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Fire buffers drought impacts on reproduction in a resprouting Mediterranean shrub

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Fire and drought increasingly co-occur, exposing plants to greater drought stress during post-fire resprouting. Yet, the effect of this combination of disturbances on plant fitness remains poorly understood. Here, we examine how post-fire resprouting influences reproductive success under drought conditions in the Mediterranean shrub *Anthyllis cytisoides*. We took advantage of a natural setting where, following a high-intensity wildfire, burned (and resprouting) individuals coexisted with unburned ones. We compared flowering and fruiting performance under a post-fire drought in both burned and unburned plants. Our results show that burned individuals were significantly less affected by drought: compared to their unburned counterparts, they had a higher probability of flowering, produced more flowers, set more fruits and seeds, and produced heavier seeds. We propose that reduced competition and enhanced physiological condition following fire may temporarily boost plant fitness despite environmental stress. These findings suggest that post-fire resprouting may confer a short-term reproductive advantage during drought ('post-fire benefit boom'). Understanding this dynamic is essential to predict plant responses under compound disturbance regimes in fire-prone ecosystems.

Keywords: *Anthyllis cytisoides*, combined disturbances, drought, fitness, post fire resprouting

Introduction

As the world becomes drier (IPCC 2023) and fire regimes shift (Pausas and Keeley 2021), the likelihood that plants will be subject to compound disturbances increases (Kane et al. 2017, Batllori et al. 2019, Nolan et al. 2021). However, how fire and drought interact to affect plants remains unclear, especially regarding to their effects on post-fire resprouting, one of the primary plant adaptations to wildfires (Keeley and Pausas 2022).

Post-fire resprouting success is constrained by fire intensity (Lloret and López-Soria 1993, Moreno and Oechel 1993) and drought severity (Pausas et al. 2016, Nolan et al.

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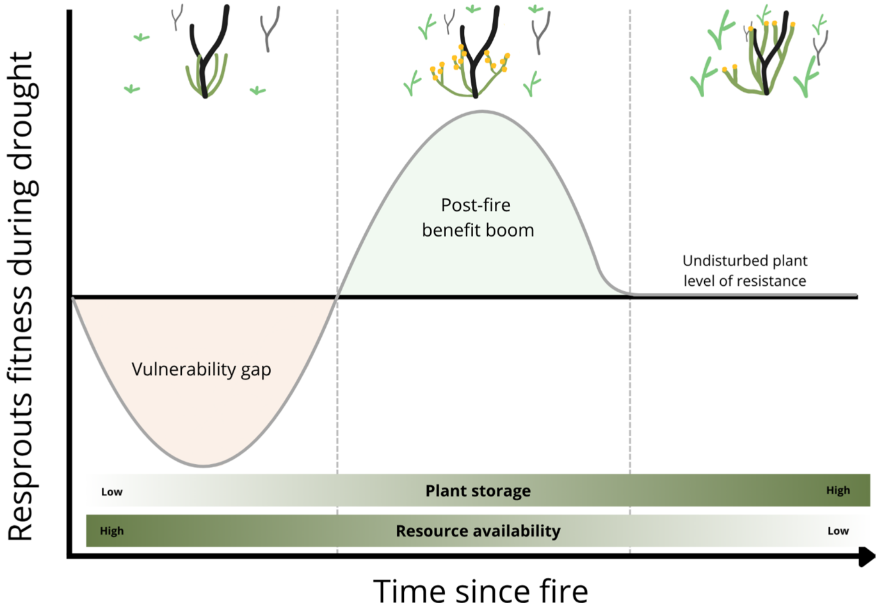
2021), yet experimental evidence of their combined effect remains mixed. Resprouting relies on stored reserves that may take years to replenish (DeSouza et al. 1986, Canadell and López-Soria 1998), making resprouts vulnerable to carbon starvation when disturbances occur within a short interval (Zedler et al. 1983, Canadell and López-Soria 1998). Hydraulic failure can also occur when resprout initiates during a drought event, as the tissues of these new shoots appear to be more vulnerable to cavitation than those of mature plants (Ramirez et al. 2012, Jacobsen et al. 2016, Schwilk et al. 2016). Indeed, in the Californian chaparral, high post-fire mortality rates due to cavitation and carbon starvation have been observed when a wildfire coincided with an extremely severe drought (Pratt et al. 2014). In contrast, under milder conditions such as moderate drought after low intensity fires, resprouting plants have been shown to outperform unburned neighbors and appear unaffected by water stress (Parra and Moreno 2017), probably due to their increased root-to-shoot ratios and deep-root systems (Oechel and Hastings 1983), as well as their increased photosynthetic rates (DeSouza et al. 1986, Stoddard and Davis 1990) and high resource availability (Silva et al. 2006, Caon et al. 2014).

These contrasting findings suggest that drought effects on resprouting plants are highly context-dependent, varying with drought and fire intensity, as well as with their temporal occurrence. Here, we propose that this variability occurs because there are two distinct post-fire phases. Immediately after fire, resprouting plants may experience a vulnerable period during which additional stressors significantly reduce survival (post- fire vulnerability gap, Fig. 1). The duration and depth of this gap depend on the intensity of both fire and subsequent stresses, as well as on species- and individual-level traits such as recovery rate and root depth. Once this vulnerable period is over (e.g. when plant reserves are higher and hydraulic integrity is restored), resprouting plants may enter a phase of enhanced resilience (post-fire benefit boom, Fig. 1). During this phase, reduced competition, high resource availability and increased root-to-shoot ratios would place resprouting individuals in a better position to withstand further disturbances. Similar effects on growth have been detected in pine trees (Marañón-Jiménez et al. 2013, Zald et al. 2022) and in other Mediterranean shrubs (Parra and Moreno 2017).

Finally, existing studies have focused on the vegetative or physiological responses of resprouting plants to these compound disturbances (e.g. survival, growth or water relations, DeSouza et al. 1986, Parra and Moreno 2017, Moore et al. 2019) while much less attention has been given to their reproductive performance. When reproduction is considered, research typically focuses on drought effects on seed bank recruitment rather than on the reproductive output of resprouting individuals during post-fire drought (Frazer and Davis 1988, Thomas and Davis 1989). Yet, understanding whether resprouting plants can maintain reproduction under such conditions is essential for predicting population persistence under changing disturbance regimes.

In this study, we aim to understand the reproductive consequences of drought and fire in a resprouting plant. To do so, we studied a population of the Mediterranean shrub *Anthyllis cytisoides* (Fabaceae) that was partially affected by a wildfire and subsequently experienced a severe drought in the second spring after the fire. This setting allowed us to compare



Q3 Figure 1. Hypothesized effects of post-fire resprouting on plant resistance to drought over time. Following a fire, resprouting plants may initially experience a period of heightened vulnerability to drought and reduced reproduction due to depleted reserves (post-fire vulnerability gap). As reserves replenish and competition levels are not fully restored, resistance to drought temporarily surpasses pre-fire levels (post-fire benefit boom); during this period, reproduction levels are high, even during drought. Eventually, as community biomass increases, competition recovers and individuals age, the effect of drought on resprouts returns to pre-disturbance levels.

burned (resprouting) and unburned individuals in close proximity. Since the study took place two years after fire, we expected that resprouting individuals would have overcome the post-fire vulnerability gap and find themselves in the benefit boom, meaning that they would be significantly less affected by drought in terms of flower and fruit production.

Material and methods

Study area

The study was conducted at the edge of a high-intensity crown fire that occurred in the summer of 2021 in Azuebar, Castellón province, eastern Spain (365 m elevation; mean annual temperature = 13.6°C, annual precipitation = 446.4 mm). The area consisted of abandoned fields colonized by *Pinus halepensis* and shrubs, including *A. cytisoides* (Supporting information). The edge of the fire formed a mosaic landscape of burned and unburned patches in close proximity (distance between plants ranged from 10 to 150 m; mean = 90 m), offering an ideal natural experiment to compare fire-affected (burned and resprouted) and unaffected (unburned) individuals under the same climatic conditions (Saiz-Blanco et al. 2025a). According to regional fire records (Alloza et al. 2021), the area had remained unburned for at least 25 years prior to the 2021 fire.

To characterise drought intensity and duration during the study period, we used the standardised precipitation–evapotranspiration index (SPEI), which integrates precipitation and potential evapotranspiration to represent the climatic water balance (Vicente-Serrano et al. 2010, Beguería et al. 2014); positive SPEI values indicating wetter-than-average conditions and negative ones drier-than-average . We extracted SPEI values for our site from 1.1 km^2 gridded maps (Vicente-Serrano et al. 2017) using two time scales: SPEI3 for May 2022 and 2023, capturing short-term water stress during the reproductive period (March–May; also referred to as ‘spring’), and SPEI12 for August 2022 and 2023, capturing cumulative conditions over the previous 12-months (the fire occurred on August 2021). SPEI values confirm that the first post-fire year (2022) was wet (SPEI12 = 1.05) and had an extremely wet spring (SPEI3 = 2.46), while 2023 was dry year (SPEI12 = −0.88), especially during the reproductive season (SPEI3 = −1.34; for further climatic information see the Supporting information).

Study species

Anthyllis cytisoides is a drought-deciduous shrub distributed across the western Mediterranean region that can reach up to 1.5 m in height. It thrives in open shrublands and abandoned fields under dry and warm low-altitude environments (de Bolòs and Vigo 1984). It is a facultative resprouter, meaning that, after a fire, it regenerates by resprouting from the root crown (Supporting information) and by seedling recruiting from a soil seed bank.

Field sampling

In spring 2022, we selected 31 *A. cytisoides* individuals within a 0.5 ha plot (16 burned and resprouting, and 15 unburned). We measured a range of phenotypic traits, including flower, seed and fitness-related traits (Saiz-Blanco et al. 2025a).

In the dry spring of 2023, we noticed that burned plants produced more flowers than unburned plants, despite they were not yet fully recovered from the fire (e.g. in terms of height or aboveground biomass). To quantify these effects, we expanded our sampling to record whether each individual produced flowers, and if so, whether it produced filled fruits (binary traits). We collected seeds and estimated seed set at the within-individual level, using several inflorescences per individual. Since *A. cytisoides* fruits are single-seeded, we defined seed set as the proportion of fruits containing a seed. To measure seed set we bagged multiple inflorescences (n ≥ 3) per individual and collected fruits during seed dispersal. Seeds were extracted by manually scrubbing hard-coated fruits with sandpaper and weighed to the nearest mg using a balance. Additionally, in 2023, we quantified each individual's total floral display by counting open flowers every seven days from March to May. Considering *A. cytisoides* flowers last approximately one week (Saiz-Blanco et al. unpubl.) and that this period spanned the entire flowering season, we can assume that we captured the whole flower production per individual. Finally, although seed production was quite low we ran germination trials with the seeds produced in 2023 (unburned = 41 seeds from 3 maternal parents; burned = 181 seeds from 10 maternal parents). Seeds were sown in commercial substrate and grown in a greenhouse for three weeks.

Statistical analyses

At individual level, we analyzed total floral display and the probability of flowering, fruiting and germinating, using linear models (GLMs in the case of probabilities: family = binomial, link = ‘log’). We fitted ‘fire’ (burned/unburned plant) as the predictor for the year 2023; in 2022 all plants flowered and set fruit and we did not register total flower production nor germination rate. For this las trait we also included mean seed weight as a predictor. For seed set and seed weight, we used linear mixed models, with the response variable being the trait of interest, while ‘fire’, ‘year’, and their interaction were included as fixed predictors. Observations were nested within individuals and included as a random factor. Model analyses were conducted using *ANOVA* function from the ‘car’ R-package (Fox et al. 2024). Predictions and confidence intervals were calculated using the ‘ggeffects’ R-package (Lüdecke et al. 2025). (Generalized) linear models were fitted with the ‘stats’ R-package (www.r-project.org) and mixed models with the ‘lme4’ R-package (Bates et al. 2025). Model diagnostics were assessed with the ‘DHARMa’ R-package (Hartig et al. 2024).

Results

During the drought year (2023), flowering and fruiting rates declined by 28 and 41%, respectively, compared to the previous year (2022) in which all individuals produced flowers and filled fruits. These reductions were greater in unburned plants (Fig. 2A, C, Table 1). Specifically, in 2023, 93.7% of burned plants flowered (only one did not), compared to 60% of unburned plants. Burned plants also produced nearly four times more flowers than unburned plants during the drought (Fig. 2B, Table 1). Among flowering individuals, 86.7% of burned plants set fruit, versus only 50% of unburned ones (Fig. 2C), although this difference was only marginally significant (Table 1). Despite an overall reduction in seed set during the drought, burned plants produced more fruits containing seeds across both years (Fig. 2D, Table 1). Seed mass was unaffected by drought, with burned plants producing heavier seeds in both study years (Fig. 2E, Table 1). Germination percentage was slightly higher in burned (32.2%) than in unburned plants (24.4%), although differences were not significant (Table 1).

Discussion

None of the studied plants died during the two-year monitoring period, consistent with the drought-avoidance strategy of *A. cytisoides* (Haase et al. 2000). However, the 2023 drought significantly reduced flower, fruit, and seed production. This reduction was much greater in unburned than in burned plants, both in the probability of flowering and setting fruit (Fig. 2A, C), reflecting a stronger drought impact on unburned individuals. To our knowledge this is the first evidence of a fire-mediated amelioration of drought in terms of reproduction in a resprouting shrub.

Considering that burned and unburned plants were located within a 0.5 ha area, it is safe to assume that they experienced similar climatic conditions and that genetic differentiation between the two groups was low. However, by mid-May, all unburned plants had started shedding leaves (a clear sign of water stress; Haase et al 2000), while none of the burned plants did. Since water stress is associated with reduced flower production and seed set (Kuppler and Kotowska 2021), lower resources for pollinators (Phillips et al. 2018) and reduced floral visitation (Gambel and Holway 2023), the better

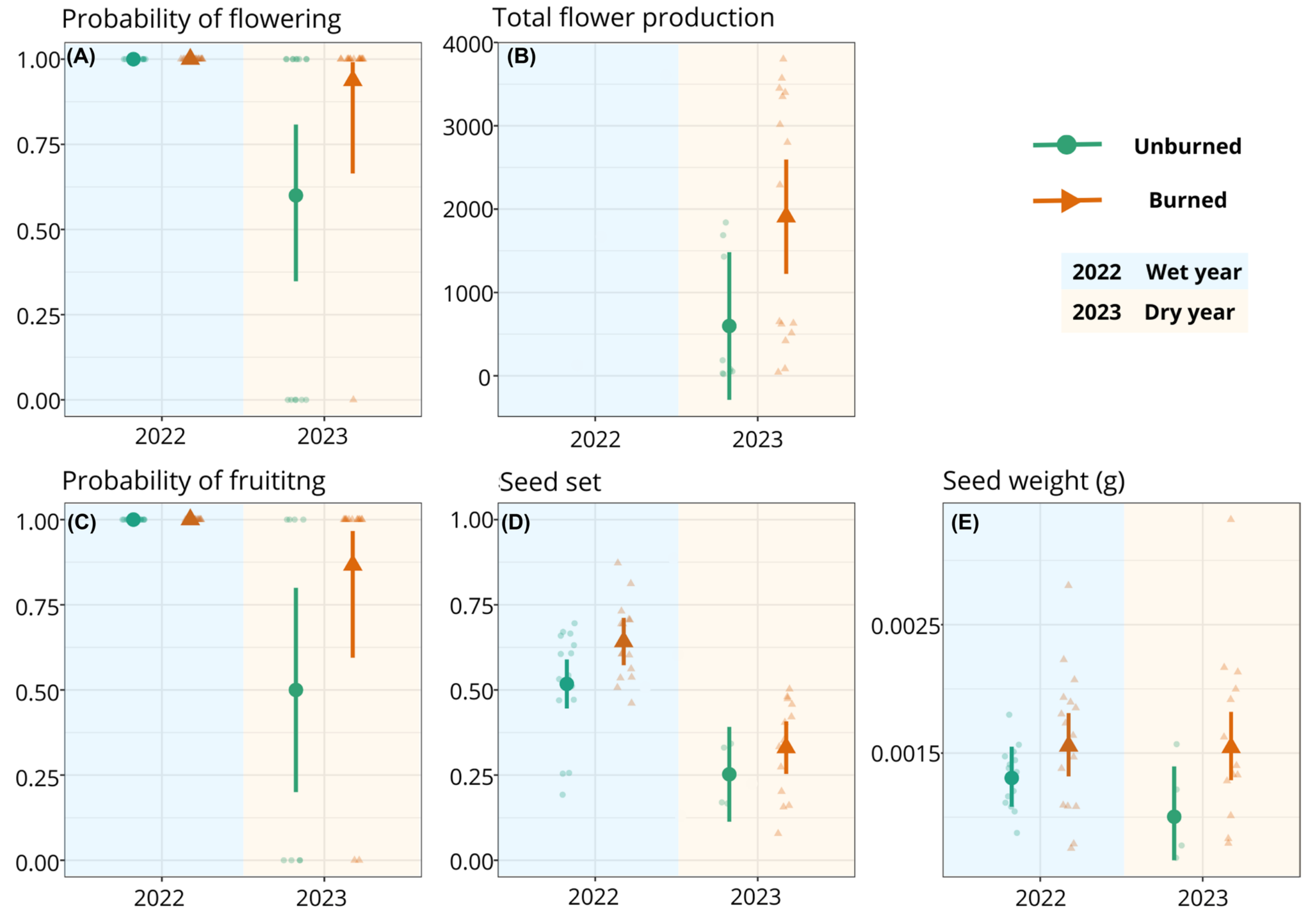


Figure 2. Model predictions (large solid symbols) and observations (small light-coloured dots) of the data analysed in 2022 and 2023; fire occurred in 2021. For flowering and fruiting, the negative effects of drought are stronger on unburned plants (A and C). Burned plants produced nearly four times more flowers than unburned plants (B), and had a higher seed set and heavier seeds than unburned plants in both years (D and E). For the statistical analyses see Table 1.

Table 1. Summary of the models fitted to assess the effects of drought on fitness using fixed effect models (F) and mixed effect models (M) depending on the response trait (first column). For 'Fixed' (F) models we only analyzed data from the dry year (2023), while for 'Mixed' (M) models, 'Year' (2022 or 2023) and its interaction with 'Fire' were also included as fixed predictor and individual as random effect. Positive (negative) estimates indicating higher (lower) values of the trait in the burned treatment and the wet year (2022). In all cases, the degree of freedom of the χ^2-test was 1.

Response trait	Predictor	Estimate	SE	χ^2	p-value	r^2
Probability of flowering (F)	Fire	2.303	1.160	5.446	**0.020**	0.163
Total flower production (F)	Fire	1311.6	540.5	9677313	**0.024**	0.175
Probability of fruiting (F)	Fire	1.872	1.038	3.532	0.060	0.158
Probability of germinating (F)	Fire	0.119	0.421	0.081	0.776	0.035
	Seed weight	822.826	343.394	5.828	**0.016**	
Seed set (M)	Fire	0.124	0.050	7.025	**0.008**	0.512
	Year	−0.265	0.078	48.074	**<0.001**	
	Year × Fire	−0.046	0.093	0.246	0.620	
Seed mass (M)	Fire	0.037	0.0250	4.211	**0.040**	0.126
	Year	−0.050	0.031	0.787	0.375	
	Year × Fire	0.048	0.036	1.714	0.191	

reproductive performance of burned plants was likely due to their improved water status, driven by higher soil moisture in burned patches (Silva et al. 2006) and greater root-to-shoot ratios in burned plants (Schafer et al. 2014).

Beyond water status, the increased reproductive performance of burned plants may result from range of interacting processes (Carbone et al. 2025), with the main causes being fire stimulated flowering (Lamont and Downes 2011) and abiotic resource pulses (Caon et al. 2014) that can trigger bottom–up effects. This could provide a mechanistic explanation for our results, since bigger floral displays with greater rewards for pollinators could enhance pollen transfer and increase seed set and seed quality (Muñoz et al. 2005). Finally, seed size is often positively correlated with germination rate (Lönnberg and Eriksson 2013), which also appears to be the case for *A. cytisoides* (Table 1). However, the increase in seed mass observed in burned plants was not sufficient to produce a significant difference in germination between groups (Table 1). Nevertheless, other factors such as changes in ant predation and/or dormancy might also affect seed mass (Rees 1996, Willott et al. 2000, Parker and Ingalls 2022).

Previous studies have proposed that when drought coincides with post-fire resprouting, resprouting plants are better adapted to short but intense droughts (Pausas et al. 2016). Our results suggest that once resprouting plants overcome the post-fire vulnerability gap (Fig. 1), they may sustain high reproductive levels even during droughts of considerable length and intensity. The next step is to identify the drivers of the magnitude and duration of this benefit boom by, for instance, long-term monitoring of resprouting individuals, or through experiments manipulating competition and water availability during the vulnerability and benefit phases. Future research should also address how this effect depends on the climatic conditions of the first year post-fire, or on traits such as storage capacity and photosynthetic efficiency (Goorman et al. 2011, Pausas et al. 2018), as well as plant age and micro-environmental factors that strongly influence disturbance responses (Moreira et al. 2012, Zomer et al. 2025). Understanding these patterns will be essential for predicting plant responses in fire-prone ecosystems and improving fire-management under increasingly extreme climate scenarios.

In conclusion, the intensity and timing of consecutive stresses are key to understanding plant responses. In particular, burned plants may outperform unburned ones when drought occurs later, even before their aboveground biomass is fully restored. This temporary post-fire advantage appears to enhance drought resilience and sustain reproduction – an effect not captured by current simulation models that aim to predict ecosystem trajectories under increasingly frequent compound disturbances.

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Conflict of interest – The authors declare no conflict of interest. Q4

Author contributions

Jaime Saiz-Blanco: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). **Conchita Alonso**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Writing – review and editing (equal). **Juli G. Pausas**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Q5 Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.XXXX (Saiz-Blanco et al. 2025b). Q6

Supporting information

The Supporting information associated with this article is available with the online version.

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