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Published in:

Journal of Vegetation Science

DOI:

[10.1111/jvs.12841](https://doi.org/10.1111/jvs.12841)

Publication date:

2020

Document version

Publisher's PDF, also known as Version of record

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Citation for published version (APA):

Phartyal, S. S., Rosbakh, S., Ritz, C., & Poschlod, P. (2020). Ready for change: Seed traits contribute to the high adaptability of mudflat species to their unpredictable habitat. *Journal of Vegetation Science*, 31(2), 331-342. <https://doi.org/10.1111/jvs.12841>

Ready for change: Seed traits contribute to the high adaptability of mudflat species to their unpredictable habitat

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Funding information

This work was financed by the Alexander von Humboldt Foundation, Germany.

Co-ordinating Editor: Hans Henrik Bruun

Abstract

Question: A better understanding of species distribution and establishment requires in-depth information on their seed ecology. We hypothesised that seed traits of mudflat species may indicate a strong environmental adaptation in their highly specialised habitat. Furthermore, we asked the question, do seeds of mudflat species have a specific trait value to contribute high adaptability to small-scale variation in their unpredictable habitat?

Location: Central Europe.

Methods: Seeds of 30 typical mudflat species were used to measure 15 traits that govern seed dispersal (buoyancy and production), persistence (seed desiccation, mass and persistence in soil), and germination and establishment (germination response to different light, temperature and oxygen conditions). Cluster analysis and phylogenetic principal components analysis (pPCA) were conducted to define potential mudflat species functional groups as per their ecological optima.

Results: Seed production and seed mass displayed extremely high variation while seed buoyancy, desiccation and persistence in soil showed almost no variation. All study species produced buoyant, desiccation-tolerant and long-term persistent seeds. Germination and establishment traits also displayed similarity in their responses to different germination treatments as the majority (73%) of species has a moderate seed germination niche width. They germinated well under light/aerobic conditions irrespective to temperature fluctuations. The cluster analysis and pPCA separated species into three potential plant functional groups as 'true', 'flood-resistant' and 'facultative', mudflat species.

Conclusion: Moderate variation in the seed traits of mudflat plants suggests they employ different ecological strategies that seem highly predictive to the peculiarity of their specific micro-habitats, which are largely controlled by the hydroperiod gradient. It implies that seed trait information, which further needs to be tested for their adaptability, can advance our understanding of how community composition at the micro-habitat level depends on trait values of participating species.

KEYWORDS

mudflats, phylogenetic PCA, regeneration niche, regeneration traits, seed dispersal traits, seed ecology, seed germination and establishment traits, seed persistent traits, wetland

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1 | INTRODUCTION

During the last two decades, there has been an increasing trend to use regeneration traits to investigate patterns and mechanisms of species distribution, abundance and community composition, due to their high environmental sensitivity (Bykova, Chuine, Morin, & Higgins, 2012; Jiménez-Alfaro, Silveira, Fidelis, Poschlod, & Commander, 2016; Poschlod et al., 2013; Poschlod, Tackenberg, & Bonn, 2005; Rosbakh, Pacini, Nepi, & Poschlod, 2018). According to Grubb's regeneration niche concept (Grubb, 1977), a plant species can neither remain part of an established community for a long time nor can it take part in a newly established community without optimising regenerative functional traits or trait values, closely matched to the environmental filter that governs the local community assembly process. Thus, it is now a prevailing view among plant ecologists that environmental factors act like filters that remove plants from local species pools if they lack certain requisite traits (Grime, 1979; Keddy, 1992). The ability of seeds of a species to disperse, persist and germinate depends on sets of trait-based ecological responses of the species (Saatkamp et al., 2019). Consequently, the inclusion of seed traits can provide significant information about how communities respond to the abiotic and biotic environment (Rosbakh & Poschlod, 2015; Tudela-Isanta et al., 2018). For instance, in a species pool of a wetland ecosystem with a fluctuating water table, if a species lacks the ability to germinate under submerged water (at constant temperature under low light and hypoxia conditions) and requires the water to recede to germinate (at fluctuating temperature under illuminated and aerobic conditions), then it will be filtered out from the local community assemblage (Keddy, 1992; Rosbakh, Phartyal, & Poschlod, 2019; van der Valk, 1981). Further, a species in a mudflat community will not survive long-term if it does not have the ability to build a persistent seed bank (Poschlod & Rosbakh, 2018).

Broadly, seed traits can be grouped into three categories as per their ecological functions, i.e., (a) dispersal, (b) persistence, and (c) germination and establishment (*sensu* Poschlod et al., 2013). Dispersal traits (e.g. seed buoyancy or seed production) mainly determine how many and how far seeds can spread to reach favourable sites for their germination and establishment. In their turn, persistence traits, such as desiccation tolerance, seed mass or soil seed bank persistence, are the determinants of how seeds interact with daily, seasonal and inter-annual variability in environmental factors to survive temporally unfavourable conditions and to sense periods favourable for seed germination and seedling recruitment conditions. Finally, seed germination and establishment traits (e.g. seed germination timing and speed, germination niche width) determine how these traits interact with local abiotic factors such as temperature, light, moisture, aerobic/hypoxic conditions and synchronise seed germination with the most favourable conditions not only for seedling development but also for juvenile plant recruitment (Saatkamp et al., 2019). However, some of these traits affect more than one of these processes, thereby allowing intermingling of a particular subset of traits into different categories as per their ecological function (see Table 1). For example, seed mass could be related to dispersal (small seeds are more easily dispersed; Weiher et al., 1999;

Westoby, Leishman, & Lord, 1996), persistence (smaller seeds persist longer in the soil; Bakker, Poschlod, Strykstra, Bekker, & Thompson, 1996; Thompson, Band, & Hodgson, 1993), and germination and establishment (larger seeds can germinate without light, while smaller seeds need light; Milberg, Andersson, & Thompson, 2000).

Freshwater mudflats are typical amphibian wetland habitats of recently exposed muddy sediments along the margin of rivers, streams, backwaters, oxbow lakes and ponds (Appendix S1). In temperate regions, these mudflat habitats are often flooded during the cool season and the period of water drawdown coincides with the growing season (Voigtlander & Poppe, 1989). Mudflats are typically moist and nutrient-rich in nature, supporting dominance and quick growth of annual herbs (Baskin, Baskin, & Chester, 1993, 2004; Chester, 1992; Salisbury, 1970; Webb, Dennis, & Bates, 1988). This kind of habitat is temporal, unpredictable and unstable in nature, often exists only for several weeks and in some extreme cases can remain under flooded conditions for decades or even centuries (Poschlod & Rosbakh, 2018). The existing studies clearly indicate that the majority of mudflat species possess life-history traits that allow them to survive under such highly unpredictable environmental conditions. Specifically, typical mudflat species are able to tolerate unpredictable flooding and drying (Leck & Brock, 2000), use a ruderal strategy (*sensu* Grime, 2002), colonise readily, are mostly fast-growing annuals and have low stature with a high degree of plasticity and adaptability towards growth (Poschlod, Böhringer, Fennel, Prume, & Tiekötter, 1999; Poschlod & Rosbakh, 2018). As for sexual reproduction, previous studies suggest that mudflat species build a long-term persistent seed bank with high seed frequency (Altenfelder, Schmitz, Poschlod, Kollmann, & Albrecht, 2016; Bissels, Donath, Hölzel, & Otte, 2005; Poschlod & Rosbakh, 2018; Šumberová, Lososová, Ducháček, Horakova, & Fabšičová, 2012) and primarily germinate at fluctuating temperature under light and aerobic conditions after water drawdown (Baskin, Baskin, & Chester, 1993, 2004; Brändel, 2004; Thompson & Grime, 1983). Yet, the majority of these studies focused either on single regeneration traits or, when several traits are considered, on a few species only. Thus, we lack a comprehensive overview of how regeneration from seed in mudflat species is adapted to the unpredictable habitat.

The present study is an attempt to close this knowledge gap by a systematic study of several seed traits related to dispersal, persistence, and germination and establishment in 30 mudflat species common in central Europe. Given the high disturbance levels in mudflats (they can be flooded at any time after becoming exposed), we first expected that the species occurring there produce a high number of buoyant seeds supported by often high nutrient availability in the mud as an adaptation to disperse in time and space by water. High seed production could facilitate the "escaping" strategy in this group, which is the transportation and deposition of a large number of diaspores by water towards other available microsites where they can germinate and establish best (Soons et al., 2017). Secondly, we expected that the seeds of mudflat species are able to persist in the soil for a long time, until the water recedes, as an adaptation to the temporal, unstable and unpredictable nature of this habitat. This long-term persistence in the soil could be

TABLE 1 Study seed traits and their ecological function in plant regeneration

Seed traits	Ecological function		
	Dispersal	Persistence	Germination and Establishment
Seed buoyancy	+		
Seed production	++	+	+
Seed mass	+	++	+
Seed desiccation tolerance		+	
Seed bank persistence	+	++	
Seed germination response to light, temperature fluctuations, and oxygen level		+	++
Seed germination speed		+	++
Seed germination niche width			++

Note: Some traits have several functions (++ indicates higher relevance of a seed trait for that particular function).

achieved by the production of smaller seeds (Fenner & Thompson, 2005) that are able to tolerate desiccation during dry periods (Dickie & Pritchard, 2002; Thompson, 2000). Thirdly, we expected that mudflat species show a narrow seed germination niche width, i.e., high similarity in seed germination response to environmental cues, which ensures post-germination seedling recruitment under the most favourable conditions, i.e., right after the water recedes. Mudflats are complex plant communities including species with ecological optima at different parts of the hydroperiod gradient ranging from typical terrestrial species, such as *Alopecurus aequalis* or *Persicaria lapathifolia* to species also adapted to survive submerged conditions of the swamp zone (e.g. *Elatine hydropiper*, *Eleocharis acicularis*; Ellenberg & Leuschner, 2010; Valdez, Hartig, Fennel & Poschlod, 2019). Thus, we expected mudflat species to show some pattern in their seed trait variation according to their germination and post-germination adaptation to different intensities and durations of flooding (or water recession) within mudflats.

2 | MATERIALS AND METHODS

2.1 | Study species

We selected 30 of the most frequent and abundant mudflat species (Appendix S2) in central Europe based on a large number of vegetation surveys carried out in Austria, Croatia, Germany, Hungary, Slovenia, the Czech Republic and the Netherlands (Bagi, 1987; Bissels et al., 2005; Csiky & Purger, 2008; Hejný, 1960; Pietsch, 1963; Täuber, 2000; von Lampe, 1996).

Seeds for the trait measurements were acquired from typical, natural populations of mudflat species located across Croatia, Germany and Slovenia (Appendix S2). Due to the rarity of fruiting in natural habitats, seeds of six species (Appendix S2) were obtained from the University of Regensburg's water basins or field greenhouse by cultivating mudflat sediments for soil seed bank studies under similar conditions as at the field sites (Poschlod & Rosbakh, 2018).

Fully ripened seed and fruits (hereafter "seeds") of the selected species were collected at maturity in four consecutive years (2012–2015). Seeds were harvested from randomly chosen individuals (>50 individuals per species) grown one step (75 cm) away from each other and thoroughly mixed. After collection, seeds were air-dried for several days, cleaned and stored dry in a cold room at 4°C until the beginning of the germination experiments (Baskin & Baskin, 2014).

2.2 | Seed trait measurements

2.2.1 | Seed dispersal traits: seed production and seed buoyancy

To measure seed production per ramet of the study species, we randomly marked 12 individuals located at one step away from each other and collected all seeds produced by an individual plant. The collected seeds were air-dried for several days, cleaned and counted. According to existing terminology, this trait is related to seed number per ramet and can be used as a proxy for the size of plant reproductive output (Knevel, Bekker, Kunzmann, Stadler, & Thompson, 2005).

To estimate seed buoyancy, one hundred seeds of each species were gently put in a separate 600 ml glass beaker (10 cm width, 12 cm height), filled with 300 ml distilled water. The beakers were placed on an orbital shaker and continuously shaken at the speed of 100 rpm to simulate a current of moving water. The water level in the flask was maintained at a constant level throughout the experiment. The orbital shaker was stopped for a short period once a day and all sunken or germinated seeds were counted and removed carefully using tweezers. The experiment lasted for 77 days at which time seeds of all species were either fully submerged or germinated. Seed buoyancy was expressed as the number of days the last seed took to sink or germinate (Römermann, 2006).

2.2.2 | Seed persistence traits: seed mass, species' ability to build a persistent seed bank, seed storage behaviour

We used the seeds from the seed production measurements to collect data on the seed mass which was obtained by weighing five batches of 100 seeds each randomly taken from seed samples and calculating the mean weight for an individual seed.

Information on the ability of mudflat species to build a persistent seed bank was gathered from a large-scale screening of mudflat seed banks in southern Germany's fish ponds (Poschlod & Rosbakh, 2018) with additional studies at the edge of a shallow water lake and on the banks of the river Rhine (Poschlod et al., 1999). Briefly, the mud or soil from the ponds, shallow water lake and river banks was systematically sampled, concentrated on a 200 μm sieve, evenly spread over the substrate and cultivated under semi-natural greenhouse conditions for five months. All emerged seedlings were identified. Since the last drainage of the ponds or water drawdown in the lake or river banks, where viable seeds of the study species were found, occurred more than 20 years ago, the studied species were categorised as having a very long-term persistent seed bank (Poschlod & Rosbakh, 2018). Missing data on seed persistence for *Cyperus glomeratus*, *C. michelianus*, *Lindernia procumbens* and *Plantago intermedia* were collected from published studies that used a similar methodology and were all of them categorised as also having a very long-term persistent seed bank (Hölzel & Otte, 2001; Šumberová et al., 2012; Wang, Jiang, Lu, & Wang, 2013; Yang & Li, 2013).

Seed storage behaviour refers to the capacity of seeds to survive desiccation and includes three categories, recalcitrant, intermediate and orthodox (Hong, Ellis, & Lington, 1998). In essence, recalcitrant seeds are not desiccation-tolerant, whereas orthodox seeds are. Intermediate seeds are more tolerant of desiccation than recalcitrant seeds, though tolerance is much more limited than is the case with orthodox seeds (Royal Botanical Gardens Kew,). The main source for these data was the Kew-Seed Information Database version 7.1 (Royal Botanical Gardens Kew,).

2.2.3 | Seed germination and establishment traits: seed germination pattern, seed germination speed (T_{50}) and seed germination niche width (J)

Prior to the germination experiments, seeds of some of the target species (Appendix S3) were cold-moist-stratified at 4°C for six weeks to meet the winter chilling requirement necessary to overcome physiological dormancy, if any (Baskin & Baskin, 2014).

To reveal the requirements for the specific germination response as an adaptation to environmental conditions in mudflats, we germinated seeds under a very broad spectrum of environmental factors, including eight different combinations of temperature, light, and oxygen (see below). In each germination test, five replications each of 20 seeds were placed on two layers of wet filter paper in a Petri dish. All the experiments were conducted in RUMED 1301 germination chambers (Rubarth Apparate GmbH, Laatzen, Germany) at constant (22°C) and diurnally fluctuating temperatures (22/14°C) and 14 hr of light (3,800 Lux) supplied by white fluorescent tubes. To test the ability of the seeds to germinate under dark conditions, the Petri dishes were wrapped with four layers of aluminium foil. Germination percentages for all dark treatments were recorded once, on the very last day of the

experiment. To simulate hypoxic conditions, the Petri dishes, supplied with vents to provide consistent gas exchange, were placed in a desiccator and its air volume was substituted with pure nitrogen. We repeated this procedure each time when germination was scored (see below). The treatments to which hypoxic conditions were not applied are referred to as aerobic. The abbreviations (LFA, LCA, LFH, LCH, DFA, DCA, DFH, and DCH) used for the different seed germination treatments in the text should be read as follows: L, light; D, dark conditions; C, constant; F, fluctuating temperatures; A, aerobic; H, hypoxic conditions.

The number of seeds germinated was scored every third day during the first two weeks, thereafter scoring was carried out once per week until the experiment was concluded after six weeks. Germination was defined as the emergence of the radicle or cotyledons through the seed coat. At the end of the incubation period, the viability of non-germinated seeds was checked by opening the seeds and checking the embryos. Seeds with white and firm embryos were considered to be viable (Baskin & Baskin, 2014).

2.3 | Statistical analysis

All statistical analyses were conducted in the R statistical environment, version 3.4.3 (R Core Team, 2018). Based on germination percentages in the treatments, we calculated germination speed (hereafter T_{50}) under optimal environmental conditions and seed germination niche width, an ability to germinate under various experimental treatments. The T_{50} values were determined as days until 50% seed germinated under the most optimal conditions (i.e., an experimental treatment in which the germination percentages were the highest). To estimate the T_{50} values, two-parameter log-logistic models were fitted to the data using the parametric event time framework developed by Ritz, Baty, Streibig, and Gerhard (2015) and Jensen, Andreasen, Streibig, Keshtkar, and Ritz (2017). Specifically, models were carried with the help of the package *drc* (Ritz et al., 2015) in the statistical environment R. Seed germination niche width was estimated for each of 30 species as per Pielou's evenness index J (Fernández-Pascual, Jiménez-Alfaro, & Bueno, 2017; Thompson, Gaston, & Band, 1999), calculated with the final germination percentages in each of the eight experimental treatments. Low J -values indicate high sensitivity to one treatment (narrow germination niche width) and values close to one indicate germination evenly distributed among the treatments (wide germination niche width).

2.4 | Cluster analysis and phylogenetic PCA

To define potential mudflat plant functional groups based on the seed ecological traits, we performed a cluster analysis with the continuous trait values. To achieve that, we firstly evaluated clustering tendency (i.e., presence of non-random structures) in the data set by applying Hopkins statistics (Hopkins & Skellam, 1954). In essence, this procedure measures the probability that a given

data set is generated by a uniform data distribution by calculating a D -value; a value of about 0.5 means that the data 'D' is uniformly distributed. Since the D -value for our data set was below the threshold 0.5 (see below), we used the *NbClust* function in the R package *NbClust* (Charrad, Ghazzali, Boiteau, & Niknafs, 2014) to determine the relevant number of clusters in the data set. Hopkins statistics simultaneously computes 30 different indices for determining the relevant number of clusters and proposes to users the best clustering scheme from the different results obtained by varying all combinations of number of clusters, distance measures, and clustering methods (Kassambara, 2017).

To visualise the (dis)similarity in the regeneration niche of mudflat species detected by the cluster analysis and determine the dominant axes of functional trait variation and to estimate the co-variation of the studied traits, we conducted a multivariate analysis on the species-trait matrix (Table 2). Given that seed germination response to the LCA and DFA treatments along with seed germination niche width, seed mass and seed number exhibited a phylogenetic signal (Table 2), we conducted a phylogenetic principal components analysis (pPCA) implemented in the package *phytools* in the statistical environment R (Revell, 2012), which accounts for non-independence among species (Revell, 2009). Due to the lack of variation (i.e., all study species possess the same trait value), the trait data on seed bank persistence and seed storage behaviour were excluded from the analysis. To make trait values comparable, the values for seed mass and seed number were $\log(\text{value} + 0.1)$ -transformed. The pPCA is based on a large dated phylogeny of the European flora (Durka & Michalski, 2012). The results of the pPCA were visualised with the help of the package *ggord* (Beck 2017) in the statistical environment R.

3 | RESULTS

3.1 | Seed dispersal traits: seed production and seed buoyancy

On average, a mudflat species in our dataset produced $4,319 \pm 1,562$ seeds/ramet. Yet, this trait value displayed extremely high variation, ranging from seven seeds/ramet in *Eleocharis acicularis* to 34,000 seeds/ramet in *Juncus bufonius*. Seed buoyancy of the studied mudflat species varied from 12 (*Persicaria lapathifolia*) to 77 days (*Mentha pulegium*) with an average of 38 ± 2.5 days; seeds of about 80% of mudflat species float on the water surface for >30 days (Appendix S3).

3.2 | Seed persistence traits: seed mass, species ability to build a persistent seed bank and seed storage behaviour

Seed mass of the studied mudflat species also varied significantly from dust-like seeds of *Lindernia procumbens* (0.003 mg) to

comparatively large ones of *Persicaria hydropiper* (2.7 mg), with an average of 0.28 ± 0.12 mg. Seed persistence in soil and seed storage ability of the mudflat species showed no variation; seeds of all species were classified as very long-term persistent and orthodox, respectively (Appendix S3).

3.3 | Seed germination and establishment traits: seed germination pattern, seed germination speed (T_{50}) and seed germination niche width (J)

We observed a high similarity in seed germination responses to the experimental treatments. The majority of the tested species (22 out of 30) were found to have a comparatively narrow germination niche with >50% of seeds germinating in only two treatments, predominantly in the LFA and LCA treatments, resulting in a comparatively moderate value (0.48 ± 0.04) for Pielou's J index (Appendix S3).

It is noteworthy that seeds of a few species were able to germinate to a high percentage under hypoxic conditions with full illumination, regardless of temperature fluctuations (treatments LFH and LCH; Appendix S3). Another small group of mudflat species germinated in darkness to the same proportion as in light but required aerobic conditions (treatments DCA and DFA; Appendix S3). The species that were able to germinate in other conditions than LFA and LCA tended to have higher values for Pielou's J index (0.64; Appendix S3) suggesting a comparatively broad seed germination niche width. None of the studied species showed any considerable response to the DCH and DFH treatments. Seed germination speed of mudflat species under optimal environmental conditions among tested treatments displayed a high variation. The T_{50} values varied from 0.2 (*Persicaria lapathifolia*) to 27 days (*Elatine hexandra*) with an average of 7.7 ± 1.2 days (Appendix S3).

3.4 | Cluster analysis and phylogenetic PCA

The 15 seed ecological traits studied could be summarised by two principal components (PCs) with eigenvalues >2.7, which together accounted for 43% of the total variance. The third PC accounted for an additional 15% of the total variation (Table 2). PC1 explained 23% of the variance and loaded most heavily and positively on seed germination responses to LFA and DFA. At the same time, PC1 loaded negatively on the seed germination response to the LCH and DCH treatments, as well as seed germination niche width. The second PC accounted for an additional 20% of the variance and loaded most heavily on seed germination's response to the LCA, DFA, DCA treatments, and seed mass (positive values). PC2 also loaded heavily and negatively on seed buoyancy and seed germination speed.

Hopkin's D -value for the six most important principal components of the pPCA was 0.39, suggesting that there were a number of species groups differing in their seed traits. Based on the majority rule (Kassambara, 2017), the *NbClust* function detected three clusters.

	PC1	PC2	PC3
Eigenvalue	2.90	2.70	1.30
Proportion of variance (%)	22.5	20.1	14.8
Cumulative proportion (%)	22.5	42.6	57.4
LFA (Light/Fluctuating temp./Aerobic condition)	0.90	0.11	0.00
LCA (Light/Constant temp./Aerobic condition)	-0.19	0.65	-0.39
LFH (Light/Fluctuating temp./Hypoxic condition)	0.20	0.39	0.67
LCH (Light/Constant temp./Hypoxic condition)	-0.84	0.12	0.26
DFA (Dark/Fluctuating temp./Aerobic condition)	0.40	0.75	0.19
DCA (Dark/Constant temp./Aerobic condition)	0.24	0.81	0.00
DFH (Dark/Fluctuating temp./Hypoxic condition)	-0.45	0.12	0.49
DCH (Dark/Constant temp./Hypoxic condition)	-0.74	0.00	0.05
Seed germination speed (T_{50})	0.02	-0.41	-0.03
Seed germination niche (Pielou's J)	-0.50	0.49	0.07
Seed mass	-0.07	0.48	-0.58
Seed number	0.31	-0.15	0.75
Seed buoyancy	0.16	-0.41	-0.24

Notes: For each axis, the eigenvalues and proportion of variance explained are provided and loadings for the first three principal components are provided. The abbreviations (LFA, LCA, etc) express the different seed incubation treatments.

Ten species were grouped into a cluster “true mudflat species.” They had a narrow germination niche (high germination percentages in the LFA experimental treatment only; low Pielou's J), comparatively low seed mass and high seed production. Contrastingly, species representing the cluster “facultative mudflat species” ($n = 5$) and the cluster “flood-resistant mudflat species” ($n = 15$) demonstrated the ability to germinate with higher germination percentages under a larger number of experimental treatments in addition to LFA and LCA (broader germination niche). Presumably, the main difference between the latter two clusters is the ability of “flood-resistant mudflat species” to germinate under hypoxic conditions (Figure 1; arrows LCH, LFH, DCH, DFH), whereas seeds of “facultative mudflat species” can additionally germinate in dark, aerobic conditions, regardless of temperature fluctuations (Table 3). In addition, species belonging to this cluster produce a higher number of large seeds as compared to the “flood-resistant mudflat species” cluster. Trait values, as well as characteristic species of the clusters, are shown in Table 3.

4 | DISCUSSION

For the mudflat plant communities, information about regenerative traits was available only for seed persistence (Altenfelder et al., 2016; Bissels et al., 2005; Poschlod & Rosbakh, 2018; Šumberová et al., 2012) or germination and establishment (Baskin, Baskin, & Chester, 1993, 2004; Brändel, 2004; Thompson & Grime, 1983). To the best of our knowledge, the present study is the first-ever detailed and comprehensive attempt to evaluate how seed dispersal, persistence, and germination and establishment traits contribute to the high adaptability of mudflat species to their unpredictable habitat.

TABLE 2 Summary of phylogenetic principal components analysis (pPCA) on a species–trait matrix of mudflat species

4.1 | Seed dispersal traits

Seed dispersal traits allow us to better understand how far and in what number seeds disperse to sites optimal for survival, germination and seedling establishment (Saatkamp et al., 2019). In the present study, we expected high seed production and high seed buoyancy potential among mudflat species to adopt long-distance dispersal in time and space by water and to facilitate the “escaping” strategy through transportation and deposition in large numbers of seeds in available habitats. However, our results supported this hypothesis only partially; although seeds of the majority of the study species floated for a similarly long time (on average, 38 days), seed production displayed extremely high variation (4,857-fold). This finding suggests that a high seed buoyancy ensures that seeds disperse longer distances, even if a species fails to produce a large number of seeds. Alternatively, high seed production can ensure abundant availability of seeds for animal dispersal, since this trait attributes more to seed dispersal through endozoochory than does seed morphology (Bruun & Poschlod, 2006). Both of these seed traits seem to increase the chances of mudflat species for establishment in temporally or spatially unpredictable but suitable microsites (Soons et al., 2017). This finding is also in line with previous research demonstrating that the structure and composition of other wetland communities might be affected by dispersal traits. Specifically, seed buoyancy was found to be lowest for communities of hydrophytes (seed sinks immediately after dispersal) and increased towards the shoreline, where seeds remained floating for several months until they are entrapped by shoreline vegetation or land at suitable locations (van den Broek, van Diggelen, & Bobbink, 2005; Soons et al., 2017). Our results on seed dispersal traits may suggest some multiple independent components of the

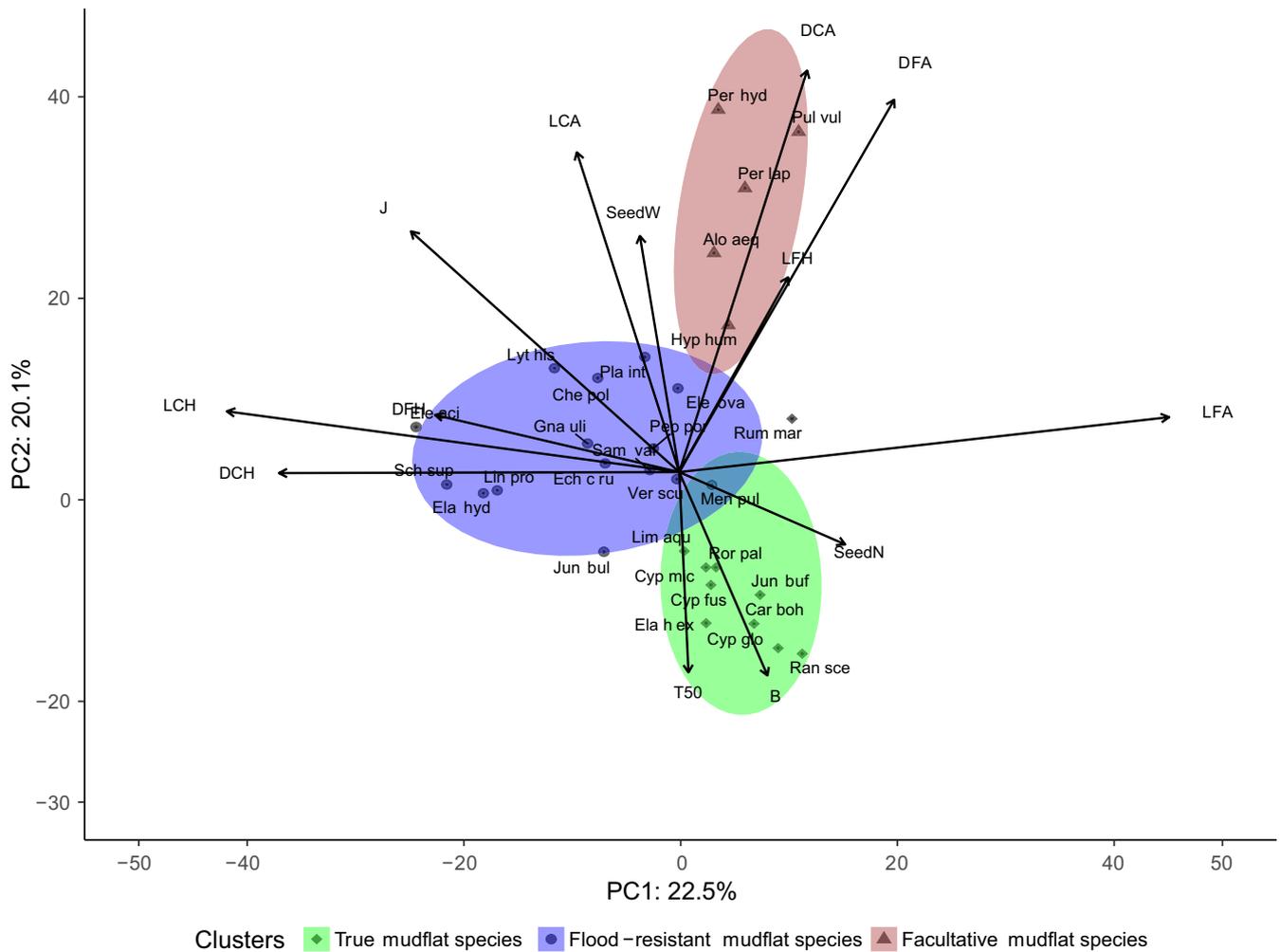


FIGURE 1 Two-dimensional illustration of the phylogenetic principal components analysis (pPCA) ordination of the species–seed trait matrix of studied mudflat species. See Table 2 for associated eigenvalues and eigenvectors and species abbreviations. Arrows indicate the direction of loading of each trait. Abbreviations LFA, DFA, LCA, DCA, LCH, DFH and DCH stand for the different environmental conditions to which seed germination responds (for more details refer to Table 2). *J* is seed germination niche width; *B*, seed buoyancy; and *SeedW* and *SeedN*, seed mass and seed number per ramet, respectively. Different symbols represent three clusters of mudflat species differing in seed traits (see Results and Table 2 for details) [Colour figure can be viewed at wileyonlinelibrary.com]

regeneration niche that make some ecological sense for temporal and spatial distribution and abundance of a species, which needs to be confirmed by further detailed studies.

4.2 | Seed persistence traits

Seed persistence traits play a crucial role in plant survival strategy; if a seed fails to germinate after dispersal, it may persist in the soil for a long time to avoid an unfavourable harsh environment until the onset of favourable conditions for establishment (Poschlod et al., 2013; Saatkamp, Poschlod, & Venable, 2014). The two main hazards for successful seedling establishment in mudflat habitats are flooding and drought. Thus, mudflat species need an adaptation in their regeneration by seed to cope with unpredictable flooding and drought events. In accordance with our hypothesis,

all studied species indicated high similarity in seed desiccation tolerance (all orthodox) and the ability to build a long-term soil seed bank (all of them have very or extremely long-term persistent seed banks; Poschlod & Rosbakh, 2018). As to the former, orthodox seed storage behaviour can be seen as an adaptation of seeds to survive unexpected droughts, which may occur on an irregular basis during summer drawdowns. For example, orthodox seeds of *Rumex maritimus* (one of our study species) survived well under different hydrological (dry, moist and wet) regimes when exhumed from artificial burial after 1.5 years (Abedi, Bartelheimer, & Poschlod, 2014) and even after 5.5 years (S. S. Phartyal, unpublished data). As to the latter, the ability of mudflat species to persist in seed banks is likely an adaptation for bridging the long periods of temporarily unsuitable (flooded) environmental conditions of their habitat (Poschlod & Rosbakh, 2018), which helps populations to recover via persistent seed banks when conditions

TABLE 3 Seed traits of three mudflat plant communities in the study obtained by *k*-means clustering

Traits*	Groups of mudflat plants		
	True mudflat species <i>n</i> = 10	Flood-resistant mudflat species <i>n</i> = 15	Facultative mudflat species <i>n</i> = 5
LFA, %	91	73	99
LCA, %	18	75	83
LFH, %	11	29	16
LCH, %	1	27	0
DFA, %	9	4	84
DCA, %	2	5	61
DFH, %	0	3	0
DCH, %	0	0	0
Seed germination width (Pielou's <i>J</i>)	0.29	0.55	0.68
Seed germination speed, days	9.78	8.09	2.64
Seed buoyancy, days	44.1	36.9	31.2
Seed mass, mg	0.06	0.18	1.04
Seed number	9,008.2	1,546.0	3,262.4
Proportion of species with long-term persistent seed bank, %	100	100	100
Proportion of orthodox seeds, %	100	100	100
Typical species	<i>Cyperus fuscus</i> <i>Juncus bufonius</i> <i>Limosella aquatica</i>	<i>Elatine hydrogiper</i> <i>Eleocharis ovata</i> <i>Schoenoplectus supinus</i>	<i>Hypericum humifusum</i> <i>Persicaria lapathifolia</i> <i>Pulicaria vulgaris</i>

*For abbreviations see Table 2.

become favourable for germination and seedling establishment (Saatkamp et al., 2019).

As expected, mudflat species produced relatively small seeds as compared to other wetland plants, but there was a high variation in seed mass among species in the study (900-fold). In contrast to the other two persistence traits, the possible reasons for dissimilarity in this trait might be the complexity of the mudflat group with "true," "flood-resistant" and "facultative" mudflat species (see more details below). "True" and "flood-resistant" mudflat species possess rather small seeds, which is in accordance with our hypothesis, whereas "facultative" mudflat species have large seeds. Small rounded seeds are able to enter the soil faster than large flat seeds (Benvenuti, 2007) and therefore are able to easily build up a persistent seed bank (Bekker et al., 1998; Saatkamp, Affre, Dutoit, & Poschlod, 2009; Thompson et al., 1993). Apart from persistence, seed mass is also linked to germination

response to light and temperature (Milberg et al., 2000) and seedling emergence from depth (Loydi, Eckstein, Otte, & Donath, 2013). The average seed mass reported for species in our study was low (0.28 mg) as compared to seed mass of other wetland species, indicating light requirement for germination (Milberg et al., 2000). Our results support this as the majority of species with small seeds failed to germinate under dark conditions, while species with large seeds germinated in both the dark and light regimes. Additionally, irrespective of a high variability in seed production, the majority of the tested species have high seed production, which supports the argument that seed bank longevity in soil is correlated with seed production, thus heightening chances of seed survival in soil if more seeds are produced (Saatkamp et al., 2009). Seed desiccation and persistence traits are expected to be highly correlated as desiccation-sensitive seeds do not tend to form a long-term persistent seed bank.

4.3 | Seed germination and establishment traits

Among regenerative traits, the seed germination period is presumed to be the most critical event in the plant life cycle (Grubb, 1977), since seed germination is an irreversible process; once it is triggered, a seedling must either establish or die. Here we hypothesised that seeds of mudflat species should have a narrow seed germination niche and a high similarity in seed germination response to environmental cues, especially for the requirements of fluctuating temperature, light and oxygen conditions, and our results confirm this hypothesis to large extent. Germination of many wetland species is largely stimulated by fluctuating temperatures, which does not occur during flooding but does occur after water drawdown, ensuring that germination takes place at a time when conditions are most conducive to the successful establishment of the seedling (Baskin, Baskin, & Chester, 1993; Thompson & Grime, 1983). Therefore, the high germination percentage of the majority of our mudflat species under LFA conditions may be related to the mechanism for detecting depth of shallow water (Ekstam, Johannesson, & Milberg, 1999; Pons & Schröder, 1986), sensing depth even under the bare muddy surface or gaps in the vegetation (Pearson, Burslem, Mullins, & Dalling, 2002; Saatkamp, Affre, Dutoit, & Poschlod, 2011). Additionally, there is often a consistent relationship between seed mass and its response to fluctuating temperatures and photoperiod. Some species with seeds that are small in size do not germinate in darkness under fluctuating temperatures, whereas others that germinate in darkness under fluctuating temperatures have a wide range of seed mass (Thompson & Grime, 1983); this is consistent with our study as well. "True mudflat species" have very small seeds (0.06 mg), which germinate well mainly in light at fluctuating temperatures (LFA) whereas "facultative mudflat species" have comparatively large seeds (1.04 mg) that germinate well both under light and darkness at fluctuating temperatures (LFA and DFA). The ecological significance of "true mudflat species" germinating mainly at LFA may provide a mechanism restricting germination to seeds at or very near the soil

surface (Thompson & Grime, 1983) or germinate as an emergent immediately after the water recedes.

4.4 | The role of seed traits at sub-community level adaptation

Being a complex group, mudflat plants also comprise those species that have their own specific ecological optima in other wetland communities. Some of them, such as *Hypericum humifusum* or *Pericaria lapathifolia*, might grow well at the comparatively dryer end of typical mudflat habitats, whereas others may grow well towards the wetter end (e.g. *Eleocharis ovata*, *Schoenoplectus supinus*; Oberdorfer, 2001). Thus, the specific microenvironments at these two contrasting ends of mudflat habitats might act differently on different species and govern their distribution and adaptability as per the variation in their seed trait functions at the sub-community level. Results of the present study support this argument, as the majority of studied seed traits seem to be highly adaptive to the peculiarities of specific micro-habitats. For example, the “true mudflat species” such as *Cyperus fuscus*, *Juncus bufonius*, *Limosella aquatica* have narrow germination niche width (J -value, 0.29), and the lowest seed mass (0.06 mg), but have the highest seed production per ramet (ca. 9,000) and a high seed buoyancy of 44 days (Table 3, Figure 1). This pioneer ephemeral community of dwarf rushes and herbs can be classified as “true mudflat species,” which includes typical representatives of the *Nano-Cyperion* alliance (Ellenberg & Leuschner, 2010), which can be found soon after the mudflats become exposed and remain dry for some time, provided no tall plants grow there.

In a wetland ecosystem, there is a pronounced hydroperiod gradient of the variation in duration, depth, and frequency of flooding (Moor et al., 2017), which occurs at relatively small scales. Thus, these “true mudflat species” border typical terrestrial communities at one end and swamp or shallow water communities at the other end, resulting in two additional clusters, i.e., “facultative mudflat species” and “flood-resistant mudflat species.” The comparatively small group of “facultative mudflat species,” such as *Pericaria lapathifolia* or *Pulicaria vulgaris*, are terrestrial species (often ruderal) that demonstrate a broader germination niche width (J -value 0.68), a comparatively low seed buoyancy of 31 days and produce large seeds (1.0 mg) in high number (3,262 seed/ramet), while the “flood-resistant mudflat species” (*Elatine hydropiper*, *Eleocharis ovata*, *Schoenoplectus supinus*) occurring towards the shallow water ends also demonstrate a broader germination niche width (J -value 0.55), have a moderate seed mass (0.18 mg) and seed buoyancy (37 days) but low seed production (1,546 seed/ramet) compared to the other two groups (Table 3). The (dis)similarity to some extent in seed traits, especially dispersal and germination and establishment traits, might play a deceptive role in ecological optima and in the fine distinction among “true,” “facultative” and “flood-resistant” mudflat species according to the variation in hydroperiod gradient at the micro-scale level, which is the most fundamental driver governing wetland plant community structure and composition (Keddy, 1992; Rosbakh,

Phartyal, & Poschlod, 2019). Nevertheless, despite the fact that these communities may coexist in various ways, they retain their distinct zonation pattern along a small hydroperiod gradient and can also occur independently elsewhere (Sculthorpe, 1967; Valdez, Hartig, Fennel & Poschlod, 2019). Considering the presence of three distinct sub-communities with three distinct seed trait values, even at a micro-habitat level, suggests that regeneration traits should be used more often in future studies on community ecology of other ecosystems, as suggested by Larson and Funk (2016) and Saatkamp et al. (2019).

5 | CONCLUSION

Considering the great importance of seed traits for plant distribution, establishment and adaptation in their natural habitat, our study has important implications for ecological research and nature conservation and/or restoration. By including the studied seed traits into ecological research they provide a comprehensive overview of how the inclusion of regenerative traits in community composition improves our understanding of how certain traits/trait values make species fit to adopt their specific and unpredicted habitats. Additionally, since the majority of mudflat species are the most threatened plant group in central Europe due to habitat degradation (Poschlod & Rosbakh, 2018), for conservation and/or restoration efforts to maintain existing communities or re-establish them, the optimal conditions for seed germination and seedling establishment should be created. That can be done by returning the natural floods and/or drainage of river banks and fish ponds to regular and more frequent intervals so that the long-term persistent sediment seed bank of the “true” mudflat plant community can be activated by allowing the favourable environmental cues for seed germination and further establishment to be sensed.

ACKNOWLEDGEMENTS

We thank the students who helped with the seed collection and germination experiment. SSP is thankful to the Alexander von Humboldt Foundation, Germany, for a Humboldt Experienced Researcher Fellowship. We also thank four anonymous referees for their valuable comments on the earlier version of this article. We would also like to thank Hayden Prouty for proofreading the paper.

AUTHOR CONTRIBUTIONS

PP, SR, and SSP conceived the study and performed the experiments; SR compiled the dataset; SR and CR analyzed the dataset; SSP and SR contributed equally to writing the manuscript. All authors helped in critically revising the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data supporting the findings of the present study are available both within the article and as its online supplementary material (Appendix S1, S2, and S3).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. A recently exposed fish pond making a typical freshwater mudflat habitat

Appendix S2. Study species and seed collection sites

Appendix S3. Details of study species and seed trait values

How to cite this article: Phartyal SS, Rosbakh S, Ritz C, Poschlod P. Ready for change: Seed traits contribute to the high adaptability of mudflat species to their unpredictable habitat. *J Veg Sci*. 2020;31:331–342. <https://doi.org/10.1111/jvs.12841>