

Article

Transient Post-Fire Growth Recovery of Two Mediterranean Broadleaf Tree Species

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Abstract: Fires affect forest dynamics in seasonally dry regions such as the Mediterranean Basin. There, fire impacts on tree growth have been widely characterized in conifers, particularly pine species, but we lack information on broadleaf tree species that sprout after fires. We investigated post-fire radial growth responses in two coexisting Mediterranean hardwood species (the evergreen *Quercus ilex*, the deciduous *Celtis australis*) using tree-ring width data. We compared growth data from burnt and unburnt stands of each species subjected to similar climatic, soil and management conditions. We also calculated climate–growth relationships to assess if burnt stands were also negatively impacted by water shortage, which could hinder growth recovery. Tree-ring data of both species allowed us to quantify post-fire growth enhancements of +39.5% and +48.9% in *Q. ilex* and *C. australis*, respectively, one year after the fire. Dry spring climate conditions reduced growth, regardless of the fire impact, but high precipitation in the previous winter enhanced growth. High June radiation was negatively related to the growth of unburnt *Q. ilex* and burnt *C. australis* stands, respectively. Post-fire growth enhancement lasted for five years after the fire and it was a transitory effect because the growth rates of burnt and unburnt stands were similar afterwards.

Keywords: *Celtis australis*; dendroecology; fire scar; *Quercus ilex*; post-fire recovery; radial growth



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1. Introduction

Wildfires are a common disturbance in seasonally dry areas such as the Mediterranean Basin, where climate warming could amplify their severity and increase their frequency, negatively impacting forest ecosystems [1,2]. Fires can damage the tree canopy, stem and root system depending on their regime, severity and species-specific heat sensitivity [3]. Moreover, drought stress could exacerbate fire damage and increase xylem cavitation leading to reduced hydraulic conductivity, growth decline or even tree death [3]. Nevertheless, several Mediterranean tree species have developed resilience mechanisms to withstand fire damage [4].

There are many adaptive responses of tree species resistant to forest fires of medium and low severity, including thick bark, deep root system and epicormic and basal sprouting, among others, which allow them to recover after fire [4,5]. However, fire injuries can also reduce the vigor of trees, often estimated as percent crown scorch, alter their water-use efficiency and trigger a temporary or permanent reduction in growth leading to tree death. This has been extensively studied in conifers, particularly pines and junipers, due to their ecological and economic relevance in regions particularly affected by fires such as southern Europe, the south-western USA and north-western Mexico [6–12]. Many of the European studies were based on prescribed burning and both European and American studies used tree-ring data to reconstruct post-fire growth and functioning (water and gas exchange) changes [7]. Nevertheless, tree-ring studies on major broadleaf species such as oaks are still scarce despite their relevance in many seasonal dry and fire-prone forests and shrublands.

Therefore, we still need assessments on the ability of broadleaf trees to recover after fires in order to improve post-fire management plans considering salvage and planting and to reduce fire risk in the long term.

Broadleaf species show extensive sprouting after fires, a trait which many conifers lack [1]. Moreover, they are resistant to drought and forecasted hotter and more arid conditions could lead to larger, high-severity fires and promote the transition from conifer forests to broadleaf woodland and shrublands dominated by resilient species such as oaks [13]. Despite the need for knowledge on post-fire recovery of broadleaf species, few studies based on tree rings exist, such as the research on *Prosopis pugionata* carried out in the dry Chaco of northern Argentina [14]. These authors found that most fire wounds affected less than 20% of the cambial perimeter and cambial damage was not related to tree age, size or bark thickness in this species, forming diffuse to semi-ring-porous wood. They concluded that this hardwood species can be used to reconstruct fire history using dendrochronology due to its ability to survive recurrent fires and form conspicuous wound scars in the wood. Similar information is lacking for Mediterranean broadleaf species also subjected to periodic fire damage and drought stress. This information is needed to improve post-fire growth and mortality projections considering growth recovery, crown scorch or sprouting intensity as has been obtained for conifers [11,15].

Here, we assessed the post-fire growth recovery in two Mediterranean hardwood species showing different functional traits (leaf habit, wood type): the widespread holm oak (*Quercus ilex* L.) and the less abundant hackberry (*Celtis australis* L.). We analyzed a fire that occurred in summer 2016 and affected a Mediterranean woodland, where both species coexist, located in north-eastern Spain. We used tree-ring data to quantify post-fire recovery in both species by comparing growth data with nearby similar stands not affected by the fire. Fire damage leads to heat-induced reductions in hydraulic conductivity and can destroy part of the cambium and the crown [3]. However, we expect that both species will react by developing wound scars and by vigorously growing and forming wider rings in stem sections where the cambium was not killed by fire. Such a post-fire reaction is linked to the need to rebuild the crown, and also due to indirect effects such as the release of soil nutrients and the reduction in tree-to-tree competition for soil water. To determine if a post-fire reduction in stem density and tree cover could favor growth by lessening competition for soil water, we also calculated climate–growth relationships. We hypothesized that the growth of both species was enhanced by wet–cool, cloudy conditions during the growing season, particularly in the burnt stands subjected to a competition release after the fire. Lastly, we also expect this post-fire radial growth recovery will result in a transitory effect once the surviving trees reach a new equilibrium between above-ground and below-ground biomass components.

2. Materials and Methods

2.1. Study Area and Species

On 10 August 2016, a wildfire spread from Huesca city (north-eastern Spain) up to the Fornillos de Apiés village, located at ca. 10 km northwards (Figure 1). It was a severe crown fire favored by warm–dry conditions and high wind speeds, which affected ca. 400 ha of coppice forests, shrublands and agricultural fields. The landscape of the study area is dominated by Mediterranean woodlands, shrublands and fields. The annual mean temperature is 12.5 °C (mean maximum and minimum temperatures are 24.1 °C and 5.3 °C, respectively) and the total annual precipitation is 474 mm (data from Huesca station, 42.08° N, 0.33° W, 541 m). There is a marked drought from July to August with precipitation peaks in spring and autumn.

The vegetation is formed by holm oak (*Quercus ilex* L. *sensu lato*, *Q. rotundifolia* Lam. or *Q. ilex* subsp. *ballota sensu stricto*; hereafter *Q. ilex*) coppice forests, shrublands and agricultural fields. The main shrub species are *Genista Scorpius* (L.) DC., *Juniperus oxycedrus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Juniperus thurifera* L., *Salvia rosmarinus* Schleid. and *Thymus* spp. Other minor plant species include *Lonicera implexa* L. and *Osyris alba* L.,

whereas grasslands are dominated by *Brachypodium retusum* (Pers.) Beauv. Hackberry trees (*Celtis australis* L.) are usually found near field margins or forming hedgerows.

The holm oak is widely distributed across sites subjected to seasonal dry summers and cold winters in the western Mediterranean basin (Figure 1). It is an evergreen tree and shrub species forming diffuse to semi-ring porous wood and resprouting from lignotubers after fire damage [16,17]. The hackberry is a fast-growing, deciduous tree forming ring-porous wood that occupies relatively wet sites near creeks and agricultural fields. It is found in areas ranging from India to the Mediterranean basin and may form part of riparian forests [18]. Both study species sprout after fire [19].

Soils are basic (pH 7.8–8.7), form on marls and limestones, rich in CaCO_3 (40–55%) and with low values of organic matter (1.5–4.4%). Soil erosion mainly affects slopes that are sparsely vegetated and the cultivated valley floors [20].

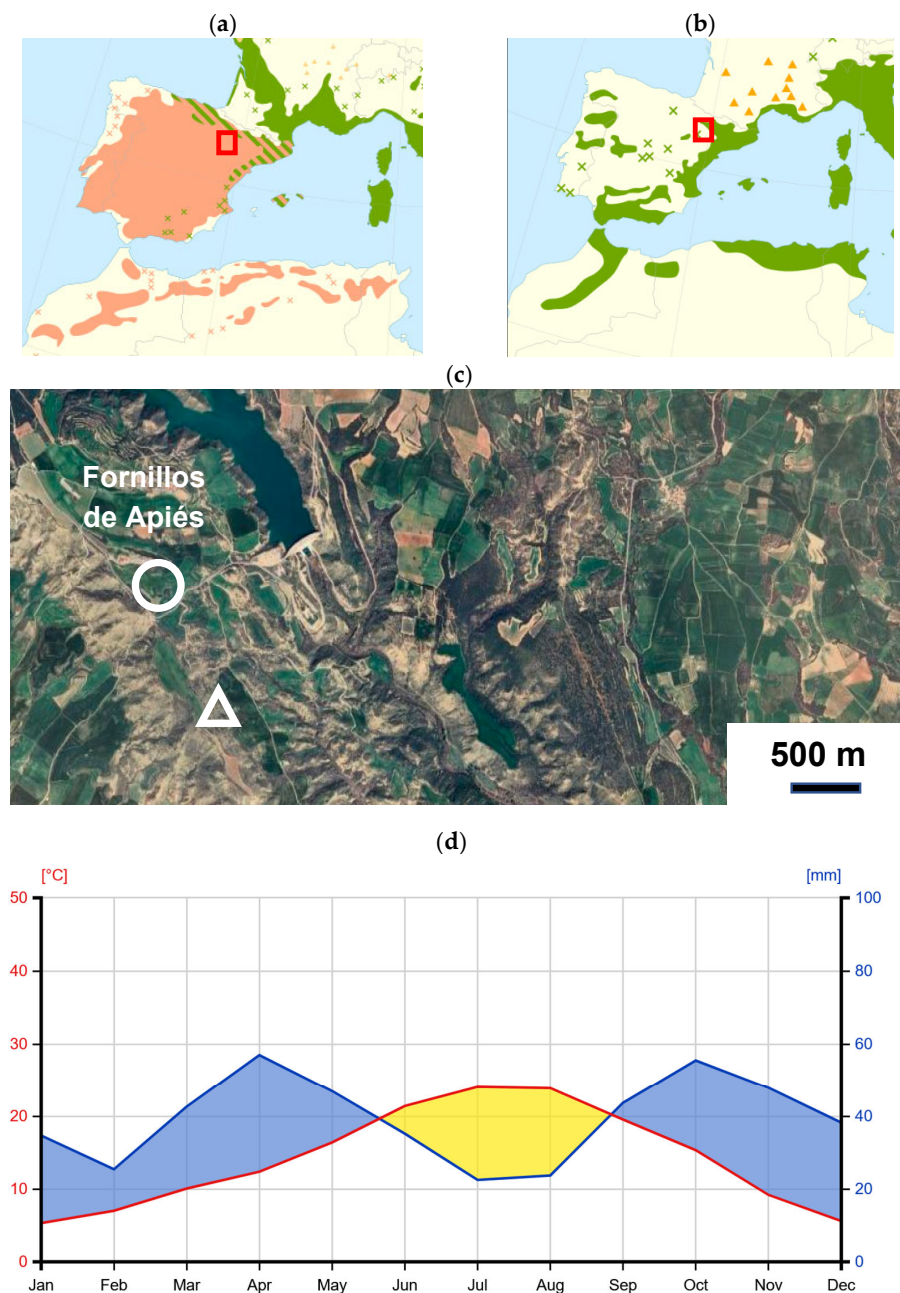


Figure 1. Distribution maps of (a) holm oak (*Q. ilex sensu lato*) and (b) hackberry (*C. australis*) in the western Mediterranean Basin. In (a), red and green patches indicate the distribution of *Q. rotundifolia*

(*Q. ilex* subsp. *ballota*) and *Q. ilex* (*Q. ilex* subsp. *ilex*), respectively. In (b), orange and green symbols or areas indicate introduced or naturalized and native populations, respectively. Modified from Caudullo et al. (2017). The red square shows the approximate location of the sampled site in NE Spain. (c) Map showing the area affected by the fire near Fornillos de Apiés with *Q. ilex* (triangle) and *C. australis* (circle) sampling sites. (d) Climate diagram of the study area (period 1993–2022). The maps shown in plots (a,b) are based on data from [21].

2.2. Field Sampling

Field sampling was carried out in late March 2023. We focused on the sampling of stands dominated by living trees showing evidence of fire damage including fire scars on the stem and main branches and stem or crown sprouting (Table 1, Figure 2). We took cross-sections near the fire scar in mature individuals of *Q. ilex* using a chain saw (Table 1). We took two cores near the fire scar in the case of *C. australis* using a Pressler increment borer. Taking cross-sections in *Q. ilex* did not kill the tree because this species forms several stems when forming coppice stands. For each species, 15 individuals were sampled and their diameter at breast height (dbh) was measured at 1.3 m with tapes. In the case of the evergreen *Q. ilex*, two visual estimates of crown defoliation were made in the field and an average was calculated. In the case of *C. australis* trees with fire scars on the stem, no defoliation was observed.

Table 1. Features of the sampled sites. Dbh is the diameter at breast height. Values are means ± SE.

Species	Latitude °N	Longitude °W	Elevation (m a.s.l.)	Slope (°)	Aspect (°)	Dbh (cm)	Crown Defoliation (%)
<i>Q. ilex</i>	42.1668	0.3690	604	20	N (30)	13.8 ± 0.8	49.7 ± 5.8
<i>C. australis</i>	42.1838	0.3709	637	5	N-NE (40)	23.5 ± 2.0	— — —

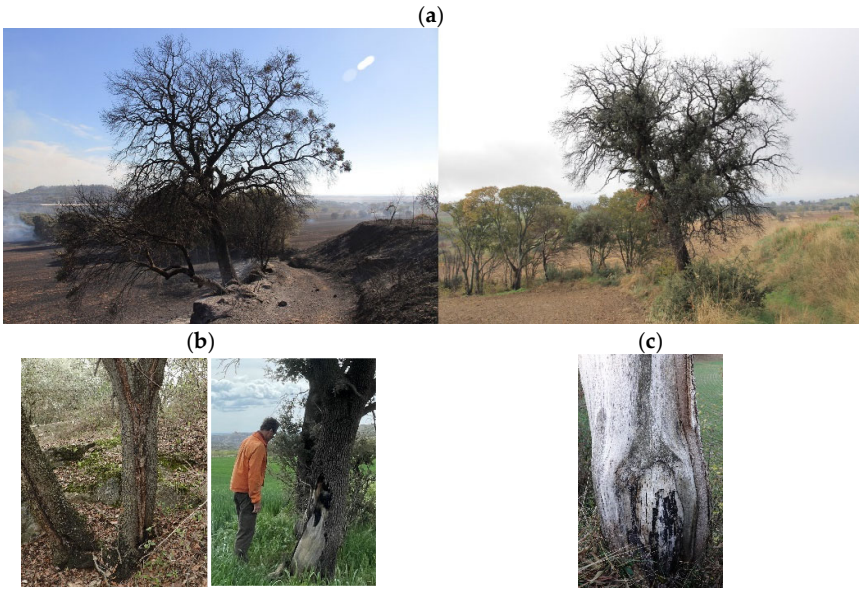


Figure 2. (a) Images of a holm oak (*Q. ilex*) affected by the studied wildfire in August 2016 and showing canopy sprouting in spring 2022. Stems scars observed in (b) *Q. ilex* and (c) *C. australis*.

To compare growth rates and growth responses to climate between stands affected by the fire and non-disturbed fires, we selected and sampled two nearby *Q. ilex* and *C. australis* populations. They were located in sites with similar climatic and edaphic conditions and were not affected by the 2016 wildfire and other previous fires at least since the 1980s. The *Q. ilex* and *C. australis* populations not affected by the fire were located near Arascués (42.2144° N, 0.4658° W, 586 m), and Fornillos de Apiés (42.2289° N, 0.3939° W, 653 m)

villages, respectively. In each population, 15 individuals of similar size to those sampled in burnt sites were selected (mean $\pm$ SE, dbh: *Q. ilex*, 13.5 ± 0.4 cm; *C. australis*, 20.1 ± 2.1 cm).

2.3. Dendrochronological Methods

Cores or cross-sections were air-dried, glued onto wooden mounts, and polished using sandpapers of progressively finer grain until ring boundaries were visible [22]. Then, samples were visually cross-dated, and tree-ring width along two radii per sample was measured with a 0.001 resolution using scanned images (resolution 2400 dpi) and the CooRecorder-CDendro software (v. 9.8.1, Saltsjöbaden, Sweden) [23]. The visual cross-dating was statistically checked using the COFECHA software, which calculates moving correlations between individual series of indexed ring-width values and the mean site series of each species [24]. The age at 1.3 m of sampled individuals was estimated by counting the number of rings along the two radii, from the bark to the pith, and keeping the maximum value.

First, to calculate radial growth patterns of trees from burnt and unburnt sites, we transformed individual tree-ring width series into basal area increment (BAI) series, which better account for geometrical constraints of stem growth [25]. The BAI series were calculated using the following equation and assuming concentric rings:

$$\text{BAI} = \pi (r_{t+1}^2 - r_t^2) \quad (1)$$

where r_t^2 and r_{t-1}^2 are the cumulative radii corresponding to the rings formed in years $t + 1$ and t , respectively. To quantify the actual impact of the fire on wood production, we directly measured the area of the 2015 and 2016 rings in a selection of scanned *Q. ilex* cross-sections ($n = 10$ trees), which showed relatively concentric growth (Figure 3). To evaluate how the 2016 fire influenced tree growth, we calculated the ratios of the BAI series of trees impacted by the 2016 fire and those not affected by the fire considering the best-replicated period (1985–2022). These ratios were standardized to compare between the two species.

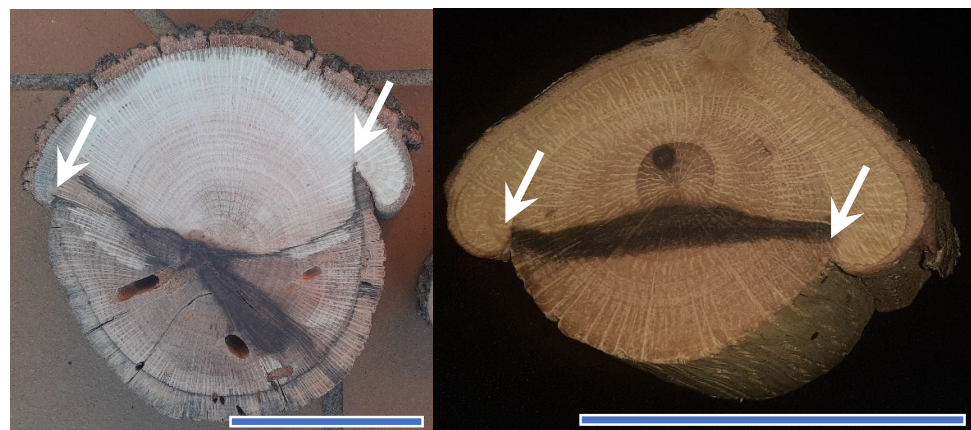


Figure 3. Images showing two cross-sections of holm oak (*Q. ilex*) individuals that formed wound scars after the 2016 fire. The part of each section with dead cambium is shown in the lowermost part of each image and it shows dark xylem zones. The white arrows indicate the scars formed after the fire. The scale bars measure 5 cm.

Second, to compute climate–growth correlations, individual tree-ring width series were detrended using a spline of two-thirds of the growth series length and a 0.5 response cut-off. Afterwards, an autoregressive model was fitted to each series to remove the first-order autocorrelation. Then, residual, pre-whitened individual series of ring-width indices were obtained and averaged by using bi-weight robust means. This allowed us to develop mean chronologies for each site and species. Several dendrochronological statistics were calculated over the period 1985–2022, including the first-order autocorrelation of raw ring-width series (AR1), the mean correlation among indexed ring-width series (r_{bar}), and the

Expressed Population Signal (EPS) that estimates the coherence and reliability of the mean series of ring-width indices [26].

2.4. Statistical Analyses

To compare tree-ring statistics between stands impacted or not affected by fire and to account for the lack of normality in the distributions of some variables, non-parametric Mann–Whitney *U* tests were used.

We calculated Pearson correlations between monthly climate data from the Huesca local station (TMx, mean maximum temperature; TMn, mean minimum temperature; Prec, total precipitation; Rad, radiation) and the mean series of ring-width indices from the prior October to current September according to previous studies in the study species [18]. This was carried out for the best-replicated period (1985–2022). In addition, to account for the collinearity between climate variables, we also calculated response functions [22]. The BAI and tree-ring width detrending and the climate–growth relationships were calculated using the packages dplR [27,28] and treeclim [29] in the R statistical software ver. 4.3.3 [30].

3. Results

3.1. Tree-Ring Data and Post-Fire Growth Changes

Regarding tree-ring statistics (mean tree-ring width, AR1) and tree age, no significant ($p < 0.05$) differences were found between sites of the same species according to Mann–Whitney tests (Table 2). Values of EPS > 0.85 indicate reliable and well-replicated mean ring-width series for the four study sites, with slightly higher rbar and EPS values for *C. australis* than for *Q. ilex*.

Table 2. Tree-ring statistics of the sampled stands affected by the 2016 fire and nearby stands not affected by the fire. Values and significance levels (p) of the Mann–Whitney *U* tests comparing burnt and unburnt stands of each species are presented. Statistics were calculated for the period 1985–2022. Abbreviations: AR1, first-order autocorrelation; rbar, mean correlation among individual series in each site; EPS, Expressed Population Signal. Values are means $\pm$ SD.

Species	Fire (F)/ No Fire (N)	No. Trees	No. Radii	Timespan	Age at 1.3 m (Years)	Tree-Ring Width (mm)	AR1	Rbar	EPS
<i>Q. ilex</i>	F	15	30	1963–2022	44 $\pm$ 8	1.06 $\pm$ 0.29	0.46 $\pm$ 0.24	0.30	0.86
	N	15	30	1942–2022	62 $\pm$ 12	0.92 $\pm$ 0.20	0.44 $\pm$ 0.20	0.32	0.87
<i>C. australis</i>		<i>U</i> (p)			683 (0.11)	764 (0.18)	825 (0.46)	–	–
	F	15	28	1943–2022	51 $\pm$ 16	2.08 $\pm$ 0.74	0.54 $\pm$ 0.15	0.34	0.89
	N	15	26	1958–2022	41 $\pm$ 14	2.06 $\pm$ 0.84	0.36 $\pm$ 0.28	0.36	0.90
		<i>U</i> (p)			712 (0.14)	803 (0.30)	725 (0.16)	–	–

In the burnt stands, BAI increased +39.5% (from to 3.5 to 4.9 cm² yr^{−1}) and +48.9% (from 14.1 to 21.0 cm² yr^{−1}) one year after fire in the case of *Q. ilex* and *C. australis*, respectively (Figure 4). However, these are estimates of basal area assuming concentric growth and calculated for rings along the stem section with living cambium (Figure 3). For comparison, if expressed in terms of xylem area increment one year after the fire, we measured a mean increment of +163% (range 122–203%) in *Q. ilex* ($n = 10$ trees). The maximum relative BAI enhancement in *Q. ilex* (+128.7%, year 2020) and *C. australis* (+99.2%, year 2018) was found four and two years after the fire, in that order. These data correspond to relative BAI increases of +210.8% in *Q. ilex* (year 2020) and +44.7% in *C. australis* (year 2018) when comparing burnt and unburnt stands.

The BAI ratios between burnt and unburnt trees showed the lowest values (+33.3% in *Q. ilex*, −9.0% in *C. australis*) in 2022. In that year, no significant difference between BAI of burnt and unburnt *C. australis* trees was found (Mann–Whitney $U = 65$, $p = 0.23$).

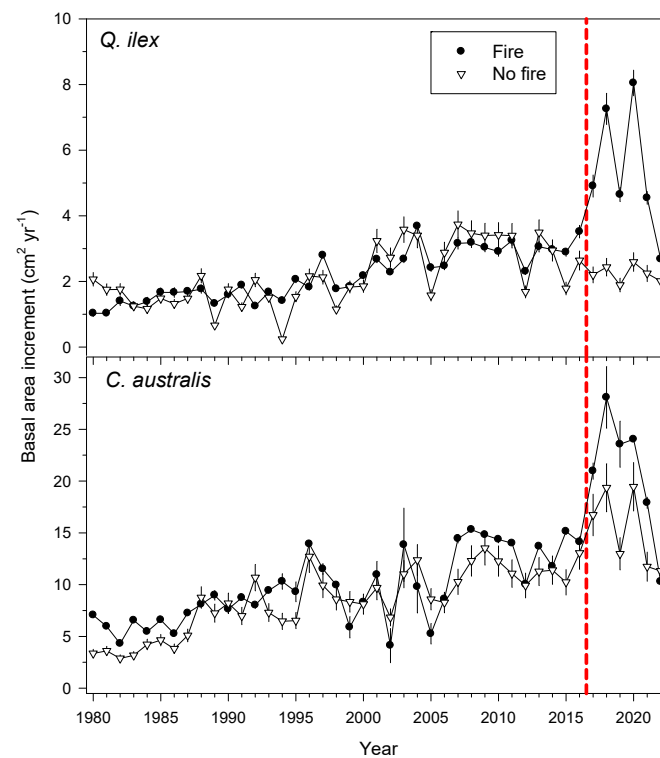


Figure 4. Series of basal area increment for the two study species in the fire sites and in nearby sites without recent fire impact. The vertical dashed line indicates the fire year (2016). Values are means $\pm$ SE.

The calculation of standardized BAI ratios between the series of burnt and unburnt trees illustrated the transitory nature of the post-fire growth increment (Figure 5). These series showed values close to 0 in 2022, i.e., six years after the fire.

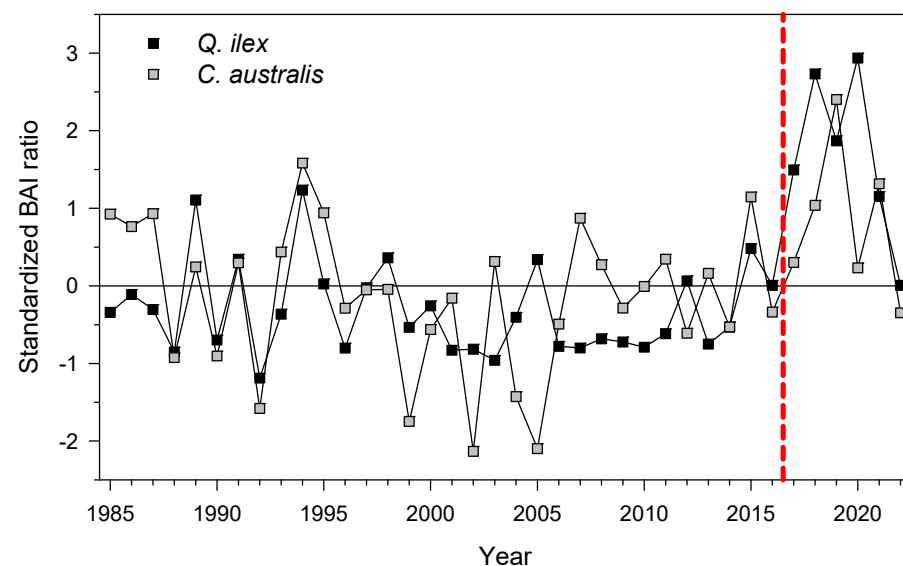


Figure 5. Standardized basal area increment (BAI) ratios between series of trees impacted by the 2016 fire and those not affected by the fire. The best-replicated period (1985–2022) is represented. The vertical dashed line indicates the fire year (2016).

Burnt trees also showed other periods with growth improvement as compared with unburnt trees (e.g., 1994 in both species, 2007–2008 in *C. australis*). Nevertheless, the mean magnitudes of the ratios in the pre-fire 1985–2016 period (-0.32 and -0.15 in *Q. ilex* and *C.*

australis, respectively) were significantly lower (*Q. ilex*, $U = 9$, $p = 0.0003$; *C. australis*, $U = 47$, $p = 0.05$) than the ratios calculated in the post-fire 2017–2022 period (1.70 and 0.82 in *Q. ilex* and *C. australis*, respectively).

3.2. Growth Responses to Climate Variables in Burnt and Unburnt Stands

In the case of *Q. ilex*, the growth of burnt stands was enhanced by cool March and wet May conditions, whereas the growth indices of unburnt trees increased in response to cool and cloud June conditions, wet January conditions and sunny conditions in the previous November (Figure 6).

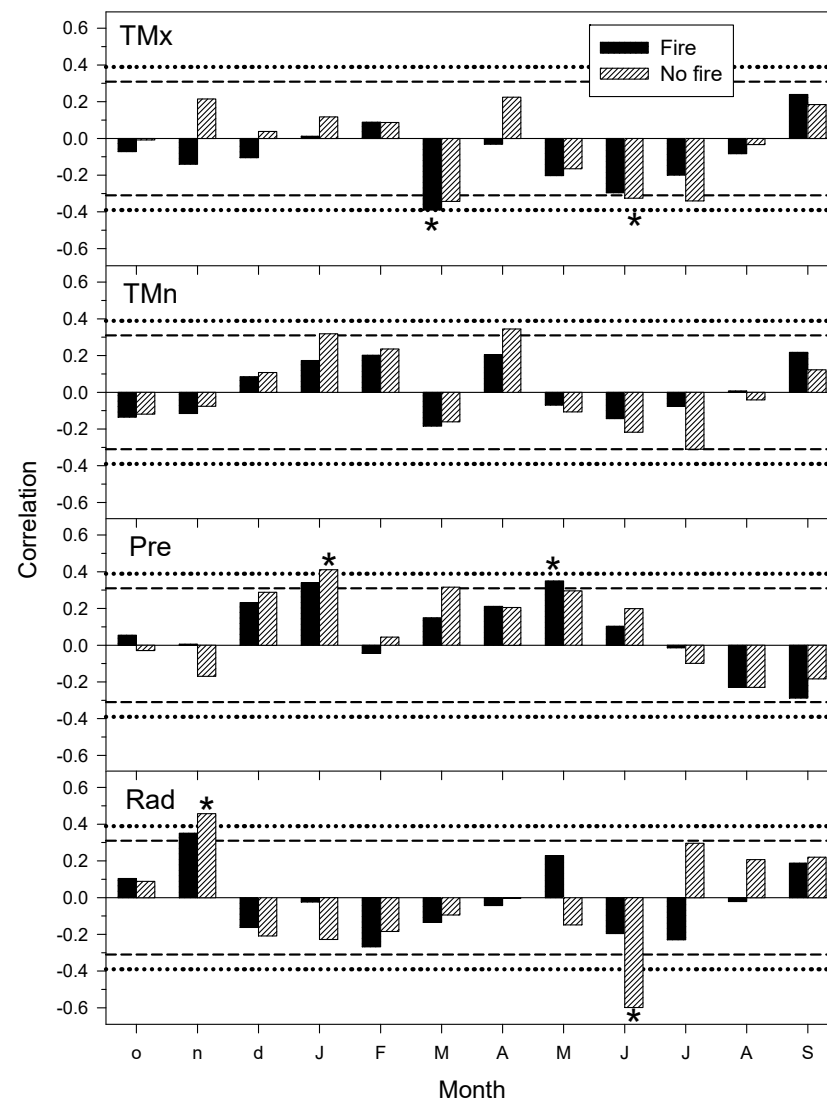


Figure 6. Correlations (Pearson coefficients) calculated by relating series of ring-width indices of *Q. ilex* from burnt (Fire) and unburnt (No fire) stands and monthly climatic variables (TMx, mean maximum temperature; TMn, mean minimum temperature; Pre, total precipitation; Rad, radiation). Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. Months abbreviated by lowercase and uppercase letters indicate the previous and current years, respectively. Asterisks indicate significant response coefficients.

In the case of *C. australis*, growth of the burnt stands was also enhanced by cloudy June conditions (Figure 7), but also by sunny September conditions. Wet June conditions and cool July conditions also improved growth in the unburnt stands (Figure 7). High precipitation in January increased growth indices in burnt and unburnt stands, with cloudy

winter conditions being more important as positive drivers of growth in the unburnt stand. June radiation accounted for 36% and 22% of the growth variability in unburnt *Q. ilex* and burnt *C. australis* stands, respectively (Figure 8).

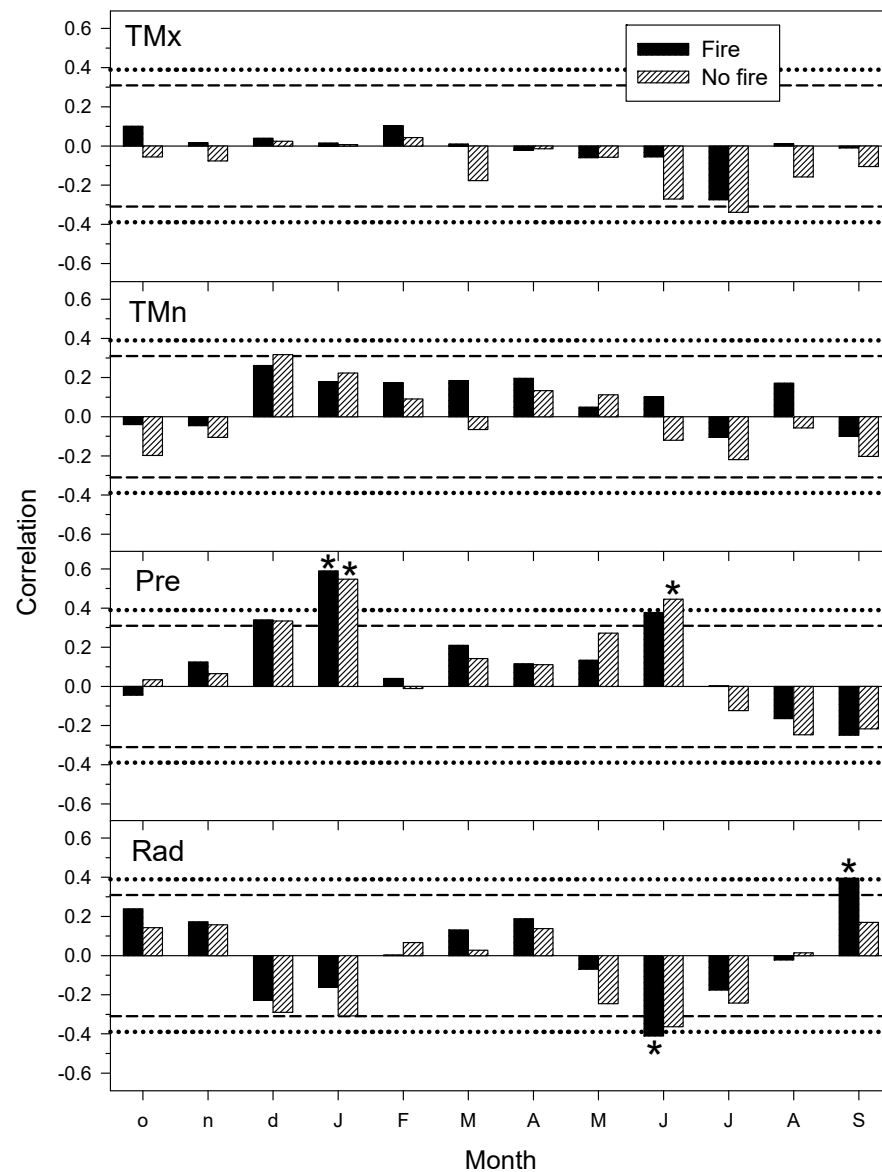


Figure 7. Correlations (Pearson coefficients) calculated by relating series of ring-width indices of *C. australis* from burnt (Fire) and unburnt (No fire) stands and monthly climatic variables (TMx, mean maximum temperature; TMn, mean minimum temperature; Pre, total precipitation; Rad, radiation). Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. Months abbreviated by lowercase and uppercase letters indicate the previous and current years, respectively. Asterisks indicate significant response coefficients.

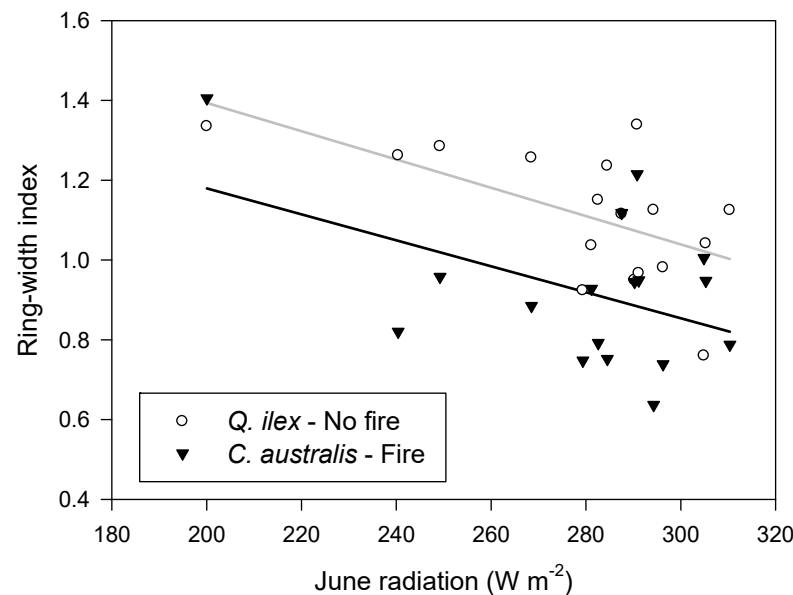


Figure 8. Positive and significant relationships between June radiation and the series of ring-width indices of unburnt (No fire) *Q. ilex* and burnt (Fire) *C. australis* stands.

4. Discussion

Both study broadleaf species formed fire scars and showed increased post-fire growth rates as hypothesized. However, this positive effect was transitory and lasted five years (period 2017–2021). Wet–cool, cloudy climatic conditions in late spring and early summer enhanced growth rates of both species (Figures 6–8) as expected, but these influences did not explain the post-fire growth enhancement and its transient decline. Therefore, the growth release after the fire was not related to a reduction in tree-to-tree competition for soil water. In addition, unburnt stands showed stronger positive impacts of growing-season cloudy (*Q. ilex*) or rainy (*C. australis*) conditions on growth rates.

We obtained high post-fire increases in BAI one to five years after fire in both species (Figure 5). However, this assessment was based on the part of the stem with living cambium forming the fire scar and producing new xylem. In some surviving *Q. ilex* individuals, the stem perimeter with cambium killed by the fire corresponded to 40–60% of the total circumference (see Figure 3). Therefore, although we measured BAI relative increases of up to +128.7% in the year 2020, they corresponded to the stem section with living cambium and fire scars. Such increments do not compensate for the total loss of biomass (wood, leaves) destroyed by the fire, at least in *Q. ilex* (see Figure 2). Perhaps in *C. australis*, the post-fire BAI enhancement could partially offset the destroyed woody tissue given that the fire scars were usually small in this species. However, comparing changes in biomass before and after the fire would require more detailed sampling and a different field setup.

Although both study species are considered isohydric trees, i.e., they are able to regulate leaf water potential [31,32], they also presented a strong growth reduction and increased stem mortality rates in response to severe water shortage [18,33–35]. Overall, our findings concur with these physiological and dendroecological findings. The dependence of both species on the precipitation of the previous winter should be noted, which could refill the soil water pools prior to the start of the growing season. In the unburnt *Q. ilex* stand, growth was enhanced by high radiation levels in the previous November, which could be explained by the higher photosynthetic rates during that month leading to the production and storage of non-structural carbohydrates used to form wood the following spring [36]. Sunny conditions in June could be related to warm–dry conditions, which are typical of Mediterranean summer, whereas the positive effect of high radiation levels in September on *C. australis* growth indices could reflect a longer growing season in the burnt stand, which was less limited by warm–dry June conditions than the unburnt stand [32].

Overall, the relationships between radiation and growth rates are novel and should be further investigated considering more species and sites, and should be disentangled from indirect effects due to precipitation. The use of gridded meteorological products could add further uncertainty to these analyses, but we used local, long-term climate data from a robust and homogeneous record.

Including hardwood species in future studies of tree-ring fire-scar records would improve the robustness of dendrochronological reconstructions of past fire dynamics [37]. For instance, the relatively poor preservation of scars by angiosperms explains why extensive tree-ring fire-scar networks are biased towards gymnosperms as is the case in North America [38,39]. In that network, angiosperms (mainly *Quercus* species and *Populus tremuloides*) only accounted for 7% of 2562 sampled sites.

This study illustrates the fire impacts on radial growth of two broadleaf species and contributes to emphasize the importance of such data to understand and forecast post-fire forest dynamics and shifts in disturbance regimes [40]. More severe and frequent fires and droughts could speed up successional dynamics from conifer- to broadleaf-dominated stands [e.g., 13]. Tree-ring data could be used to constrain simulations of post-fire vegetation transitions from seeder (conifer) to sprouter (oak) dominance, which is expected to occur after large crown fires followed by severe drought [41].

5. Conclusions

To conclude, we examined how tree-ring data of two Mediterranean broadleaf species (*Q. ilex*, *C. australis*) can be used to quantify post-fire growth changes. Both species showed strong radial-growth enhancements after fire, but they were transient and lasted five years. Further monitoring of the affected individuals could be performed to assess their long-term growth and mortality rates, but the similar BAI values between unburnt and burnt stands suggest a high resilience of the forests impacted by the fire. Hardwood species such as oaks should be more widely considered in tree-ring studies of fire ecology to reconstruct and to assess fire–forest interactions.

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