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Fire season differentially affects resprouters in a *Cistus-Erica* shrubland of central Spain

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Abstract

Background Many plants survive fire by resprouting from lignotubers partially or completely buried in the ground. Resprouting success after fire could vary with fire season due to changes in plant carbohydrate reserves, soil moisture, and plant water status, among other factors. It may also depend on plant size, as this affects lignotuber depth in the soil. We investigated the effects of fire season on resprouting success (%) and speed (time to reach 50% of resprouting, t_{50}) in two lignotuberous species (*Erica arborea* and *Phillyrea angustifolia*) in a shrubland of central Spain. Over three consecutive years, three 13 × 14 m plots were burned early (ES) and late (LS) in the fire season (end of June and early October, respectively). Before fire, individuals were permanently marked after being classified as small, medium, or large. Predawn plant water potential (Ψ_{pd}) was measured during the fire season. Resprouting was monitored for up to two years. We used repeated measures ANOVA to test the effects of fire season and year (within-subjects effects), and plant size (between-subjects effects) on resprouting success (%) and t_{50} .

Results Resprouting success in *E. arborea* increased from ES to LS fires, and with plant size, while *P. angustifolia* was unaffected by fire season or plant size. The fire year did not directly affect resprouting success but interacted with fire season (for both species) and plant size (*E. arborea*). t_{50} was unaffected by fire season in *E. arborea*, but it significantly affected *P. angustifolia*, which showed smaller values after ES burns. t_{50} varied by fire year in both species, especially when plant water potentials were low. Plant size also affected t_{50} in *P. angustifolia*. Ψ_{pd} and t_{50} for both species combined were negatively related, with a more pronounced effect in LS fires.

Conclusions Our results show that the demography of the two resprouters will be differentially affected by fire season, alone or in interaction with the fire year and plant size. *E. arborea* was highly sensitive to fire season, particularly the smaller individuals, and to ES burns. In contrast, *P. angustifolia* was highly insensitive. t_{50} response among species differed by fire season, fire year, or size. Ψ_{pd} determined t_{50} of both species combined. These responses could impact long-term population structure and community dynamics of this Mediterranean shrubland.

Resumen

Antecedentes Muchas plantas sobreviven al fuego rebrotando de un lignotúber parcial o completamente enterrado en el suelo. El éxito del rebrote después del incendio podría variar con la estación de incendios debido a los cambios en las reservas de carbohidratos de las plantas, la humedad del suelo y el estado hídrico de las plantas, entre otros factores. También puede influir el tamaño de la planta, ya que afecta a la profundidad del lignotúber en el suelo. En

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este trabajo se han investigado los efectos de la estación de incendios sobre el éxito (%) y la velocidad (tiempo para alcanzar el 50% de rebrote, t_{50}) del rebrote en dos especies con lignotúber (*Erica arborea* y *Phillyrea angustifolia*) en un matorral del centro-oeste de la Península Ibérica. Durante tres años consecutivos, tres parcelas de 13×14 m se quemaron al principio (ES) y final (LS) de la estación de incendios. Antes de la quema, los individuos de cada especie se marcaron indeleblemente y se clasificaron como pequeños, medianos o grandes. Se midió el potencial hídrico de las plantas (Ψ_{pd}) antes del amanecer durante la estación de incendios. El rebrote se monitoreó hasta dos años. Se utilizó un test de ANOVA de medidas repetidas para testar los efectos de la estación de incendios y el año del fuego (efectos entre sujetos) y el tamaño de la planta (efectos intrasujetos) sobre el éxito del rebrote (%) y t_{50} .

Resultados El éxito rebrotador de *E. arborea* aumentó de los incendios ES a los LS y lo hizo también con el tamaño de la planta, mientras que *P. angustifolia* no fue afectada por la estación de incendios o el tamaño de la planta. El año del fuego no afectó directamente al éxito rebrotador, pero interactuó con la estación de incendios en ambas especies y el tamaño de la planta (*E. arborea*). t_{50} no fue afectado por la estación de incendios en *E. arborea*, pero sí en *P. angustifolia*, siendo menor después de las quemas ES. t_{50} también varió según el año de la quema en ambas especies, especialmente cuando el potencial hídrico de las plantas fue bajo. El tamaño de la planta en *P. angustifolia* también influyó en t_{50} . En general, hubo una relación negativa significativa entre Ψ_{pd} y t_{50} para ambas especies juntas, más pronunciada en los incendios LS.

Conclusiones Nuestros resultados muestran que la demografía de las dos especies rebrotadoras fue afectada de manera diferencial por la estación de incendios, por sí sola o en interacción con el año del incendio y el tamaño de la planta. *E. arborea* fue muy sensible a la estación de incendios, particularmente los individuos pequeños y tras incendios ES. Por el contrario, *P. angustifolia* fue altamente insensible. La respuesta de t_{50} entre las especies difirió entre la estación de incendios, el año del fuego o el tamaño. Ψ_{pd} se relacionó con t_{50} en ambas especies juntas. Estas respuestas podrían afectar a largo plazo a la estructura de las poblaciones y a la dinámica de la comunidad de este matorral mediterráneo.

Keywords Fire season, Lignotuber, Postfire resprouting, Postfire regeneration, Mediterranean-type shrub, Resprouting success, Resprouting speed, Time to resprouting, Plant-size, Lignotuber depth

Background

Mediterranean-type shrublands are often dominated by plant species whose individuals survive the blaze and resprout after fire from lignotubers (Clarke et al. 2013; Pausas and Keeley 2023). These are swollen structures at the root crown, partially or totally buried in the soil, with buds, carbohydrates, and other nutrients necessary for bud development (James 1984). Since the soil has a large insulation potential, some buds will survive and resprout after the fire, thus regenerating the plant (Auld 1990). However, not all individuals of resprouting lignotuberous species survive fire, and large variations have been reported in postfire resprouting success both among and within species (Quevedo et al. 2007; Enright et al. 2011; Pratt et al. 2014). Differences in mortality have been widely studied in relation to changes in fire regime characteristics, focusing on the effects of changes in fire frequency and fire intensity or severity (Noble 1984; Lloret and López-Soria 1993; Moreno and Oechel 1994; Fairman et al. 2016). However, the timing of fire throughout the year has received much less attention (Miller et al. 2019). This is important because the fire season is expanding due to the overwhelming role of human ignition sources, which are widespread throughout the year compared to the much more temporally

restricted lightning ignitions (Vázquez and Moreno 1998; Balch et al. 2017; Cattau et al. 2020). The fire season is also expanding due to climate change, which brings suitable fire weather toward spring or fall (Jolly et al. 2015), a process that is projected to continue as global warming remains unabated (Son et al. 2021).

In seasonal climates, the time of the year when fires occur can affect resprouting success and performance after the fire through various mechanisms (Miller et al. 2019; Bison et al. 2022). First, fire intensity varies throughout the year due to the temporal variation in fuel moisture and load, and weather conditions (Goven-der et al. 2006; Johnson and Balice 2006). Consequently, out-of-season fires, which occur in cooler months, tend to be less intense than within-season ones (Oliveira et al. 2015; Parks et al. 2018). This would have consequential effects on resprouting success due to the negative impact of increased fire intensity or severity on plant populations (Moreno and Oechel 1994). Second, plants respire and construct the new resprouting tissue at the expense of stored carbohydrates (Partelli-Feltrin et al. 2020). It has been shown that non-structural carbohydrate (NSC) reserves vary throughout the year, with peak values observed in late winter, before spring growth, and minimum values at the beginning of summer, after which they start recovering until the next winter (Jones

and Laude 1960; Cruz and Moreno 2001a, b; Martínez-Vilalta et al. 2016). Consequently, a fire at a time of the year when NSC are lowest could reduce resprouting success and vigor (Resco de Dios et al. 2020). Third, the typical drought period of Mediterranean-type climates causes large fluctuations in plant water hydration, with increased levels of water stress being observed as the seasonal summer drought progresses until the fall rains (Rhizopoulou and Mitrakos 1990; Lansac et al. 1994). Hydraulic failure due to increased water stress can prevent reaching the needed levels of hydration at the bud to initiate cell division and elongation, which could affect plant survival and growth (Cruz et al. 2003b, a; Resco de Dios et al. 2020). Drought-induced cavitation can further increase the death of the resprouting plant (Pratt et al. 2014). Fourth, bud resistance to fire may change throughout the season, thus affecting their survival and resprouting success (Bison et al. 2022). This is important for plants that resprout from aerial buds, which are more exposed to the heat of the fire, than for those resprouting from buds buried in the soil, although this effect has not been studied. Fifth, and final, the timing of fire will determine the period available to grow and develop new leaves that will allow restoring the photosynthetic capacity until the onset of the dormant, winter season. Fires late in the season will delay resprouting due to reduced temperatures in fall and winter, among other possible causes (Jones and Laude 1960). Despite the above, few studies have addressed the impact of fire season on plant demography and performance after fire in lignotuberous plants in seasonal climates, like the Mediterranean-type climates of the world. Moreover, studies until now are largely inconclusive (Miller et al. 2019; Fill and Crandall 2020), since fire effects might be blurred by other factors, including the size of the plant, which are less often included (Werner and Franklin 2010; Werner and Prior 2013). The larger the plant, the deeper the lignotuber in the soil (Moreno et al. 1999), hence the higher resprouting success.

Here, we assessed how plants of different sizes of two lignotuberous species resprout after fires conducted early (ES) or late (LS) in the fire season. Additionally, since rainfall in Mediterranean-type climates fluctuates largely from year to year (Cowling et al. 2005), we wanted to determine whether the resprouting response would also vary over the years. We chose two dominant species of shrublands growing in acidic substrates in mesic areas in central Spain: *Erica arborea* and *Phillyrea angustifolia*. The main hypotheses to be tested were (1) resprouting success (%) would be lower after ES than LS burns; (2) resprouting success (%) will be lower in dry years compared to higher rainfall ones; (3) resprouting success (%) would be higher in large-size individuals than in smaller

ones; (4) the speed of resprouting would be lower after ES than LS burns. The reasons would be as follows: (1) plant non-structural carbohydrate (NSC) reserves are lowest at the end of the growing season, before the onset of the summer drought. Since these will drive resprouting capacity, the percentage of plants resprouting after fire would be lower early in the fire season, just after completing spring growth, than later in the fire season. Additionally, resprouting under the increased water stress of summer, following ES fires, will also negatively affect resprouting success compared to LS fires, which will normally be followed by the rainy season. (2) Since water stress reduces resprouting, fires in dry years will result in lower resprouting success than in humid years. The negative effect of water stress on resprouting will make dry years produce lower resprouting success than humid ones. (3) Smaller plants will be more exposed to fire than larger plants due to more superficial lignotubers; additionally, they will have lower NSC reserves owing to lesser storage capacity and higher water stress due to a reduced root system to reach deeper soil layers. (4) Plants burned in ES will resprout faster than those in LS, due to the cooler temperatures of autumn and winter. While the above hypotheses and explanations focus on individual factors controlling resprouting, we anticipated that interactions among these factors would also occur. For example, the effect of fire season may depend on the year of burning, such that its impact is amplified in dry years, when overall resprouting is expected to be lower. Similarly, the effect of fire season may vary with plant size, with larger individuals being less affected. Moreover, the year of burning may interact with plant size, so that the negative impact of a dry year is more pronounced in smaller individuals. We tested the roles of both main effects and interactions by including them in the statistical models.

Methods

The study was carried out at the Los Quintos de Mora property of the Spanish National Parks Autonomous Agency (Los Yébenes, Toledo, 39°23'N, 4°00'W). The mean annual temperature is 14.6 °C, and the mean annual precipitation is 683 mm, of which only 13.2% falls during the extended summer months (June–September), as is characteristic in Mediterranean climates (data from the nearby Los Cortijos Meteorological Station, 39°19' N, 4°04' W; AEMET). In an old (> 45 years) shrubland, a stand was chosen on a south-facing slope at 900 m elevation and 17% inclination. The dominant shrubs were *Cistus ladanifer* L. (2.1 individuals m⁻²), *Erica arborea* L. (1.5 individuals m⁻²), *Erica umbellata* Loebl. ex L. (0.6 individuals m⁻²), *Phillyrea angustifolia* L. (2.5 individuals m⁻²), and *Salvia rosmarinus* Spenn.

(former *Rosmarinus officinalis* L.) ($0.5 \text{ individuals m}^{-2}$). *C. ladanifer*, *E. umbellata*, and *S. rosmarinus* are seeders and will not be treated further since all individuals died during the fire. *E. arborea* and *P. angustifolia* are obligate resprouters. Resprouting after fire occurs from lignotubers (Paula et al. 2009) that are partially or fully buried in the soil, respectively, and will be the object of this investigation. *E. arborea* produces very small seeds that are widely dispersed beneath the other plants. In contrast, *P. angustifolia* produces drupes that are dispersed by birds. Both species are spatially associated, probably because *E. arborea* serves as a perch for the birds that disperse the drupes of *P. angustifolia* (Moreno et al. 2023).

Experimental fires were carried out for three consecutive years (Year 1, Year 2, and Year 3), starting in 1997. Fires were conducted either early in the fire season (ES) (about 1 week before the end of June) or at the end of the fire season (second week of October) (LS). During each year, three $13 \times 14 \text{ m}$ paired plots were burned at each season (ES, LS), resulting in 18 plots burned over the three years. Paired plots were 5–10 m distant from one another. All plots within a season were burned on the same day, and each plot was burned separately. Burning was always conducted on clear, sunny days and under stable conditions. Fires were lit uphill and upwind. Soil surface temperatures during the fire were recorded with 10–15 K-type thermocouples placed 1 cm above the soil surface and connected to a data logger (Campbell Scientific, Logan, Utah, USA) for all except the first set of fires. These were arranged to cover the plot from the bottom to the top. Residence time above 100°C , in 50°C intervals up to 600°C , was calculated. Subsequently, the area under the temperature–time curve was determined using numerical integration. The time–temperature integral was used as an indicator of fire intensity (for details, see Moreno et al. 2011). Predawn, plant shoot water potentials (Ψ_{pd}) were measured in three individuals per plot for each of the two species (*E. arborea* and *P. angustifolia*) using a Scholander-type pressure chamber (Model 1000; PMS Instrument Company, Albany, OR, USA). Measurements were conducted in early April (spring), June (early summer, one or two weeks before fire), July (midsummer), September (early fall), and October (midfall, shortly before or after fire). The property was being used for hunting, and deer were stocked at much higher densities than normal. To avoid trampling and herbivory by these animals, the plots were fenced. For further details of the experiment, see Moreno et al. (2011).

In each plot, two $10 \times 1 \text{ m}$ transects were established, and along each $1 \times 1 \text{ m}$, all living plants of *E. arborea* and *P. angustifolia* were marked with numbered metal

rings, and surrogates for their size were measured. In *E. arborea*, the lignotuber is visible, and the largest two diameters perpendicular to one another were measured and used to calculate lignotuber area, assuming an ellipsoidal form. From these measures, each individual was assigned a size category: small [$0\text{--}25 \text{ cm}^2$], medium [$>25\text{--}100 \text{ cm}^2$], and large [$>100 \text{ cm}^2$]. In *P. angustifolia*, the lignotuber is fully buried and is not visible at the surface. We measured the largest stem diameter at its base and used it as a surrogate for its size. Based on this, three size categories were made: small [$0\text{--}1 \text{ cm}$], medium [$>1\text{--}1.5 \text{ cm}$], and large [$>1.5 \text{ cm}$]. After the fire, plants were identified based on their marks and periodically (approximately every 1 to 2 months, depending on the time of the year, and for at least nine months) monitored for signs of resprout emergence. If a plant resprouted at the end of the monitoring period, it was considered that it had succeeded in surviving the fire. Based on this, the resprouting success (%) was calculated. However, some plants died sometime after resprouting, but this mortality was minimal, and no further analysis could be done. A total of 238, 264, and 203 individuals of *E. arborea* were monitored in the small, medium, and large size categories, respectively, and 239, 309, and 260 individuals of *P. angustifolia* in the same categories. Resprouting speed was calculated based on resprouting emergence time. We calculated the time to reach 50% resprouting (t_{50}) (Soltani et al. 2015) by linearly interpolating between two consecutive samplings encompassing 50% resprouting success. When the first reading was larger than 50%, we calculated t_{50} assuming a linear relationship between fire and the first observation. When resprouting success was below this figure, this variable was not calculated since, in some cases, the values were very low.

Statistical methods

Differences in resprouting success (%) for each species (*E. arborea* and *P. angustifolia*) among the various factors were analyzed using repeated measures ANOVA with two within-subjects factors (burning year (Yr1, Yr2, and Yr3, $n=3$) and fire season (early-season [ES] and late-season [LS], $n=2$)) and one between-subjects factor (plant size [small, medium, and large, $n=3$]). Resprouting success proportion data were arcsine transformed. Normality and homogeneity of variances among groups (size classes) were checked, using, respectively, the Shapiro–Wilk and Levene’s test based on the median to account for high skewness in the data. Additionally, resprouting speed (t_{50}) was tested for *P. angustifolia* using a similar model as above. The t_{50} variable was square root transformed, which is most appropriate for percentage data. In the case of *E. arborea*, t_{50} could not be calculated for small- and medium-sized individuals. Calculation and

testing of this variable were possible only for the large-sized individuals using a similar model as above, without the between-subject factor. When tests for within-subjects effects did not meet sphericity assumptions, we used the Greenhouse–Geisser correction when this estimate (ϵ) was <0.75 , or the Huynh–Felt correction when $\epsilon > 0.75$ (Field 2009). The relationship between t_{50} and plant water potential for the large individuals and both species was explored using regression models. The best model was a linear one for ES, and an exponential one for LS. The data were analyzed using IBM SPSS Statistics (Version 28). Plotting was done using Microsoft Excel and ggplot of R (Wickham 2016).

Results

Precipitation from the beginning of the hydrological year until before the ES fires (October–May) was high during the first two years (Yr1 and Yr2) (931 and 930 mm, respectively) and well below average (377 mm) during the third (Yr3). Extended summer (June through September) precipitation was similar for each fire year. Fall and winter precipitation following the LS fires was high (677 mm) after Yr1 fires and very low for the next two years (Yr2 and Yr3) (377 and 344 mm, respectively). Winter minimum temperatures (December through February) were high (2.7 °C) after Yr1 LS fires and low following LS fires of the next two years, with mean temperatures of 0.5°C and 0.3°C for Yr2 and Yr3, respectively (Fig. 1).

The mean maximum temperatures registered at the soil surface during the experimental fires varied from

422 ± 20 to 655 ± 27 °C; mean residence time above 350°C varied from 115 ± 7 to 185 ± 8 s. There were no statistically significant differences for time-integrated temperatures during fires between seasons and years. See (Moreno et al. 2011) for the full data.

Plant water potentials were generally lower for *E. arborea* than for *P. angustifolia*. Plant water stress was very different during the three years of experimentation: Yr1 was the mildest, while Yr3 was the most extreme, with plant-shoot water potentials being very low since late spring. Additionally, plant water potentials for both species were higher at the time of ES than LS fires, except in Yr3 fires, when they were much lower than usual, especially at the driest time of the year, and much lower also than for LS fires (Fig. 2).

Resprouting success, that is the plants that resprouted and remained alive during the whole monitoring period, of *E. arborea* varied by size. It was low in the smaller individuals (36%), intermediate in the medium ones (70%), and very high in the largest size category, with most individuals in this category surviving the fire (94%). Additionally, resprouting success varied by season, whereby it was lower (54%) after ES fires than after LS ones (79%). Finally, there was some variability in resprouting success between the years of fire. The lowest figure was obtained in the first year (62%) while the highest was in the third (72%), with the second year being in between (Figs. 3 and 5). Plant size and fire season produced statistically significant effects on resprouting success (%), although they did not interact with each other. Additionally, the burning

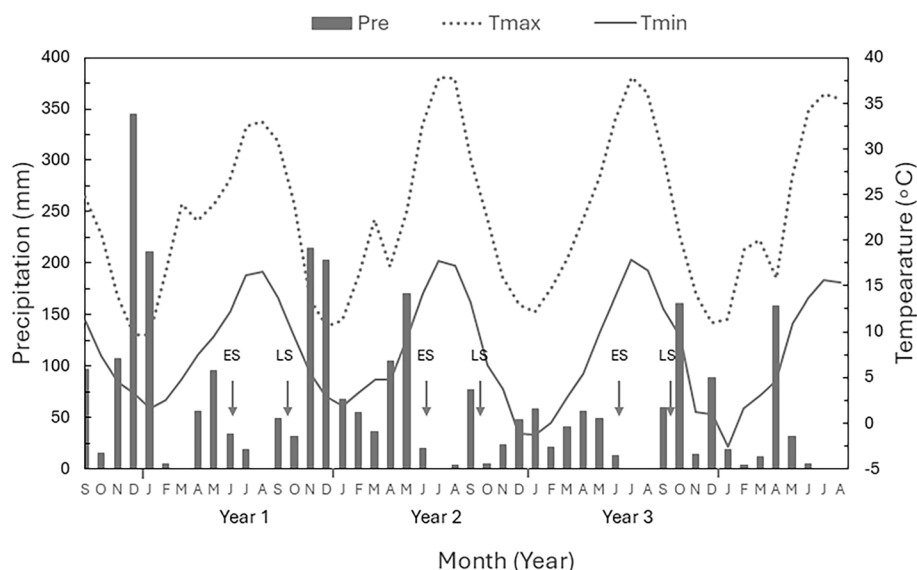


Fig. 1 Monthly precipitation (Pre) and maximum (Tmax) and minimum (Tmin) temperatures at Los Cortijos Meteorological Observatory during the three consecutive years (Year 1 to Year 3) in which experimental fires were conducted early and late in the fire season (indicated by arrows) in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Arrows indicate the time of fire in early season (ES) or late season (LS)

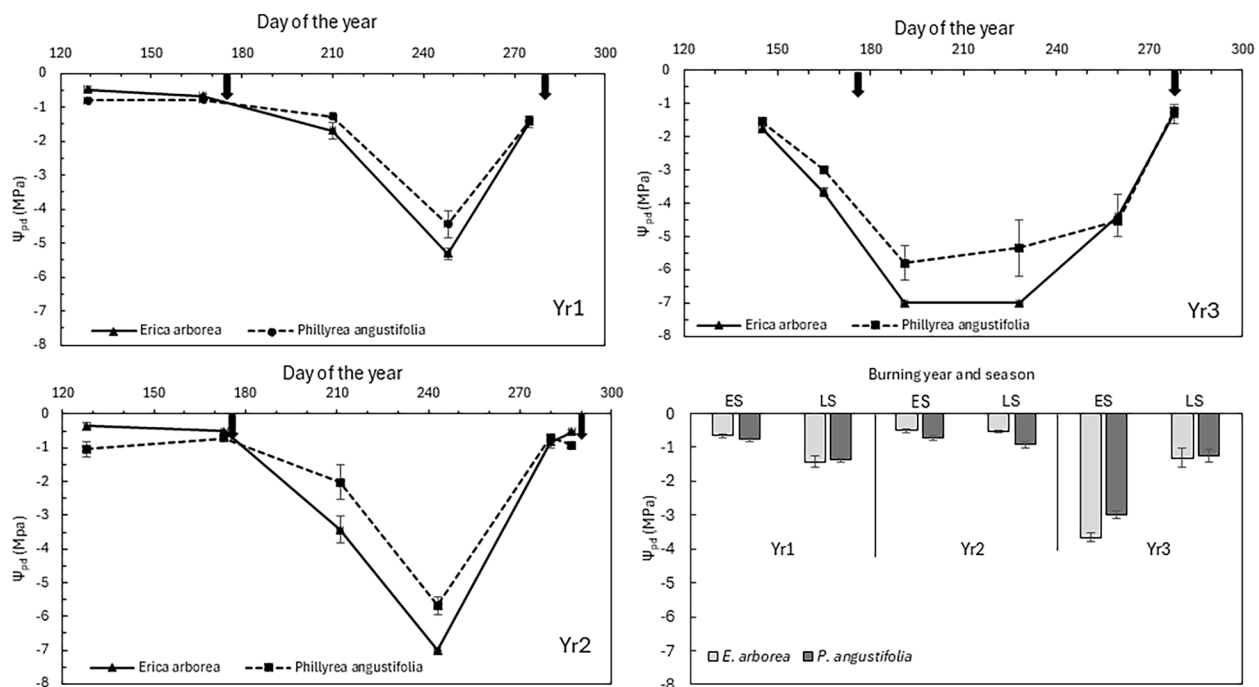


Fig. 2 Predawn plant-shoot water potential (Ψ_{psd} , MPa) (mean $\pm$ SEM) ($n=3$) of *Erica arborea* and *Phillyrea angustifolia* from spring to fall over three consecutive years (Year 1 to Year 3) during which experimental fires were carried out early or late in the fire season (indicated by arrows), in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Pre-fire values are shown in the bottom right panel

year significantly interacted with plant size and burning season but was not statistically significant by itself (Table 1).

Resprouting of *P. angustifolia* was very high and independent of plant size (96%, 97%, and 98%, for the small-, medium-, and large-sized individuals, respectively), fire season (97% and 97%, for early-season and late season fires, respectively), and year of burning (96%, 97%, and 98% for the first, second, and third fire year, respectively). Neither plant size nor year nor season produced statistically significant effects on resprouting, there being only significant interactions between season and year, and season, year, and plant size (Figs. 4 and 5; Table 2).

Resprouting speed (t_{50}) in the largest size category of *E. arborea* was non-statistically significantly different among seasons (85 days on average), but highly variable and statistically significant among years (from 47 days on average in the second year to 124 days on average in the third), there being also a significant interaction between season and year (Fig. 6; Table 3).

Resprouting was slower in *P. angustifolia* than in *E. arborea*, and its t_{50} was statistically significantly different between seasons (averages of 95 and 153 days for early-season and late-season fires, respectively), years (averages of 115, 110, and 146 days for years one, two, and three, respectively), and plant size (averages of 134, 123,

and 110 days). Additionally, there was a significant interaction between fire season and year (Fig. 6; Table 4).

There was no significant relationship between predawn plant-shoot water potential before fire and resprouting success (%) for either *E. arborea* ($F_{1,4}=0.46$; $P=0.84$; $R^2=0.01$) or *P. angustifolia* ($F_{1,4}=2.26$; $P=0.21$; $R^2=0.36$). There was a significant negative relationship between plant-shoot water potential and t_{50} for early-season (linear model) and late-season (curvilinear model) fires for both species combined (Fig. 7).

Discussion

Our results document that fire season differentially affected resprouting success in the two shrubs investigated; *E. arborea* was greatly affected by it, but *P. angustifolia* was not. For *E. arborea*, fires in early season produced lower resprouting success than those in late season, a pattern that was consistent over the three years investigated. Fire season effects have often been attributed to changes in fire intensity (Miller et al. 2019); however, our experimental fires were similar in this respect (Moreno et al. 2011), so other factors must have been involved in the observed pattern. Resprouting success was related to plant size, whereby it increased with increasing size, as shown in other lignotuberous shrubs (Moreno and Oechel 1994). Thus, while large individuals had always very high resprouting success (> 75%), the

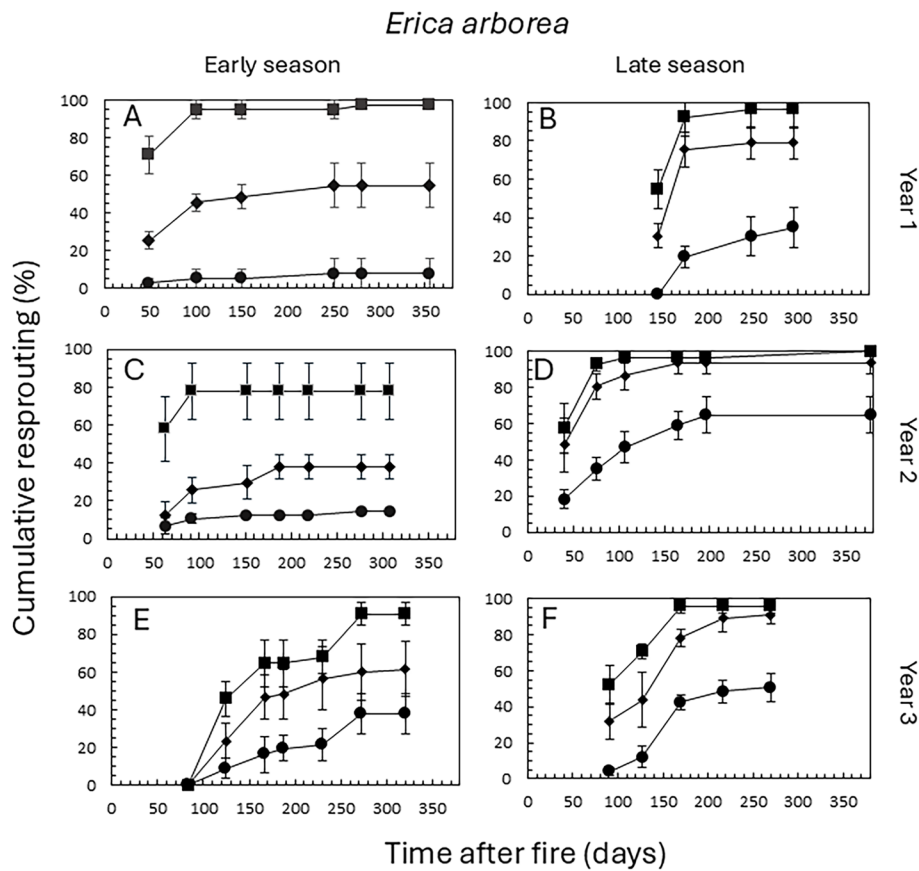


Fig. 3 Cumulative resprouting success (%) of *Erica arborea* by plant size (small [circles], medium [rhomboid], and large [squares]) after early (ES) (left panels) or late (LS) (right panels) season fires carried out during three consecutive years (Year 1 to Year 3) (top to bottom) in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain)

Table 1 Results of the repeated measures ANOVA test for the effects of fire season (early [ES] or late [LS]), year (Year 1 to Year 3) (within-subjects), and plant size (small, medium, and large) (between-subjects) on resprouting success (%) after fire by *Erica arborea* in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Plant size was determined based on lignotuber area (small: 0–25 cm²; medium: 25–100 cm²; large: > 100 cm²). Experimental fires were conducted for three consecutive years. Bold: Statistically significant ($P \leq 0.05$)

Factor	F	d.f	P
Within-subjects			
Season	13.937	1, 6	0.010
Season Plant size	0.673	2, 6	0.545
Year	0.271	2, 12	0.107
Year x Plant size	3.435	4, 12	0.043
Season x Year	4.266	2, 12	0.040
Season x Year x Plant size	1.423	4, 12	0.285
Between-subjects			
Plant size	30.850	2, 6	<0.001

smallest-sized individuals varied largely among the three years (from 8 to 65%). It appears that the size of the lignotuber, which is related to plant size, played a major role in resprouting success. Thus, smaller plants, which have smaller lignotubers and are less deeply buried in the soil (Moreno et al. 1999), could not withstand the heat of the fire as did larger plants.

The response of *E. arborea* fits in part with the hypothesis that differences in NSC content at the time of fire could explain this response. Unfortunately, we did not have such measures. Yet, we can argue that lower NSC content at the end of the growing season, which is amply documented in the literature, including in closely related species (Cruz and Moreno 2001a, b; Martínez-Vilalta et al. 2016; Davidson et al. 2021), could reduce resprouting success after fire since plants will need to mobilize carbon reserves for their new growth (El Omari 2022), which could particularly affect small-sized plants. The reduced resprouting success of the smaller individuals

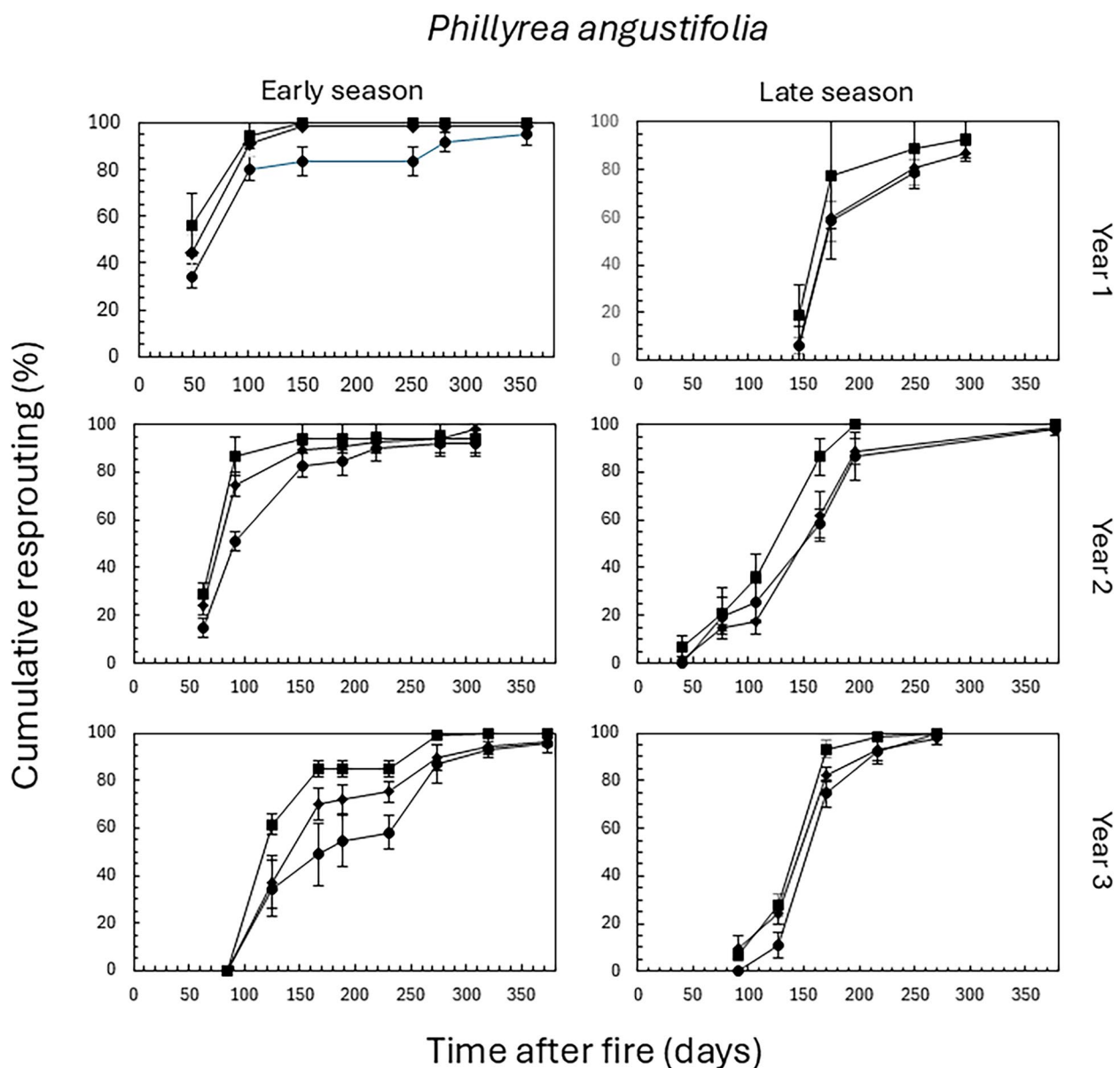


Fig. 4 Cumulative resprouting success (%) of *Phillyrea angustifolia* by plant size (small [circles], medium [rhomboid], and large [squares]) after early (ES) (left panels) or late (LS) (right panels) season experimental fires carried out during three consecutive years (Year 1 to Year 3) (top to bottom) in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain)

could also be due to factors that affect their lower storage of NSC. First, it has been shown that NSC concentration and pools increase with plant size (Zhang et al. 2018; Qi et al. 2022); thus, the available NSC will usually be lower in smaller individuals. Second, smaller individuals may be shaded by larger plants, thus would have reduced assimilation and lower NSC stores (Resco de Dios et al. 2020). Third, shaded plants tend to invest more in growth rather than in storage until they reach the upper canopy, which could reduce their reserves (Maguire and Kobe 2015; Deng et al. 2020).

Our results show that fire season can strongly influence the population dynamics of *E. arborea* by disproportionately affecting smaller individuals. Once plants reach a certain size, however, the impact of fire would be greatly reduced due to their deeper bud reserves and sufficient non-structural carbohydrate (NSC) stores that support resprouting. This is consistent with earlier findings in the closely related species (*Erica australis* L.) in which large plants were little responsive to burning or clipping in their resprouting response, even when NSC had been reduced through shading (Cruz et al. 2003b, a). None of

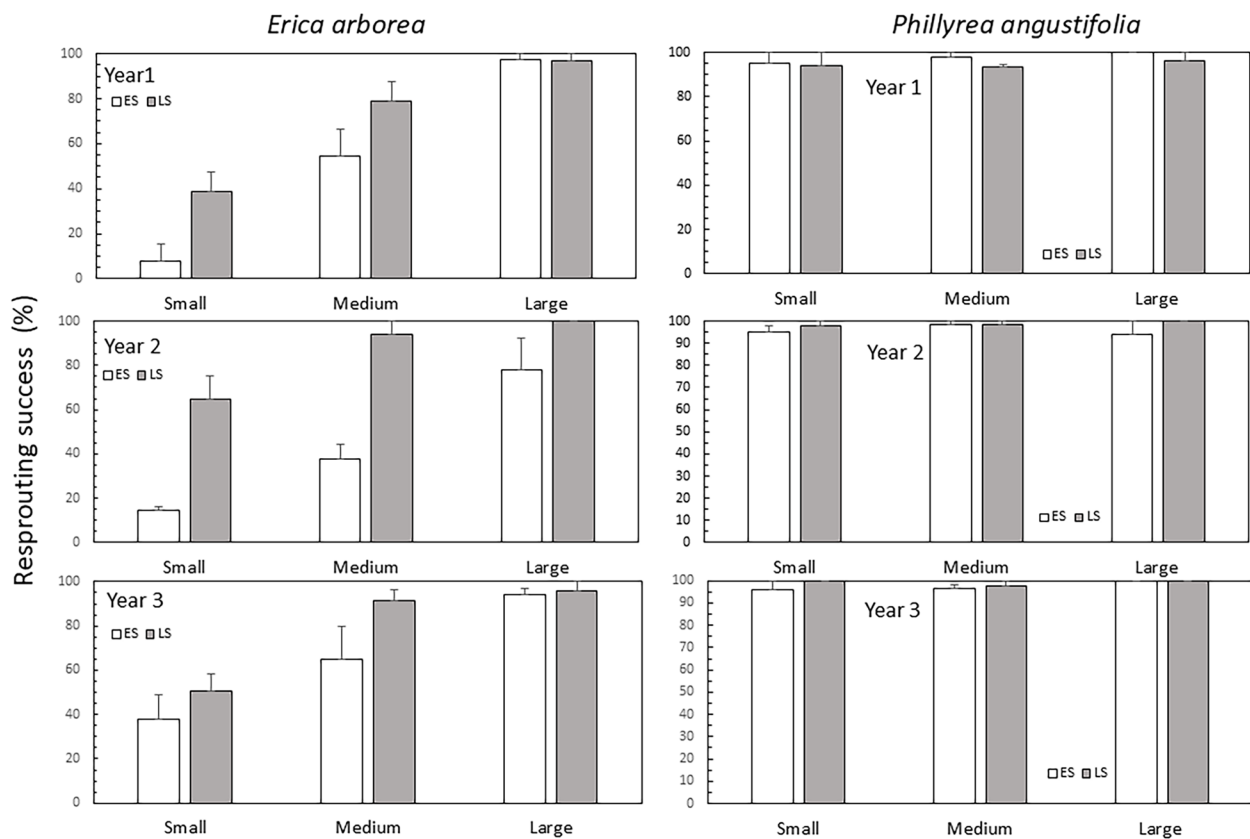


Fig. 5 Mean ($\pm$ SEM) resprouting success (%) of plants of three sizes (small, medium, and large) of *Erica arborea* (left panels) and *Phillyrea angustifolia* (right panels) after experimental fires over three consecutive years (Year 1, Year 2, and Year 3) in early-season (ES) and late-season (LS) burns, in an old *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). For statistical results, see Tables 1 and 2

Table 2 Results of the repeated measures ANOVA test for the effects of fire season (early [ES] or late [LS]), year (Year 1 to Year 3) (within-subjects), and plant size (small, medium, and large) (between-subjects) on resprouting success (%) after fire by *Phillyrea angustifolia* in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Plant size was determined based on the basal diameter of the main shoot (small: 0–1 cm; medium: 1–1.5 cm; large: > 1.5 cm). Experimental fires were conducted for three consecutive years. Bold: Statistically significant ($P \leq 0.05$)

Factor	F	d.f	P
Within-subjects			
Season	0.074	1, 6	0.794
Season x Plant size	0.044	2, 6	0.957
Year	0.504	2, 12	0.616
Year x Plant size	0.056	4, 12	0.993
Season x Year	6.170	2, 12	0.014
Season x Year x Plant size	3.552	4, 12	0.039
Between-subjects			
Plant size	2.223	2, 6	0.190

these experiments used smaller-sized plants. The large variability in survival of the smaller plants from year to year indicates that there are factors that can greatly affect resprouting success. In fact, we found that fire season effects were related to the fire year and that the effect of plant size also interacted with this. That is, the year of the fire was important in determining the overall survival patterns, as we had anticipated. Yet, it was hypothesized that dry years would produce lower resprouting success, but that was not the case. The driest year of experimentation was the third one, when low water potentials were observed at the time of ES fires and remained so until nearly the LS fires. Yet, the lowest resprouting success in the smaller-sized plants was observed in the first year of experimentation, not in the third. Assuming that NSC was behind the mortalities observed, it can be argued that a spring favorable for growth and reproduction might deprive NSC reserves more than a stressful one due to drought, since growth is more sensitive to water stress than photosynthesis, which would lead to increased carbohydrate reserves under such circumstances (Hartmann et al. 2018). Seed production measured at an adjacent

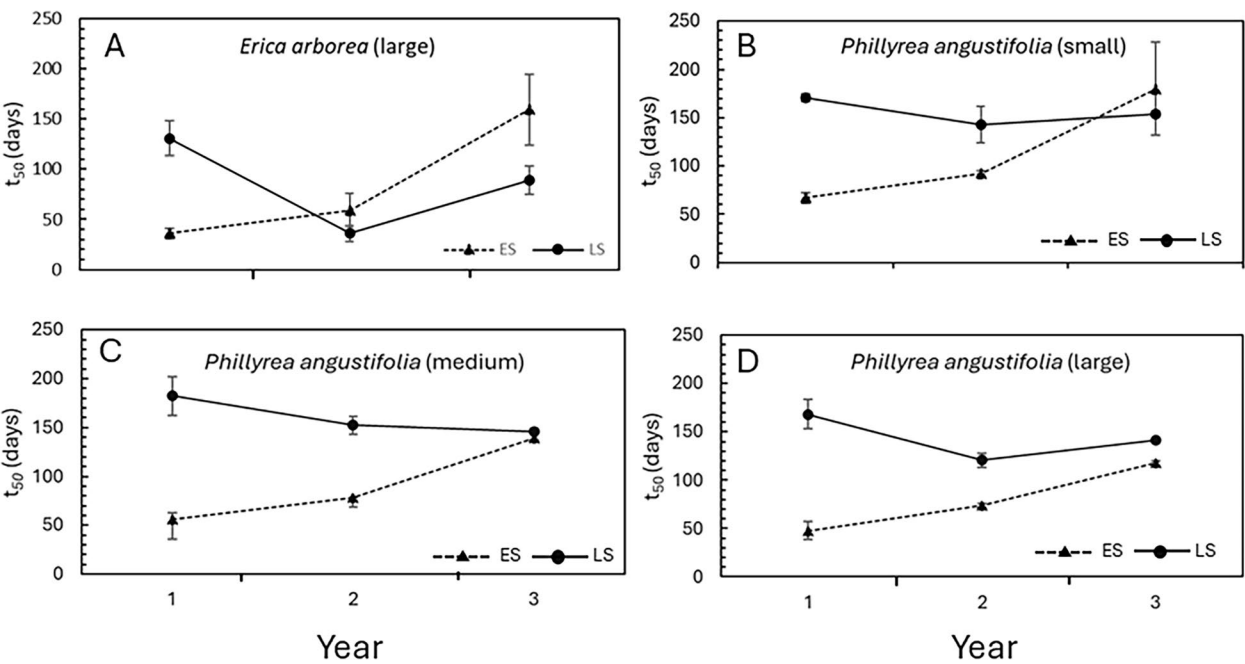


Fig. 6 Resprouting speed (i.e., time to reach 50% of resprouting) (t_{50}) of *Erica arborea* (A) (large plants only) and *Phillyrea angustifolia* (small (B), medium (C) and large (D) plants, respectively) over 3 years (Year 1 to Year 3), after burning in early-season (ES) or late-season (LS), in an old *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain)

Table 3 Results of the repeated measures ANOVA test for the effects of the fire season (early [ES] or late [LS]) and year (Year 1 to Year 3) (within-subjects), on resprouting speed (i.e., time to reach 50% of resprouting) (t_{50}) by large plants (lignotuber area > 100 cm²) of *Erica arborea* in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Experimental fires were conducted for three consecutive years. Bold: Statistically significant ($P \leq 0.05$)

Factor	F	d.f	P
Within-subjects			
Season	0.001	1, 2	0.974
Year	9.598	2, 4	0.036
Season × Year	12.054	2, 4	0.020

plot was highest in the first year, while it was minimum in the second and intermediate, although still low, in the third; these patterns were not related to the weather of the corresponding year (Moreno et al. 2023). If higher-than-average seed production year (i.e., mastings) were related to a process of accumulation of resources (Pearse et al. 2016), it is arguable that the internal process of accumulating NSC to produce flowering and fruiting at certain years might further contribute to reducing plant survival after fire. Notwithstanding, in the closely related species (*E. australis*), no relationship was found between

Table 4 Results of the repeated measures ANOVA test for the effects of fire season (early [ES] or late [LS]), year (Year 1 to Year 3) (within-subjects), and plant size (small, medium, and large) (between-subjects) on resprouting speed (i.e., time to reach 50% of resprouting) (t_{50}) by *Phillyrea angustifolia* in a *Cistus-Erica* shrubland at Los Quintos de Mora (Toledo, Spain). Plant size was determined based on the basal diameter of the main shoot (small: 0–1 cm; medium: 1–1.5 cm; large: > 1.5 cm). Experimental fires were conducted for three consecutive years. Bold: Statistically significant ($P \leq 0.05$)

Factor	F	d.f	P
Within-subjects			
Season	95.008	1, 6	0.001
Season × Plant size	1.588	2, 6	0.280
Year	19.411	2, 6	< 0.001
Year × Plant size	0.368	4, 12	0.827
Season × Year	27.024	2, 12	< 0.001
Season × Year × Plant size	0.343	4, 12	0.844
Between-subjects			
Plant size	8.470	2, 6	0.018

investment in reproductive structures and resprouting thereafter following a clipping experiment in early season (Cruz and Moreno 2001a, b). Since in that experiment plants were all of large size, it is unclear whether that

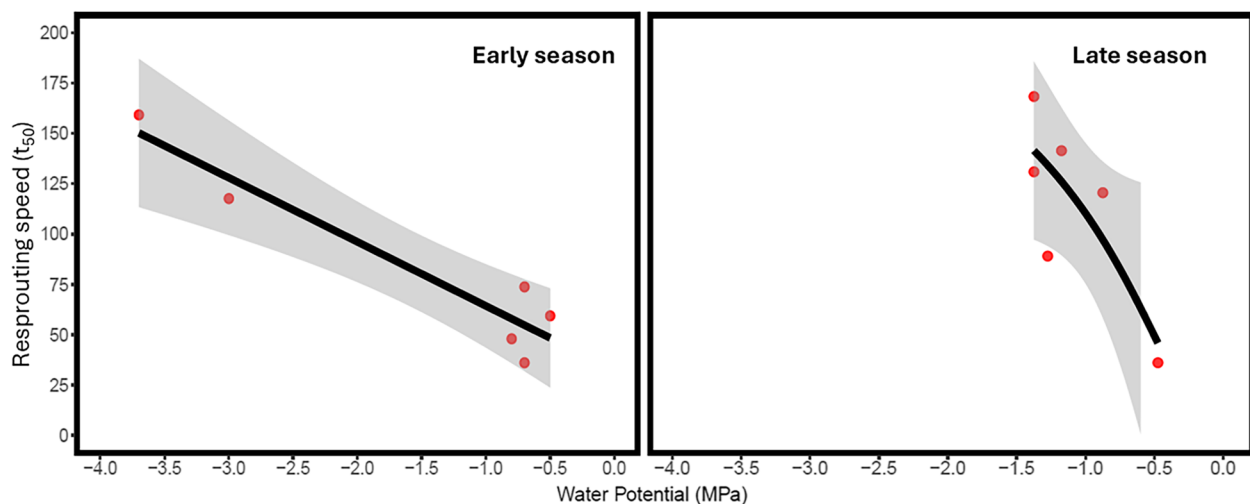


Fig. 7 Relationship between predawn plant-shoot water potential (Ψ_{pd} , MPa) and resprouting speed (t_{50}) (days) for early-season (left) and late-season (right) fires, for both species (*E. arborea* and *P. angustifolia*) combined

would apply to smaller-sized plants and is consistent with the idea that carbohydrates in large plants are plentiful to sustain resprouting (Cruz et al. 2003b, a). In addition, the degree of water stress after spring would further control the degree of replenishment of the NSC, which would explain the reduced resprouting success of the smaller individuals during the third year, the most severe of the studied ones. Resprouting success will further be affected by the level of water stress through its effect on resprouting speed, a delay of which would imply higher respiration costs. Resprouting speed after ES fires in the third year was the lowest (159 days, only for large-size individuals), which means that resprouts did not appear until autumn, when cold temperatures would prevent them from growing, thus further stressing the plants until they could develop a large leaf area that would facilitate growth and storage.

As for *P. angustifolia*, in contrast to *E. arborea*, neither fire season nor plant size directly affected resprouting success. This pattern is inconsistent with NSC playing a role in survival after fire. *P. angustifolia* is a midsuccessional species that recruits under *E. arborea* plants (Moreno et al. 2023). The fruit of this species is a drupe that is dispersed by birds that probably perch on *E. arborea*. Hence, these two species differ in shade tolerance: *P. angustifolia* is more shade-tolerant than *E. arborea*, and often grows under *Quercus ilex* canopies. It has been shown that shade-tolerant species accumulate higher NSC, conferring them a higher survival when suffering defoliation damage (Kobe 1997; Wiley 2020). If that were the case, this would explain the contrasting response of these two species, but further studies are needed to elucidate this.

Moreover, during the three years of experimentation, no significant seed production was measured in this species at an adjacent plot (Moreno et al. 2023). Resprouting success in this species was always very high (above 90%), because its lignotubers are fully buried in the soil and not directly exposed to fire (Paula et al. 2016). This lack of exposure was likely determinant for the high level of resprouting success even in the smallest individuals. Moreover, studies in the same study area have corroborated that *P. angustifolia* is a species whose functionality and resprouting success are hardly affected by weather conditions and post-fire drought events, in contrast to *E. arborea* (Parra and Moreno 2017; Parra and Moreno 2018).

Our results show that once the plants burn, the speed of resprouting is influenced by several factors, including the fire season, the year of the fire, and plant size, as demonstrated in the case of *P. angustifolia*. Unfortunately, the large number of deaths of the smaller-sized individuals in *E. arborea* did not allow us to calculate time to resprouting except in the large-sized individuals, which were not sensitive to the fire season. Our results show that the speed of resprouting can strongly vary from year to year. For instance, resprouting by 50% of the plants after ES fires took from about 50 days (year 1) to about 150 days (year 3). That is, resprouting speed varied by more than three times. That would mean that a plant burned in late June would resprout from mid-August until mid-November, which is a rather large fluctuation. In the first case, the plant would still benefit from the autumn months to grow, while in the latter case, the cooler temperatures of fall would further delay growth until the next spring. In the case of LS fires, resprouting would be delayed until

March in the case of *P. angustifolia*, but varied greatly in *E. arborea*, with delays from nearly one month to more than 4 months. Again, we show that fluctuations are considerable and can substantially affect the rate of recovery after fire. The role of the fire year was similar in both species for ES fires, but not for LS ones. It appears that the level of water stress directly determined the speed of emergence of resprouts in the case of ES fires. The relationship was more pronounced in LS fires; that is, even high water potentials led to long delays in resprouting. This suggests that less stressful conditions still caused significant delays in resprouting, likely due to the combined effects of water stress and cold temperatures following LS.

Overall, fires at different times in the year will have a very different effect on the populations of these two competing species. While the population of *E. arborea* may severely suffer from fire, particularly by the smaller-sized individuals, and more so in early-season fires, *P. angustifolia* will practically not be affected by fire season. By reducing the number of smaller-sized plants of *E. arborea*, fire will significantly change the structure of the population of this species. Furthermore, an increase in fire frequency will lead to a population with increasingly larger individuals. Since the population studied here did not include very large individuals, it is unclear whether very large individuals will continue to be little affected by fires. In contrast, fires will virtually maintain the structure of the population of *P. angustifolia* unaltered, hence facilitating the course of succession driven by the open spaces caused by the mortality of *E. arborea* and toward the dominance of *Quercus* forests (Santana et al. 2011). *Erica* shrublands have been proposed to be a stable state of *Quercus ilex* woodlands with the aid of fires (Ruffault et al. 2020; Schwörer et al. 2024). Yet, that depends on fire frequency, since its increase would facilitate the dominance of *P. angustifolia*.

Our data support arguing that climate change, by expanding the fire season toward spring, and increasing fire frequency (Bedia et al. 2015; Ruffault et al. 2020), has the potential to alter the dynamics after fire of this community dominated by the two resprouters. Fire management should be aware of these findings and use different fire seasons for prescribed fires depending on their objectives, being aware that the time of burning throughout the year has the potential to modify the relative dominance of these two competing species.

Conclusions

Fires at different times of the year differentially affected the populations of two dominant shrubs, *Erica arborea* and *Phillyrea angustifolia*, in a *Cistus–Erica* shrubland

in central Spain by reducing resprouting success in *E. arborea*, due to increased mortality of smaller individuals, while having no significant effect on *P. angustifolia*. This difference is likely due to the more superficial lignotubers of *E. arborea*, in contrast to the deeply buried lignotubers of *P. angustifolia*, which are therefore much better protected from the heat of the fire. Furthermore, early-season fires were more detrimental than late-season ones, likely due to lower carbohydrate reserves following spring growth, compared to early fall, when plants have had time to replenish their reserves during summer. Contrary to expectations, resprouting success was not influenced by plant water potential at the time of fire in either species. Moreover, resprouting success in *E. arborea* was lowest in the year with the most favorable moisture conditions for spring growth, reinforcing the idea that carbohydrate reserves play a key role. However, that did not apply to *P. angustifolia*, so further research is still needed to clarify the role of carbohydrate reserves in resprouting success.

Resprouting in *P. angustifolia* occurred more rapidly after early-season than late-season fires, and in larger individuals compared to smaller ones. Additionally, the year of fire, alone or interacting with fire season, affected both species, likely due to variations in plant water potential (in early-season fires) and in both water potential and air temperature (in late-season fires). Differences in resprouting timing can span several months, potentially resulting in significant long-term effects on resprout growth.

Overall, fire season, either alone or in interaction with plant size and the weather conditions of the fire year, can significantly influence resprouting success and timing. This highlights its considerable potential to directly shape the population structure of these two shrubs and/or alter their competitive interactions by affecting resprout timing. Managers should consider the differential sensitivities of these species when planning prescribed burns in this shrubland.

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Authors' contributions

JMM designed the study and obtained funding. EZ carried out research with field and laboratory assistance by AV. JMM and CMF conducted data analysis and modelling. JMM implemented the analysis and produced the first draft. All authors contributed to the final manuscript. All authors read and approved the manuscript.

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Data availability

No datasets were generated or analysed during the current study.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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