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REPORT

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Maternal plant exposure to fire enhances offspring germination

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Abstract

Plants that resprout after fire experience drastically altered conditions in post-fire environments. However, the effects of plant exposure to fire on offspring traits remain understudied. Many resprouting species are herbaceous plants that flower and fruit rapidly after fire (i.e., fire-stimulated flowering), developing their seeds under increased resource availability and modified biotic interactions, particularly enhanced pollination. We hypothesize that these changes may improve early offspring development through maternal provisioning and increased quality of floral visitation and pollen deposition. To test this, we selected three Mediterranean geophytes (*Asphodelus cerasifer*, *Drimia maritima*, *Narcissus assoanus*) and compared seed mass (3161 seeds) and total germination (2262 seeds) between paired burned and adjacent unburned plants during the first post-fire fruiting season, sampling six populations over 4 years. Although responses varied among localities and species, on average, seeds from burned plants were 13.9% heavier and had a 16.9% higher germination than those from unburned plants. Our results demonstrate that plant exposure to fire can enhance seed mass and germination and suggest that these improvements may be largely influenced by maternal effects. These fire-driven increases in offspring performance may have important consequences for recruitment, regeneration dynamics, and the long-term persistence of plant populations in fire-prone ecosystems.

KEYWORDS
fire ecology, geophyte, maternal effects, post-fire germination, post-fire resprouting

INTRODUCTION

Fire is a key ecological factor shaping the dynamics of communities in many ecosystems worldwide (He et al., 2019; Keeley & Pausas, 2022). The regeneration strategies of plants living in fire-prone ecosystems are broadly classified into three main categories (Keeley et al., 2011; Pausas & Keeley, 2014): (1) Post-fire obligate seeders, species that are fire-killed and whose populations regenerate from a persistent dormant seed bank that germinates in response to fire (Pausas & Lamont, 2022); (2) obligate resprouters, in which it is the

burned plant itself that regenerates from a bud bank and produces seeds afterwards; and (3) facultative seeders, that combine both mechanisms of post-fire regeneration. Research on post-fire germination ecology has mainly focused on post-fire seeders, both obligate and facultative, showing that fire-related cues like heat or smoke often stimulate seed germination (Auld & O'Connell, 1991; Brown, 1993; Moreira et al., 2010; Pausas & Lamont, 2022). However, the post-fire germination ecology of obligate resprouting species remains comparatively understudied (it is now receiving some attention in tropical ecosystems; Miranda et al., 2024; Tosatto et al., 2025; Zirondi et al., 2024), probably because the links to fire are less evident given that the seeds themselves are not exposed to it. This knowledge gap means that we understand little about how fire affects seed germination and offspring performance within a crucial plant life history type in fire-prone communities, and this is especially relevant in herbaceous species as they may flower and seed soon after fire (Gegunde et al., 2026; Lamont & Downes, 2011).

It is well established that the environment in which a plant grows may influence the early development of its offspring through maternal effects (Roach & Wulff, 1987; Weiner et al., 1997). These effects are known to be induced by environmental stressors such as herbivory (Agrawal, 2001; Steets & Ashman, 2010) or drought (Matesanz et al., 2022; Riginos et al., 2007); however, the role of fire as a driver of maternal effects has received almost no attention. Fire represents a profound ecological disturbance capable of reshaping the conditions where resprouting plants grow, often resulting in increased light and nutrient availability (Caon et al., 2014). Plants growing under favorable conditions tend to increase seed provisioning (Herman & Sultan, 2011; Sultan et al., 2009), which is often associated with improved seed quality and germination success (Wulff, 1986a). We therefore expect that favorable post-fire abiotic conditions could alter maternal allocation patterns of burned resprouting plants and directly influence offspring phenotypes through enhanced seed provisioning.

Plants resprouting after fire may also experience altered biotic conditions, such as changes in predation (García et al., 2016) or pollination (García et al., 2018); the latter is particularly notable in herbaceous species that flower rapidly and profusely after fire (i.e., fire-stimulated flowering; Lamont & Downes, 2011). Fire stimulates and synchronizes flowering in these species, increasing both the flower production per individual and the density of flowering individuals, which together enhance the floral availability in the population (Wagenius et al., 2020). This can enhance floral visitation and pollen deposition on stigmas (Carbone et al., 2025; Gegunde et al., 2026; Tosatto et al., 2025) which, in turn, may not only promote seed production but also enhance seed quality, in some cases, via increased gametophytic competition (Labouche et al., 2017; Marshall & Ellstrand, 1988; Snow, 1986). Moreover, this post-fire mass flowering may increase opportunities for outcrossing with genetically distant mates, reducing inbreeding depression and promoting genetic diversity (Fenster & Galloway, 2000), which could in turn enhance seed quality and performance. However, flowering after fire may also have the opposite effect on seed quality by increasing the risk of inbreeding through geitonogamy (Harder & Barrett, 1995) or biparental mating, particularly in self-incompatible species (LoPresti et al., 2018; Richardson & Wagenius, 2022) and in spatially structured populations (e.g., species with limited seed dispersal or that are clonal; Vallejo-Marín et al., 2010).

These modifications in both abiotic and biotic aspects of the maternal environment represent two complementary and potentially interacting pathways (Bañuelos & Obeso, 2003; Recart & Campbell, 2021; Shi et al., 2005) through which fire may influence offspring performance of maternal plants exposed to fire. Yet, this remains largely unexplored. We hypothesize that the post-fire environment experienced by resprouting plants may enhance the performance of the seeds they produce. To test this hypothesis, we studied species with fire-stimulated flowering that set seed shortly after a fire and thus provide a unique opportunity to investigate the ecology and development of seeds produced by burned plants. We focused on wild populations of three geophytes to compare seed mass and germination between seeds produced by burned and unburned maternal plants.

MATERIALS AND METHODS

Study species and seed collection

Our study was conducted in shrublands of the southeastern Iberian Peninsula, a region with a typical Mediterranean climate where summer wildfires are common. We selected three geophyte species with fire-stimulated flowering that are widely distributed in the study region: *Asphodelus cerasifer* (Asphodelaceae), *Drimia maritima* (Asparagaceae), and *Narcissus assoanus* (Amaryllidaceae). All species usually have completely dry leaves at the time of fire and resprout from underground storage organs: rhizomes with tuberous roots in *A. cerasifer* and bulbs in *D. maritima* and *N. assoanus*. All species are pollinated by insects, exhibit short-distance seed dispersal, and do not form a permanent seed bank (obligate resprouters).

Seed sampling was conducted in six different burned areas during the first post-fire fruiting season (i.e., within 1 year after fire), and adjacent unburned areas (i.e., a paired design) carefully chosen to be representative of the pre-fire conditions (e.g., same plant species composition, dominant species, and soil characteristics). *A. cerasifer* was sampled in three localities (i.e., burned–unburned pairs), *D. maritima* in two, and *N. assoanus* in a single locality. We collected fruits from spatially separated sites within each locality and fire treatment (burned and unburned), with the number of seeds determined by the local availability of each species. All sampled sites had remained unburned for at least 10 years before the fires considered in this study, and fire frequency ranged from 0 to 2 fires over the available fire history records (see Appendix S1: Table S1 for details). Fire history was obtained from maps provided by the regional governments of Valencia and Andalucía and covered 1978–2024 and 1975–2021, respectively.

For each species and locality, fruits were collected during their dispersal period from 16 to 60 plants per fire treatment (burned and unburned), distributed across sites. Seeds were then manually removed from the fruits and stored in paper bags in the dark at room temperature for 6–10 months until the start of the germination trials (see Appendix S1: Table S1 for further details). Overall, we collected between 100 and 400 seeds per locality and fire treatment. For each species, locality, and site, a subset of seeds was individually weighed to the nearest 0.01 mg using an analytical balance, resulting in 3161 weighed seeds (for details, see Appendix S1: Table S1).

Germination trials

Germination trials consisted of placing seeds on moist filter paper in Petri dishes in germination chambers to assess germination rates. For each species and locality, we sowed eight dishes per fire treatment distributed among sites, except for *D. maritima*, where we used six and seven replicates in the two localities, respectively. We sowed 24 ± 5 seeds in each dish for *A. cerasifer*, 25 ± 1 for *D. maritima*, and 29 ± 2 seeds for *N. assoanus*, totaling 2262 seeds. Seeds were subjected to a 12-h light/dark cycle, with temperatures of 20 and 15°C, respectively. We recorded the number of germinating seeds with a radicle protruding at least 1 mm from the seed coat every 2 days until the end of the experiment. Each trial ended when no additional seeds had germinated after at least 6 days, and its duration varied between species (see Appendix S1: Table S1). Before data analysis, the initial number of seeds sown was adjusted by discarding empty nonviable seeds that lacked an embryo or storage tissues.

Data analysis

To assess differences in seed mass and germination rate between seeds from burned and unburned maternal plants, we fitted separate models for each species and each response variable. Fire (i.e., burned vs. unburned), locality, and their interaction were included as predictor variables in models for *A. cerasifer* and *D. maritima*, and only fire was included in models for *N. assoanus* (sampled in one locality). Seed mass was included as the response variable in linear mixed models (LMMs) with the identity of the maternal plant nested within site as random effect. Total germination (relative to the number of seeds sown) was used as the response variable in generalized linear mixed models (GLMMs) with a binomial error distribution and the identity of the dish nested within site as random effect. For *D. maritima*, site was not included as a random effect in either model because site replication was limited and among-site variance was negligible.

GLMMs and LMMs were performed with the "lme4" R package (Bates et al., 2015). Significance of fixed effects and interactions were obtained using the Anova function from the "car" R package (Fox & Weisberg, 2019). In the cases when the fire × locality interaction term was significant, we conducted post hoc analysis by conducting pairwise comparisons of the estimated marginal means with the "emmeans" R package (Lenth & Piaskowski, 2026). Uniformity of residuals was checked using the "DHARMa" package (Hartig, 2019). All statistical analyses were performed in the R software version 4.4.1 (R Core Team, 2024).

RESULTS

Fire had a significant positive effect on both seed mass and total germination across the three study species, although the magnitude of the response varied among species and localities (Figure 1 and Appendix S1: Table S2). Seed mass increased significantly in four of the six localities, whereas total germination increased in five of the six localities. In no cases did these variables decrease with fire.

For *A. cerasifer*, the fire × locality interaction was significant when testing both differences in seed mass ($\chi^2 = 17.27$, df = 2, $p < 0.001$) and total germination ($\chi^2 = 6.23$, df = 2, $p = 0.044$). Post hoc comparisons showed that fire increased seed mass in Azuébar and in Vall d'Ebo, but not in Bejís (Appendix S1: Table S3). Fire increased total germination in Azuébar and Bejís, but had no significant effect in Vall d'Ebo (Appendix S1: Table S4).

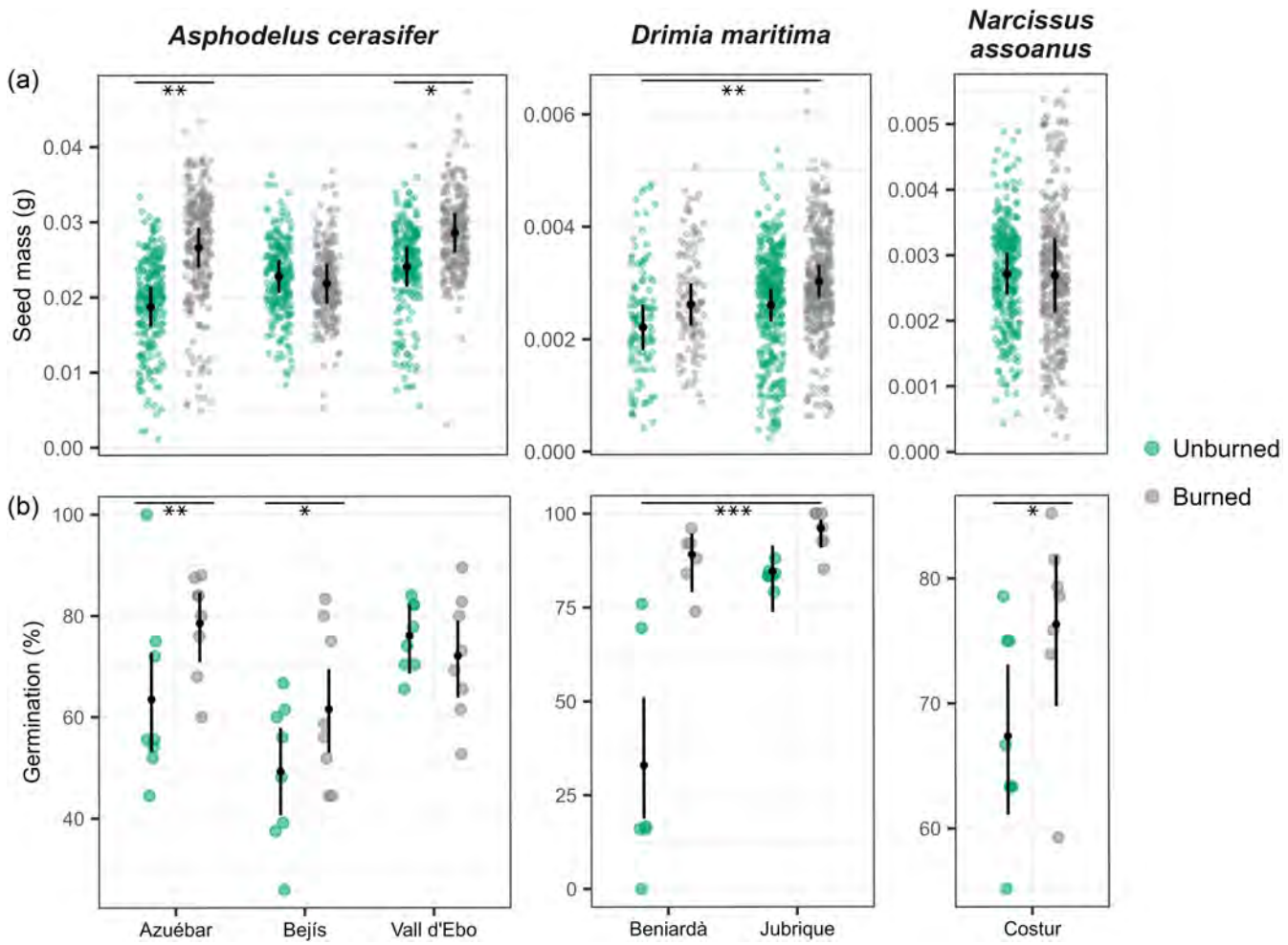

FIGURE 1 (a) Seed mass and (b) total germination (in percentage) of seeds from burned (gray) and unburned plants (green) for *Asphodelus cerasifer*, *Drimia maritima*, and *Narcissus assoanus*. Background dots represent: (a) individual seed mass values and (b) germination values of individual Petri dishes. Black dots with error bars indicate estimated marginal means ±95% CIs in both cases. Asterisks indicate significant differences between burned and unburned plants, shown per species or per locality when the fire effect differed among localities (significant fire × locality interaction; ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$). See Appendix S1: Table S2 for summary statistics and Appendix S1: Tables S3 and S4 for post hoc analysis.

In *D. maritima*, seeds from burned plants were heavier ($\chi^2 = 6.21$, df = 1, $p = 0.013$) and showed higher total germination per dish ($\chi^2 = 28.66$, df = 1, $p < 0.001$) than seeds from unburned plants, and increases in both variables were consistent across localities (nonsignificant interaction between fire and locality in both models). Seed mass ($\chi^2 = 5.24$, df = 1, $p = 0.022$) and total germination ($\chi^2 = 22.00$, df = 1, $p < 0.001$) also differed between localities, being generally higher in Jubrique than in Beniardà.

For *N. assoanus*, fire did not affect seed mass but had a significantly positive effect on total germination ($\chi^2 = 4.06$, df = 1, $p = 0.044$).

Overall, across all populations studied, there was an increase of 13.9% in seed mass and in 16.9% in total germination in burned plants.

DISCUSSION

Seeds from burned maternal plants were heavier and exhibited higher total germination than those from unburned plants across the three study species. These results suggest that the post-fire environment experienced by maternal plants can have ecological consequences in the early development of their offspring, at least in resprouting species that flower quickly after fire.

By increasing soil nutrient availability and reducing competition (Caon et al., 2014), fire improves the nutritional condition of surviving plants. This promotes vegetative growth in resprouting species that often translates into larger plants (Tosatto et al., 2025) and greater flower production (Borchert & Tyler, 2009; Gegunde et al., 2026; Wagenius et al., 2020). There is also evidence of post-fire

increases in pollinator visitation (Carbone et al., 2025) and pollination success (Gegunde et al., 2026; Richardson & Wagenius, 2022; Wagenius et al., 2020), which may further increase the reproductive efficiency of flowering plants (fruit and seed set). This concurrent improvement in both abiotic and biotic conditions following fire could enhance total seed production per plant, as has been reported for many fire-stimulated flowering species (Carbone et al., 2025), including the same populations studied here (Gegunde et al., 2026). According to the well-known trade-off between seed number and seed mass (Labouche et al., 2017; Moles & Leishman, 2008; Smith & Fretwell, 1974), such increase in total seed production would be expected to result in reduced seed mass. However, our results show that seed mass was not compromised despite an increase in seed number, and even increased in some populations. Taken together, these findings suggest that post-fire improvements in both abiotic (e.g., nutrient availability) and biotic (e.g., pollination) conditions may act synergistically to enhance both the quantity and quality (in terms of seed mass) of seeds produced by burned plants or at least to compensate potential negative effects associated with any of these mechanisms (Shi et al., 2005).

Total germination increased consistently in seeds from burned plants across all study species and in nearly all populations. Increases in germinability may be explained by higher seed viability, reduced dormancy, or both (Zirondi et al., 2024). Although seed viability was not directly assessed in this study, increased viability appears to be a plausible contributor to the higher germination of seeds from burned plants, as seed mass can reflect seed viability (e.g., Huayta-Hinojosa et al., 2025), and we found higher seed mass in many of the populations where germinability increased. By contrast, reduced seed dormancy seems unlikely because these species are not known to exhibit physical or physiological dormancy and do not form persistent seed banks.

Furthermore, germination also increased in some populations without a corresponding increase in seed mass, suggesting that factors other than those typically linked to seed mass may underlie the beneficial effects of the maternal post-fire environment on seed germination. These could include changes in pollinator community composition (Herrera, 2000) or epigenetic changes in maternal plants, as suggested by recent evidence of post-fire shifts in DNA methylation in a resprouting species (Saiz-Blanco et al., 2025). Further research is needed to assess the extent to which these mechanisms contribute to germination responses. In addition, population-level variation in seed mass and germination responses could be influenced by differences in local fire history (Gómez-González et al., 2011; Zirondi et al., 2024). However, in our study, differences in fire frequency among sites were small and all burned areas had remained unburned for at least 10 years before the study fire, suggesting that fire history is unlikely to explain variations among localities.

The enhanced seed mass and germination observed in burned plants might be partly explained by maternal effects induced by fire. If such effects persist into subsequent generations, they would represent a form of adaptive transgenerational plasticity (Herman & Sultan, 2011; Marshall & Uller, 2007), a hypothesis that warrants further research across generations. Some evidence also suggests possible fire-driven paternal effects through enhanced germination success of pollen produced by burned plants (Travers, 1999). The extent and ecological significance of these fire-driven maternal and paternal effects deserve further research.

Our results demonstrate that maternal exposure to fire can enhance germination in obligate resprouting species and, if this response is driven by higher seed viability, as seems plausible based on our results, it may also improve early offspring performance beyond germination (Wulff, 1986b). The combination of high seed availability, improved germination, increased light and nutrient availability, and low competition creates a unique window of opportunity for these species to recruit shortly after fire, as reported previously in the field for some of the studied species (Gegunde et al., 2026). This strategy aligns fire-stimulated flowering species with the "best-bet strategy" typical of post-fire seeders (Pausas et al., 2022), revealing a previously underappreciated pathway through which fire contributes to the regeneration dynamics of fire-adapted species.

AUTHOR CONTRIBUTIONS

Julia Gegunde, Maria Clara Castellanos, and Juli G. Pausas designed the research. Julia Gegunde conducted the sampling, performed the analyses with assistance from Juli G. Pausas, and wrote the first draft of the manuscript. Maria Clara Castellanos and Juli G. Pausas contributed to the discussion of the results and the final writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Gegunde, 2026) are available in Figshare at https://doi.org/10.6084/m9.figshare.33071153.v2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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