



Dormant or non-dormant seeds: different germination strategies used by common aquatic plants in Mediterranean temporary ponds

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Abstract In temporary ponds, the re-establishment of aquatic plant assemblages after desiccation mainly depends on seed germination. We analysed the seed germination dynamics of common aquatic plants in Mediterranean temporary ponds to evaluate how the ponds' dry phase could affect the persistence of plant populations. We collected seeds of *Callitriche brutia* Petagna, *Ranunculus peltatus* Schrank, and *Myriophyllum alterniflorum* DC. For each species, one half of the seeds were used in germination trials one day after collection, and the other half were kept in a dry after ripening treatment for two months before being used in germination trials. We placed the seeds in inundated wells kept at 20 °C and 12L:12D; we recorded the number of germinated seeds per well and the time to germination. For *C. brutia*, both treatments led to a high percentage of germination. For *R. peltatus* and *M. alterniflorum*, only the dry after ripening treatment led to a high percentage of germination. Most *C. brutia* seeds are non-dormant; thus, only its late-produced seeds would germinate in subsequent germination cycles. In contrast, most

R. peltatus and *M. alterniflorum* seeds seem to go through a dormancy period, which is broken during the dry phase, allowing germination during future inundation cycles.

Keywords Aquatic plants · Reproduction · Dormancy · Doñana · Seeds

Introduction

Macrophytes play an important role in aquatic ecosystems where they provide food and complex habitat structures for aquatic organisms and help improve water quality by releasing oxygen and removing excessive nutrients (Lesiv et al., 2020). Temporary ponds are singular aquatic ecosystems that experience recurrent dry phases. As a result, they tend to harbour specialised aquatic flora (and fauna) that have developed different strategies for coping with desiccation (Grillas et al., 2004). While plants in permanent aquatic habitats mainly reproduce via vegetative propagules, plants in temporary aquatic habitats usually decay at the end of the annual inundation cycle and therefore rely on seeds to re-establish their populations after intense dry periods (Cronk & Fennessi, 2001; Deil, 2005). Seeds may germinate during the following inundation cycle, or they may persist in the soil seed bank for long periods, germinating during later pond flooding events (Brock et al., 2003; Aponte et al., 2010; Brock, 2011; Cross et al., 2015).

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In temporary ponds, aquatic plants do not germinate during the dry period; instead, during each new inundation cycle, some fraction of the soil seed bank will germinate (Brock et al., 2003), a process that is triggered by favourable environmental cues. Some aquatic plant species produce non-dormant seeds, which can germinate under a wide range of environmental conditions after dispersal from the mother plant. However, many aquatic plant species produce dormant seeds, whose germination remains blocked even under conditions that favour seedling emergence and survival (Baskin & Baskin, 1998, 2004). There are several types of seed dormancy: morphological, physiological, and physical, or a combination of these, such as morphophysiological dormancy (Baskin & Baskin, 1998; Fenner & Thompson, 2005). Furthermore, dormant seeds may experience both primary and secondary dormancy. Primary dormancy occurs when the seeds are still on the mother plant and is broken if the seeds undergo certain physical or chemical processes (after ripening), which may coincide with the dry period. Seeds may enter into secondary dormancy if they do not experience suitable conditions for germination after primary dormancy is broken (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006).

In this study, we describe the germination dynamics of common aquatic plants in Mediterranean temporary ponds. Usually small and shallow, these ponds contain a distinctive form of biodiversity and host a large number of rare, endemic, or threatened plant and animal species (Grillas et al., 2004; Ruiz, 2008). Additionally, Mediterranean temporary ponds experience pronounced variability in the annual timing of pond inundation; in some years, it happens in the autumn, and in other years, it happens in the winter or spring, resulting in broad differences in the ponds' initial aquatic conditions (Fernandez-Zamudio et al., 2018). Inundation is the key trigger of seed germination for the most common aquatic plant species in Mediterranean temporary ponds (Fernández-Zamudio et al., 2018). Furthermore, environmental conditions at the time of seed germination will influence seedling survival as well as plant growth and the probability of successful reproduction (Donohue et al., 2010). Thus, interannual differences in the timing of pond inundation can influence seed germination, seedling survival, and seedling growth. When ponds are filled in the autumn, water turbidity, pH, and

conductivity are lower than when ponds are filled in the winter or spring. While water temperatures gradually decrease in autumn, they increase in ponds that fill in the winter and spring (Florencio et al., 2020). Most Mediterranean temporary ponds are dry in the summer, making it an unfavourable period for aquatic plant persistence and seed germination. To persist under unsuitable environmental conditions (e.g. dry periods or cold temperatures during winter inundation), aquatic plants may utilise different reproductive strategies, including different germination responses. It may be crucial to understand the germination ecology and characteristics of macrophyte seeds when reintroducing plants as part of pond restoration efforts (Prausova et al., 2022; Verhoeven et al., 2024).

We examined the differences in seed germination dynamics among three common plant species found in Mediterranean temporary ponds. The objective was to assess whether the plants had different reproductive strategies for persisting in the ponds and for re-establishing their populations across inundation cycles. Specifically, we analysed how seeds from the three species responded to experiencing a dry phase, with a view to evaluating the role of the dry phase on long-term plant persistence. To this end, we compared the germination of fresh seeds (which had always remained submerged) with the germination of seeds that had been stored under dry conditions. Overall, our hypothesis was that the three plant species would produce seeds that could survive the ponds' dry phase, whose germination can be improved by a dry after ripening period.

Materials and methods

Study area

In this study, we examined the seed germination dynamics of three common aquatic plant species found in the temporary ponds of Doñana National Park (36,991 N/ 6.443 W). This protected area of approximately 54,300 ha is located in southwestern Spain, between the mouth of the Guadalquivir River and the Atlantic coast. The park includes two distinct areas: an extensive marsh on clay substrate and a sandy area with stable and moving dunes. The climate is Mediterranean with an Atlantic influence, characterised by mild winters (mean

winter temperature: 10.9 °C), hot dry summers (mean summer temperature: 23.5 °C), and a mean annual rainfall of around 550L/m². In the sandy area of the park, there is a large pond network in which more than 3,000 Mediterranean temporary ponds may be filled in very wet years (Díaz-Paniagua et al., 2015). These ponds are groundwater dependent; they fill with accumulated rainfall as groundwater levels rise above the bottom of the pond. Pond inundation commonly occurs when heavy rains start falling in the autumn, winter, or spring—timing varies across years. Ponds are commonly dry during the summer (Díaz-Paniagua et al., 2010, 2015).

The plant species found in Doñana's ponds have been extensively described (García-Murillo & Fernández-Zamudio, 2015; Fernández-Zamudio et al., 2016). In the ponds' inner zones, the predominant plants are annual species that commonly develop aquatic morphs during the ponds' wet phase; however, they may develop terrestrial morphs during the ponds' dry phase (Fernández-Zamudio et al., 2021). The most abundant of these annual species are *Ranunculus peltatus* Schrank, *Myriophyllum alterniflorum* DC, several *Callitriche* species (*Callitriche brutia* Petagna, *Callitriche stagnalis* Scopoli, and *Callitriche obtusangula* Le Gall), and *Juncus heterophyllus* Dufour. At the edge of the ponds, helophytes may form a dense vegetated zone, where *Juncus maritimus* Lam. and *Scirpoides holoschoenus* (L.) Soják are common (García-Murillo & Fernández-Zamudio, 2015).

Study species

For this study, we selected three of the most common species in Doñana's temporary ponds (Fernández-Zamudio et al., 2016, 2018). The three species have different reproductive characteristics. *Callitriche brutia* and *Ranunculus peltatus* start producing flowers and fruits around two months after germination, generally from February onwards (Fernández Zamudio et al., 2018). *Myriophyllum alterniflorum* produces flowers and fruits about 2–3 months later than the other two species (reaching maximum flower number in May), closer to the end of the inundation phase (Pintero-Rodríguez et al., 2021). *Callitriche brutia* and *R. peltatus*

seeds produced early in the annual inundation cycle could germinate during that same cycle. However, most *M. alterniflorum* seeds germinate during subsequent inundation cycles, as do the later produced seeds of the other two species.

Seed collection and germination trials

During the spring of 2017, we transplanted rooted plants of the three species, moving them from the temporary ponds to 55L tanks located outdoors and exposed to the natural conditions of the park's research facilities. The tanks contained a layer of sand, pond sediment, and well water. The plants were left to grow under natural ambient conditions. We placed plastic containers at the bottom of the tanks that served as seed traps, from which we collected the mature seeds that had fallen from the plants. We collected a total of 480 seeds from *C. brutia*, 1082 seeds from *R. peltatus*, and 430 seeds from *M. alterniflorum*. We then created two approximately equal-sized groups of seeds for each species. One group (i.e. the fresh seeds) was immediately used in germination trials (start date: 13 July 2017); the germination trials began the day after the seeds were collected from the tanks, meaning that the seeds did not experience drying. These conditions simulated a scenario in which seed production and germination took place within the same inundation cycle. The other group of seeds (i.e. the dry after ripening treatment) were wrapped in filter paper and stored under dry conditions at room temperature (mean temperature: 29.1 °C, range: 25–33 °C) for two months; after this dry period (i.e. the after ripening period), the seeds were used in germination trials (start date: 12 September 2017). These conditions simulated a scenario in which germination took place during subsequent inundation cycles (following the summer dry phase).

During both sets of germination trials, we placed 10–12 seeds in the wells of 24-well polystyrene plates; the wells were filled with dechlorinated tap water. For each species, we considered that the seeds in each well were replicates. In the case of the dry seeds, for *R. peltatus*, there were 41 wells with 12 seeds each and 1 well with 10 seeds; for *C. brutia*, there were 30 wells with 10 seeds; and for *M. alterniflorum*, there were 23 wells with 10 seeds. In the case of the fresh seeds, for *R. peltatus*, there were 58 wells with 10 seeds; for *C. brutia*, there were 18

wells with 10 seeds; and for *M. alterniflorum*, there were 20 wells with 10 seeds. The plates were then placed in germination chambers (20 °C, 12L:12D). We observed the seeds every day until we detected the first seedling. Then, we monitored the seeds twice a week to remove and count all the seedlings; we interrupted the experiment when two or three weeks passed without recording any new germination. We considered that a seed had germinated when we observed that its radicle had emerged from its seed coat. Once detected, seedlings (and their remaining seed coats) were removed to make it easier to see newly germinated seeds.

Data analyses

We carried out our analyses in R (v. 4.5.0; R core team, 2025). We used generalised linear models (GLMs) to compare germination levels among species and seed groups (fresh or dry seeds). The models had a quasibinomial error distribution (due to overdispersion). The response variable was the number of germinated versus ungerminated seeds in each well, and the explanatory variables were species and treatments (i.e. fresh vs dry after ripening). We also tested the interaction of the variables (species:treatment).

We similarly used GLMs to examine time to germination. The models had either a Poisson or quasi-Poisson error distribution, depending on the presence of overdispersion. The response variable was the day of germination (measured from the beginning of the trial), and the explanatory variables were species and seed treatments, testing also the interaction of these variables. For GLM estimation and diagnostics, we used the R packages *MASS* (Venables & Ripley, 2002) and *car* (Fox & Weisberg, 2019). When we observed a significant interaction among the variables, Tukey's tests were employed to conduct post hoc comparisons; we utilised the *multcomp* R package (Hothorn et al., 2008).

We counted the number of seeds that germinated and determined the day of germination for each seed in each well. We used these values to calculate the mean ($\pm$ standard error) percentage of germinated seeds and time to germination for each species and treatment.

Results

We observed differences in the percentage of germinated seeds among species ($P_{2, 185}=152.01$, $P<0.00005$) and between treatments ($P_{1, 185}=175.80$, $P<0.00005$). The species-by-seed treatment interaction was also significant ($P_{2, 185}=18.66$, $P<0.00005$) (Fig. 1).

The seeds of *C. brutia* had similarly high germination levels in both seed treatments (fresh: $95.5 \pm 2.02\%$, dry: $92.3 \pm 1.49\%$; Tukey's test, $P=0.952$), which were significantly different from the germination levels of the other two species ($P<0.0005$ for both comparisons). For *R. peltatus* and *M. alterniflorum*, the percentage of germinated seeds was very low for the fresh seeds but considerably higher for the dry seeds (Fig. 1). In the case of *R. peltatus*, the percentage of germinated seeds was almost sevenfold higher for the dry seeds ($45.2 \pm 2.65\%$) than for fresh seeds ($6.21 \pm 2.33\%$) (Tukey's test: $P<0.0001$). This difference was similarly large for *M. alterniflorum* (dry: $88.7 \pm 2.13\%$, fresh: $12.5 \pm 1.76\%$; Tukey's test: $P=0.0001$).

Overall, time to germination significantly differed among species ($F_{2, 937}=4.98$, $P=0.005$) and between treatments ($F_{1, 937}=1394.13$, $P<0.00005$). The species-by-seed treatment interaction was again significant ($F_{2, 937}=14.68$, $P<0.00005$). For the dry seeds, there were no differences in time to germination among species (Tukey test: $P>0.08$ in all cases). For the fresh seeds, all the paired comparisons were

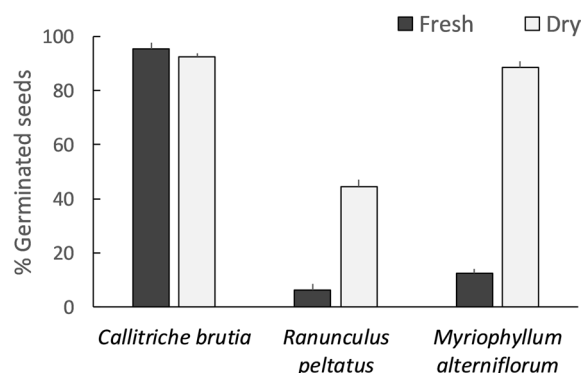


Fig. 1 Percentage of germinated seeds for the three aquatic plant species. Fresh seeds were used in germination trials after their collection, meaning that they remained wet; dry seeds experienced two months of dry storage before being used in germination trials

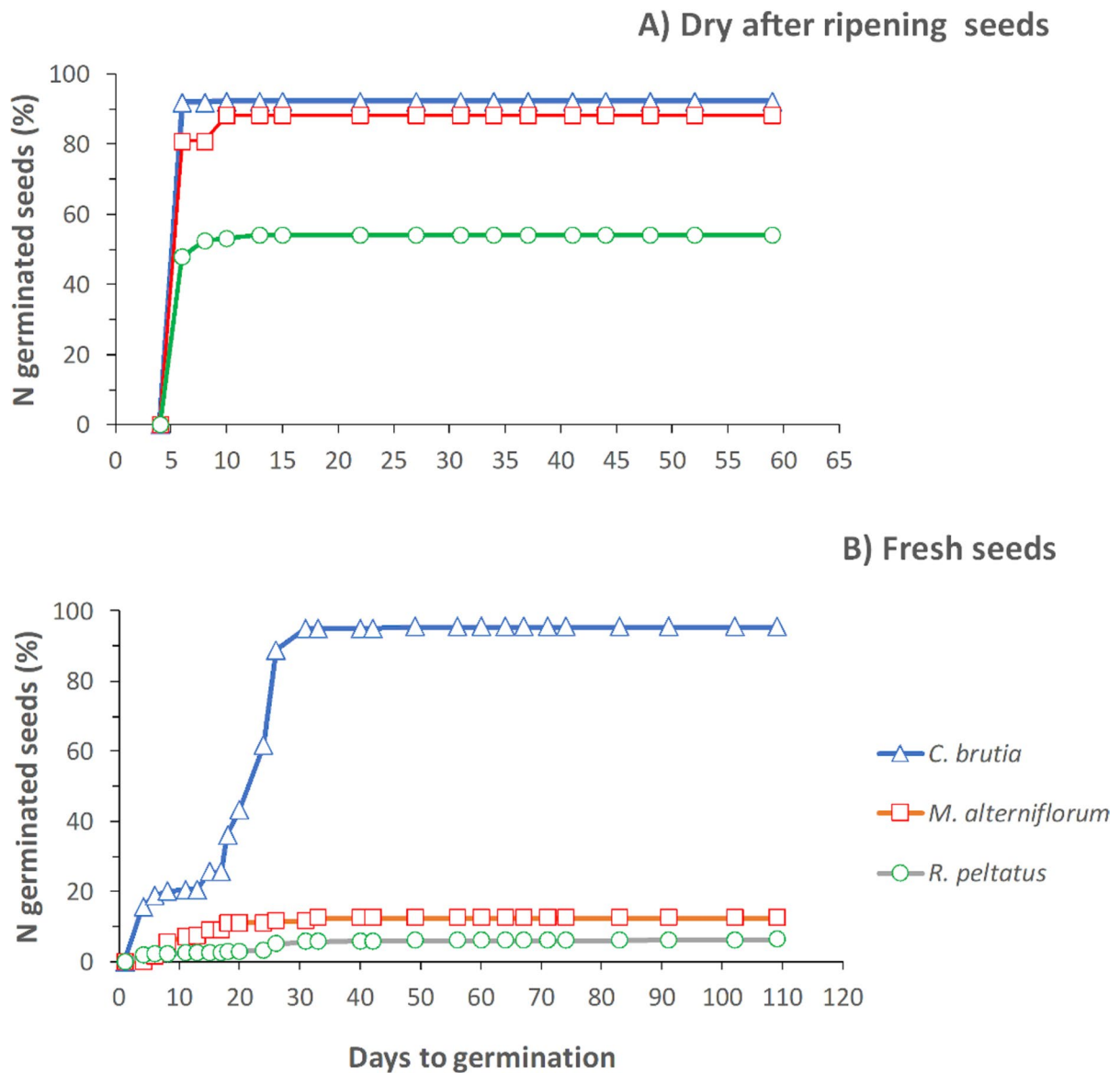


Fig. 2 Cumulative curve of the percentage of dry after ripening seeds (A) and fresh seeds (B) that germinated over time for the three plant species

significantly different ($P < 0.0005$), except for the comparison between *C. brutia* and *R. peltatus*, which was not ($P > 0.08$). Fresh seeds generally germinated across a long period during the first month of the germination trial, with a few seeds germinating during the second month or even later (Fig. 2). There were two different germination peaks for *C. brutia* and *R. peltatus*. For the fresh seeds, the mean time to germination was 13.5 ± 1.55 d for *M. alterniflorum*,

22.4 ± 3.50 d for *R. peltatus*, and 19.6 ± 0.67 d for *C. brutia*. For the dry seeds, germination occurred rapidly once the trial began, mostly within the first week. Their mean time to germination was 6.01 ± 0.01 d for *C. brutia*, 6.33 ± 0.08 d for *M. alterniflorum*, and 6.24 ± 0.07 d for *R. peltatus*.

Discussion

In this study, we examined the germination dynamics of newly produced seeds. The three aquatic plant species produce seeds that can survive the dry phase of the ponds but differed in their percentages of seed germination. For *C. brutia*, germination levels were high, regardless of whether seeds were exposed to dry conditions. In contrast, germination levels were only high for *M. alterniflorum* and *R. peltatus* seeds that had experienced drying.

The fact that *C. brutia* seeds displayed high germination levels in our germination trials while their parent plants were still alive suggests that the species produces non-dormant seeds that do not require special conditions to germinate. Most of the fresh *C. brutia* seeds germinated. Under real-life conditions, the result would have been new plants emerging within the ongoing inundation cycle, which would have contributed to increased plant density and continuous plant renewal in temporary ponds. The aquatic form of *C. brutia* has thin stems, with little to no branching, but the species is the earliest to produce fruits and seeds in the Mediterranean temporary ponds of Doñana, a process that continues uninterrupted until the end of the plant's life cycle (Fernández Zamudio et al., 2018) in late spring. Thus, seeds are responsible for the plant's continuous and dense presence in the ponds throughout the spring, and the absence of seed dormancy may allow seedlings to emerge while conditions are favourable for plant growth and reproduction. The high percentage of seed germination that we observed here implies that *C. brutia* makes a limited contribution to the seed bank. However, the re-establishment of *C. brutia* populations during the subsequent inundation cycles must draw upon a source of seeds, notably the small fraction of ungerminated seeds remaining in the pond basin. These seeds may have been produced at the end of the season, when increased temperatures or drier conditions are not favourable to germination. Our data do not allow us to determine whether these ungerminated seeds were non-viable, dormant, or whether they were seeds that did not experience conditions suitable to germination by the end of the inundation cycle in which they were produced. After the dry phase, these seeds may germinate in the newly filled ponds at around the same time as seeds of the other two species, resulting in *C. brutia* re-colonising the ponds just after they have

filled. At the same time, *C. brutia* is known to use other strategies to survive unfavourable periods (i.e. drought), allowing its long-term persistence. Under dry conditions, the species may develop terrestrial forms whose seeds have higher germination rates than the seeds of aquatic forms, and these terrestrial forms play an essential role in ensuring the persistence of the populations after severe dry periods (Fernández-Zamudio et al., 2021).

In the case of *M. alterniflorum* and *R. peltatus*, the percentage of germination was low for fresh seeds: they appeared to enter a dormant phase that prevented seedling emergence within the same inundation cycle. *Myriophyllum alterniflorum* is a common plant and tends to have the largest amount of biomass in Mediterranean temporary ponds (Fernández-Zamudio et al., 2018). It produces flowers and fruits in late spring or early summer (Pinero-Rodríguez et al., 2021), when environmental conditions are likely unsuitable for seedling survival and plant growth. Under these conditions, delaying germination to subsequent inundation cycles may increase the probability of the successful reproduction and persistence of the population. During the ponds' dry phase, seed dormancy may be broken, and germination may be triggered by pond refilling. This hypothesis is supported by the fact that the fresh *M. alterniflorum* seeds displayed low levels of germination whereas the seeds which underwent a dry after ripening period had high levels of germination. Like *C. brutia*, *M. alterniflorum* had a low percentage of ungerminated seeds that could be stored in the seed bank for later inundation cycles. This low contribution to the seed bank may be due to the species' great capacity to regenerate from rhizomes or vegetative propagules, which may play a more important role than seeds in the long-term persistence of populations (Schulthorpe, 1967). Therefore, in *M. alterniflorum*, population re-establishment is not exclusively dependent on seeds; however, seeds may be essential when conditions are extremely unfavourable, such as during periods of severe drought, because seeds may survive when vegetative propagules do not.

In this study, most *R. peltatus* seeds did not germinate during the inundation cycle, which suggests they might enter a dormancy stage after being released by their mother plant. In *R. peltatus*, dispersed seeds contain underdeveloped embryos (Carta et al., 2012). They therefore must complete embryo development

before they can germinate, which may explain the absence of germination after seed dispersal. Even though embryo development may be completed within 30 d (Carta et al., 2012), we observed a longer absence of germination for the fresh *R. peltatus* seeds. Therefore, although Carta et al. (2012) classified the seeds of *R. p. baudotii* as non-dormant, our study suggests that the seeds of *R. peltatus* were dormant and may have also undergone an additional period of physiological dormancy before or after the embryos completed development.

Pond drying is a factor that can help break dormancy (Tuckett et al., 2010), which means that seeds are ready to germinate when favourable conditions appear after pond refilling. Pond inundation determines the timing of seed germination and synchronises the emergence of most seedlings, restoring the plant assemblage (Fernández-Zamudio et al., 2018). In this study, we observed two different germination strategies used by three submerged aquatic plants in temporary ponds.

The first strategy is producing seeds with a dormancy period that is broken during the dry phase; these seeds can then respond to favourable conditions after the pond refills, and their synchronised germination and early growth occur rapidly after the beginning of the new inundation cycle. In this study, we observed that only a fraction of *R. peltatus* seeds germinated during the trials; around 50% of seeds may remain in the seed bank and germinate during future inundation cycles (Fernández-Zamudio et al., 2021), increasing population resilience. The second strategy is producing seeds that germinate within the same inundation cycle, before the dry phase. Although we observed that seeds of all three species germinated even if they did not experience dry conditions, only *C. brutia* produced a large percentage of these non-dormant seeds. This species starts to produce flowers and seeds early in the inundation cycle (Fernández-Zamudio et al., 2018) and, because these seeds then germinate, the plants can continuously produce new individuals throughout the cycle, increasing their abundance and total number of seeds produced per year. At the end of the inundation phase, the final seeds produced are unlikely to encounter suitable conditions for germination and plant growth. As a result, they must make it through the dry phase and await the occurrence of favourable conditions during

the next inundation cycle, at which point the percentage of seed germination is again high.

Both strategies ensure that the species can re-establish themselves during future inundation cycles, but they differ in their patterns of greatest investment: *C. brutia* produces seeds constantly during a given inundation cycle and only its late-produced seeds will germinate in the next inundation cycle; *M. alterniflorum* produces all its seeds at the end of the inundation phase, leaving their germination for the next inundation cycle; and *R. peltatus* uses a conservative strategy, where seed germination occurs over several subsequent inundation cycles as it makes a large contribution to the seed bank that can help promote its long-term persistence. Nevertheless, these results must be interpreted with caution as they were obtained using an experimental approach and have not been validated by germination data from the field. Also, the Mediterranean is one of the global regions most affected by climate change: annual precipitation has declined and temperatures have increased (Lionello & Scarascia, 2018). Climate change has especially affected the dynamics of Mediterranean temporary ponds, including the dates of pond inundation and drying as well as pond water characteristics such as temperature, conductivity, and pH, shifts that we have recently observed in our study area. Mediterranean temporary ponds have also been affected by declines in groundwater level, which have reduced the extent of pond inundation and shortened pond hydroperiod (de Felipe et al., 2023, 2026). These changes may have severe impacts on seed germination and seedling viability, which will, in turn, negatively influence the persistence of plant communities in these aquatic habitats. It is necessary to conduct complementary studies focused on these species' seed germination dynamics in the field, which could help reveal whether their germination strategies mean that they could benefit from population conservation efforts.

Conclusion

In temporary ponds, the re-establishment of aquatic plant populations during each new inundation cycle is mostly dependent on the plants' seeds. Our study species appear to utilise different strategies for persisting in temporary ponds. Two species, *R. peltatus*

and *M. alterniflorum*, produced dormant seeds with low germination levels post dispersal, but their seeds displayed higher germination levels when they had experienced a dry (i.e. after ripening) period prior to a new period of inundation. Furthermore, a certain fraction of their seeds remained ungerminated—in nature, these seeds would remain in the seed bank and allow longer population persistence. The third species, *C. brutia*, produced non-dormant seeds, which would allow for continuous seedling emergence during a given inundation cycle (Fernández-Zamudio et al., 2018). The dry period did not promote germination of the species' seeds. However, its later produced seeds, which would be more likely to face the unfavourable conditions in drying ponds, would likely withstand drying and delay germination until the subsequent inundation cycle.

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Author contributions The two authors contributed to the conception and design of the experiments. MJPR collected the seeds and CDP monitored the seeds in the experimental trials. CDP wrote a first draft of the manuscript and both authors reviewed and approved the final version to be published.

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Data availability Data will be available upon request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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References

- Aponte, C., G. Kazakis, D. Ghosn & V. P. Papanastasis, 2010. Characteristics of the soil seed bank in Mediterranean temporary ponds and its role in ecosystem dynamics. *Wetland Ecology Management* 18: 243–253. <https://doi.org/10.1007/s11273-009-9163-5>.
- Baskin, C. C. & J. M. Baskin, 1998. *Seeds: ecology, Biogeography, and Evolution of Dormancy and Germination*, Academic Press, San Diego.
- Baskin, J. M. & C. C. Baskin, 2004. A classification system for seed dormancy. *Seed Science Research* 14: 1–16. <https://doi.org/10.1079/SSR2003150>.
- Brock, M. A., 2011. Persistence of seed banks in Australian temporary wetlands. *Freshwater Biology* 56: 1312–1327. <https://doi.org/10.1111/j.1365-2427.2010.02570.x>.
- Brock, M. A., D. L. Nielsen, S. J. Shiel, J. D. Green & J. D. Langley, 2003. Drought and aquatic community resilience: The role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology* 48: 1207–1218. <https://doi.org/10.1046/j.1365-2427.2003.01083.x>.
- Carta, A., G. Bedini & B. Foggi, 2012. Laboratory germination and seed bank storage of *Ranunculus peltatus* subsp. *baudonii* seeds from the Tuscan Archipelago. *Seed Science and Technology* 40: 11–20. <https://doi.org/10.15258/sst.2012.40.1.02>.
- Cronk, J. K. & M. S. Fennessy, 2001. *Wetland Plants: biology and Ecology*, CRC Press, Boca Raton.
- Cross, A. T., S. R. Turner, M. Renton, J. M. Baskin, K. W. Dixon & D. J. Merritt, 2015. Seed dormancy and persistent sediment seed banks of ephemeral freshwater rock pools in the Australian monsoon tropics. *Annals of Botany* 115(5): 847–859.
- de Felipe, M., D. Aragonés & C. Díaz-Paniagua, 2023. Thirty-four years of Landsat monitoring reveal long-term effects of groundwater abstractions on a World heritage site wetland. *Science of the Total Environment* 880: 163329. <https://doi.org/10.1016/j.scitotenv.2023.163329>.
- de Felipe, M., L. Colorado-Pedrero, C. Keller, L. Serrano, A.C. Andreu, R. Arribas, M. Ramírez-Soto & C. Díaz-Paniagua, 2026. Groundwater overexploitation drives freshwater turtle declines in Doñana National Park. *Biological Conservation* 315: 111730. <https://doi.org/10.1016/j.biocon.2026.111730>.
- Deil, U., 2005. A review on habitats, plant traits and vegetation of ephemeral wetlands—A global perspective. *Phytocoenologia* 35: 533–706. <https://doi.org/10.1127/0340-269X/2005/0035-0533>.
- Díaz-Paniagua, C., R. Fernández-Zamudio, M. Florencio, P. García-Murillo, C. Gómez-Rodríguez, A. Portheault, L. Serrano & P. Siljestrom, 2010. Temporary ponds from the Doñana National Park: a system of natural habitats for the preservation of aquatic flora and fauna. *Limnetica* 29: 41–58. <https://doi.org/10.23818/limn.29.04>.

- Díaz-Paniagua, C., R. Fernández-Zamudio, L. Serrano, M. Florencio, C. Gómez-Rodríguez, A. Sousa, P. Sánchez Castillo, P. García-Murillo & P. Siljestrom, 2015. El Sistema de Lagunas Temporales de Doñana, Una Red de Hábitats Acuáticos Singulares. Organismo Autónomo de Parques Nacionales, Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid:
- Donohue, K., R. Rubio de Casas, L. Burghardt, K. Kovach & C. G. Willis, 2010. Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* 41: 293–319. <https://doi.org/10.1146/annurev-ecolsys-102209-144715>.
- Fenner, M. & K. Thompson, 2005. *The Ecology of Seeds*, Cambridge University Press, New York:
- Fernández-Zamudio, R., P. García-Murillo & C. Díaz-Paniagua, 2016. Aquatic plant distribution is driven by physico-chemistry and hydroperiod in a Mediterranean temporary pond network. *Hydrobiologia* 774: 123–135. <https://doi.org/10.1007/s10750-016-2701-2>.
- Fernández-Zamudio, R., P. García-Murillo & C. Díaz-Paniagua, 2018. Effect of the filling season on aquatic plants in Mediterranean temporary ponds. *Journal of Plant Ecology* 11: 502–510.
- Fernández-Zamudio, R., P. García-Murillo & C. Díaz-Paniagua, 2021. Terrestrial morphotypes of aquatic plants display improved seed germination to deal with dry or low-rainfall periods. *Plants* 10: 741. <https://doi.org/10.3390/plants10040741>.
- Finch-Savage, W. E. & G. Leubner-Metzger, 2006. Seed dormancy and the control of germination. *New Phytologist* 171: 501–523. <https://doi.org/10.1111/j.1469-8137.2006.01787.x>.
- Florencio, M., R. Fernández-Zamudio, M. Lozano & C. Díaz-Paniagua, 2020. Interannual variation in filling season affects zooplankton diversity in Mediterranean temporary ponds. *Hydrobiologia* 847: 1195–1205. <https://doi.org/10.1007/s10750-019-04163-3>.
- Fox, J. & S. Weisberg, 2019. *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks. <https://www.john-fox.ca/Companion/>
- García-Murillo, P. & R. Fernández-Zamudio, 2015. Las Plantas de Las Lagunas Temporales de Doñana. In Díaz-Paniagua, C. (coord.) *El Sistema de Lagunas Temporales de Doñana, una Red de Hábitats Acuáticos Singulares*. Organismo Autónomo de Parques Nacionales, Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, pp. 119–148.
- Grillas, P., P. Gauthier, N. Yavercovski & P. Perennou, 2004. *Mediterranean Temporary Pools; vol 1- Issues relating to conservation, functioning and management*. Station Biologique de la Tour du Valat, Arles.
- Hothorn, T., F. Bretz & P. Westfall, 2008. Simultaneous Inference in General Parametric Models. *Biometrical Journal* 50: 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Lesiv, M. S., A. I. Polishchuk & H. L. Antonyak, 2020. Aquatic macrophytes: ecological features and functions. *Studia Biologica* 14: 79–94. <https://doi.org/10.30970/sbi.1402.619>.
- Lionello, P. & L. Scarascia, 2018. The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change* 18: 1481–1493. <https://doi.org/10.1007/s10113-018-1290-1>.
- Pinero-Rodríguez, M. J., I. Gomez-Mestre & C. Díaz-Paniagua, 2021. Herbivory by spadefoot toad tadpoles and reduced water level affect submerged plants in temporary ponds. *Inland Waters* 11: 457–466. <https://doi.org/10.1080/20442041.2021.1933855>.
- Prausová, R., H. Holzbauerová, I. Špringrová, N. Jará, I. Šafářová, S. T. Cross & I. Adamec, 2022. Seed germination ecology of common bladderwort (*Utricularia vulgaris* L.). *Aquatic Botany* 182: 103545. <https://doi.org/10.1016/j.aquabot.2022.103545>.
- R Core Development Team, 2025. *R: a Language and Environment for Statistical Computing*; R Foundation for Statistical Computing.
- Ruiz, E., 2008. Management of Natura 2000 habitats. 3170 *Mediterranean temporary ponds: European Commission
- Schulthorpe, C. D., 1967. *The Biology of Aquatic Vascular Plants*, Edward Arnold Ltd:
- Tuckett, R. E., D. J. Merritt, F. R. Hay, S. D. Hopper & K. W. Dixon, 2010. Dormancy, germination and seed bank storage: a study in support of ex situ conservation of macrophytes of southwest Australian temporary pools. *Freshwater Biology* 55: 1118–1129. <https://doi.org/10.1111/j.1365-2427.2010.02386.x>.
- Venables, W.N. & B.D. Ripley, 2002. *Modern Applied Statistics with S*, Fourth edition. Springer, New York. <https://www.stats.ox.ac.uk/pub/MASS4/>
- Verhoeven, M. R., J. A. Bacon & D. J. Larkin, 2024. Effects of seed traits and dormancy break treatments on germination of four aquatic plant species. *Aquatic Botany* 192: 103746. <https://doi.org/10.1016/j.aquabot.2023.103746>.

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