyzed incorporating sampling year as a repeated-measures factor. An identity link function was specified for these normally distributed variables. The relative stem diameter increment was calculated by dividing the absolute annual increment by the initial stem diameter. GLMs were also made to analyze annual growth in each year.

The changes in seed production in response to thinning and throughfall exclusion for the whole period were analyzed using a repeated-measures approach. Seeds from all traps per treatment were pooled for processing until 2006 ($n=3$ plots). For the last two crops (2007 and 2008), differences in seed production (separated into their three different categories) by effect of both factors were evaluated using a factorial ANOVA, with $n=36$ traps.

Binomial distribution and logit link function were specified for the presence of sprouts per stump/stem. For abundance of sprouts, following a Poisson distribution, we used GLMs with logarithmic link functions. Finally, we specified an identity link function to compare the diameter of the dominant sprout per stump/stem between treatments.

To check for a potential confounding effect of the plot border on results, those trees less than 2 m from the border were excluded from the data set and the analyses of stem mortality and growth repeated. Since similar results were obtained in both cases, we present the analyses made with the whole data set. Seed traps and trees sampled for sprouting were already more than 2 m away from the border.

Finally, we used GLMs to test for differences in structural features at the stand level between treatments and dates. Whenever significant (at $P<0.05$), post-hoc Tukey's HSD tests were used to separate means.

3 Results

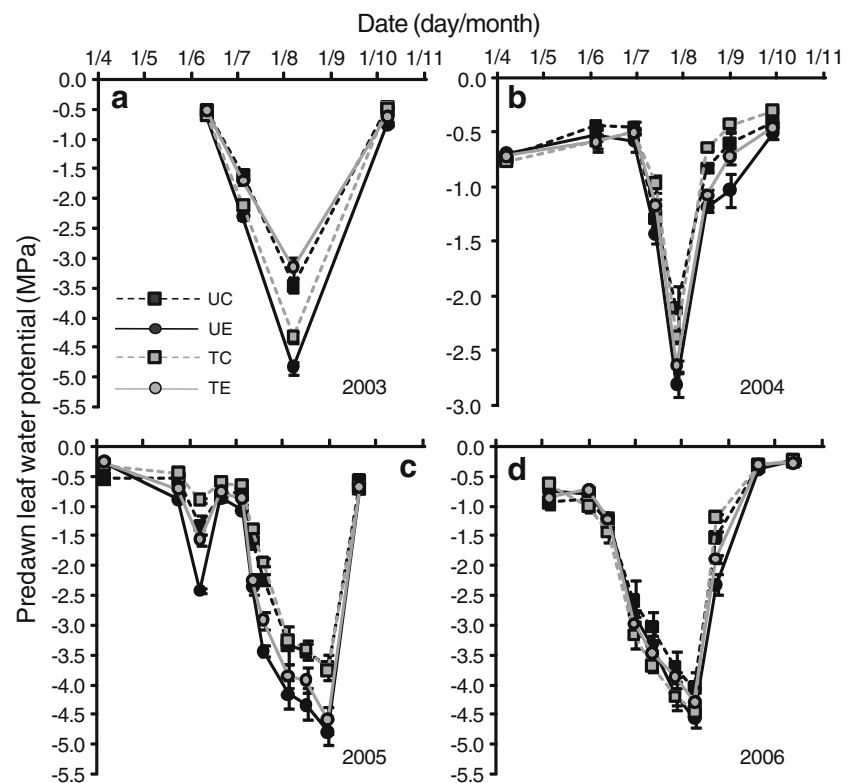
3.1 Tree water status

Predawn leaf water potential (Ψ_{pd}) was significantly affected by thinning and throughfall exclusion, but differences strongly varied as a function of year and sampling season (Fig. 1). Ψ_{pd} was significantly higher in the thinned subplots than in the unthinned subplots during summer in two years ($F=15.4$, $P<0.01$ for 2003 and $F=7.1$, $P<0.05$ for 2004), but no effect of thinning was generally seen in spring (all $P>0.10$, except in 2005 with $F=74.1$ and $P<0.001$). Throughfall partial exclusion caused a reduction in Ψ_{pd} in all years (all $P<0.01$) except 2006 ($P>0.10$). This effect was again stronger in summer than in spring, as indicated by the significant interaction between sampling date (treated as repeated measures) and throughfall exclusion factors (all $P<0.001$). The only exception occurred during the dry spring of 2005 (Fig. 1), when water deficit was lower in the control subplots ($F=64.9$, $P<0.001$). Finally, a significant interaction between both factors (thinning and throughfall exclusion) was detected during the summer of 2003 ($F=305.3$, $P<0.001$), thinning exercising a positive effect on Ψ_{pd} in the throughfall exclusion subplots ($F=170.8$, $P<0.001$) and a negative effect in the control subplots ($F=139.2$, $P<0.001$).

3.2 Stem mortality

As expected, stem mortality was higher in the unthinned subplots (3% year⁻¹, i.e., 197 stems ha⁻¹ year⁻¹) than in the thinned subplots, where only five stems died by the end of the study ($\chi^2=5.59$, $P<0.001$, Fig. 2). Mortality in the unthinned subplots was mainly of small stems, with 69% of

Fig. 1 Seasonal variation of predawn leaf water potential from 2003 to 2006 (a–d) in thinned and unthinned subplots (gray and black symbols and lines, respectively) further subject to either throughfall exclusion (circles, solid lines) or not (squares, dotted lines). Notice the different Y-scale for 2004. Symbols are means \pm SE ($n=4$)



stems smaller than 4 cm dbh dying through the study period but none greater than 8 cm dbh (P for the covariate initial stem diameter < 0.05 in all analyses). Mortality thus had a minor influence in terms of stand biomass, reaching 0.18% of initial above-ground biomass over the course of the study. Throughfall exclusion accelerated stem death in the unthinned subplots (Fig. 2). By the end of the second year, cumulative mortality reached 8.3% of initial stems (533 stems ha^{-1}) in the exclusion subplots and 4.9% (300 stems ha^{-1}) in the control subplots (Wald=6.01, $P < 0.05$; Fig. 2a). However, differences by effect of exclusion disappeared for the last 4 years (all $P > 0.10$).

3.3 Stem growth

Mean absolute stem diameter increments were significantly higher in the thinned than the unthinned subplots in all years except 2007, such that cumulative growth by the end of 2008 was clearly higher in the thinned subplots ($F=45.2$, $P < 0.001$, year treated as repeated measures; Fig. 3). Stem diameter growth rates averaged for the 6 years of study were 0.9 and 0.5 mm year^{-1} in the thinned and unthinned subplots, respectively. The same result was obtained when diameter increments were expressed relative to the initial diameter. Relative stem growth rates through the 6 years of study were 1.07% year^{-1} in the thinned subplots and 0.69% year^{-1} in the unthinned subplots ($F=38.1$, $P < 0.001$). On the contrary, the rainfall partial exclusion did not exercise

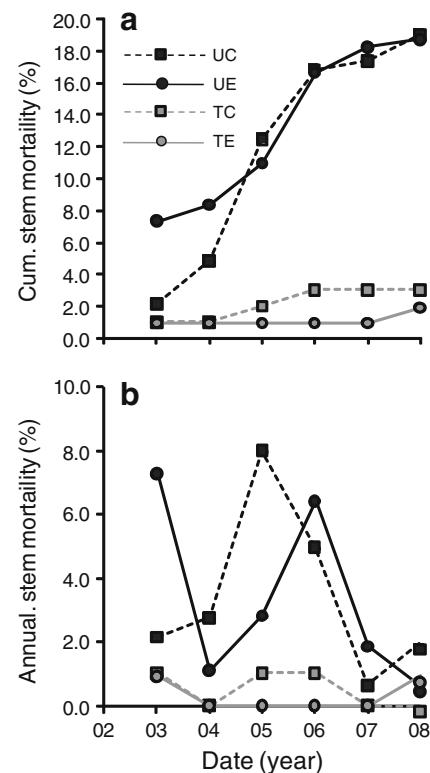


Fig. 2 Cumulative (a) and annual mortality (b) in thinned and unthinned subplots (gray and black symbols and lines, respectively) further subject to either throughfall exclusion (circles, solid lines) or not (squares, dotted lines). Symbols are means \pm SE ($n=98$ –180 for year 2003)

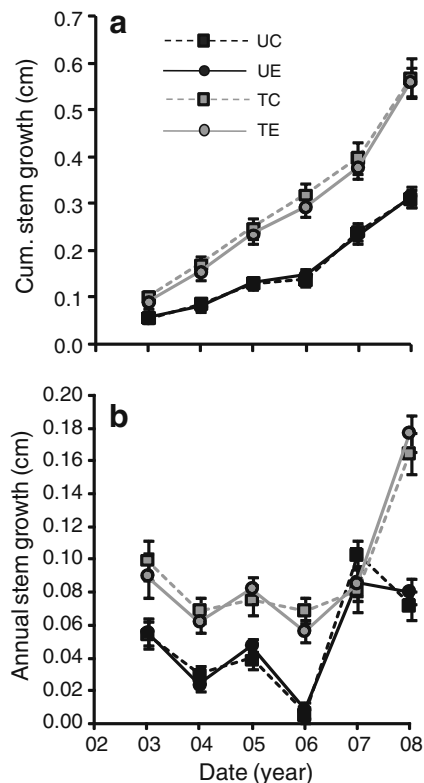


Fig. 3 Cumulative absolute stem diameter growth (a) and annual absolute stem diameter growth (b) in thinned and unthinned subplots (gray and black symbols and lines, respectively) further subject to either throughfall exclusion (circles, solid lines) or not (squares, dotted lines). Symbols are means \pm SE ($n=95-177$ for year 2003)

any significant effect on the absolute ($P>0.10$; Fig. 3) and relative stem growth rates ($P>0.10$; 0.85% year⁻¹ in the control subplots and 0.90% year⁻¹ in the subplots with throughfall exclusion). Similar effects of thinning and throughfall exclusion were obtained when growth was separated by diametric classes (data not shown) and when it was estimated at the stand level (Supplementary Table 1).

3.4 Seed production

The seeding process was largely influenced by thinning and throughfall exclusion. On one hand, total seed production was higher in the thinned than the unthinned subplots ($F=13.08$, $P<0.001$; Fig. 4). When analyzed separately by categories (Fig. 5), thinning caused a significant increment on the number of aborted acorns ($F=5.01$, $P<0.05$), but had no significant effect on the number of sound ($F=3.30$, $P=0.07$) or infested acorns ($P>0.10$). On the other hand, throughfall exclusion did not affect total seed production ($P>0.10$), but induced a significant reduction in the production of sound acorns ($F=4.13$, $P<0.05$; in terms of biomass) and a significant increase in the number of aborted seeds

($F=4.31$, $P<0.05$). This effect was more marked in the thinned than in the unthinned subplots, as indicated by the marginally significant interaction between thinning and throughfall exclusion factors for the number of aborted seeds ($F=3.30$, $P=0.07$; Fig. 5). Interestingly, differences by effect of both factors (thinning and throughfall exclusion) were significant for 2007 (a masting year), but not for 2008 (when the seed crop was substantially lower; Fig. 5).

This specific pattern of enhanced seed production in thinned and control (throughfall not excluded) subplots holds when the complete 6-year cycle is examined (Fig. 4). Nevertheless, the differences between treatments were only statistically significant for certain years due to the low number of replicates considered in the analyses ($n=3$) when samples were grouped per plot.

3.5 Sprouting

Six years after thinning, 79% of stumps had resprouted in the thinned subplots and 55% of stems had sprouted in the unthinned subplots (Wald=19.7, $P<0.001$). Interestingly, in the unthinned subplots, the proportion of stems with sprouts was higher in those areas subject to throughfall exclusion (64%) than in those with natural rainfall (46%) (Wald=4.46, $P<0.05$; Fig. 6a). Similarly, the number of living sprouts per stem in the unthinned subplots increased with exclusion of throughfall (Wald=22.4, $P<0.001$; Fig. 6b). The diameter of the dominant sprout per stump/stem was higher in the thinned than the unthinned subplots ($F=89$, $P<0.001$), but it was not affected by throughfall exclusion ($P>0.10$; Fig. 6c).

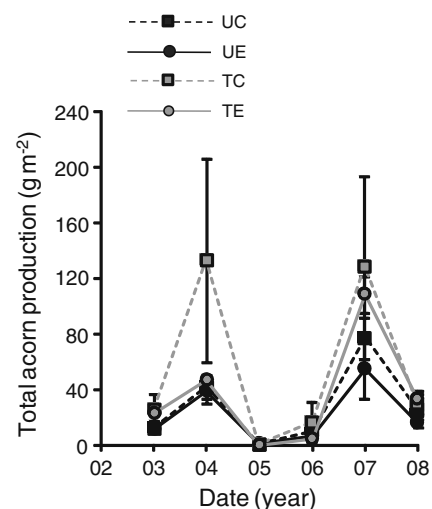
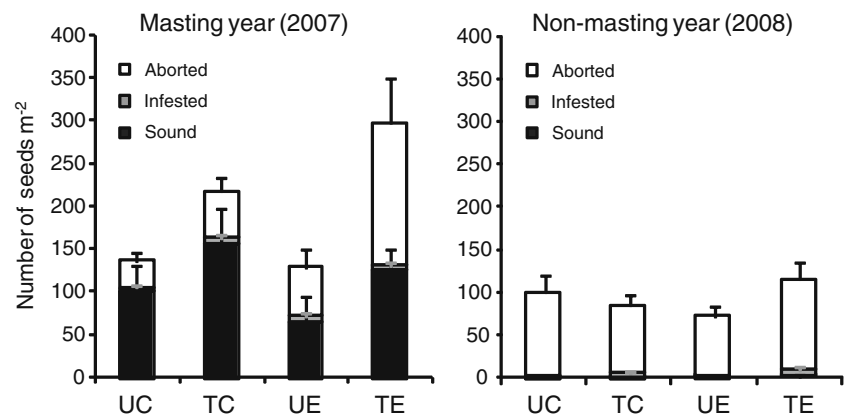


Fig. 4 Annual seed production (gram dry weight per square meter) in thinned and unthinned subplots (gray and black symbols and lines, respectively) either subject to throughfall exclusion (circles, solid lines) or not (squares, dotted lines). Symbols are means \pm SE ($n=3$)

Fig. 5 Seed production separated by categories in a masting and a non-masting year. *Error bars show 1 SE (n=36)*



4 Discussion

The selective thinning of suppressed stems in an abandoned *Q. ilex* coppice stand had positive consequences for the remaining stems: survival and growth was higher than in areas that were left unthinned. Similar positive effects of thinning were found under natural conditions and experimental conditions imposing a 29% reduction of net precipitation, a value predicted by some climate models for the western Mediterranean region for the end of this century (Giorgi 2006). Our results suggest that thinning is a suitable measure for adapting forests to climate change, at least in the short term (Cotillas et al. 2009; Misson et al. 2003; Spittlehouse and Stewart 2003).

4.1 The impact of throughfall reduction on stem mortality and growth and the feasibility of thinning for mitigating drought effects in the short term

Felling suppressed stems with a high probability to die is a way of accelerating the competitive exclusion that occurs through self-thinning. While 19% of stems died in the unthinned areas over the 6 years of study, almost all stems survived in those areas subject to thinning. The increased competition for water caused by the onset of the experimental throughfall exclusion exacerbated mortality, but this effect rapidly disappeared, as probably the initial wave of mortality of weaker stems increased the amount of water available for the surviving ones (Brando et al. 2008; Millar et al. 2007). Adaptive measures in forest management to cope with climate change in Mediterranean-type ecosystems should involve reducing the risk of associated hazards, such as wildfires and pathogen outbreaks. Removing trees that are about to die will reduce the accumulation of dead biomass and lessen the probability of occurrence of both perturbations (González et al. 2006; Waring and Pitman 1985).

Contrary to our hypothesis, stem diameter growth was not affected by throughfall reduction. Previous studies have

reported contrasting results under comparable levels of reduced throughfall. Seven years of partial exclusion was insufficient to cause any effect on the radial growth of some tree species in mixed deciduous temperate forests (Hanson et al. 2003), whereas clear reductions in radial growth were reported for trees in tropical (Brando et al. 2008) and Mediterranean forests (Ogaya and Peñuelas 2007a). The variable response of tree growth to throughfall reduction among experiments is likely underpinned by the structure and composition of forests, for instance, by the drought tolerance of species, the alteration that enhanced water deficit may cause on competitive interactions, and the present deviation of physical and climatic conditions from optimal species requirements.

It is worth noting that our study comprised the driest 6-year period since 1812–1817 (*unpublished data*). All trees suffered from severe water deficits, which probably curtailed an effect of throughfall exclusion on growth. Moreover, the impact of water deficit on plant vegetative and reproductive mechanisms depends on their phenology. In part, throughfall exclusion had no impact on growth because it enhanced water deficit at the end of summer, when *Q. ilex* has completed most of its annual radial growth (Allard et al. 2008; Castro-Díez and Montserrat-Martí 1998; Gea-Izquierdo et al. 2009; Gratani 1996; Körner 2003). The uncoupling between stem growth phenology and timing of peak water stress has been suggested by Hanson et al. (2003, 2007) for explaining the resilience of deciduous oaks to a continued exclusion of throughfall. Buds and seeds, however, continue to develop during late summer (Montserrat-Martí et al. 2009) and seem to be affected by an increase of water deficit at this time. As such, an 18% reduction in leaf area index (LAI) has been reported for plots subject to throughfall exclusion with respect to control ones (Limousin et al. 2009). Apparently, trees responded to a further enhancement in water deficit by decreasing the leaf area/sapwood area ratio, thus reducing the transpiration surface area and the risk of xylem cavitation (Corcuera et al. 2006; Mencuccini and Grace

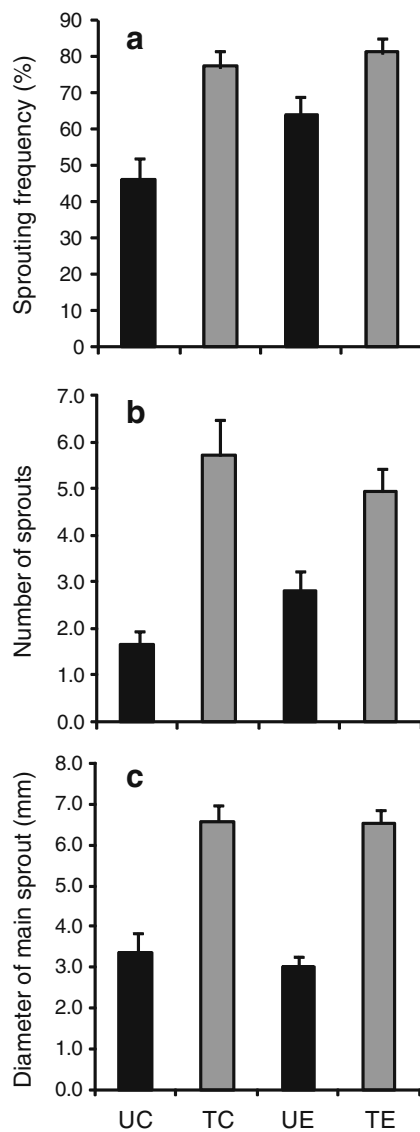


Fig. 6 Proportion of stumps/stems with at least one sprout (a), number of sprouts per stump/stem (b), and diameter of the dominant sprout per stump/stem (c) 6 years after application of thinning and throughfall exclusion. *Black bars* correspond to sprouts from uncut stems in the unthinned subplots and *gray bars* to sprouts from stumps in the thinned subplots. *Error bars* show 1 SE ($n=76-113$ for a and b and $n=35-92$ for c)

1995). This is supported by our data on apical branches, which reveal a significant decline in the leaf area per unit cross-sectional area of sapwood following 6 years of throughfall exclusion (Limousin et al. 2010b). Upon increased drought severity, decreased LAI and sustained diameter growth could help trees to maintain leaf-specific hydraulic conductance (Limousin et al. 2009).

How is it possible that drought-induced reductions in canopy leaf area and summer net CO_2 uptake rates per unit leaf area (Limousin et al. 2010a) are not having delayed impacts on stem growth? An eventual decline in net carbon

gain may have no effect on stem diameter increment if (1) less carbon is invested per kilogram of wood (Hanson et al. 2003; Limousin et al. 2010b) and/or (2) a change in the allocation of carbon occurs (Reich et al. 1993). Either the old root system of *Q. ilex* coppiced trees acts as a carbon reservoir and maintains provisionally stem growth or new carbohydrates are allocated to wood formation rather than storage. Although stem growth generally occupies a low position in the carbon allocation hierarchy (Eilmann et al. 2009; Hoff et al. 2002; Waring and Pitman 1985), maintaining early wood formation upon increased drought may be a priority in trees whose radial growth is already at a minimum.

Our results supported the expectation that reducing stem density would improve growth of residual stems. The felling of suppressed and diseased stems increased the diameter growth rate of residual stems from 0.5 to 0.9 mm year^{-1} (0.69% to 1.07% year^{-1} relative to the initial diameter), as observed for similar oak coppice stands subject to comparable percentages of basal area removal (Corcuera et al. 2006; Ducrey and Toth 1992; Mayor and Roda 1993). This increment reflects the pulse of resources and the physiological improvements (e.g., in tree water status, net carbon assimilation, and hydraulic conductivity; Bréda et al. 1995; Corcuera et al. 2006; Gracia et al. 1999; Moreno and Cubera 2008) that occurs after thinning, at least for residual single stems. The growth rate increment of residual stems within clumps is partly attributed to the increase in light and water resulting from felling adjacent stems within the clump, and also to the mobilization of carbon reserves from the root system, at least initially (Dickmann and Pregitzer 1993). Felling all but the largest stem in a clump might be considered to minimize within-clump competition and boost photosynthesis and growth (Johnson et al. 2002). Furthermore, higher differences in water status and growth would probably have been observed if we had cut trees from higher diameter classes (Bréda et al. 1995).

The existence of a centennial root system in these coppiced trees could contribute to explain some of the unexpected differences between the thinned areas subject to reduced or natural rainfall, i.e., the slightly higher growth in terms of stand biomass in the former despite the 23.3% lower throughfall caused by the exclusion system.

4.2 The impact of throughfall reduction on sprouting and seed production and the feasibility of thinning for mitigating drought effects in the long term

Long-term adaptation to climate change calls for increasing the genetic diversity of some forests via plantation and/or stimulation of natural sexual regeneration (Spittlehouse and Stewart 2003). Thinning, often combined with other

silvicultural practices (e.g., burning), aids in increasing seed production and natural regeneration in oak forests, including old oak coppices (Johnson et al. 2002). Yet, we ignore how current practices will be modified by future warmer and drier conditions. Flowering and acorn formation and development are processes sensitive to summer water deficit (Espelta et al. 2008; Montserrat-Martí et al. 2009; Ogaya and Peñuelas 2007b; Siscart et al. 1999) and thus vulnerable to a potential increase in drought intensity.

In the absence of thinning, throughfall exclusion did not affect the annual seed crop but significantly reduced the amount of sound acorns. While the exclusion of throughfall did not affect tree water status in spring and thus seemed to have a negligible effect on flowering and early seed formation, it enhanced late summer water deficit and thus constrained the final development of seeds (Alejano et al. 2008; Carevic et al. 2010). Other authors (e.g., Espelta et al. 2008; Siscart et al. 1999) have documented high abortion rates during the dry season in Mediterranean evergreen oaks, which can be interpreted as the excess fruit the tree is not able to keep as a function of the available water (Lloyd 1980). These results suggest that acorn ripening is more sensitive to a constant reduction in precipitation than flowering and early seed formation. However, we must note that future reductions in rainfall will not be constant through the year. An increase in the frequency and intensity of spring droughts could have a larger impact on the reproductive (and vegetative) output of *Q. ilex* trees than an intensification of summer drought, as remarked by Hanson et al. (2003) for deciduous temperate trees.

Thinning resulted in an increase in total acorn production, but with a large proportion of abortions. We suggest that increased CO₂ assimilation (Moreno and Cubera 2008) and likely mobilization of carbon reserve compounds from the roots (Dickmann and Pregitzer 1993) stimulated flowering and seed formation in residual stems, but that summer water deficit impeded the normal development of seeds, as suggested by the larger proportion of abortions in the thinned areas that were subject to throughfall exclusion. Therefore, drier future conditions might attenuate the success of thinning in promoting oak sexual regeneration. A higher crop may increase the probability of an acorn to escape from predators due to a satiating effect (Kelly and Sork 2002; Pérez-Ramos and Marañón 2008), but the probability of seedling establishment is low in smaller size acorns (Gómez 2004).

In the absence of thinning, small sprouts emerged from the base of the stems, more frequently and more abundantly when throughfall was reduced. We think this response is related to the decline in leaf area that has occurred since the onset of throughfall exclusion (Limousin et al. 2009), which could somewhat act as a triggering signal for the activation of dormant buds. After thinning, most stumps

resprouted vigorously. The proportion of stumps that resprouted and the abundance and vigor of resprouts did not change with throughfall reduction as these responses could be primarily governed by the amount of resources stored in the roots (Bond and Midgley 2001; Lloret et al. 2004). Profuse resprouting may constrain the success of thinning. On the one hand, resprouts may divert significant amounts of carbon and water otherwise destined to the growth and/or reproduction of residual stems (Cotillas et al. 2009). On the other hand, competitive interactions between resprouts and seedlings can also affect stand dynamics (Lloret et al. 2004). Favored by the possession of a more developed root system, sprouts grow faster than seedlings and can eventually deter seedling recruitment. The strong resprouting capacity of *Q. ilex* confers this species a high degree of resilience to recover from perturbations, but it might compromise a longer-term adaptation to future environmental changes by limiting sexual regeneration and genetic diversification (Espelta et al. 1999).

In conclusion, our results suggest that a reduction in rainfall can exacerbate the problem of seedling regeneration in abandoned *Q. ilex* coppice forests owing to a reduction in seed development. Felling suppressed and diseased stems increased the production of sound seeds in the remaining stems and also the proportion of aborted seeds. It is thus questionable whether this practice will favor seedling recruitment, especially if no further control of resprouts is made. We found, however, some evidence that selectively thinned abandoned coppices of *Q. ilex* are better prepared than dense unthinned ones to face future drier and warmer conditions, at least in the near term. First, thinning improved the vigor of residual stems, which is related to an enhanced capacity to respond to situations of impaired CO₂ assimilation (McDowell et al. 2008); second, thinning reduced dead biomass accumulation, which fuels wildfires and pathogen outbreaks (González et al. 2006; Waring and Pitman 1985).

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