Aquatic Botany 130 (2016) 21–26

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Comparative seed germination traits in bog and fen mire wetlands☆

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ARTICLE INFO

Article history:
Received 23 November 2015
Received in revised form 5 January 2016
Accepted 5 January 2016
Available online 11 January 2016

Keywords:
Arnica
Carex
Dormancy
Drosera
Eleocharis
Eriophorum
European mire indicator
Narthecium
Poor fen
Regeneration strategy
Rhynchospora
Trichophorum

ABSTRACT

Mires are continental wetlands of high scientific and conservation interest. Knowing the seed germination traits of mire species is essential for understanding their regeneration ecology and conducting active restoration policies. Here, a comparative study of seed germination traits was performed with 34 plant species from bog and fen communities, including many European indicators of these habitats. Freshly collected seeds were exposed to a laboratory germination experiment designed to characterize their response to (1) cold stratification and (2) simulated field temperatures. Germination strategy groups were interpreted according to these responses, and the relation between these groups and different mire types was discussed. Seeds of all tested species had physiological dormancy. Most of them showed conditional type 2 non-deep physiological dormancy: fresh seeds could germinate only at warm temperature, but attained the ability to germinate at colder temperature as they lost dormancy. Most mire species from bogs, poor fens and base-rich fens followed a warm germination strategy analogous to that of other wetland species. Species from this warm group responded to very warm temperatures which rarely occur in the field, and this was interpreted as a gap-detecting mechanism. In contrast, species from calcareous springs and flushes had a cold germination strategy, which would fit with the cold and stable soils where they occur. Finally, a group of species associated with the pioneer *Rhynchosporion* vegetation of bare peat areas had very low germination, suggesting an intermediate or deep seed dormancy and a long term seed bank.

1. Introduction

A mire is a permanent semi-terrestrial wetland where soils remain waterlogged but not inundated during most of the year (Wheeler and Proctor, 2000). Mire classification is a rich field of study, with different criteria being emphasized in different academic and geographic contexts. Broadly, these communities are divided into rain-fed bogs and groundwater-fed fens; with fens further divided by their water and soil properties, derived from topology and the bedrock (Hájek et al., 2006). These mire types are also established according to indicator plant species that are strongly associated to each type (Wheeler and Proctor, 2000; Hájek et al., 2006). Generally, mires are regarded as habitats of high scientific and conservation interest. During the Quaternary, they provided refuge to wetland plants affected by climate change and human colonization (Jamrichová et al., 2014). At present, they hold a valuable biological diversity and are considered priority habitats for conservation in several parts of the world (e.g., Council Directive 92/43/EEC). Moreover, they are increasingly attracting attention as potential refugia against climate change (Raney et al., 2014; Fernández-Pascual et al., 2015a). At the same time, mires provide valuable ecosystem services, like regulating the water cycle and acting as carbon sinks (Bragg and Lindsay, 2003). Nevertheless, their conservation status is uncertain, with most European countries having lost more than half of their original mire surface (Bragg and Lindsay, 2003).

Active restoration policies require understanding the seed germination traits of mire species in order to benefit from seed collections conserved *ex situ*. The patchy distribution of mires favors short-distance dispersal and persistence through vegetative reproduction (Sosnova et al., 2010). Nonetheless, reproduction by seed is still essential for the colonization of new sites, the reoccupation of disturbed gaps and the long-term maintenance of mire species at the landscape level (Herben et al., 2014). As an example, massive germination of *Rhynchospora fusca* quickly occupies all safe niches following a disturbance, and subsequent propagation is mainly vegetative (Kesel and Urban, 1999). Similarly, seedling emergence patterns respond to microhabitat heterogeneity in

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☆ Nomenclature follows the Euro+Med PlantBase (http://www.emplantbase.org/home.html, accessed 21 Oct 2015)

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http://dx.doi.org/10.1016/j.aquabot.2016.01.001
0304-3770/

Drosera intermedia (De Ridder and Dhondt, 1992) and *Eriophorum vaginatum* (Gartner et al., 1986). Although successful seedling establishment tends to be low (Gartner et al., 1986; De Ridder and Dhondt, 1992), mire seeds can remain viable at depths (c. 50 cm) that suggest very long-term seed banks (Jauhiainen, 1998). Thus, successful regeneration events by seed likely occur in long time scales. The importance of seed reproduction in detecting these 'opportunity gaps' is highlighted by several strategies that accelerate germination in special situations, such as pseudo-vivipary (Leck and Schütz, 2005), the response to extraordinary heat (Fernández-Pascual et al., 2013), and the effect of the diurnal thermal amplitude (Fernández-Pascual et al., 2015b).

Comparative community-wide assessments of mire germination traits are relatively scarce. Work has focused mainly on alkaline environments, such as mountain base-rich fens (Fernández-Pascual et al., 2013) and lowland fen grasslands (Maas, 1989; Patzelt et al., 2001; Jensen, 2004). Species from these habitats usually have conditional non-deep physiological dormancy (Baskin and Baskin, 2014) and follow a 'warm germination strategy' (Thompson and Grime, 1983). At the time of dispersal in autumn, they can germinate at very warm temperatures that rarely occur in fen soils (Fernández-Pascual et al., 2015a). Subsequently, their temperature range for germination widens toward colder temperatures as they loss dormancy, either in the short term through increased diurnal thermal amplitudes (Fernández-Pascual et al., 2015b) or in the long term through overwintering (Fernández-Pascual et al., 2013). Such germination strategy is common in the fen-dominant *Carex* genus (Schütz, 2000) and in Cyperaceae in general (Leck and Schütz, 2005). This 'warm strategy' has been proposed to detect changes in the water table (Thompson and Grime, 1983; Baskin and Baskin, 2014) and gaps opened by disturbances (Gartner et al., 1986; Fernández-Pascual et al., 2013). An alternative 'cold germination strategy' has been proposed for spring fen species that live close to water flushes, where soil temperatures are kept cold and stable throughout the year (Fernández-Pascual et al., 2013; Albrecht and Long, 2014).

Compared to base-rich fens, germination in bogs and poor fens has received less attention. Community-wide assessments have analyzed emergence from the soil seed bank (Salonen, 1987; Jauhiainen, 1998) rather than germination requirements. Species-specific studies indicate however that the 'warm germination strategy' might be prevalent also in bog and poor fen species; e.g., in *Carex canescens* (Schütz and Milberg, 1997), *E. vaginatum* (Wein and MacLean, 1973; Gartner et al., 1986) and *Narthecium ossifragum* (Summerfield, 1973).

The aim of our study was to conduct a comparative analysis of the seed germination traits of European mire species. Such a comparative and community-wide assessment can be a useful contribution toward understanding the regeneration ecology of mires. To this end, we studied 21 species associated with bogs and poor fens, and analyzed them together with previous work on an additional 13 base-rich fen species (Fernández-Pascual et al., 2013). Our specific research aims were to (1) test the germination response to treatments that simulate the natural thermal conditions; (2) group mire species according to their germination response; and (3) discuss the relation of these germination groups to specific mire types.

2. Material and methods

2.1. Study system

This study took place in the temperate oceanic region of north-western Spain (43°N, 5°W). Local geography and climate are dominated by the Cantabrian Mountains (>1500 m above sea level) that run parallel to the coast and trap the prevailing NW Atlantic winds. The resulting wet climate supports the south-western limit of mire communities in Europe (Jiménez-Alfaro et al., 2014). These communities encompass a wide variety of mire types, as defined in the EUNIS habitat classification (http://eunis.eea.europa.eu/habitats.jsp). Exclusively rain-fed blanket bogs (EUNIS code D1.2) are locally rare and occur on flat mountaintops close to the sea (Fernández Prieto et al., 1985). Acid valley mires (D2.11) can be found from the lowlands to just below the treeline, in poorly drained valleys and former glacial lake beds (Fernández Prieto et al., 1985). Glacial lakes undergoing silting develop transition mires and quaking bogs communities (D2.3) in the water-to-land transition (Martínez Cortizas et al., 2009). Spring fens appear in the mountains above 1000 m, and they range from soft-water poor fens (D2.2) on acid bedrocks (Fernández Prieto et al., 1985) to base-rich and calcareous fens (D4) on limestone (Jiménez-Alfaro et al., 2012).

2.2. Seed collection

Dispersal units (hereafter 'seeds') were collected from 53 accessions of 21 bog and poor fen species during 2012–2014 (Table 1). Sampling regularly covered the entire area of occupancy of the target populations and included all individuals bearing ripe seeds. After collection, seeds spent 3 weeks in the laboratory (21 °C, 50% RH) to ensure homogeneous maturation. Then, they were cleaned and the germination experiments started.

2.3. Seed germination

Laboratory germination experiments were conducted with seeds of all species. For each experimental treatment, four Petri dishes holding 1% distilled water agar were prepared. As a standard, 25 seeds were sown in each Petri dish, but in some accessions with low seed numbers 15 or 20 seeds were sown instead (Table S1). During the experiments, dishes were sealed with parafilm to prevent desiccation. Experiments were fully factorial with two factors, pre-treatment and germination temperature. Pre-treatment had two levels: fresh seeds, incubated immediately after sowing; and cold-stratified seeds, which spent 12 weeks at 3 °C in 1% agar and in darkness to simulate overwintering. Germination temperature had three levels or daily alternating regimes: 14/4 °C (autumn or spring); 22/12 °C (summer); and 30/20 °C (unusual heat). Although the latter temperature regime rarely occurs in nature, it promotes germination in many fen species (Fernández-Pascual et al., 2013, 2015a). These germination temperatures were programed inside incubators (Grow-S 360, Ing. Climas, Barcelona, Spain) and coupled to a 12 h-light/12 h-darkness photoperiod (c. 20 μmol m^{-2} s^{-1} during the light phase, provided by six Philips TLD30W/54-765 cool fluorescent tubes).

During incubation, germination was scored weekly as radicle emergence, and seedlings were removed. After the end of the experiments, non-germinated seeds were cut open and classified as apparently viable, empty and fungi infected. Germination percentages and further statistical analyses were calculated only with potentially germinable seeds (germinated + apparently viable, Table S1).

2.4. Statistical analyses

All statistical analyses were performed in R (v3.1.2, The R Foundation for Statistical Computing, Vienna, Austria). First, germination proportion data were analyzed separately for each species using Generalized Linear Mixed Models (GLMM) with binomial error distribution and logit link function. Germination temperature (14/4 °C, 22/12 °C and 30/20 °C), pre-treatment and their interac-