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Selecting plant species and traits for phytometer experiments. The case of peatland restoration

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ABSTRACT

Phytometers are indicator transplants that provide information on site conditions based on plant survival, growth and reproduction. Since this is a relatively new approach, standards for its implementation remain to be defined, for example, during peatland restoration. Peatland restoration frequently aims at recovering characteristic communities, and a key attribute of successfully restored ecosystems is their capacity to sustain viable populations of target species. When not actively introduced, these species are expected to establish on their own after improving site conditions, for example by rewetting. Assessments to determine whether this goal is met require the long-term monitoring of species' presence, whereas the underlying causes of these observations, i.e. site or dispersal limitation, often remain unknown. Using phytometers within ecological restoration helps addressing this question. The goal of this study is to compare the responses of several species and traits to environmental conditions in restored peatlands. Three target species (*Drosera rotundifolia, Eriophorum vaginatum, Vaccinium oxycoccos*) were planted in restored montane peatlands in central Germany, while in a greenhouse experiment, the same species were grown on peat from the field sites and exposed to two water levels. Several plant traits were measured and compared with variation in light, water and soil conditions. The response to habitat conditions was species-specific, indicating that the use of different phytometers increases the reliability of monitoring. Survival and growth traits were suitable to assess a wide range of abiotic conditions, while differences in reproductive output were more time-consuming to measure. Survival provided the most conclusive results for species sensitive to stressful habitat conditions. Biomass and other size metrics of the phytometers, as well as growth and reproductive traits were partly redundant. Thus, we suggest recording survival and biomass and use non-destructive growth measurements for repeated assessments, while the choice of the most suitable size trait should depend on the growth form. Our study stresses the potential of phytometers for monitoring the restoration outcome, while highlighting the importance of species and trait selection.

1. Introduction

Ecological restoration aims at counteracting the negative effects of land degradation (Hobbs, 2007). It has the potential to protect endangered species by increasing the amount of suitable habitat on a local scale and by improving connectivity on a regional scale (Miller and Hobbs, 2007). However, especially in fragmented landscapes (Battaglia et al., 2008), in ecosystems with little seed banks and in early-successional sites (Turnbull et al., 2000), seed availability is limiting, when attempting to achieve a characteristic species composition (Bakker et al., 1996; Soons et al., 2005). As both habitat conditions and seed availability are drivers of a species' distribution (Ehrlen and Eriksson, 2000), disentangling them (i.e. site vs. dispersal limitation) is crucial for potential reintroduction, and one promising approach for doing so are phytometer experiments.

These problems also arise in peatland restoration with recovering plant communities (Pfadenhauer and Grootjans, 1999). As peatlands have been extensively degraded by drainage, peat cutting and conversion (Joosten and Clarke, 2002), specialised species inhabiting these habitats have become rare (Haapalehto et al., 2011). Peatland restoration commonly consists of raising and stabilising the water table and ultimately aims at re-establishing a peat-accumulating system (Vasander et al., 2003). This means that abiotic conditions are improved first (Pfadenhauer and Grootjans, 1999), while peatland species are often not actively introduced, although they have only short-lived seed banks (Huopalainen et al., 2000) and many have poor dispersal abilities. Even if there is evidence for the spontaneous recovery of plant communities (González et al., 2014), re-establishment might also be

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restricted by a lack of seed sources. It is claimed that the verification of the underlying causes for target species absence requires experimental approaches (Ehrlen and Eriksson, 2000); thus we should integrate them in the monitoring of restored peatlands.

For detecting dispersal limitation, it has to be proven that not all suitable habitats are occupied, i.e. that site limitation is excluded (Ehrlen and Eriksson, 2000). This can be achieved through complementing assessments of target species with seed-addition or phytometer experiments (Clark et al., 2007; Bourgeois et al., 2016). The phytometer approach, in which standardised plants are transplanted to indicate site-specific differences (Antonovics et al., 1982), was first used by Clements and Goldsmith (1924), while in restoration ecology the idea of using plants as measuring instruments is relatively new (Dietrich et al., 2013). Early applications dealt with agronomic crops, extending later to population genetics, biotic interactions and assessments of habitat conditions (Dietrich et al., 2013). In recent years, using phytometers was introduced, for example, for the restoration of secondary forests (Verheyen and Hermy, 2004, Baeten et al., 2010), dune slacks (Bakker et al., 2006) and riparian zones (e.g. Dietrich et al., 2015; Bourgeois et al., 2016). Thereby, most phytometer experiments used site-specific species (Verheyen and Hermy, 2004; Bakker et al., 2006; Baeten et al., 2010; Bourgeois et al., 2016), while others relied on standardised plant material like commercial sunflowers (Dietrich et al., 2015). For reasons of time or resource constraints, many studies plant only one or few species, whereas Dietrich et al. (2013) suggested the use of a suite of complementary species, highlighting that further research on the species selection process is needed before standardising the approach.

Phytometer experiments take advantage of the fact that plants represent an integrative measure of average site conditions (Ellenberg et al., 2001). Within its physiological limitations, a plant reacts to environmental variation by adjusting its growth and development (Baeten et al., 2010). This can be assessed by measuring its traits (Violle et al., 2007). Between-species differences are best described by three fundamental traits that control plant strategies, namely specific leaf area (SLA) as well as height and seed mass (Westoby, 1998). SLA is positively correlated with relative growth rate (Poorter et al., 2009) and negatively with leaf longevity (Pérez-Harguindeguy et al., 2013); it is correlated with light and water availability (Poorter et al., 2009), which are decisive in peatlands. However, in contrast to terrestrial ecosystems, wetland plants generally have a low SLA despite high water availability, which can be explained by anoxia under water saturation (Moor et al., 2017). The height of a plant is usually used as a surrogate for its competitive ability (Violle et al., 2007) and expresses a trade-off of its efficiency in capturing resources and the disturbance frequency in the environment (Grime, 1974). In wetlands, both SLA and height are expected to increase with higher nutrient levels (Moor et al., 2017). Seed mass determines the ability to colonise new environments and controls seedling survival in unfavourable environments (Westoby, 1998). Varying independently from each other and being easily measurable, these traits represent a plant's capacity to overcome challenges it faces in life, i.e. dispersal, establishment and persistence, and they are particularly useful for differentiating between plant communities (Weiher et al., 1999).

In transplant experiments, intraspecific trait variability along environmental gradients is highly important because conclusions on habitat variation are drawn based on differences in plant performance, measured as survival, growth and reproductive output (Violle et al., 2007; Scheepens et al., 2010). Wetland plants could hypothetically show high intraspecific variability, since they adjust to varying microenvironments in terms of soil water, oxygen and pH (Moor et al., 2017). Generally, intraspecific trait variability contributes to overall variability by 30% (Albert et al., 2010), but which traits are most closely correlated with fitness is species-specific and depends on the life history, e.g. of short- vs. long-lived species (Adler et al., 2014). Transplant experiments have used various traits, including germination (Dietrich et al., 2015; Egawa and Tsuyuzaki, 2015), survival (Bakker et al., 2006; Dietrich et al., 2015; Egawa and Tsuyuzaki, 2015, Bourgeois et al., 2016), biomass (Bakker et al., 2006; Baeten et al., 2010; Dietrich et al., 2015; Egawa and Tsuyuzaki, 2015), leaf number (Verheyen and Hermy, 2004; Baeten et al., 2010; Bourgeois et al., 2016), plant height (Verheyen and Hermy, 2004; Baeten et al., 2010; Bourgeois et al., 2016), and inflorescence or flower number (Verheyen and Hermy, 2004; Baeten et al., 2010). This heterogeneity in response variables (Dietrich et al., 2013) indicates the need for standardisation.

For monitoring ecological restorations, these considerations should be made against the background of practical feasibility, including a compromise between informative value and resource constraints. Even if it is claimed that phytometer experiments should be more commonly applied in restoration (Bourgeois et al., 2016), they are laborious and costly, while most restoration monitoring lacks time and funding (Kondolf et al., 2007). In research projects, a large number of traits have been analysed (Verheyen and Hermy, 2004; Baeten et al., 2010), while this is not feasible in monitoring routines. Furthermore, restoration projects often focus on rare or endangered species whose acquisition is difficult, while standardised plant material is often not commercially available or cannot be collected in sufficient numbers in field sites. The selection of a few effective traits and species would help overcome this constraint.

This study aims at extending the phytometer method to peatland restoration by comparing the responses of different species and traits to changing environmental conditions. We approach this by exposing three peatland species (*Drosera rotundifolia, Eriophorum vaginatum, Vaccinium oxycoccos*) to restored site conditions in the field and in the greenhouse. We measured a wide range of performance traits (sensu Violle et al., 2007), i.e. survival, vital leaf number, leaf number, shoot number, rosette diameter, tussock diameter, height, shoot length, vegetative and total biomass, SLA, capsule number, inflorescence number and mass per inflorescence. The study identifies those traits that represent the most effective and efficient response of phytometers to environmental stress, and to evaluate the benefits of using different indicator species. In particular, we address the following questions: (1) Do the phytometer species show a complementary response to site conditions? (2) Which phytometer traits show the highest intraspecific variability? (3) Which traits are redundant or unreliable? (4) Which environmental stress does intraspecific trait variability reflect?

We expected differences in performance (especially survival and reproduction) among sites and species, as species are more or less sensitive to habitat deterioration, and both site and dispersal limitation might occur. We also anticipated many growth traits (leaf number, shoot number, rosette diameter, tussock diameter, height, shoot length, biomass, SLA) to be correlated, while showing differences in plasticity. Furthermore, we hypothesised higher survival, increased growth and more reproductive output under restored field conditions, i.e. high water level and peat water holding capacity, low pH, low nutrient content and reduced shading. Water level effects were analysed under controlled conditions in a greenhouse experiment. We expected species-specific differences in response of traits, as the importance of survival, growth and reproduction for fitness depend on growth form.

2. Material and methods

2.1. Study sites

The study was conducted in restored peatlands of the mountains 'Fichtelgebirge' and 'Steinwald' in north-eastern Bavaria (longitude E11°44′59″–12°5′5″, latitude N49°53′46″–50°5′45″, 660–1000 m a.s.l., Fig. A.1). The study sites were (transitional) bogs and acidic fens, all developed on slopes or saddles under a positive water balance with an annual temperature of 5.5–6.2 °C and 910–1120 mm precipitation (Bayerisches Landesamt für Umwelt, 2017). Peat thickness was 0.2–2.0 m, with a mean of 0.6 m. Water levels were variable with a