

Seed germination traits shape community assembly along a hydroperiod gradient

Sergey Rosbakh^{1,*}, Shyam S. Phartyal^{1,2,†} and Peter Poschlod¹

¹University of Regensburg, Ecology and Conservation Biology, Institute of Plant Sciences, Regensburg, Germany and ²H. N. B. Garhwal University, Department of Forestry and NR, Srinagar-Garhwal, India

*For correspondence. E-mail sergey.rosbakh@ur.de

†Present address: Nalanda University, School of Ecology and Environment Studies, Rajgir, India.

Received: 5 June 2019 Returned for revision: 17 July 2019 Editorial decision: 7 August 2019 Accepted: 13 August 2019
Published electronically 17 August 2019

- **Background and Aims** Hydroperiod drives plant community composition in wetlands, resulting in distinct zonation patterns. Here, we explored the role of seed germination traits in shaping wetland community assembly along a hydroperiod gradient. Specifically, we tested the hypothesis that seeds of reed, mudflat, swamp, shallow- and deep-water communities only germinate under a specific set of environmental factors characterized by the community-specific optimal conditions for seedling survival and growth.
- **Methods** In a three-factorial experiment, we tested the seed germination response of 50 species typical for temperate wetlands of Europe to temperature fluctuations (constant vs. fluctuating temperature), illumination (light vs. darkness) and oxygen availability (aerobic vs. hypoxia). Phylogenetic principal component analysis, cluster analysis and phylogenetic linear regressions were used to confirm the community-specific seed germination niches.
- **Key Results** Our study revealed the presence of five distinct, community-specific seed germination niches that reflect adaptations made by the study communities to decreasing light intensity, temperature fluctuations and oxygen availability along the hydroperiod gradient. Light as a germination trigger was found to be important in mudflats, swamps and shallow water, whereas the seeds of reed and deep-water species were able to germinate in darkness. A fluctuating temperature is only required for seed germination in mudflat species. Germination of species in the communities at the higher end of the hydroperiod gradient (reed and mudflat) demonstrated a strict requirement for oxygen, whereas swamp, shallow- and deep-water species also germinated under hypoxia.
- **Conclusions** Our study supports the recent argument that the inclusion of seed germination traits in community ecology adds significant insights to community response to the abiotic and biotic environment. Furthermore, the close relationship between seed germination adaptations and community assembly could help reach a better understanding of the existing patterns of wetland plant distribution at local scales and wetland vegetation dynamics, as well as facilitate nature conservation measures and aquatic habitat restoration.

Key words: Community assembly, hydroperiod gradient, regeneration niche, seed germination, trait, wetland

INTRODUCTION

Understanding plant community assembly rules, that are ecological processes selecting for or against species from the regional species pool and thus determining local community composition (Keddy, 1992), is one of the most challenging tasks of vegetation ecologists. Disentangling the different processes involved in community assembly is not only important to explain current community compositions (both species occurrence and abundance) along spatial and temporal gradients but is also crucial for an understanding of how these communities will respond to future environmental changes (Götzenberger *et al.*, 2012).

An adult plant cannot become a part of an established community if its seeds are not able to germinate and/or its seedlings cannot establish themselves. Thus, these two stages are important drivers of community assembly (Grubb, 1977; Poschlod *et al.*, 2013). Despite the fact that seed germination and seedling traits are extremely sensitive to abiotic factors and represent a

major bottleneck to species recruitment (Fenner and Thompson, 2005), they are still overlooked when inferring community assembly rules (Laughlin, 2014). Yet, some recent studies (though very scarce) clearly indicate that the inclusion of such traits in community ecology adds significant insights to community response to the abiotic and biotic environment (Rosbakh and Poschlod, 2015; Tudela-Isanta *et al.*, 2018). Specifically, seed germination traits are powerful predictors of community assembly at a regional scale (i.e. among different habitats; Rosbakh and Poschlod, 2015; Tudela-Isanta *et al.*, 2018). However, studies exploring the role of seed germination traits in community assembly at a local scale are still very scarce (e.g. Kos and Poschlod, 2007, 2010; Fernández-Pascual *et al.*, 2017).

Wetlands are habitats that are inundated or saturated by water at a rate sufficient to support a prevalence of vegetation typically adapted for life in saturated soil conditions (Mitsch and Gosselink, 2015). The presence of numerous key

environmental gradients occurring at relatively small scales and the resulting high trait variation of plant species occurring along these gradients make wetlands a powerful ‘natural experiment’ for examining the drivers of community assembly on a local scale (Shipley *et al.*, 1989). Hydroperiod (duration, depth and frequency of flooding; Moor *et al.*, 2017) is the most fundamental driver of wetland plant community structure and composition (Keddy, 1992). In an idealized example (Sculthorpe, 1967; Spence, 1982; Fig. 1), permanently or long-term flooded parts of the hydroperiod gradient with large water tables (up to 10 m depth) are dominated by communities of floating-leaved, rooted nympheoids, such as *Nuphar lutea* or *Nymphoides peltata* occurring in shallow waters (Fig. 1) or permanently submerged hydrophytes (e.g. *Potamogeton* spp.), respectively, at deeper sites (‘deep water’ zone; Fig. 1). They are spatially succeeded by swamp communities occurring on exposed or submerged soils, where the water table is ≥ 50 cm beneath the soil surface to where the soil is covered by ≥ 150 cm of water. This ‘swamp’ zone is occupied by emergent hydrophytes or helophytes (e.g. *Alisma lanceolata* or *Typha latifolia*) well adapted to such ‘amphibian’ conditions, i.e. alternation between terrestrial and aquatic growing conditions. The ‘dry’ end of the hydroperiod gradient, the ‘reed’, where the water table lies below the soil surface during the growing season and rises for a short time during the wet season, is occupied by dense communities of tall helophytes – predominantly grasses and sedges, such as *Phalaris arundinacea*, *Phragmites australis* and *Carex rostrata*, or species-rich wet meadows. Additionally, pioneer ephemeral mudflat communities of annual dwarf rushes and herbs (e.g. *Cyperus fuscus* and *Limosella aquatica*) can appear in each of these zones during drawdowns, when the substratum is free of standing water and litter. Finally, in sheltered places, free-floating plants may also be present in any of the three first zones provided that the water table remains stable. Other environmental gradients including those of soil and water chemical composition (pH, type and concentration of available

nutrients, and salinity), sediment type and flow velocity, as well as the terrain morphology and land use, can modify this zonation, resulting in the well-documented high variability of wetland communities (Hejný, 1960; Sculthorpe, 1967; Spence, 1982; Santamaria, 2002; Chepinoga, 2015; Landucci *et al.*, 2015; Moor *et al.*, 2017). Despite the fact that these communities may coexist in various ways, they retain their distinct zonation pattern along the hydroperiod gradient and can occur independently elsewhere (Sculthorpe, 1967).

Although vegetative reproduction by the formation of clones and turions predominates among wetland plants, particularly in submerged and free-floating hydrophytes, seed reproduction plays an important role in wet habitats (Sculthorpe, 1967; Hutchinson, 1975; Barrett *et al.*, 1993; Grace, 1993). Specifically, certain wetland species rely on seeds for population persistence (e.g. seed banks; Poschlod and Rosbakh, 2018), colonization of gaps in existing communities (Shipley *et al.*, 1989) and long-distance dispersal (Charalambidou and Santamaría, 2002), due to their higher resistance to environmental stress as compared with vegetative propagules (Hay *et al.*, 2000). Previous studies have suggested that wetland community structure and composition might be affected by the seed traits of corresponding species along the hydroperiod gradient. For instance, studies on seed dispersal in wetlands demonstrate that community occurrence along the hydrologic gradient is correlated with seed buoyancy. Specifically, buoyancy was found to be lowest for floating-leaved hydrophytes (seed sunk immediately after dispersal) and increased towards the shoreline (seeds of some shoreline plants remained floating for several months) (van den Broek *et al.*, 2005; Soons *et al.*, 2017). Soons *et al.* (2017) conclude that wetland plants produce seeds with adaptations to promote transportation and deposition by water towards microsites along the hydroperiod gradient where they germinate and become established. Similarly, the requirements for seed germination of some wetland species demonstrate strong associations with corresponding

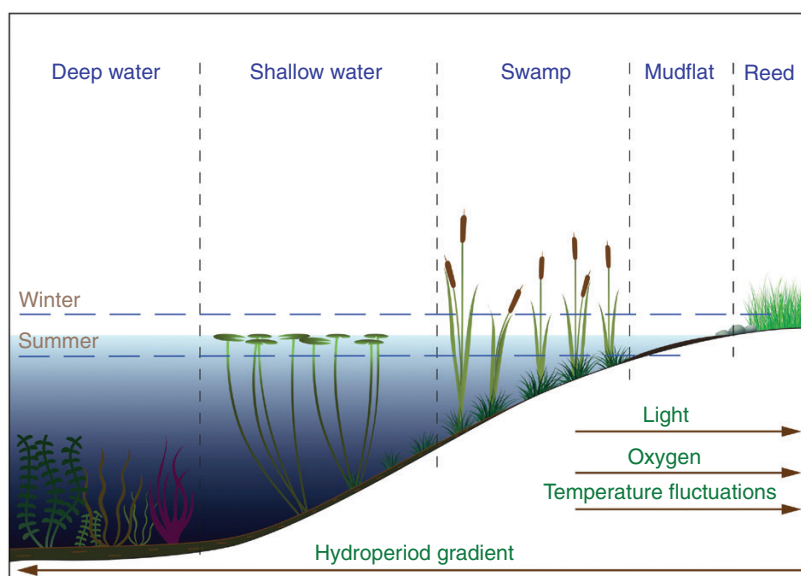


FIG. 1. Wetland vegetation zonation along a hydroperiod gradient. The arrows in the lower right corner indicate decreasing light availability, oxygen concentrations and temperature fluctuations, which are important environmental clues for seed germination, along the hydroperiod gradient. The dashed lines indicate different water levels in winter and summer.

communities (reviewed by Baskin and Baskin, 2014). Data indicate that the majority of emergent species from reed and swamp, as well as species of mudflat communities, germinate primarily on exposed soils or sediments free of vegetation, whereas submerged, free-floating and floating-leaved aquatics produce seeds that germinate best under flooded substrate conditions (Sculthorpe, 1967; van der Valk and Davis, 1978; Shipley *et al.*, 1989). The seeds of the former species usually require exposure to light and/or fluctuating temperatures, and germinate to low percentages under low oxygen conditions (Baskin and Baskin, 2014). In the latter case, seeds display high germination in shaded conditions, constant temperatures and hypoxia, or even strictly anaerobic conditions (Baskin and Baskin, 2014). Consequently, the intensity and duration of flood or drawdown are thought to shape wetland local community assembly by filtering species from the species pool according to their ability to germinate under water (van der Valk, 1981; Baskin and Baskin, 2014). However, this hypothesis has not been explicitly tested yet.

In the present study, we explore the role of seed germination traits in shaping wetland community assembly along the hydroperiod gradient. Given the high environmental variability among wetland plant communities along the hydroperiod gradient, we hypothesized that seeds of the corresponding species should germinate under the set of specific environmental factors that indicate the onset of optimal conditions for seedling survival and growth (i.e. possess a narrow community-specific germination niche; Fenner and Thompson, 2005; Donohue *et al.*, 2010; Fernandez-Pascual *et al.*, 2017). Specifically, we suggest that species of reed, mudflat, swamp, shallow- and deep-water communities differ in their seed germination requirements for light, temperature fluctuation and oxygen, since these factors are the most important determinants of plant recruitment along the hydroperiod gradient (van der Valk, 1981; Galinato and van der Valk, 1986; Baskin and Baskin, 2014), and their interaction may serve as environmental cues for dormancy break or germination, and for post-germination seedling establishment.

MATERIALS AND METHODS

Study system and species

Based on vegetation surveys (Hejný, 1960; Sculthorpe, 1967; Landucci *et al.*, 2015) and the authors' field observations carried out in the temperate wetlands of Europe, we selected 50 of the typical herbaceous plant species occurring in five distinct wetland plant communities along the hydroperiod gradient (Fig. 1): deep-water zone, shallow-water zone, swamps, reeds and mudflats ('DW', 'SW', 'S', 'R' and 'M', respectively; Table 1). At the local scale, the majority of these species are confined to one of these communities and demonstrate (with a few exceptions) a very high level of specialization to the particular water table level, flood/drought characteristics and the corresponding abiotic factors (Hejný, 1960; Sculthorpe, 1967; Spence, 1982; Chepinoga, 2015; Landucci *et al.*, 2015). This study is restricted to species occurring in continental waterbodies with standing or slow running waters of temperate Europe, and excludes saline habitats.

Seed germination experiments

Mature dispersal units (hereafter 'seeds') of the 50 study species were sourced from typical, natural populations of wetland species located across Germany, Croatia, Russia and Slovenia (Supplementary data Appendix S1). Seeds of some species were obtained from the University of Regensburg's water basins or greenhouses by cultivating sediment samples for soil seed bank studies under natural or semi-natural conditions due to the rarity of fruiting naturally (Poschold and Rosbakh, 2018). We collected the seeds from randomly chosen individuals (>50 individuals per species and thoroughly mixed). After collection, the seeds of non-aquatic species were air-dried for several days, cleaned and kept dry in a cold room under 4 °C until the beginning of the germination experiments, following recommendations by Baskin and Baskin (2014). The seeds of aquatic plants (e.g. *Nuphar lutea*, *Potamogeton natans*, *Trapa natans*, etc.) were stored wet in plastic containers at room temperature, to avoid their desiccation (Hay *et al.*, 2000). Prior to the germination experiments, the seeds of all the species were allowed to overwinter moist at 4 °C for 6–9 weeks, to meet winter chilling requirements necessary to overcome physiological dormancy, if any, in some of the target species (Baskin and Baskin, 2014). Due to the presence of their permeable but hard seed coat, seeds of *Potamogeton* spp. were mechanically scarified before the wet chilling to ease dormancy break and seed germination.

To reveal the requirements for optimal germination as an adaptation to environmental conditions in the study communities, we used a three-factorial experiment to test seed germination response to temperature fluctuations (constant vs. fluctuating temperature), illumination (light vs. darkness) and oxygen availability (aerobic vs. hypoxia). Previous research suggests that these three environmental factors are the most important seed germination triggers in wetlands (reviewed in Baskin and Baskin, 2014) and are assumed to represent the environments in wetland communities along the hydroperiod gradient that the seeds may encounter (Fig. 1; Table 2). For example, the quality and quantity of light (Silvertown, 1980; Vazquez-Yanes and Orozco-Segovia, 1987), daily temperature fluctuations (Thompson, 1974) and oxygen concentrations (Pons, 1989) were found to decrease with water depth. Therefore, seed germination of species inhabiting the 'deep-water' zone is expected to be independent from light and triggered by constant temperatures and low oxygen concentrations (Baskin and Baskin, 2014).

In each germination test, 20 seeds were placed on two layers of wet filter paper in a Petri dish; each treatment was replicated five times. All the experiments were conducted in RUMED 1301 climatic chambers (Rubarth Apparate GmbH, Laatzen, Germany) at constant (22 °C; no temperature fluctuations) or diurnal fluctuating temperatures (22/14 °C; temperature fluctuations) with 14 h of light supplied by white fluorescent tubes. To test the ability of the seeds to germinate under dark conditions, the Petri dishes were wrapped immediately with four layers of aluminium foil. Germination proportions for all dark treatments were recorded once, on the very last day of the experiment. For the light treatment, the Petri dishes remained unwrapped for the whole experiment. Oxygen availability had two levels: hypoxic and aerobic. To simulate hypoxic conditions, the Petri dishes

TABLE 1. Study species, their occurrence along the hydroperiod gradient and seed germination traits

Species	Abbreviation	Wetland community	Seed germination niche			Seed germination, %						Seed germination speed (T_{50}), d	Seed germination niche width (J)
			LFA	LCA	LFH	LCH	DFA	DCA	DFH	DCH			
<i>Alisma lanceolatum</i>	Ali lan	S, SW	4.8	9.2	96.4	65.7	0	0	100	42.5	26.7	0.71	
<i>Alisma plantago-aquatica</i>	Ali pla	S, SW	0	0	100	32.1	0	0	80.6	1.6	24.7	0.50	
<i>Alopecurus aequalis</i>	Alo aeq	R	100	88.7	0	0	63.8	0	0	0	2.8	0.65	
<i>Butomus umbellatus</i>	But umb	S, SW	1.6	12.5	40.5	100	0	0	1.6	0	6	0.47	
<i>Carex bohemica</i>	Car boh	M	100	4.1	0	0	0	0	0	0	9.3	0.08	
<i>Carex pseudocyperus</i>	Car pse	M	100	92.3	0	0	7.7	0	2.6	2.6	11.1	0.45	
<i>Chenopodium polyspermum</i>	Che pol	M	100	87.4	31.4	3.4	16.8	42.2	16.8	0	12.8	0.78	
<i>Cyperus fuscus</i>	Cyp fus	M	100	15.5	0	0	0	0	0	0	7	0.19	
<i>Cyperus glomeratus</i>	Cyp glo	M	100	1	0	0	0	0	0	0	7.9	0.03	
<i>Dichosyris micheliana</i>	Dic mic	M	100	17	0	0	0	0	0	0	6.9	0.20	
<i>Echinochloa crus-galli</i>	Ech cru	M, R	100	72.7	2.4	18.8	12.4	6.3	0	2.4	15.1	0.63	
<i>Elatine hexandra</i>	Ela hex	M, S	100	30.7	5.7	0	3.7	3.7	0	0	27	0.43	
<i>Elatine hydrophiper</i>	Ela hyd	M, S	47.6	73.2	0	100	0	0	0	0	6.5	0.51	
<i>Eleocharis acicularis</i>	Ele aci	M, S	74.3	100	81.2	74.2	1.8	3.5	12.4	5.3	5.7	0.77	
<i>Eleocharis ovata</i>	Ele ova	M, S	100	89.2	98	2	9.1	2	5.1	0	3.8	0.64	
<i>Eleocharis palustris</i>	Ele pal	S	96.3	100	98.8	96.3	6.3	2.5	22.5	2.5	7.2	0.78	
<i>Gnaphalium uliginosum</i>	Gna uli	M	57	100	0	0	0	0	0	0	2.5	0.32	
<i>Hypericum humifusum</i>	Hyp hum	M	100	100	0	0	71	3.5	0	0	5.7	0.63	
<i>Iris pseudacorus</i>	Iri pse	S, R	100	19.1	1.1	0	25.3	12.9	0	0	7.3	0.52	
<i>Juncus bafionius</i>	Jun buf	M	100	31.3	50.8	2.5	0	0	0	0	19.2	0.50	
<i>Limosella aquatica</i>	Lim aqu	M, S	100	61.9	0	5.1	1.7	0	0	0	8.4	0.40	
<i>Lindernia procumbens</i>	Lin pro	M, S	61	50.8	0	100	0	0	0	0	7.4	0.51	
<i>Lytirum hyssopifolia</i>	Lyt hys	M, S	100	96.8	96.8	84.9	0	0	5.4	0	2.2	0.69	
<i>Mentha pulegium</i>	Men pul	M, R	99	100	0	3	10.1	14.2	0	0	2.8	0.53	
<i>Nasturtium officinale</i>	Nas off	S	95.5	100	0	0	0	0	0	0	6.1	0.33	
<i>Nuphar lutea</i>	Nup lut	SW	0	1.4	91.3	100	0	0	20.5	25	12.5	0.58	
<i>Nymphaea alba</i>	Nym alb	SW	31.4	30	100	97.6	5	9.9	16.5	16.7	19.4	0.81	
<i>Nymphoides peltata</i>	Nym pel	SW, S	100	71.4	76.8	80.4	0	0	0	0	1.3	0.66	
<i>Peplis portula</i>	Pep por	M	100	99.9	0	0	0	0	0	0	3.3	0.33	
<i>Persicaria hydropiper</i>	Per hyd	R, M	100	92.4	0	0	95.8	85.8	1.1	1.1	2.2	0.68	
<i>Persicaria lapathifolia</i>	Per lap	R, M	100	39.4	3.3	0	99	42	0	0	0.2	0.65	
<i>Phalaris arundinacea</i>	Pha aru	R	99.9	24.7	49.8	0	100	46.8	25.5	0	0.9	0.79	
<i>Plantago intermedia</i>	Pla int	M	100	68	56.3	1.1	19.1	17	9.6	0	2.6	0.74	
<i>Potamogeton compressus</i>	Pot com	DW, SW	100	100	100	100	100	100	100	100	2.2	1.00	
<i>Potamogeton gramineus</i>	Pot gra	DW, SW	100	97.6	97.6	100	99.2	97.6	97.6	98.4	2	1.00	
<i>Potamogeton natans</i>	Pot nat	DW	98.4	98.4	98.4	97.6	96.8	97.6	98.4	100	1.9	1.00	
<i>Potamogeton pectinatus</i>	Pot pec	DW	99	97.6	97.6	100	99.2	97.6	97.6	98.4	2	1.00	
<i>Pulicaria vulgaris</i>	Pul vul	R, M	100	100	74.9	0	96.9	92.4	0	0	2.2	0.77	
<i>Ranunculus peltatus</i>	Ran pel	SW	100	55.5	0.5	7.5	67.1	0.5	0	0	12	0.58	
<i>Ranunculus sceleratus</i>	Ran sce	R, M	100	2.5	0	0	0	0	0	0	10.2	0.06	
<i>Ranunculus trichophyllus</i>	Ran tri	SW	100	43	0	0	31.6	0	0	0	11.3	0.47	
<i>Rorippa palustris</i>	Ror pal	R, M	100	40.1	7.2	0	2.8	0	0	0	0.5	0.41	
<i>Sagittaria sagittifolia</i>	Sag sag	SW	14.9	52	100	98.9	1	5	96	96	3.1	0.83	
<i>Schoenoplectus lacustris</i>	Sch lac	SW	89.4	95.3	96.5	100	65.9	54.1	83.5	92.9	8.2	0.99	
<i>Schoenoplectus supinus</i>	Sch sup	M, S	7.5	47.4	75.4	100	0	0	0	1.9	14.3	0.58	
<i>Scirpus radiicans</i>	Sci rad	R	100	3	0	0	0	0	0	0	13.4	0.06	
<i>Sparganium erectum</i>	Spa ere	R	100	58.7	25.8	7	85.3	96.3	18.8	7	20.8	0.85	
<i>Trapa natans</i>	Tra nat	DW	100	100	88.9	75	100	100	81.3	81.3	5.9	1.00	
<i>Typha angustifolia</i>	Typ ang	S, SW	7.7	1.3	96.8	100	6.4	1.3	3.8	0	14.3	0.52	
<i>Typha latifolia</i>	Typ lat	S, SW	95.2	82.1	98.8	100	6	3.6	41.7	22.6	5.2	0.85	

Wetland community: R, reed; M, mudflat; S, swamp; SW, shallow water; DW, deep water. The classification is based on Hejny (1960), Sculthorpe (1967), Spence (1982), Chepings (2015) and Landucci et al. (2015). Seed germination requirements: L, light; D, darkness; C and F, constant and fluctuating temperatures, respectively; A, aerobic conditions; H, hypoxia. See the Materials and Methods for further details.

TABLE 2. Seed germination conditions in the studied wetland communities and expected optimal seed germination conditions in the experiment

Wetland community	Hydroperiod	Seedling establishment conditions in the field			Expected optimal germination conditions in the experiment
		Light	Temperature	Oxygen levels	
Reed	Water table during growing season lies below the soil surface and rises for a short time during the wet season	Dense vegetation, light available in open gaps only	Constant temperatures under dense plant cover, larger fluctuations in open gaps	Almost high, low when flooded	LFA, LCA, DFA, DCA
Mudflats	Can appear at each part of the hydroperiod gradient, given that the sub-stratum is free of standing water and litter	Fully illuminated	Large fluctuations	Almost high, low when flooded	LFA
Swamp	High variation in duration, depth and frequency of flooding. Water table ranges from ≥ 50 cm beneath the soil surface to where the soil is covered by ≥ 150 cm of water	Fully illuminated, but could be moderate or low when flooded	Both constant and fluctuating depending on the water table	Moderate, vary depending on water table	LFA, LCA, LCH, DCH
Shallow water	Permanently or long-term flooded. Shallow water table	From moderate to no illumination	Mainly constant, but can fluctuate when shallowly flooded	Low, usually hypoxic	LCH, LFH
Deep water	Permanently or long-term flooded. Deep water table	No light, especially when seeds are buried in sediments	Constant	Very low, usually anoxic or hypoxic conditions	DCH

L, light; D, darkness; C and F, constant and fluctuating temperatures, respectively; A, aerobic conditions; H, hypoxia. See the Materials and Methods for further details.

were supplied with vents to provide consistent gas exchange and then placed in a desiccator where the air was substituted with pure nitrogen. We repeated this procedure each time germination was scored. The treatments to which this treatment was not applied are referred to as aerobic.

The dishes were examined initially twice a week and later once a week for germination, and any seeds with a protruding radicle or evidence of cotyledons were classed as germinated; these were removed once the checks had been completed. After 6 weeks, the experiments were terminated and the viability of non-germinated seeds was checked by inspection of embryos. Seeds with white and firm embryos were considered viable (Baskin and Baskin, 2014). The abbreviations used for the different seed incubation treatments through the text read as follows: L, light; D, dark conditions; C, constant, F, fluctuating temperatures; A, aerobic, H, hypoxia conditions.

Statistical analysis

*T*₅₀ and seed germination niche width Based on seeds that germinated in the treatments, we calculated germination speed under optimal environmental conditions (hereafter *T*₅₀) and seed germination niche width. The *T*₅₀ values are determined here as the number of days taken by 50 % of total germinated seeds under the most optimal conditions (i.e. an experimental

treatment in which the germination rates were the highest). When two or more treatments produced similar final germination, the *T*₅₀ values were calculated for all of them and the lowest value was considered in the analysis. To estimate the *T*₅₀ values, a two-parameter log-logistic model was fitted to the data using the statistical method developed by Ritz *et al.* (2013) and Jensen *et al.* (2017). The curve fit as well as the estimation of *T*₅₀ values were carried out with the help of the drc package (Ritz *et al.*, 2015) for R software.

Seed germination niche width was estimated for each of the 50 species as Pielou's evenness index (*J*; Thompson *et al.*, 1999; Fernández-Pascual *et al.*, 2017), calculated with the final germination proportions in each of the eight experimental treatments. Low *J* values indicate high sensitivity to one treatment (narrow germination niche) and values close to one indicate germination evenly distributed among the treatments (wide germination niche).

Phylogenetic signal in seed germination traits To estimate the extent to which seed germination traits are constrained by the relatedness between species, we first tested for a phylogenetic signal in each of our traits using Blomberg's *K* (Blomberg *et al.*, 2003) in the phytools package of the statistical environment R (Revell, 2012). Briefly, low *K* values indicate a weak phylogenetic signal in the trait data, and values close to one indicate a strong phylogenetic signal. Calculations of the *K* values, as well as phylogenetic principal component analysis (pPCA; see

below) were based on a phylogeny of a large European flora (Durka and Michalski, 2012).

Community-specific seed germination niche and phylogenetic PCA To confirm the community-specific seed germination niches of the study species detected in the laboratory treatments (see above), we performed a cluster analysis on the species–trait matrix. We grouped the species into five clusters corresponding to the five target wetland communities by *k*-means clustering. To visualize the (dis)similarity in the seed germination traits within the target wetland communities and determine the dominant axes of trait variation, we conducted multivariate analysis on the species–trait matrix (Table 1). Given that we detected phylogenetic signals in almost all seed germination traits (Table 3), we conducted a pPCA, which accounts for non-independence among species (Revell, 2009). The results of the pPCA were plotted with the help of the *ggord* package (Beck, 2017) in R.

Differences in wetland communities in their response to the experimental treatments, seed germination speed and seed germination niche width were tested with the help of phylogenetic generalized linear models (pGLMs; method ‘Poisson GEE’), which account for phylogenetic relatedness among the study species (Paradis and Claude, 2002), implemented in the package *phylolm* (Ho et al., 2018). The pairwise comparisons were done by releveling the baseline group; Bonferroni correction was applied to adjust for multiple testing. All statistical analyses were conducted in R 3.4.3 (R Core Development Team, 2018).

RESULTS

Phylogenetic signal in seed germination traits

We detected a strong phylogenetic signal in seed germination response to all experimental treatments, as well as in seed germination speed under optimal environmental conditions (Table 3). Little phylogenetic signal was found in the seed germination niche width, as evidenced by low Blomberg’s *K* ($K = 0.18$, $P = 0.51$), indicating a lack of trait association with phylogeny.

TABLE 3. Summary of phylogenetic principal components analysis (pPCA) on species–trait matrix of 50 study wetland species and Blomberg’s *K* test for phylogenetic signal in each trait

	PC1	PC2	PC3	Blomberg’s <i>K</i>
Eigenvalue	3.5	1.7	1.3	
Proportion of variance	34.9	17.3	13.5	
Cumulative proportion	34.9	52.2	65.7	
LFA	−0.2	−0.6	−0.1	0.74*
LCA	−0.3	0	0.56	0.39*
LFH	−0.3	0.27	−0.3	0.73*
LCH	−0.2	0.6	0.02	0.40*
DFA	−0.4	−0.3	0.11	0.39*
DCA	−0.4	−0.3	−0.2	0.66*
DFH	−0.4	0.12	−0.3	0.88*
DCH	−0.4	0.09	−0.3	0.62*
T_{50}	0.08	0	−0	0.63*
<i>J</i>	−0.3	0.09	0.61	0.18

For each axis, the eigenvalues and proportion of variance explained are provided, as well as loadings for the first three principal components. Asterisks indicate a strong phylogenetic signal in the trait. For abbreviations refer to Table 1.

Phylogenetic PCA

The ten seed traits studied could be summarized by two principal components (PCs) with eigenvalues of 1.5, which together accounted for 52.2 % of the total variance. The third PC was not well supported and only accounted for an additional 13.5 % of total variation (Table 3). PC1 explained 34.9 % of the variance and loaded most heavily (Pearson’s $r > 0.37$) and negatively on seed germination response to all dark treatments (DCA, DFA, DCH and DFH). Thus, PC1 separated the deep-water species characterized by a comparatively wide germination niche from species of the other four zones that required more specific conditions for seed germination (Fig. 2). The second PC accounted for an additional 17.3 % of the variance and loaded most heavily on seed germination response to the LFA ($r = -0.6$) and LCH ($r = 0.6$) treatments. Therefore, PC2 separated reed and mudflat species requiring light, fluctuating temperatures and high oxygen supply, from the shallow-water communities which had seed germination optima under full illumination, constant temperatures and hypoxic conditions. Swamp species were ordinated on the PC2 between these two different groups of wetland communities (Fig. 2).

Community-specific seed germination traits

Seed germination requirements for temperature fluctuations, light and oxygen, as well as germination speed and seed germination niche width varied among the communities studied (Table 1; Figs 3 and 4). Trait values, as well as characteristic species of the clusters obtained by *k*-means clustering, are shown in Table 4. The results of pGLMs are presented in the Supplementary data Appendix S2.

Reeds

Seven species (e.g. *Alopecurus aequalis* and *Phalaris arundinacea*) were grouped into cluster ‘reed’ and demonstrated the ability to germinate best under LFA, LCA, DFA and DCA treatments, indicating that while oxygen was crucial, neither light nor temperature fluctuations were an important prerequisite for seed germination in this community (Fig. 3). This relatively broad germination niche was also reflected by a comparatively high Pielou’s *J* index (0.72; Fig. 4B). On average, seeds of a species from this cluster only took 5 d to reach 50 % germination under the most optimal conditions, in this case with sufficient oxygen (Fig. 4A).

Mudflats

The majority of the mudflat species ($n = 21$), such as *Dichostylis micheliana* and *Limosella aquatica*, demonstrated clear germination preferences that were reflected in comparatively low *J* values (0.38; Table 4; Fig. 4B). Their seeds required light, full oxygen supply and fluctuating temperature to achieve high germination (>50 %; Table 4; Fig. 3) and had comparatively low seed germination speed ($T_{50} = 9.4$ d). Moreover, the low seed germination response to the remaining experimental factors (just a few species were able to germinate under the LCA treatment) confirms the very specific nature of the seed germination niche in this community.

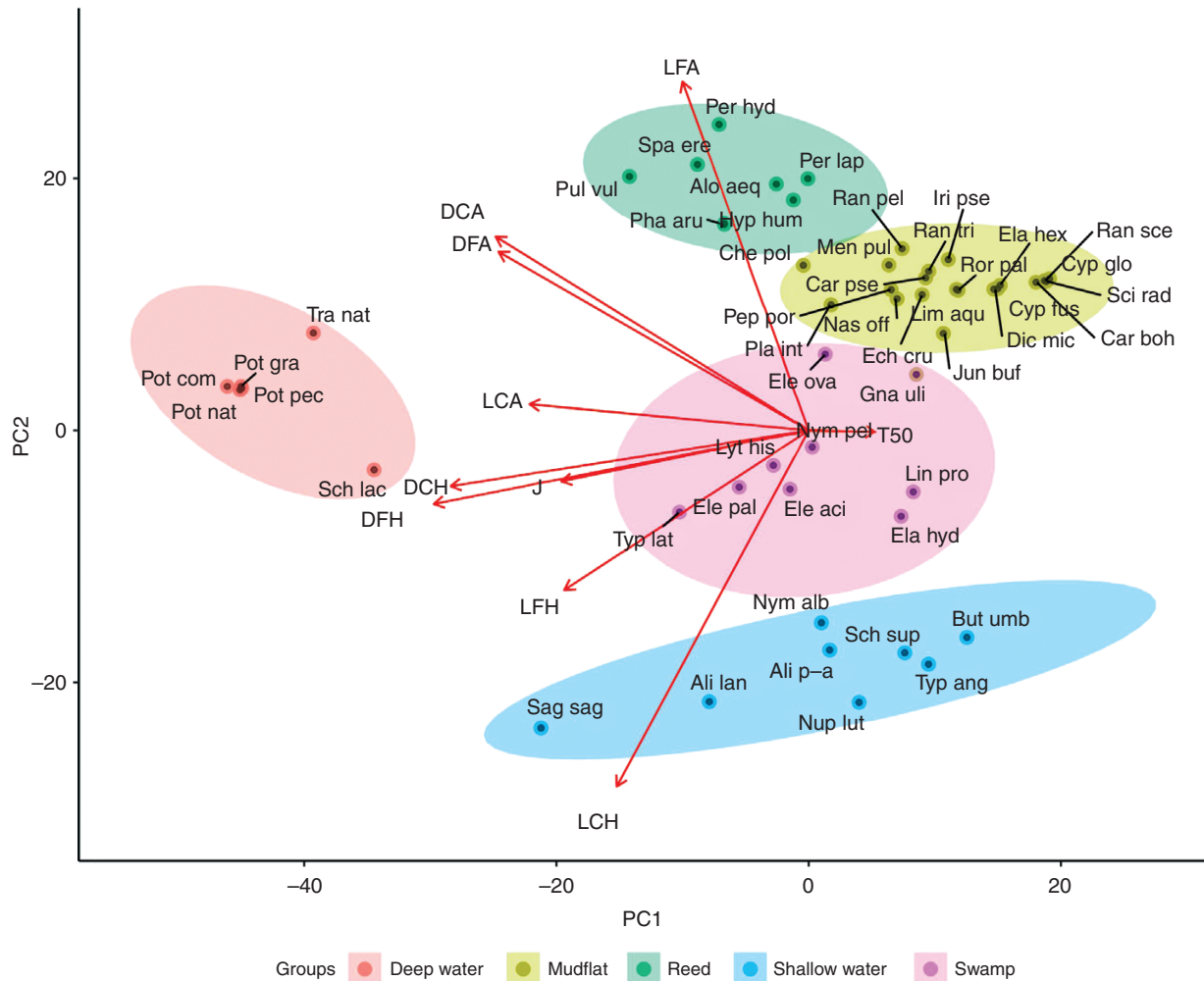


FIG. 2. Two-dimensional illustration of the phylogenetic PCA ordination on the species–seed trait matrix of the studied wetland species. See Tables 1 and 2 for species abbreviations, and associated eigenvalues and eigenvectors, respectively. Arrows indicate the direction of loading of each trait. LFA, LCA, LFH, LCH, DFA, DCA, DFH and DCH are seed germination response to different environmental conditions (see the Materials and Methods for details). ‘ J ’ and ‘ T_{50} ’ are seed germination niche width and seed germination speed, respectively.

Swamp

The seed germination pattern of the eight species belonging to the ‘swamp’ cluster (e.g. *Alisma plantago-aquatica* and *Typha latifolia*) included characteristics of terrestrial reed and mudflat communities and permanently or long-term flooded shallow-water communities. Seeds of swamp species germinated well under both aerobic and hypoxic conditions under full illumination regardless of the temperature fluctuations (Fig. 3), resulting in a broad seed germination niche width (Pielou’s $J = 0.68$; Fig. 4B). Additionally, species belonging to this cluster demonstrated high seed germination speed; on average, 50 % of a swamp species germinated within 4.9 d (Fig. 4A).

Shallow-water communities

In contrast to the reed and mudflat communities, seeds of eight species from the ‘shallow-water’ cluster were able to germinate to high percentages only under hypoxia conditions and full illumination regardless of temperature fluctuations (Table 4;

Fig. 3); the comparatively low J value (0.63; Fig. 4B) confirmed this specific germination behaviour. Several species of this cluster (e.g. *Nuphar lutea* and *Sagittaria sagittifolia*) also had substantial seed germination proportions in the DFH and DCH experimental treatments. Seeds of ‘shallow-water’ species had the lowest seed germination speed (on average 15.1 d to reach 50 % seed germination; Fig. 4A) among the wetland communities studied.

Deep-water communities

We observed high similarity in seed germination responses to all experimental treatments among the species occurring in deep-water communities (Table 4; Fig. 3). Specifically, they germinated to high percentages (>90 %) and equally well under all treatments suggesting that these species possess a very wide germination niche, which was also confirmed by very high J values (0.99; Fig. 4B). The seeds of the deep-water species, such as *Potamogeton pectinatus* and *Trapa natans*, demonstrated a fast germination response to the most optimal

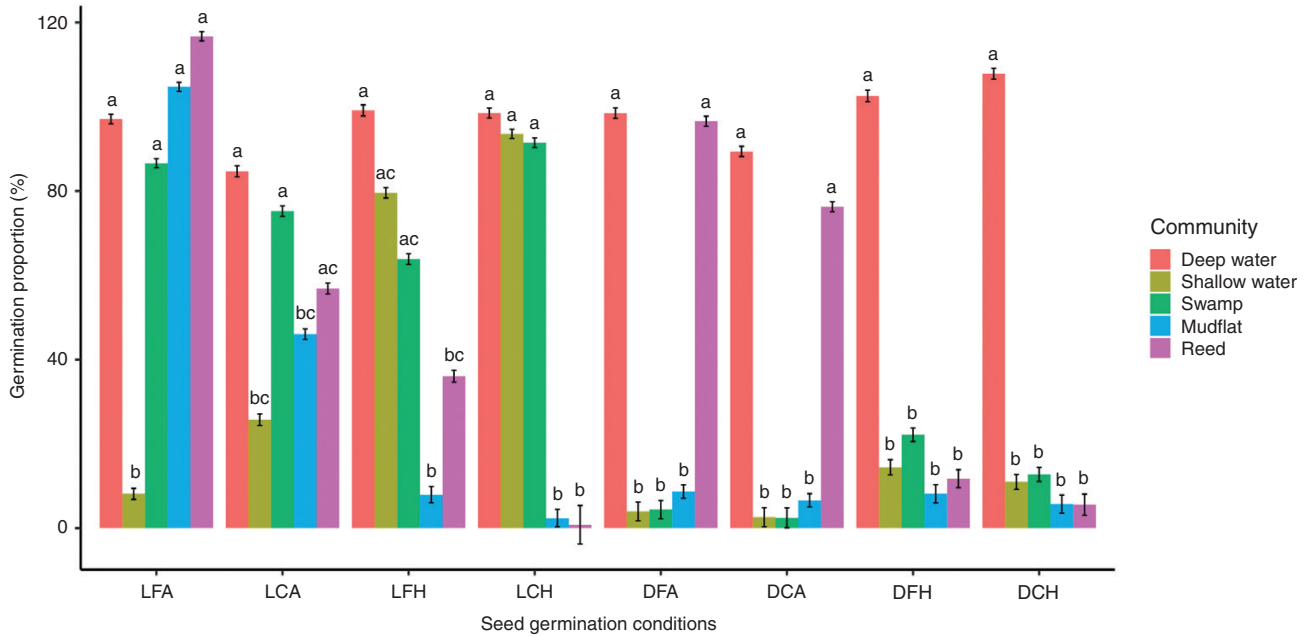


FIG. 3. Seed germination traits in the five wetland communities studied. LFA, LCA, LFH, LCH, DFA, DCA, DFH and DCH are seed germination response to different environmental conditions (see the Materials and Methods for details). Different letters indicate statistically significant ($P < 0.05$) differences among the communities as estimated by phylogenetic generalized linear models. Bars represent the mean values for each community; error bars are standard errors.

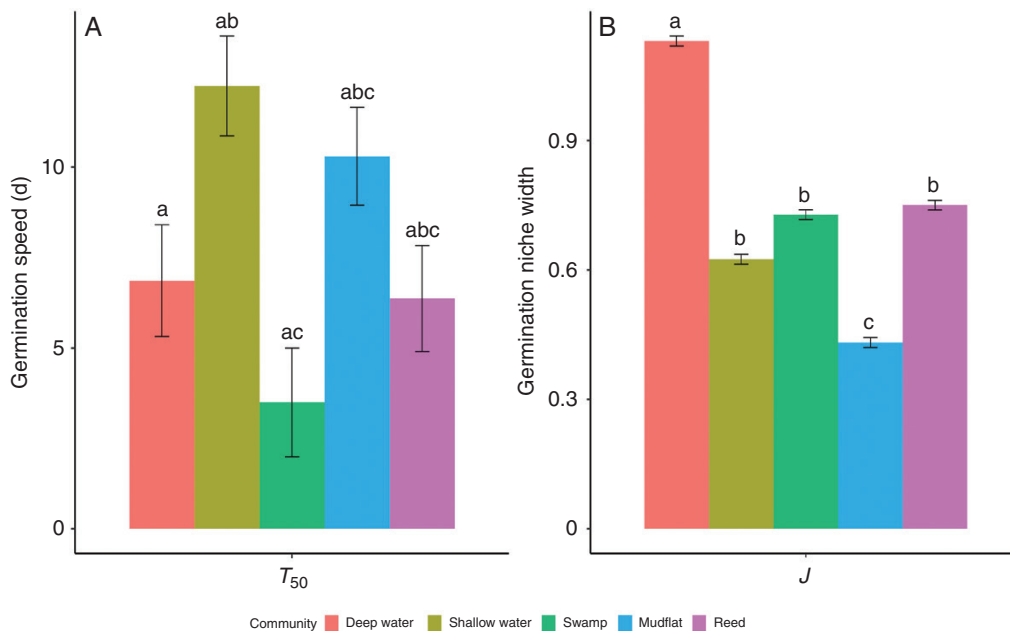


FIG. 4. Seed germination speed (A) and seed germination niche width under optimal conditions (B) in the five wetland communities studied. Different letters indicate statistically significant ($P < 0.05$) differences among the communities as estimated by phylogenetic generalized linear models. Bars represent the mean values for each community; error bars are standard errors.

germination conditions; on average, it took seeds only 3.7 d to reach 50% germination under optimal conditions (Fig. 4A).

DISCUSSION

The spatial and temporal variation in duration, depth and frequency of flooding along the hydroperiod gradient turns wetlands

into an extremely heterogeneous environment (Santamaria, 2002; Moor *et al.*, 2017). Thus, specific combinations of environmental factors at different parts of the hydroperiod gradient act as ‘sieves’, filtering out maladapted species and favouring species possessing traits best adapted to these conditions, resulting in the clear pattern of wetland community structure and composition (Sculthorpe, 1967; Spence, 1982; Keddy, 1992).

TABLE 4. Seed germination characteristics of the five study wetland communities obtained by k-means clustering

Seed germination trait	Wetland communities				
	Reed	Mudflat	Swamp	Shallow water	Deep water
	<i>n</i> = 7	<i>n</i> = 21	<i>n</i> = 8	<i>n</i> = 8	<i>n</i> = 6
LFA, %	100.0	97.7	84.3	8.5	98.0
LCA, %	72.0	49.8	82.9	19.2	98.1
LFH, %	22.0	7.4	68.8	87.6	96.5
LCH, %	1.0	2.0	79.7	86.8	95.4
DFA, %	87.4	9.4	2.9	1.6	93.5
DCA, %	64.9	4.6	1.5	2.0	91.2
DFH, %	6.5	1.4	10.9	39.9	93.0
DCH, %	1.2	0.2	3.8	23.2	95.2
Seed germination niche width (Pielou's <i>J</i>)	0.72	0.38	0.68	0.63	0.99
Seed germination speed (T_{50}), d	5.0	9.4	4.9	15.1	3.7
Typical species	<i>Alopecurus aequalis</i> <i>Phalaris arundinacea</i> <i>Sparganium erectum</i>	<i>Dichostylis micheliana</i> <i>Limosella aquatica</i> <i>Plantago intermedia</i>	<i>Alisma plantago-aquatica</i> <i>Eleocharis palustris</i> <i>Typha latifolia</i>	<i>Nuphar lutea</i> <i>Nymphaea alba</i> <i>Sagittaria sagittifolia</i>	<i>Potamogeton pectinatus</i> <i>Schoenoplectus lacustris</i> <i>Trapa natans</i>

For abbreviations refer to Table 1.

As for seedling survival and growth, ecological theory suggests (Götzenberger *et al.*, 2012; de Bello *et al.*, 2013) that each of these communities should be characterized by the set of specific environmental factors that indicate the onset of optimal conditions for seed germination, permitting the establishment of only community-specific species (van der Valk, 1981). Our results confirm this theory to a large extent by demonstrating the presence of distinct, community-specific seed germination niches in wetlands. In accordance with our hypothesis, the existing diversity of germination response types in wetlands reflected adaptations to decreasing light intensity, temperature fluctuations and oxygen availability along the hydroperiod gradient (Fig. 1; Table 2).

Reeds and mudflats

Reeds, plant communities located at the upper end of the hydroperiod gradient, are characterized by prolonged flooding with a comparatively low water table during winter and exposed soil surfaces during growth periods when the water recedes. The strict requirements for oxygen detected for the reed species reflect the adaptation of seed germination to these environmental conditions. In contrast to hydro- and helophytes occupying open waters and swamps (see below), the species of this group lack adaptations to permanent flooding and submergence. Consequently, if seeds of a reed species germinate under hypoxic, submerged conditions (a water layer of a few centimetres over the soil considerably reduces oxygen concentration in water; Wetzel, 1983; Smits *et al.*, 1990), the seedlings might not be able to grow to the surface and thus would die. Therefore, the requirement for oxygen will either prevent seedling emergence under flooded conditions or will allow seeds to germinate in/on the bare, well-aerated soil. The rise of soil oxygen concentrations after a drawdown indicates, for the reed species, the onset of favourable conditions for seedling establishment that triggers very fast germination; on average, they reached 50 %

germination within 5 d under optimal conditions. The fast germination speed in the reed community may be an adaptation to take early advantage of aerobic conditions prevailing soon after water drawdowns. In the case of a slow seed germination rate, an inundation may hamper seed germination and seedling establishment.

Apart from the sensitivity to oxygen, seeds of reed species were able to germinate equally well in both darkness and full illumination regardless of temperature fluctuations, indicating a comparatively broad germination niche (Pielou's $J = 0.72$). This germination behaviour appears to be an adaptation to establishment within reed stands (van der Valk, 1981), often made up of communities of tall species with a thick litter cover. In such communities, dense vegetation reduces temperature fluctuations and light availability at the soil surface (Thompson *et al.*, 1977; Grime *et al.*, 1981), thereby diminishing their role as reliable cues for the onset of favourable conditions for germination. Furthermore, the lack of sensitivity of seeds to temperature fluctuations and light explains the fact that many reed species lack persistent seed banks (van den Broek *et al.*, 2005); a seed bank can only be built if seeds are inhibited by darkness in the soil (Grime, 1989; Pons, 1991).

Compared with other wetland communities, the position of the mudflat community in the pPCA ordination was found to be very close to the reeds, indicating similarities in seed germination strategy, namely similar strict requirements of oxygen for germination. Like the reeds, the mudflat communities are mainly comprised of terrestrial species, whose seedling growth and development might be negatively affected by long-term flooding (Baskin *et al.*, 1993). Thus, to avoid high seedling mortality and optimize establishment, seed germination of mudflat species is triggered by high oxygen concentrations that are typical for exposed soil or sediment surfaces after the retreat of flood water (Coops and Velde, 1995). As for other environmental factors tested, seeds of mudflat species were not able to germinate in darkness and germinate better in fluctuating than in constant temperatures that limit the seed germination niche

to a comparatively narrow range (Pielou's $J = 0.38$). This specific seed germination behaviour, to germinate at full illumination and fluctuating temperature, might have evolved as a gap detection mechanism (Thompson *et al.*, 1977), an adaptation to enhance mudflat seedling establishment in open patches and vegetation gaps. Since the majority of mudflat species are short in stature and shade intolerant, they cannot become established from seeds within stands of existing vegetation or under water, because the shading from the plant canopy or water column reduces temperature fluctuations and prevents the seeds from being exposed to direct sunlight (van der Valk, 1981). Thus, seed germination of mudflat species is inhibited when they are covered with soil or vegetation and is triggered in open gaps and litter-free patches (van der Valk, 1981; Baskin *et al.*, 1993, 2004).

Mudflats are unpredictable, unstable, ephemeral habitats that can appear at every part of the hydroperiod gradient, provided they are drained, open and free of litter. To bridge the long periods of temporarily unsuitable environmental conditions in this community, mudflat species are able to persist in seed banks for very long periods, at least 50 years in many cases (Poschlod and Rosbakh, 2018). The germination inhibition detected by darkness and constant temperatures explains this common characteristic of mudflat species (S. Rosbakh, pers. obs.); once flooded or covered with sediments and or litter, seed germination is inhibited until conditions become favourable for germination and seedling establishment. In its turn, the relatively fast seed germination speed ($T_{50} = 9.4$ d) explains how mudflat species tune their seedling establishment to the temporal nature of this community; germination is initiated once the open soil surface is exposed to full illumination and alternating temperature after the water recedes (Shipley and Parent, 1991).

Shallow- and deep-water communities

Like reeds and mudflats, the environment in open waters shapes the corresponding communities by selecting those species that are best adapted for each part of the hydroperiod gradient from the local species pool, in this case submerged conditions. Yet, the shallow- and deep-water species differed considerably in their germination strategies, putatively due to the water table depths at the parts of the hydroperiod gradient they occupy. As for the former, germination was mainly triggered under hypoxia and full illumination, two environmental cues indicating optimal ecological conditions for growth and development under long-term or permanent shallow flooding (Smits *et al.*, 1990; Ellenberg and Leuschner, 2010). In terms of adaptations, the inhibition of germination by oxygen ensures that the emergence of shallow-water species does not take place in drained soil (Pons and Schröder, 1986; Coops and Velde, 1995), because post-germination of such species largely depends on the aquatic environment and usually does not tolerate desiccation, even for short periods of time (Sculthorpe, 1967; Hay *et al.*, 2000). Contrastingly, the low oxygen concentrations in water-saturated soils (Wetzel, 1983; Smits *et al.*, 1990) indicate the onset of favourable conditions for seedling establishment. Thus, along with the light requirement for seed germination and insensitivity to temperature fluctuations, which act as a depth-sensing mechanism [deep flooding considerably

reduces light intensity (van der Valk, 1981) and temperature fluctuations (Thompson *et al.*, 1977)], seedling emergence of shallow water species is restricted to waterlogged or shallowly flooded soils. The comparatively slow germination speed under such conditions (on average, it took a shallow water species 15.1 d to reach 50 % germination) suggest that germination is triggered once the soil remains waterlogged or flooded for several days.

According to our hypothesis, we expected seeds of deep-water species to be adapted to germinate best under dark, hypoxic conditions with no temperature fluctuations (Table 1), since the seeds of deep-water species are known for their very poor floating ability (Smits *et al.*, 1990; Boedeltje *et al.*, 2003; van den Broek *et al.*, 2005; Soons *et al.*, 2017). However, they demonstrated an extremely broad seed germination niche (Pielou's $J = 0.99$), germinating well irrespective of light or darkness, aerobic or hypoxic conditions (Figs 3 and 4). This opportunistic behaviour indicates that the seedlings of these species can establish under almost all possible environmental (constant and fluctuating temperature, light and darkness, aerobic and hypoxic) conditions in wetlands. There are several possible explanations for this phenomenon. First, the majority of these species have a physical or physiological dormancy (Baskin and Baskin, 2014) and require some kind of dormancy-breaking treatments. It is often noticed that soon after dormancy is broken via responses to specific environmental cues, non-dormant seeds in the majority of terrestrial and wetland species germinate under a wide range of environmental conditions, allowing species to exploit low resource competition and take advantage of early establishment (Baskin and Baskin, 2014) as seen in the seeds of *Trapa natans* (Phartyal *et al.*, 2018). This broad germination niche indicates that the establishment of the deep-water community is governed, primarily, through their dormancy-breaking environmental cues rather than through seed germination cues. Secondly, the broad germination niche is probably a bet-hedging strategy that minimizes the risk of seed germination at a specific narrow environmental cue and improves the chances for survival and further establishment of the species at a local scale (Venable, 2007; Donohue *et al.*, 2010). Thirdly, species with wide germination niches are more likely to have wide ecological niches and geographical distribution, although it is still difficult to draw generalizations, suggesting that a broader germination niche provides a greater opportunity for post-germination adaptation to a wide range of environmental conditions than a narrow germination niche (Donohue *et al.*, 2010). It seems true to a large extent for our deep-water plant communities since some of them have a pan-continental distribution under wide hydrological gradients from tropical to temperate regions.

Swamp communities

Due to their intermediate position at the hydroperiod gradient, swamp communities are regularly subjected to short- and long-term fluctuating water levels, resulting in alternation between terrestrial and aquatic growing conditions. Therefore, only species whose seedlings are able to establish on both exposed and shallowly flooded soils can occur in such communities. The results of our study confirm that seeds of swamp

species germinate equally well under the combination of experimental conditions typical for mudflat and reed species (LFA and LCA treatments), as well as shallow-water species (LFH and LCH treatments resulting in a broad seed germination niche; Pielou's $J = 0.68$). The lack of germination under dark conditions suggests that seedling establishment is prevented when water tables are too high.

CONCLUSIONS

The results of our study clearly demonstrate that seed germination traits can play an important structuring role in community assembly at the local scale, in our case in wetlands. This finding has two important implications for research in community assembly in general, and wetland vegetation dynamics and restoration ecology in particular. As to the former, it confirms earlier suggestions that a species' position along environmental gradients is determined by the characteristics of its regeneration niche (Grubb, 1977; Smits *et al.*, 1990; Rosbakh and Poschlod, 2015; Valdez *et al.*, 2019) and that the formation of vegetation zonation along such gradients, particularly in wetlands, starts the very early stages of plant establishment (Spence, 1982; Coops and Velde, 1995; Moor *et al.*, 2017). Therefore, it endorses the recent argument by Larson and Funk (2016), Jiménez-Alfaro *et al.* (2016) and Saatkamp *et al.* (2019) that such traits should be included in studies on plant community composition in trait-filter assembly frameworks (Keddy, 1992), because they encompass functions that cannot be explained solely by adult plants (Jiménez-Alfaro *et al.*, 2016).

Wetlands are a well-known ecosystem for the short- and long-term changes in vegetation structure and composition caused by various environmental factors, including disturbance, the physical or chemical conditions of the habitat, interactions among plants or the invasion and establishment of new species (van der Valk, 1981; Keddy, 2010). Since the establishment of a newcomer or re-establishment of already existing species (e.g. from the soil seed bank) from seeds in available gaps is controlled by the specific, and sometimes very narrow, seed germination niche, realistic predictions about changes in the composition of wetland vegetation can be made (van der Valk, 1981; Valdez *et al.*, 2019).

As regards restoration ecology, the results obtained for seed germination requirements in wetland communities may help to improve restoration outcomes (Jiménez-Alfaro *et al.*, 2016). Our main recommendation for practitioners is that seeds of wetland species should be germinated under known community-optimal conditions, to increase establishment success in restoration areas or optimize production of greenhouse-grown plants for transplantation into these areas. For example, we recommend bringing back natural drawdowns of river banks and lake/pond shorelines to create suitable sites for seedling establishment from seed banks of mudflat species, one of the most threatened wetland plant communities in Central Europe (Poschlod and Rosbakh, 2018).

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following.

Appendix S1: seed collection sites.

Appendix S2: results of pGLMs

FUNDING

This work was partially financed by the Alexander von Humboldt Foundation, Germany (S.S.P.), as well as the German Academic Exchange Service and Russian Ministry of Science and Education (S.R.).

ACKNOWLEDGEMENTS

We wish to thank all the students who participated in this project helping with the seed germination experiment. We also thank Fernando Silveira for constructive comments on earlier versions of this manuscript.

LITERATURE CITED

- Barrett SCH, Eckert CG, Husband BC. 1993. Evolutionary processes in aquatic plant populations. *Aquatic Botany* **44**: 105–145.
- Baskin CC, Baskin JM. 2014. *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Amsterdam: Elsevier Science.
- Baskin CC, Baskin JM, Chester EW. 1993. Seed germination ecophysiology of four summer annual mudflat species of Cyperaceae. *Aquatic Botany* **45**: 41–52.
- Baskin CC, Baskin JM, Chester EW. 2004. Seed germination ecology of the summer annual *Cyperus squarrosus* in an unpredictable mudflat habitat. *Acta Oecologica* **26**: 9–14.
- Beck MW. 2017. *Ggord: ordination plots with ggplot2. Version 1.0.0*.
- de Bello F, Lavorel S, Lavergne S, *et al.* 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* **36**: 393–402.
- Blomberg SP, Garland T Jr, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–45.
- Boedeltje G, Bakker JP, Bekker RM, Van Groenendael JM, Soesbergen M. 2003. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology* **91**: 855–866.
- van den Broek T, van Diggelen R, Bobbink R, Collins B. 2005. Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. *Journal of Vegetation Science* **16**: 579–586.
- Charalambidou I, Santamaría L. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecologica* **23**: 165–176.
- Chepinoga V. 2015. *Flora and vegetation of waterbodies in Baikal Siberia*. Irkutsk: V.B. Sochava Institute of Geography SB RAS, 468.
- Coops H, Velde G. 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshwater Biology* **34**: 13–20.
- Donohue K, de Casas RR, Burghardt L, Kovach K, Willis CG. 2010. Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* **41**: 293–319.
- Durka W, Michalski SG. 2012. Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology* **93**: 2297–2297.
- Ellenberg H, Leuschner C. 2010. *Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht*. Stuttgart: Ulmer.
- Fenner M, Thompson K. 2005. *The ecology of seeds*. Cambridge: Cambridge University Press.
- Fernandez-Pascual E, Perez-Arcoiza A, Prieto JA, Diaz TE. 2017. Environmental filtering drives the shape and breadth of the seed germination niche in coastal plant communities. *Annals of Botany* **119**: 1169–1177.
- Galinato IM, van der Valk AG. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. *Aquatic Botany* **26**: 89–102.
- Götzenberger L, de Bello F, Bräthen KA, *et al.* 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews* **87**: 111–127.

- Grace JB. 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* **44**: 159–180.
- Grime J. 1989. Forward. Seed banks in ecological perspective. In: Leck MA, Parker VT, Simpson RL, eds. *Ecology of soil seed banks*. Amsterdam: Elsevier, xv–xxii.
- Grime JP, Mason G, Curtis AV, et al. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**: 1017–1059.
- Grubb PJ. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**: 107–145.
- Hay F, Probert R, Marro J, Dawson M. 2000. *Towards the ex situ conservation of aquatic angiosperms: a review of seed storage behaviour*. Wallingford, UK: CAB International.
- Hejný S. 1960. *Ökologische Charakteristik der Wasser-und Sumpfpflanzen in den slowakischen Tiefebene (Donau-und Theissgebiet)*. Verlag der Slowakischen Akademie der Wissenschaften.
- Ho LST, Ane C, Lachlan R, et al. 2018. Package 'phyloilm'.
- Hutchinson GE. 1975. *A treatise of limnology*. New York: John Wiley & Sons.
- Jensen SM, Andreassen C, Streibig JC, Keshtkar E, Ritz C. 2017. A note on the analysis of germination data from complex experimental designs. *Seed Science Research* **27**: 321–327.
- Jiménez-Alfaro B, Silveira FAO, Fidelis A, Poschlod P, Commander LE. 2016. Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science* **27**: 637–645.
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**: 157–164.
- Keddy PA. 2010. *Wetland ecology: principles and conservation*. Cambridge: Cambridge University Press.
- Kos M, Poschlod P. 2007. Seeds use temperature cues to ensure germination under nurse-plant shade in Xeric Kalahari Savannah. *Annals of Botany* **99**: 667–675.
- Kos M, Poschlod P. 2010. Why wait? Trait and habitat correlates of variation in germination speed among Kalahari annuals. *Oecologia* **162**: 549–559.
- Landucci F, Reznickova M, Sumberova K, et al. 2015. WetVegEurope: a database of aquatic and wetland vegetation of Europe. *Phytocoenologia* **45**: 187–194.
- Larson JE, Funk JL. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology* **104**: 1284–1298.
- Laughlin DC. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102**: 186–193.
- Mitsch WJ, Gosselink JG. 2015. *Wetlands*. Chichester, UK: Wiley.
- Moor H, Rydin H, Hylander K, Nilsson MB, Lindberg R, Norberg J. 2017. Towards a trait-based ecology of wetland vegetation. *Journal of Ecology* **105**: 1623–1635.
- Paradis E, Claude J. 2002. Analysis of comparative data using generalized estimating equations. *Journal of Theoretical Biology* **218**: 175–185.
- Phartyal SS, Rosbakh S, Poschlod P. 2018. Seed germination ecology in *Trapa natans* L., a widely distributed freshwater macrophyte. *Aquatic Botany* **147**: 18–23.
- Pons TL. 1989. Breaking of seed dormancy by nitrate as a gap detection mechanism. *Annals of Botany* **63**: 139–143.
- Pons TL. 1991. Induction of dark dormancy in seeds – its importance for the seed bank in the soil. *Functional Ecology* **5**: 669–675.
- Pons TL, Schröder HFJM. 1986. Significance of temperature fluctuation and oxygen concentration for germination of the rice field weeds *Fimbristylis littoralis* and *Scirpus juncoides*. *Oecologia* **68**: 315–319.
- Poschlod P, Abedi M, Bartelheimer M, Drobnik J, Rosbakh S, Saatkamp A. 2013. Seed ecology and assembly rules in plant communities. In: van der Maarel E, Franklin J, eds. *Vegetation ecology*, 2nd edn. Chichester, UK: John Wiley & Sons, Ltd.
- Poschlod P, Rosbakh S. 2018. Mudflat species: threatened or hidden? An extensive seed bank survey of 108 fish ponds in Southern Germany. *Biological Conservation* **225**: 154–163.
- R Core Development Team. 2018. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Revell LJ. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–68.
- Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Ritz C, Pipper CB, Streibig JC. 2013. Analysis of germination data from agricultural experiments. *European Journal of Agronomy* **45**: 1–6.
- Ritz C, Baty F, Streibig JC, Gerhard D. 2015. Dose–response analysis using R. *PLoS One* **10**: e0146021. doi: 10.1371/journal.pone.0146021.
- Rosbakh S, Poschlod P. 2015. Initial temperature of seed germination as related to species occurrence along a temperature gradient. *Functional Ecology* **29**: 5–14.
- Saatkamp A, Cochrane A, Commander L, et al. 2019. A research agenda for seed-trait functional ecology. *New Phytologist* **221**: 1764–1775.
- Santamaria L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica* **23**: 137–154.
- Sculthorpe CD. 1967. *The biology of aquatic vascular plants*. London: Edward Arnold Ltd.
- Shipley B, Parent M. 1991. Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. *Functional Ecology* **5**: 111–118.
- Shipley B, Keddy PA, Moore DRJ, Lemky K. 1989. Regeneration and establishment strategies of emergent macrophytes. *Journal of Ecology* **77**: 1093–1110.
- Silvertown J. 1980. Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist* **85**: 109–118.
- Smits AJM, Vanavesaath PH, Vandervelde G. 1990. Germination requirements and seed banks of some nymphaeid macrophytes – *Nymphaea alba* L., *Nuphar lutea* (L.) Sm and *Nymphoides peltata* (Gmel) O Kuntze. *Freshwater Biology* **24**: 315–326.
- Soons MB, de Groot GA, Ramirez MTC, Fraaije RGA, Verhoeven JTA, de Jager M. 2017. Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. *Functional Ecology* **31**: 499–508.
- Spence DHN. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* **12**: 37–125.
- Thompson K, Grime JP, Mason G. 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* **267**: 147–149.
- Thompson K, Gaston KJ, Band SR. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *Journal of Ecology* **87**: 150–155.
- Thompson PA. 1974. Effects of fluctuating temperatures on germination. *Journal of Experimental Botany* **25**: 164–175.
- Tudela-Isanta M, Ladouceur E, Wijayasinghe M, Pritchard HW, Mondoni A. 2018. The seed germination niche limits the distribution of some plant species in calcareous or siliceous alpine bedrocks. *Alpine Botany* **128**: 83–95.
- Valdez J, Hartig F, Fennel S, Poschlod P. 2019. The recruitment niche predicts plant community assembly across a hydrological gradient along ploughed and undisturbed transects in a former agricultural wetland. *Frontiers in Plant Science* **10**: Article 88.
- van der Valk AG. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* **62**: 688–696.
- van der Valk AG, Davis CB. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**: 322–335.
- Vazquez-Yanes C, Orozco-Segovia A. 1987. Light gap detection by the photoblastic seeds of *Cecropia obtusifolia* and *Piper auritum*, two tropical rain forest trees. *Biologia Plantarum* **29**: 234–236.
- Venable DL. 2007. Bet hedging in a guild of desert annuals. *Ecology* **88**: 1086–1090.
- Wetzel RG. 1983. *Limnology*. Philadelphia: Saunders.