



Soil moisture level and substrate type determine long-term seed lifespan in a soil seed bank

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Abstract

Aims Seeds are usually classified as short- or long-term persistent. It is still hardly understood how environmental conditions influence seed persistence. The study aimed to monitor the long-term effects of different moisture and substrate on seed persistence.

Methods Seeds of three *Rumex* species buried in autumn 2009 in combinations of moisture and substrate were exhumed in spring 2015 and 2021 to test their persistence in the soil after 5.5 and 11.5 years, respectively. Long-term persistence data were compared with data from previous short-term experiment for the same species and environmental conditions

reported in Abedi et al. (Plant Soil 374:485–495, 2014).

Results No seeds of *R. acetosa* were found viable after 1.5 years. Seeds of *R. acetosella* retained viability after 11.5 years mostly in dry-loam (~60%) and moist-sand (~25%) test conditions and moisture levels were identified as the main driver. *R. maritimus* retained ≥80% viability in moist and wet test conditions and >40% in the dry test conditions.

Conclusions For one (*R. acetosella*) of the three investigated species, the classification of soil seed bank type depended on environmental conditions, emphasizing the need to introduce a more detailed classification scheme for soil seed persistence and to include the information about extrinsic parameters in databases. However, in the other two species with transient (*R. acetosa*) and long-term persistent (*R. maritimus*) seed banks, there are rather intrinsic parameters that affect seed viability. Hence, both site-specific environmental factors as well as seed

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germination traits need full consideration in the classification of future soil seed bank studies.

Keywords Burial seed bank · *Rumex* spp. · Seed longevity in soil · Seed persistence · Soil seed bank classification · Soil substrate type

Introduction

Seed bank persistence plays a crucial role in population dynamics (Grubb 1977) since it allows the plant to disperse through time by remaining viable and avoiding germination in unfavorable environmental conditions (Kiss et al. 2018; Long et al. 2015). Persistence classification schemes categorize species as forming either of three types of soil seed bank: (1) transient seed banks—if viable seeds are present in the soil for < 1 year, (2) short-term persistent seed bank—if viable seeds are present in the soil for > 1 but < 5 years, and (3) long-term persistent seed banks—if viable seeds are present in the soil for > 5 years (Bakker 1989; Maas 1987; Thompson and Fenner 1992; Thompson and Grime 1979). However, even within a species and among seeds of the same cohort, there is variability in the time seeds may survive in the soil seed bank (Genna and Perez 2021; Saatkamp et al. 2014). The post-dispersal environment influences seed persistence that includes microclimate (temperature, moisture), soil properties (physical, chemical, biological), and other features (e.g., burial depth, light, disturbance, predation) of the site into which seeds are dispersed (Long et al. 2015; Ma et al. 2017).

It is now well known that seeds of some species can persist and remain viable for millennia if hidden or buried under relatively stable, cool, dark, and dry or wet conditions, as evident from the germination of 2000-years old date palm seed (*Phoenix dactylifera*) excavated from Masada near the Dead Sea, Israel (Sallon et al. 2008) or of a 1300-years old lotus seed (*Nelumbo nucifera*) from the sediment from an ancient lake bed at Pulantien, Liaoning Province, China (Shen-Miller et al. 1995). Dr. William Beal's famous seed burial experiments showed that some plant species' seeds (*Malva rotundifolia*, *Verbascum blattaria*, and *Verbascum* sp.) could retain their viability even under semi-ambient field conditions for at least a century, in that case, buried in a glass

bottle with dehydrated soil (Telewski and Zeevaart 2002; another viable seed sample was excavated in 2021, i.e., after 142 years). After Beal's experiment, many studies have been carried out in which freshly matured viable seeds were buried in soil under ambient natural conditions, and their viability was determined after various periods (see table 7.1 in Baskin and Baskin 2014).

For most of these seed burial studies, it was hard to distinguish which individual environmental factors (extrinsic parameters such as moisture level, soil substrate type, or temperature) have the most pronounced effect on seed longevity in soil. On the other hand, several burial experiments have been carried out involving older stages of seed banks to distinguish the impact of an individual environmental factor on seed longevity. However, attention has rarely been focused on how the interaction of two or more factors affects seed longevity in the soil in a longer time span (but see Abedi et al. 2014; Chen et al. 2021; Long et al. 2009; Schafer and Kotanen 2003; Skálová et al. 2019; Van et al. 2005, for relatively short-term experiments). Nevertheless, to the best of our knowledge, there is still no long-term experiment carried out to address this issue. Abedi et al. (2014) varied two environmental factors and detected significant soil moisture and substrate types interactions on seed longevity based on 1.5 years of burial duration. However, a burial time of only 1.5 years was likely not sufficiently informative as far as the point of the longevity of seed survival is concerned. Also, the relative effects of intrinsic and extrinsic parameters on seed survival might differ when examined for the long-term instead of the short-term.

Exact measurement of seed persistence in the soil may only be possible through long-term burial experiments (Poschlod et al. 2013), as seed persistence potential, in the long run, depends on the overall quality of the seeds and soil conditions at the burial sites (Schafer and Kotanen 2003). Hence, the general aim of the present study is to investigate the long timescales changes in seed viability of three *Rumex* species, i.e., closely related species differing substantially with respect to the natural conditions in which they typically grow (especially precipitation regimes and soil types). Abedi et al. (2014) reported findings for the initial three burial time-steps (up to 1.5 yrs). However, it is known that seeds of these species can persist in the soil much longer. The specific aim of

the study is to (1) monitor a decline in seed viability after 5.5 and 11.5 years of burial, and (2) evaluate the effect of moisture level, soil substrate, and their interaction on soil seed persistence in a long-run. We hypothesized that species reported to be short-term persistent (*R. acetosella*) and long-term persistent (*R. maritimus*) by Abedi et al. (2014) will show different persistence behaviour, e.g., less impact of extrinsic parameters on seed viability for long-term persistent species. This may be affected either by intrinsic (e.g., storage physiology, germination ecophysiology) or extrinsic (i.e., moisture level, soil substrate type) parameters.

Materials and methods

We used three native *Rumex* species with different specific habitat requirements (*R. acetosella* from dry-sandy grasslands communities, *R. acetosa* from mesic-loamy meadows, and *R. maritimus* from wet-muddy amphibious habitats such as ponds and river banks) to test the long-term effect of soil conditions and moisture regime to seed viability. Ripe fruits of *R. acetosella*, *R. acetosa*, and *R. maritimus* were collected in Siegenburg, Regensburg, and Charlottenhof (all Southern Germany), respectively, in summer 2009. In autumn 2009, an outdoor pot experiment was set up using the water-basin facilities of the Botanical Garden of Regensburg University, Germany.

Eight rain-water-filled basins were used to adjust desired water levels throughout the long-term experiment. Three different soil substrates (sand, loam, mud) and moisture levels (dry, moist, wet) were used. These soil types and moisture levels were chosen to match the natural conditions in which the three study species typically occur. A block design representing 8 basins*3 soil substrate types*3 water levels*5 burial-time steps for seed excavation was set up. In each pot, 25 seeds of each species were separately buried in three nylon bags at 5 cm depth to minimize light and fluctuating temperature effects on seed germination. Metal grids in two different positions were placed into the basins to carry the pots, allowing that the water level within the pots was adjusted either to 1 cm above (wet treatment) or 10 cm below (moist treatment) seed position. The pots with dry treatment were placed directly next to the respective basin, hence receiving water only from rainfall. Further

details about the choice of species, experimental strategy, and experimental setup can be found in Abedi et al. (2014). In the present study, seeds of all three species for the fourth and fifth burial-time steps were exhumed in spring 2015 and 2021 after 5.5 and 11.5 yrs of burial, respectively. Obtained long-term data were analyzed together with data of the previous short-term investigation described in Abedi et al. (2014).

Exhumed seeds were sterilized for two minutes with sodium-hypochlorite (5%) before incubating in 90-mm-diameter Petri-dishes at 22/14 °C alternating temperature and 14/10 h day/night light regimes in the laboratory for 45 days. Seeds of all three species were in the non-dormant stage, as they already cold-stratified during winter seasons. Still, some seeds remained non-germinated at the end of the test period. These were then cold stratified again at 4 °C for six weeks and then exposed once more for another 45 days to germinating conditions as described above. If seeds still failed to germinate, then their viability was evaluated by tweezer-testing the seed coat for integrity and (if intact) by tetrazolium (TTZ) test (Moore 1985). Seed viability was calculated as percentage of all seeds that were viable (number of germinated seeds before and after stratification + number of seeds found viable in TTZ test).

Soil moisture in the pots was measured by use of a moisture meter (Theta Probe ML2x Delta-T Devices Ltd, UK) before seed excavation. Soil samples were collected from about the same soil depth as from where the seeds were retrieved. These samples were analyzed to monitor changes in physiochemical properties after 5.5 and 11.5 yrs of using the same procedure as described in Abedi et al. (2014). The dried and sieved soil samples were extracted using calcium lactate and analyzed for phosphorus content (Thermo Spectronic UV1), potassium, sodium, and magnesium content (Solaar Atomic Absorption Spectrometer Thermo Elemental). Nitrogen and carbon content were measured with a C/N analyzer Vario EL (Elementar Analysentechnik GmbH, Germany).

Statistical analysis

Effects of different sets of moisture levels and substrate types on seed viability after 5.5 and 11.5 yrs of burial-time were analyzed using an independent sample Kruskal–Wallis one-way ANOVA for k samples.

Further, to evaluate the effect of burial time-steps, species, moisture level, substrate types, and their interactions on seed viability, present data (5.5 and 11.5 yrs) along with data collected by Abedi et al. (2014) for the three earlier burial time-steps (0.5, 1.0, and 1.5 yrs) were pooled and analyzed using a generalized linear model (GLM) with binomial family. To not over-parametrize the model, separate models were performed for individual *Rumex* species. Post-hoc Tukey tests were used if glm showed significant differences. No seeds of *R. acetosa* were found viable in the fourth and fifth burial-time steps. Therefore, to avoid of repeating the statistical analysis made by Abedi et al. (2014), *R. acetosa* was excluded from the long term investigation. All statistical analyses were carried out using R software (version 4.1.2; R core Team 2021).

Results

No seeds of *R. acetosa* were found viable after 1.5 yrs of burial. In *R. acetosella*, different substrate and soil moisture combinations resulted in significant differences in viability after 5.5 yrs of burial (Kruskal–Wallis one-way ANOVA, $H=54.40$, $df=8$, $p<0.001$). The species retained high viability in dry-muddy soil but low viability in the wet-loamy and wet-muddy substrate, while the other treatments lay in between (Fig. 1A). Similarly, after 11.5 yrs of burial, the viability of *R. acetosella* seeds significantly differed ($H=45.17$, $df=8$, $p<0.001$) in different combinations of substrate and soil moisture with the highest viability in the dry-loamy and moist-sandy substrate and almost no viable seeds in all other conditions (Fig. 1C). Quite different to this, seeds of *R. maritimus* retained $\geq 85\%$ and 70% viability in all combinations of moisture and soil substrate, except for in the dry-sandy and dry-muddy substrates after 5.5 and 11.5 yrs, respectively ($H=25.79$, $H=41.43$, $df=8$, $p<0.001$; Fig. 1B and 1D).

Separate glms were performed individually for seed viability of the two *Rumex* species for the effects of moisture levels, substrate types, burial-time steps, and their respective interactions (Table 1). For *R. acetosella*, burial-time steps, moisture levels, and their interactions had strong and significant effects on seed viability. For *R.*

maritimus, all interactions between moisture levels, substrate types and burial-time steps were significant. *R. acetosella* retained the highest seed survival in dry-mud and least in wet-mud consistently over initial four burial time-steps, but showed no or low seed survival in all combinations of soil and moisture (with the exception in dry-loam and moist-sand) after 11.5 yrs of burial (Fig. 2). *R. maritimus* retained comparatively high viability consistently over all five burial time-steps in all test conditions (Fig. 3).

R. acetosa had lost viability dramatically within one year of burial. It was already reported by Abedi et al. (2014), that even within a short survival period, *R. acetosa* retained significantly higher viability in wet conditions than in the other moisture conditions. In the case of *R. acetosella*, seed viability declined significantly during the first two burial time-steps, thereafter remaining constant and after 11.5 years almost completely losing viability. Under dry conditions and in sandy substrate seeds retained high viability (Fig. 2). On the contrary, seeds of *R. maritimus* were almost unaffected by duration up to the fourth burial time-step, however a slight decrease was detected during 11.5 years of burial time, mostly due to a decreased viability in dry conditions and in the muddy substrate (Fig. 3).

The physicochemical properties of soil varied considerably among substrate types (Appendix S1). The overall difference in soil moisture level between the dry substrate and moist substrate was about $252 \pm 42\%$, and between dry and wet substrate, it was about $318 \pm 35\%$. These increases also varied considerably between substrate types (see Appendix S1). Soil contents in mineral nutrients (P, K, and Mg) ranked as follows: loam > mud > sand after 5.5 yrs and mud > loam > sand after 11.5 yrs, while N, C, and C/N-ratio ranked as mud > loam > sand after 5.5 yrs and loam > mud > sand after 11.5 yrs. The pH of the muddy substrate was slightly acidic (mean overall moisture levels for pH in water = 6.4) as compared to sand and loam (6.9) after 5.5 yrs and slightly increased over time (6.6, 7.4, and 7.1 after 11.5 yrs for loam, mud, and sand substrate type, respectively). Soil conductivity decreased from loam > mud > sand after 5.5 yrs and from mud > loam > sand after 11.5 yrs.

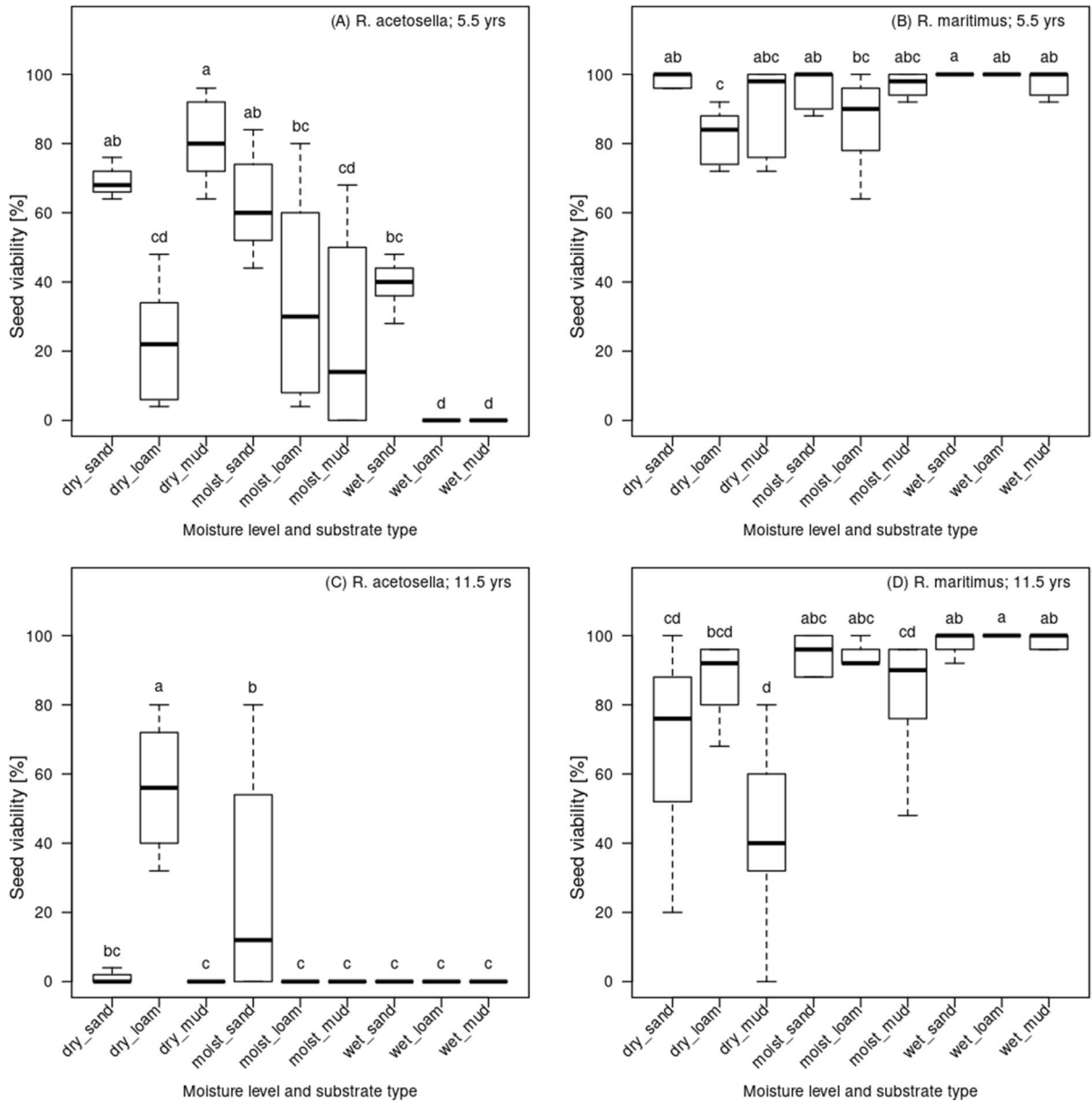


Fig. 1 Box plots illustrating median and quartiles of overall mean seed viability percentage in different combinations of moisture and soil substrate after 5.5 and 11.5 yrs of burial in

R. acetosella (A and C) and *R. maritimus* (B and D). Letters represent subsets with significant differences (Kruskal–Wallis test, $n=8$, $p < 0.05$)

Discussion

Species-specific soil seed bank persistence

No seeds of *R. acetosa* stayed viable after the third burial time-step in any test condition, further confirming a transient nature of soil seed bank (Abedi

et al. 2014), although there were several entries in the database of Thompson et al. (1997) and Kleyer et al. (2008), respectively, where the soil seed bank was classified as long-term persistent. Under ex-situ gene banking conditions (Royal Botanical Garden Kew 2021), seeds of *R. acetosa* show orthodox storage behavior (i.e., seeds survive considerable desiccation

Table 1 Results of two generalized linear models performed individually for each of the two *Rumex* species for effects of moisture level, substrate type, burial time-step, and their respective interactions on seed viability; boldface indicates significance

Species	Factors	df	LR	Pr(> Chisq)
<i>R. acetosella</i>	Moisture (M)	2	372.84	< 0.001
	Substrate type (S)	2	0	1
	Burial time-step (T)	4	973.76	< 0.001
	M×S	4	68.04	< 0.001
	M×T	8	225.03	< 0.001
	S×T	8	198.27	< 0.001
	M×S×T	16	343.74	< 0.001
<i>R. maritimus</i>	Moisture (M)	2	38.63	< 0.001
	Substrate type (S)	2	78.63	< 0.001
	Burial time-step (T)	4	21.82	< 0.001
	M×S	4	23.6	< 0.001
	M×T	8	22.61	0.004
	S×T	8	36.72	< 0.001
	M×S×T	16	60.88	< 0.001

and their longevity is increased with decrease in moisture content and temperature) and retained 88–95% viability for 13 years of storage. However, the storage physiological attributes of *R. acetosa* seeds do not appear to correlate with their inability to persist in the soil in our experiment. Rather than extrinsic, it is more likely that another intrinsic parameter, i.e., seed germination ecophysiology, seems to be primarily responsible for the low persistence of *R. acetosa* seeds. Their ability to germinate both under light/dark and entirely dark conditions does not allow building up a soil seed bank. We suggest that this is the main reason for this species not to form short- to long-term persistent soil seed banks despite of its orthodox seeds (see Abedi et al. 2014). Grime (1989), Saatkamp et al. (2011), and Mašková and Poschlod (2022) already suggested that a species' demand for light to germinate (as a mechanism to detect depth of burial or gaps in vegetation) explains the potential to establish a persistent seed bank.

Our results show that seeds of *R. maritimus* persist in all studied moisture and soil substrate types more than 11.5 years. Under ex-situ gene banking conditions, seeds of *R. maritimus* show an orthodox storage behavior by retaining 88–100% viability for 15 yrs (Royal Botanical Garden Kew 2021). Together with our results, we can conclude that seed longevity in

this species is rather affected by intrinsic than extrinsic parameters. This interpretation is also supported by studies showing that seed persistence in the field or uncontrolled storage conditions tend to be positively correlated with their longevity under controlled storage conditions (Bekker et al. 2003; Long et al. 2008; Nagel and Börner 2010). Seeds of *R. maritimus* with a long-term persistent seed bank were found to be non-sensitive to post-dispersal site-specific environmental factors (here: soil moisture and substrate type). This indicates that neither conditions resembling the species natural habitat nor conditions different to that have effects on their seed persistence, but rather, intrinsic germination ecophysiology will govern their persistence. Another study by our research group investigating the impact of constant vs. fluctuating temperatures, light vs. dark, and hypoxia vs. oxic conditions on seed germination of *R. mar*

itimus reveals that its seeds germinate well at a range of alternating temperature regimes with 14/10 h light/dark and oxic conditions. However, seed germination was significantly retarded at constant temperature regimes both with 14/10 h light/dark and complete dark and hypoxia conditions (Phartyal et al. 2020). Further, the fully imbibed seeds of *R. maritimus* were found to be very sensitive to light. They required a short flux of white light exposure (at least 15 min) to achieve a high (> 90%) germination percentage (Phartyal et al. unpublished). These findings confirm that the seed longevity of *R. maritimus* in the soil is governed by its storage physiology and germination ecology since most of the burial conditions (e.g., constant temperature, complete darkness) in the present study were unfavorable for its seed germination.

In contrast to the other two studied species, long-term burial results reveal that *R. acetosella* demonstrates a long-term persistent seed bank under optimum dry conditions. Under suboptimal wet conditions, it is merely indicated to form a short-term persistent or even transient seed bank. This confirms previous results of Abedi et al. (2014), who found moisture as the most important factor for *R. acetosella* seeds' persistence and highlighted the impact of extrinsic parameters in the long-term. On the other hand, this pattern coincides with the results of another burial experiment with eight fen meadow species which showed a substantial decrease in soil seed bank persistence with increasing groundwater

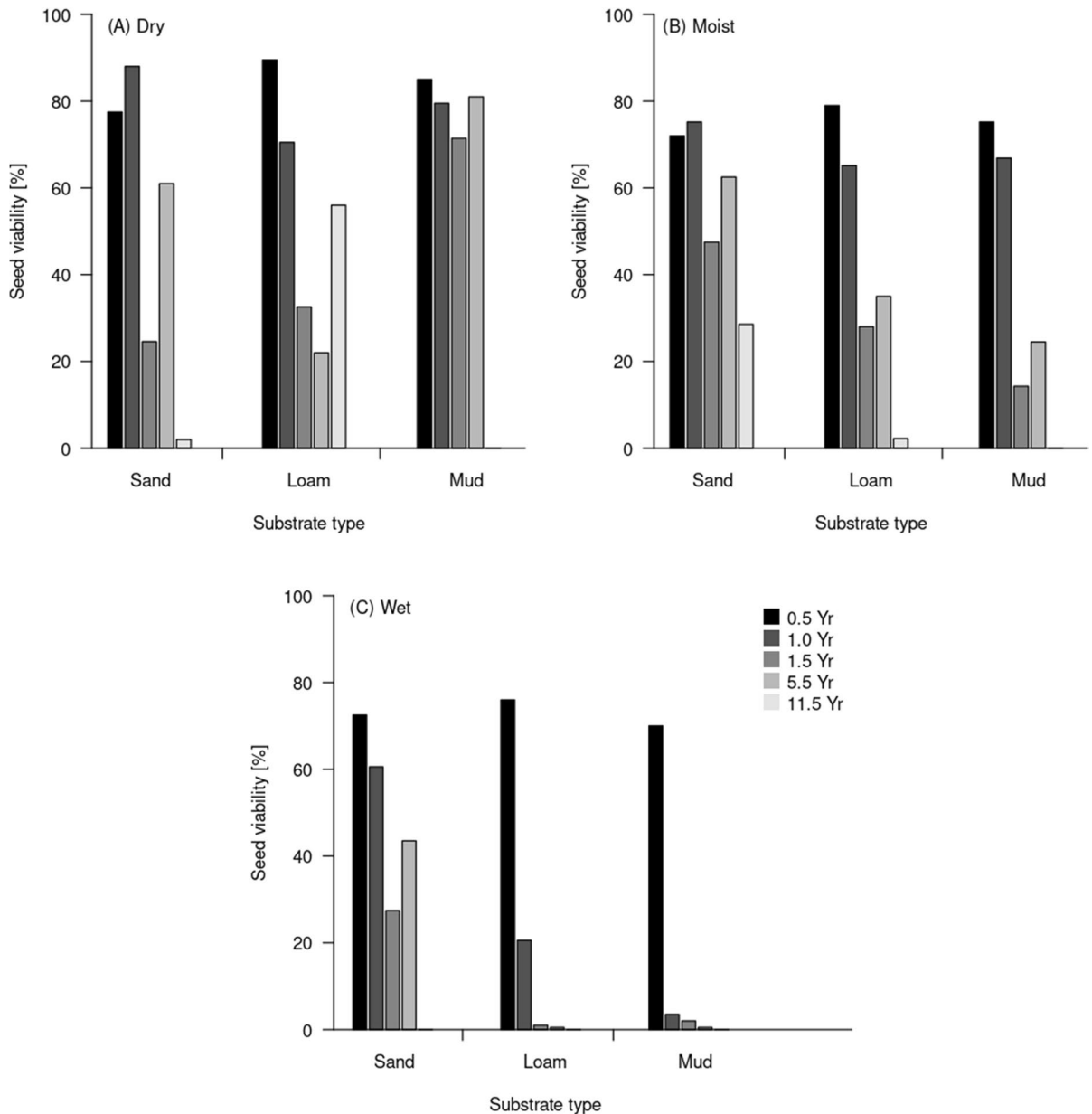


Fig. 2 Comparison of seed viability percentage in *R. acetosella* after each time step (0.5, 1.0, 1.5, 5.5 and 11.5 yrs) of seed excavation from burial in different moisture and soil sub-

strate types. Bars represent means, $n=8$. Factors responsible for variation in seed viability percentage are statistically analysed as shown in Table 1

levels (Kaiser and Pirhofer-Walzl 2015). Therefore, soil seed bank persistence of *R. acetosella* and of those species examined by Kaiser and Pirhofer-Walzl (2015) appear to be driven by extrinsic parameters. Our study reveals that seeds of *R. acetosella* can persist for long-term periods only under moisture conditions similar to the natural habitat of the species.

Under ex-situ gene bank conditions, the storage physiology of seeds of *R. acetosella* is still uncertain and reported as ‘probable orthodox’ considering their ability to withstand desiccation (Royal Botanical Garden Kew 2021).

Our findings confirm that both, species-specific intrinsic characteristics as well as post-dispersal

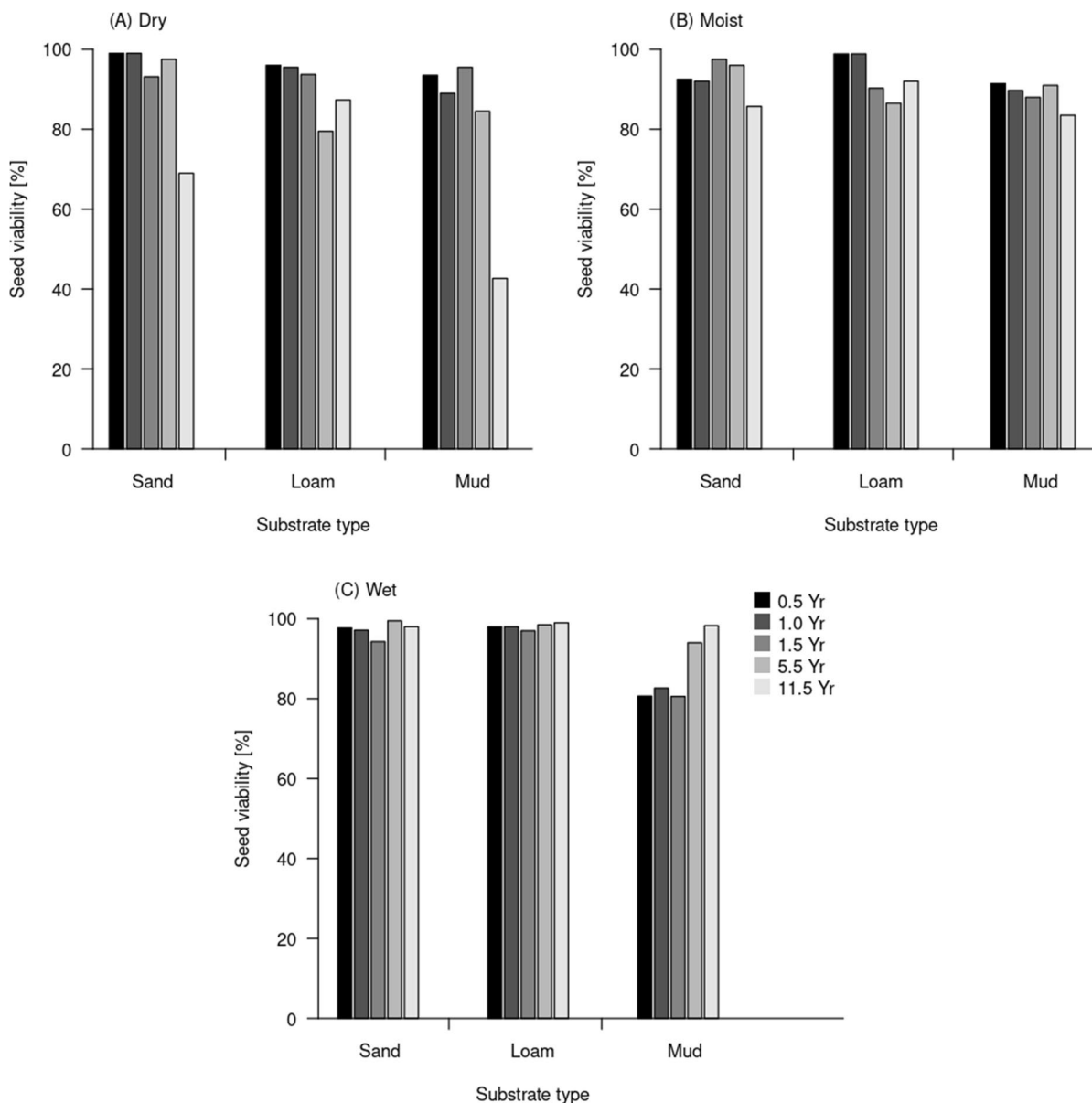


Fig. 3 Comparison of seed viability percentage in *R. maritimus* after each time step (0.5, 1.0, 1.5, 5.5 and 11.5 yrs) of seed excavation from burial in different moisture and soil substrate

type. Bars represent means, $n=8$. Factors responsible for variation in seed viability percentage are statistically analysed as shown in Table 1

site-specific extrinsic factors (Long et al. 2015) like moisture, substrate types, and their interactions, determine seed longevity in a soil seed bank persistence (compare Abedi et al. 2014; Benvenuti and Mazzoncini 2019; Van et al. 2005; Volis and Dorman 2019). Nevertheless, intrinsic parameters seem to be of higher importance for transient and very long-term persistent species, while

short- to long-term persistent species rather depend on extrinsic parameters.

Soil properties

Parameters other than moisture and substrate such as soil pH and C:N ratio also might have affected the survival of buried seeds as well, with high

values of these factors generally being associated with decreased seed longevity (Pakeman et al. 2012). However, there are contrasting results concerning the impacts of these factors in other experiments (Yang et al. 2021). Basto et al. (2015) studied the effect of soil pH on the persistence of seeds of grassland species in a seed burial experiment. They concluded that the size and longevity of grassland plants' soil seed banks decrease as soil pH increases. Our results indicate that the potential of soil seed bank persistence over time was significantly reduced in loam and mud substrate under moist and wet conditions for *R. acetosella* and in mud substrate under dry conditions for *R. maritimus*, respectively. However, Long et al. (2009) did not find an effect of soil substrate on seed persistence. A closer look at soil properties (Appendix S1) reveals that muddy substrate was more acidic at the initial (0.5 yrs) stage of burial; later (5.5 yrs) turned slightly acidic than the two other substrates; after 11.5 yrs its pH was comparable with that of the others substrates. Initial acidity of muddy substrate could potentially retards seed longevity of both *R. acetosella* and *R. maritimus*. Further, loam and mud substrates have a higher C:N ratio than sand, which could also contribute to a reduction of soil seed bank persistence. These results agree with Pakeman et al. (2012) but contradict Basto et al. (2015).

Conclusion

We conclude that soil seed bank longevity of species with long-term persistent (*R. maritimus*) or transient (*R. acetosa*) seed bank depends mainly on intrinsic parameters. In contrast, soil seed bank longevity of species with short- to long-term persistent seed bank (*R. acetosella*) rather depends on extrinsic parameters. For the latter species, seed persistence was increased by moist conditions similar to the conditions from natural habitat. To better understand the relevant processes, we need a more extensive overview of soil seed bank persistence of target species under long-term conditions and with combinations of several outdoor burial conditions. Information about extrinsic parameters should also be included in databases on soil seed bank persistence. Finally, transient soil seed banks of many species may often be simply explained by their seed germination characteristics,

such as light and diurnally fluctuating temperature requirements for germination (Grime 1989; Mašková and Poschlod 2021; Saatkamp et al. 2011).

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Author Contributions P.P., M.B. and M.A. designed the study. S.S.P. and T.M. performed the fourth and fifth excavations and lab experiments, T.M., S.S.P., and M.A. analyzed the data, S.S.P. and T.M. interpreted results, S.S.P. and T.M. jointly wrote the first draft of the manuscript with contributions of all authors. All authors approved the final version of the manuscript.

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Data Availability The datasets generated during the previous study, pooled and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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