



# 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 (Ehrlén 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 (Ehrlén 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 (Ehrlén 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 micro-environments 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

median ranging from  $-95$  cm to  $+2$  cm in summer months (June–September). All sites were previously drained and afforested with *Picea abies*. They were restored between 1998 and 2015 through the filling and damming of drainage ditches, and by cutting trees along the ditches, more specifically in 1998, 2000, 2002, 2007, 2011, 2014 and 2015 (Table A.1).

The main objective of these measures was to restore habitat conditions by raising the water level and by re-establishing a peat-accumulating system. A characteristic plant community was expected to colonise spontaneously, while sites were left largely unmanaged and subject to natural succession, following rewetting measures. Plant target species were *Drosera rotundifolia*, *Eriophorum vaginatum*, *Sphagnum* spp., *Vaccinium oxycoccos* and *Vaccinium uliginosum*. With time since restoration, both vegetation cover and height linearly increased in the sites (K. Strobl, unpublished data). ‘Younger’ sites, i.e. 1–2 years after restoration, showed a high cover of bare peat, remnants of dead wood and comparatively low total vegetation cover. After 2–5 years, most sites developed an increased abundance of graminoids, especially *Calamagrostis villosa*, *Carex* spp. and *Juncus effusus*, but generally below 50% cover (mean of six plots of  $0.5$  m<sup>2</sup>), and intermediate abundance of *Sphagnum* spp. and ericaceous dwarf shrubs (10–30%). In ‘older’ sites, after 9–18 years, graminoid cover was lower, while *Sphagnum* spp. and ericaceous species became more abundant. A species list with the frequency of vascular plants and bryophytes is given in Table A.1; nomenclature of vascular plants follows Buttler and Hand (2008), nomenclature of bryophytes fits Koperski et al. (2000).

## 2.2. Phytometer species

Three specialist bog species, naturally occurring in the study area and commercially available, were selected as phytometers, i.e. *Drosera rotundifolia* L., *Eriophorum vaginatum* L. and *Vaccinium oxycoccos* L. They differ in life and growth form as well as sensitivity to environmental conditions. *D. rotundifolia* is a carnivorous hemicryptophyte (Nordbakken et al., 2004) with leaves that form a rosette of 3–6 cm (Bruzzese et al., 2010); *E. vaginatum* is a tussock-forming hemicryptophyte (Bennington et al., 2012) with mature tussocks of 300–600 tillers (Fetcher and Shaver, 1982); and *V. oxycoccos* is an evergreen chamaephyte with thread-like stems up to 80 cm long (Jacquemart, 1997).

Following the leaf-height-seed (LHS) scheme proposed by Westoby (1998), all three species are ‘stress tolerators’ (mean height  $< 0.5$  m; Kleyer et al., 2008). However, the species differ in SLA (*D. rotundifolia* with  $59$  mm<sup>2</sup> mg<sup>-1</sup>, *V. oxycoccos* with  $35$  mm<sup>2</sup> mg<sup>-1</sup>, *E. vaginatum* with  $24$  mm<sup>2</sup> mg<sup>-1</sup>; Kleyer et al., 2008) and relative growth rate. *D. rotundifolia* sprouts every year from a hibernaculum with relatively fast growth, while *E. vaginatum* and *V. oxycoccos* have persistent leaves for  $> 2$  years (Fetcher and Shaver, 1983; Jacquemart, 1997). The species were purchased from nurseries to minimise intraspecific genetic variation, the effects of different cultivation methods and variation in plant age (*D. rotundifolia*: Gärtnerei Carow, Nürdingen; *E. vaginatum*: Staudenkulturen Stade, Borken; *V. oxycoccos*: Baumschule Pflanzenvielfalt GmbH, Zetel). The plants differed in size: *D. rotundifolia* had 1–2 cm rosette diameter, *E. vaginatum* had 3–7 cm tussock diameter (15–25 cm height) and *V. oxycoccos* had up to 70 cm long shoots.

Naturally occurring individuals of all three species were systematically searched along the study transects (see below) within a buffer of 10 m on both sides (ca.  $85$  m  $\times$   $42$  m), surveyed in parallel stripes of 3 m distances. *D. rotundifolia* was naturally occurring in none, *E. vaginatum* in four sites, and *V. oxycoccos* in one of eight sites (Table A.1).

## 2.3. Field and greenhouse experiments

The field experiment was conducted in eight sites within seven peatlands. For each site, a transect of 65 m was randomly chosen along a former drainage ditch, and six plots were randomly established along

the transects, with three plots within the ditch and three at 2, 4 and 11 m distance to the ditch, resulting in a total of 48 plots (Fig. A.2). In order to reduce the effects of competition at the time of planting, we removed all naturally present vascular plants within a triangle with 45-cm-long sides in May 2015. We only removed the upper layer of 2–3 cm of moss, as the transition between living *Sphagnum* spp. and subjacent peat was gradual in most cases.

One individual of each of the three phytometer species (*D. rotundifolia*, *E. vaginatum*, *V. oxycoccos*) was planted in the corners of the triangular plots at a distance of 25 cm from each other and 10 cm away from the edges of the plot, totalling six individuals per species and site. Possible competing vegetation (such as herbaceous plants and *Sphagnum* spp.) was removed from the plots every other month in April–October. However, belowground competition could not be fully excluded, as removing roots caused too much disturbance.

At each plot, peat characteristics (water holding capacity, nutrient content, pH) and light conditions were recorded. Light conditions below canopy were measured at 1.5 m above ground level using a Solariscope (SOL 300, Ing.-Büro Behling, Wedemark), which analyses hemispherical photographs. For subsequent analysis, the total site factor (TSF) was chosen as the most appropriate measure. It is defined as the proportion of direct (DSF) and diffuse (ISF) solar radiation and expressed as a percentage of the radiation received above the canopy (Rich, 1990). To perform laboratory analyses of peat, samples were taken with the help of soil corers (mixed sample of  $3 \times 100$  ml) at each plot in August 2015. The maximum water holding capacity was defined as the amount of water absorbed by 100 g of dry peat. We placed the peat samples in filters and poured 200 ml of distilled water over them to determine the saturated ‘fresh mass’. ‘Dry mass’ was obtained after oven drying at  $65$  °C for  $> 72$  h. We measured the pH in 5 g peat (dry mass) stirred up in 100 ml distilled water. Nutrient concentrations (anions and cations) were obtained using ion chromatography (Dionex ICS-1600, Thermo Fisher Scientific Inc.). Mean values of peat characteristics per site are listed in Table A.2–4.

In addition to the field study, we conducted a greenhouse experiment to understand the effects of different ‘peat provenances’ corresponding to the field sites as well as two water levels on the performance of the phytometers. Fig. A.3 shows the experimental design: two individuals of each species were planted in separate pots (one individual per pot) with mixed peat obtained from the eight field sites, totalling 16 pots per species and four pots per peat provenance. Pot diameter was chosen according to the size of the species (5 cm for *D. rotundifolia*, 15 cm for *E. vaginatum*, 19 cm for *V. oxycoccos*). The two sets of pots of the three species with the same peat provenance were placed in 16 trays to apply two water level treatments. Trays containing pots with the same peat were flooded with rain water at either 3 or 8 cm below upper pot level, imitating belowground water levels in the study sites. Water tables lower than  $-8$  cm were found in the field, but were not feasible in the greenhouse.

Each block (peat provenance  $\times$  water level) was repeated twice, leading to a total of 32 trays and 96 pots. A constant water level was assured by watering 2–3 times a week depending on weather conditions. The experiment was kept in a greenhouse with a constant temperature of about  $10$  °C during winter and transferred to a half-open greenhouse with wire mesh walls in summer, allowing for more natural variation of temperature. Light was not manipulated in the greenhouse and corresponded to natural conditions in Freising, where the greenhouse was located ( $48^{\circ}24'20.87''$ N,  $11^{\circ}41'29.69''$ E). The trays were randomly placed on four tables and their position was changed once per month.

In both experiments, we planted *E. vaginatum* and *V. oxycoccos* in May 2015 and harvested aboveground biomass in October 2015 for a preliminary analysis (C. Schmidt, unpublished data). Data used for our final analysis corresponds to measurements in June 2016 (flowering of *D. rotundifolia*) and September 2016 (survival, growth, reproduction of *E. vaginatum* and *V. oxycoccos*). As *D. rotundifolia* did not survive the

**Table 1**

To measure the performance of the phytometer species (*Drosera rotundifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*), 14 traits related to plant fitness were selected. The survival of *E. vaginatum* could not be studied, since almost all individuals survived. The reproduction of *V. oxycoccos* was not addressed because no individual flowered ( $\Delta$ , difference in initial and final size; Veg, vegetative; SLA, specific leaf area).

Variable	<i>Drosera rotundifolia</i>	<i>Eriophorum vaginatum</i>	<i>Vaccinium oxycoccos</i>
Survival	Survival [1/0]	Survival [1/0]	Sprouting [1/0]
Growth	Diameter [cm]	Veg biomass [g]	Veg biomass [g]
	$\Delta$ diameter [cm]	Total biomass [g]	Shoot length [cm]
	Leaf number [cm]	Height [cm]	Shoot number [count]
	$\Delta$ leaf number [count]	Diameter [cm]	SLA [cm <sup>2</sup> g <sup>-1</sup> ]
	Vital leaf number [count]	SLA [mm <sup>2</sup> mg <sup>-1</sup> ]	
Reproduction	Capsules [count]	Inflorescences [count]	–
		Mass per inflorescence [g]	

harvest in 2015, it had to be replanted at the beginning of the second season in April 2016. The initial size of this species was measured at this time. This schedule resulted in a growing period of 17 months for *E. vaginatum* and *V. oxycoccos* (with a first aboveground harvest after five months), and six months for *D. rotundifolia*, corresponding to its main growing season. Reproduction had to be measured after three months for *D. rotundifolia* in order to not miss any capsules.

#### 2.4. Trait measurements

To describe plant fitness, we measured 14 traits related to survival, growth and reproduction, 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 (Table 1). Survival or sprouting from the roots was recorded for all three species. Leaf number as well as vital leaf number (many leaves in each rosette were withered by the end of the experiment) of *D. rotundifolia* were measured at the time of planting and harvesting. We included the final value as well as the difference between the initial and final size in the analysis. The shoot number of *V. oxycoccos* was determined by counting. The rosette diameter of *D. rotundifolia* and tussock diameter of *E. vaginatum* were defined as the mean of two orthogonal measurements. The height of *E. vaginatum* and shoot length of *V. oxycoccos* corresponded to the mean value of the three longest leaves or shoots, respectively. The vegetative aboveground biomass of *E. vaginatum* and *V. oxycoccos* was measured by cutting the plant at ground level and then drying (65 °C, > 48 h) and weighing it. The total biomass of *E. vaginatum* also included the dry mass of inflorescences and buds. For the determination of SLA, ten leaf sections of *E. vaginatum* and 15 entire leaves of *V. oxycoccos* were scanned, their area analysed with Image J (Rasband, 1997) and dry weighed, and the ratio of dry weight and area calculated. Before processing, sections of 5 cm were cut from the middle of *E. vaginatum* leaves in order to exclude differences in area or mass related to the leaf

tip or basis. In the field, SLA could not be determined for *V. oxycoccos* since the phytometer plants did not produce enough leaves. The flowers or capsules of each *D. rotundifolia* and inflorescences of each *E. vaginatum* individual were counted and the weight per inflorescence was determined after drying (65 °C, > 48 h). None of the *V. oxycoccos* individuals produced flowers.

#### 2.5. Data analysis

Data analysis was performed using R version 3.2.3 (R Core Team, 2015) and packages bestglm (McLeod and Xu, 2014), hmisc (Harrell, 2016), lme4 (Bates et al., 2015), piecewiseSEM (Lefcheck and Freckleton, 2016) and vegan (Oksanen et al., 2016). Packages ggplot2 (Wickham, 2016) as well as ggbiplot (Vu, 2011) and ggrepel (Slowikowski, 2016) were used for plotting. P values are abbreviated throughout the manuscript including appendices (\*, p < 0.05; \*\*, p < 0.01; \*\*\*, p < 0.001). For the analysis of survival, all individuals were considered. All other calculations concerning growth and reproduction were done with reduced datasets that considered only living individuals (defined as those having vital leaves) at the time of harvest or only flowering individuals, respectively.

The percentages of all surviving and reproducing individuals per experiment were calculated (Table 2). In addition, we determined percentages separately for occupied and non-occupied patches, i.e. those containing naturally occurring populations of the study species, and plotted the results in a bar graph (Fig. B.1).

A Principal Component Analysis (PCA) based on trait values was calculated for each species and both experiments. It was then used for further analysis. First, for the field experiment the relationship of growth traits to environmental conditions was tested using a posteriori correlation of a second matrix containing measured abiotic conditions (nitrate, phosphate, potassium, water holding capacity, light and pH) with the ordination objects of the field data (Table B.1). This was visualised in PCA biplots with trait data as a first matrix and

**Table 2**

Coefficients of variation (CV) were calculated for all living (growth) and flowering (reproduction) phytometer species in the field and greenhouse (GH) experiments. Inconsistencies in the number of flowering (25) and living (23) individuals of *Drosera rotundifolia* in the greenhouse are related to the time of measurement in which capsules could still be recorded but all leaves had died.

<i>Drosera rotundifolia</i>			<i>Eriophorum vaginatum</i>			<i>Vaccinium oxycoccos</i>		
	CV			CV			CV	
Trait	Field	GH	Trait	Field	GH	Trait	Field	GH
Growth (n) (% alive)	27 (56)	23 (72)		44 (92)	32 (100)		18 (38)	27 (84)
Diameter	51.1	34.4	Veg biomass	154.1	23.7	Veg biomass	111.9	94.6
$\Delta$ diameter	45.2	34.4	Tot biomass	160.0	23.4	Shoot length	76.9	34.8
Leaf number	38.2	29.9	Height	44.4	14.7	Shoot number	63.5	46.8
$\Delta$ leaf number	47.1	29.3	Diameter	54.3	13.9	SLA	–	21.2
Vital leaves	46.9	30.5	SLA	22.4	8.5			
Reproduction (n) (% flowering)	16 (33)	25 (78)		18 (38)	18 (56)		0	0
Capsules	79.5	68.4	Inflorescences	127.9	148.2			
			Mass/inflor.	67.5	31.0			

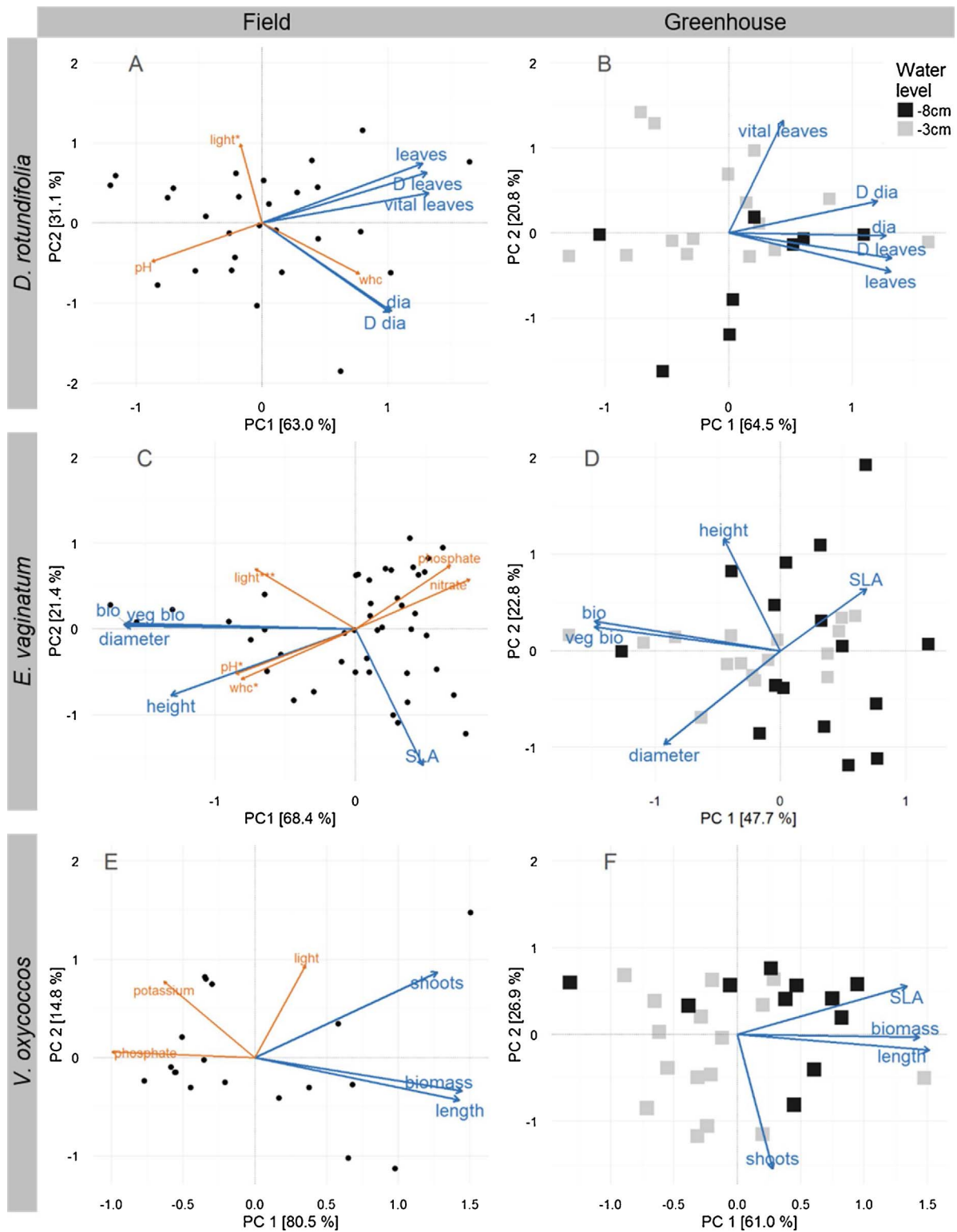


Fig. 1. PCA plots of measured growth traits (blue lines) for all three species and both experiments. Points represent phytometer individuals. For the field experiment, environmental covariates (orange lines), which are correlated with the first matrix on a 0.5 level, are shown (see also Tables B.1). For the greenhouse experiment, points were coloured according to water level treatment (light and dark grey). Numbers in brackets indicate explained variation by respective axis. Only the growth traits of surviving individuals are shown. This led to a different number of data points per graph, as the mortality rate differed depending on the species and treatments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

environmental covariates as a second matrix (Fig. 1). For the greenhouse experiment, points in the biplot were coloured according to water level treatment, and permutational multivariate analysis of variance (PERMANOVA) was used to test for the significant effect of

treatments on trait variability in the greenhouse (Table B.2).

The intraspecific variability of traits was compared using the coefficient of variation (Table 2), which indicates the relationship of the standard deviation to the mean. It is a measure of relative variability

**Table 3**Correlation matrix (Spearman's pairwise correlation) of measured traits of *Drosera rotundifolia* in a field and greenhouse (GH) experiment. Bold indicates the threshold  $|\rho| > 0.7$ .

Traits	Diameter		$\Delta$ diameter		Leaf number		$\Delta$ leaf number		Vital leaves	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
Experiment										
$\Delta$ diameter	<b>0.99***</b>	<b>0.62**</b>								
Leaf number	0.19	<b>0.72***</b>	0.15	0.46*						
$\Delta$ leaf number	0.28	<b>0.63**</b>	0.26	<b>0.53**</b>	<b>0.94***</b>	<b>0.95***</b>				
Vital leaves	0.40*	0.26	0.35	0.39	<b>0.72***</b>	0.10	<b>0.72***</b>	0.22		
Capsules	0.49	<b>0.72***</b>	0.37	0.45*	<b>0.68**</b>	0.31	<b>0.73**</b>	0.30	0.59*	0.03

**Table 4**Correlation matrix (Spearman's pairwise correlation) of measured traits of *Eriophorum vaginatum* in a field and greenhouse experiment. Bold indicates the threshold  $|\rho| > 0.7$ .

Traits	Veg bio		Tot bio		Height		Diameter		SLA		Infloresc	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
Experiment												
Tot bio	1.00***	<b>0.98***</b>										
Height	<b>0.78***</b>	0.25	<b>0.77***</b>	0.30								
Diameter	<b>0.90***</b>	0.45**	<b>0.90***</b>	0.40*	<b>0.74***</b>	-0.13						
SLA	-0.22	-0.25	-0.22	-0.27	0.27	-0.19	-0.18	-0.20				
Infloresc	<b>0.91***</b>	-0.40	<b>0.91***</b>	-0.26	0.59**	0.12	<b>0.86***</b>	-0.29	0.12	0.22		
Mass per infloresc	0.68**	0.25	0.68**	0.30	0.69**	0.32	<b>0.77***</b>	-0.40	0.20	-0.40	0.58*	0.09

**Table 5**Correlation matrix (Spearman's pairwise correlation) of measured traits of *Vaccinium oxycoccos* in a field and greenhouse experiment. Bold indicates the threshold  $|\rho| > 0.7$ .

Traits	Veg. biomass		Shoot length		Shoot number	
	Field	GH	Field	GH	Field	GH
Experiment						
Shoot length	<b>0.87***</b>	<b>0.92***</b>	1			
Shoot number	0.60**	0.19	0.57*	0.24	1	
SLA	-	<b>0.72***</b>	-	<b>0.75***</b>	-	-0.06

that allows for the comparison of variables with different units. To calculate the coefficient of variation, variables with negative values were transformed by adding the absolute minimum value plus one. This was necessary for *D. rotundifolia* ( $\Delta$  diameter,  $\Delta$  leaf number), where the initial size value was subtracted from the final one and the individual had decreased in size.

The redundancy of measured traits was analysed using Spearman's correlation coefficient (Tables 3–5). A strong correlation was assumed, when  $|\rho| > 0.7$  (Dormann et al., 2012). PCA plots and biplots also represent a visualization of redundancy.

Trait sensitivity to physical conditions was analysed for both the field and greenhouse experiment in separate analyses due to differences in design. For the field experiment, the response of traits to environmental conditions was tested using regression analysis with site as a random factor in order to compensate for spatial autocorrelation (Table 6). Distance from the former drainage ditch was used as a covariate in the models to detect effects linked to the position of plots within a site. For the analysis of survival as a function of environmental conditions, binomial generalised linear mixed models (GLMM) were calculated; for the analysis of count data, i.e. inflorescence, capsule and leaf number, a GLMM with a Poisson error distribution was selected. For biomass, diameter and height, data were transformed if not normally distributed, and then linear mixed effect models with a Gaussian error distribution were applied (data transformation:  $\log_{10}(x + 1)$  for biomass and diameter of *E. vaginatum* and shoot length of *V. oxycoccos*; square root for biomass of *V. oxycoccos*). Models were simplified using R function 'bestglm' based on the Akaike information criterion (AIC). For these models, significance was calculated using the likelihood ratio test. In order to avoid the collinearity of explanatory variables in the models, only independent variables were chosen out of a list of measured variables (Table A.5). Dependency was analysed using

Spearman's correlation coefficient ( $\rho < 0.4$ ), variation inflation factors (VIF  $< 3$ ) and PCA for graphical interpretation. Explanatory variables were standardised through scaling via subtraction of the mean and division by standard deviation of the variables. Confidence intervals were calculated using the adjusted Wald method. Conditional  $R^2$  values (Nakagawa et al., 2013, Johnson, 2014) were identified using function sem.model.fits.

For the greenhouse experiment, the response of individual traits to water treatment (two levels) and peat provenance (eight levels) was analysed using two-way ANOVA with water and peat type as fixed factors (Table 7). Data were transformed when necessary to meet the assumptions of normality ( $\log_{10}(x + 1)$  for biomass of *E. vaginatum* and *V. oxycoccos*). The interaction between peat and water was considered when it produced a better model based on the AIC.

### 3. Results

#### 3.1. Comparison of species

The performance of the phytometer plants differed among species, sites and experiments. In the field, more than half of *D. rotundifolia* (56%, Table 2) survived and 33% flowered, while no natural population could be detected within the study sites (Fig. B.1). Almost all *E. vaginatum* individuals survived (92%, Table 2), and this was similar in sites with and without naturally occurring populations (Fig. B.1); 38% produced inflorescences. 38% of *V. oxycoccos* survived (Table 2), but they did not flower. They showed a better score in occupied sites: 67% in occupied vs. 33% in non-occupied sites (Fig. B.1). Growth of *D. rotundifolia* only significantly responded to light conditions ( $p < 0.05$ , Fig. 1, Table B.1), while the one of *E. vaginatum* was an indicator for water holding capacity, light and pH ( $p < 0.05$ ,  $p < 0.01$ ,  $p < 0.05$ , Fig. 1, Table B.1), and the growth of *V. oxycoccos* was unrelated to any of the measured field conditions (Fig. 1, Table B.1).

In the greenhouse, 72% of *D. rotundifolia* survived, and all of them flowered (78%, Table 2). All *E. vaginatum* individuals survived and 56% produced inflorescence buds, while 84% of *V. oxycoccos* survived but did not flower (Table 2). Concerning greenhouse treatments, *D. rotundifolia* did not reflect any of the treatments, *E. vaginatum* showed a significant response to peat provenance and its interaction with water level (both:  $p < 0.01$ , Table B.2), and *V. oxycoccos* only to water level ( $p < 0.05$ , Table B.2).

**Table 6** Effect of nutrients, water holding capacity (Whc), light and pH on the survival, growth and reproduction of phytometers in the field. The table shows simplified models, estimate ± confidence interval. Asterisks indicate significances. D.r., *Drosera rotundifolia*; E.v., *Eriophorum vaginatum*; V.o., *Vaccinium oxycoccos*; \*\*\*, P < 0.001; \*\*, P < 0.01; \*, P < 0.05.

Survival	Growth	Reproduction	Sp.	Trait	Cond. R <sup>2</sup>	Distance	Nitrate	Phos-phate	Potas-sium	Whc	Light	pH
			D.r.	Diameter	0.324	-	-1.055 ± 1.517	-	-0.915* ± 0.815	1.396** ± 1.063	-	-
			V.o.	Leaf number	0.332	-	-	-	-	0.782 ± 0.854	-0.774 ± 0.947	-
			D.r.	Log biomass	0.319	-	-	-	-	0.604** ± 0.385	0.285 ± 0.533	-
			E.v.	Log diameter	0.046	-	-	-0.283 ± 0.346	-0.356 ± 0.388	0.144* ± 0.146	0.761*** ± 0.363	-
			V.o.	Sqrt biomass	0.549	-0.044** ± 0.030	-	-0.084 ± 0.123	-0.140* ± 0.141	-	0.228*** ± 0.120	-
				Log shoot length	0.057	-	-	-0.029 ± 0.059	-	-	-	-
			D.r.	Caps	0.177	-	-	-0.302 ± 0.309	-0.403** ± 0.274	0.640*** ± 0.259	0.249* ± 0.201	-
			E.v.	Inflorescences	0.870	-0.225*** ± 0.042	-	-0.729*** ± 0.336	0.042 ± 0.189	0.044 ± 0.227	0.757*** ± 0.427	-0.516*** ± 0.169
					0.985	-	-	-0.707*** ± 0.361	-	-	-	-

**Table 7**

Effect of greenhouse treatments on survival, growth and reproduction of the phytometer species. Only results of simplified ANOVA models are shown (+, positive relationship).

Species		Peat provenance		Water level		Peat x Water	
		F		F		F	
<i>Drosera rotundifolia</i>	Survival	1.86		16.33**		+	3.38*
	Diameter	0.78		0.18			1.62
	Leaf number	0.54		0.20			1.66
	Capsules	1.62		1.36			1.46
<i>Eriophorum vaginatum</i>	Log(Biomass)	0.82		3.37			2.72*
	Diameter	1.85		4.51*		+	-
	Inflorescences	1.40		3.15			1.45
<i>Vaccinium oxycoccos</i>	Sprouting	1.48		8.33*		+	1.48
	Log(Biomass)	1.20		1.42			-
	Shoot length	1.41		3.91			2.27

3.2. Comparison of traits

3.2.1. Intraspecific variability of traits

We observed largest coefficients of variation for biomass and reproduction traits in both experiments, while those of SLA were rather low (Table 2). However, there were some species-specific differences: For *E. vaginatum*, both vegetative and total biomass showed the highest plasticity in the field (Table 2). Among growth traits, height and diameter of *E. vaginatum* were more variable than SLA. Reproductive traits were most variable in the greenhouse, and inflorescence number was more plastic than mass per inflorescence. For *D. rotundifolia*, where biomass was not measured, capsule number showed the overall largest variability in both experiments (Table 2). Diameter at the end of the experiment was slightly more variable than other growth parameters for this species. For the non-flowering *V. oxycoccos*, biomass was also more plastic than other growth traits (Table 2). The shoot length of *V. oxycoccos* was more variable than the shoot number in the field, while it was the inverse in the greenhouse experiment.

3.2.2. Redundancy of traits

Both experiments showed a high correlation among growth traits, as well as between growth and reproduction (Fig. 1, Tables 3–5). Biomass – measured for *E. vaginatum* and *V. oxycoccos* – was highly redundant with other size traits. This is shown by high correlation coefficients between biomass and tussock diameter or height (*E. vaginatum*, Table 4) as well as between biomass and shoot length or SLA (*V. oxycoccos*, Table 5). Count data, however, were less related to biomass as demonstrated by the shoot number of *V. oxycoccos* (Table 5). In general, vegetative and total biomass showed the same results (*E. vaginatum*), and no large differences were observed comparing relative growth (difference between final and initial value) and final values alone (*D. rotundifolia*, Table 3). Reproduction traits – measured for *D. rotundifolia* and *E. vaginatum* – were generally closely related to growth traits (Tables 3–5). Examples include the correlation of the number of capsules with the leaf number (*D. rotundifolia*, Table 3), as well as the inflorescence number and mass with biomass and diameter (*E. vaginatum*, Table 4).

3.2.3. Trait sensitivity to physical field conditions

Not all phytometer traits reflected environmental conditions measured in the field. The survival, biomass and shoot length of *V. oxycoccos* as well as the diameter and leaf number of *D. rotundifolia* were not significantly influenced by any of the measured physical conditions (Table 6). In general, the abiotic variables most closely reflected by phytometer performance were phosphate, potassium, water holding capacity and light (Table 6). The survival of *D. rotundifolia* was negatively influenced by potassium (Est.  $-0.92 \pm 0.82^*$ , Table 6) and positively by water holding capacity (Est.  $1.40 \pm 1.06^{**}$ ), while the survival of *V. oxycoccos* did not show a significant response to any

abiotic variable. Significant impacts on growth could only be observed for *E. vaginatum* (Table 6). Both its biomass and diameter increased with higher water holding capacity (Est.  $0.60 \pm 0.39^{**}$ ,  $0.14 \pm 0.15$ , Table 6) and higher light conditions (Est.  $0.76 \pm 0.36^{***}$ ,  $0.23 \pm 0.12^{***}$ ). Its diameter also decreased with increasing potassium concentrations (Est.  $-0.14 \pm 0.14^*$ ) and the distance to the former drainage ditch (Est.  $-0.044 \pm 0.03^{**}$ ). Reproductive output decreased with phosphate (*D. rotundifolia*: Est.  $-0.73 \pm 0.34^{***}$ , *E. vaginatum*:  $-0.71 \pm 0.36^{***}$ ), potassium (*D. rotundifolia*:  $-0.40 \pm 0.27^{**}$ ) and pH (*E. vaginatum*: Est.  $-0.52 \pm 0.17^{***}$ ), while it increased with water holding capacity and light conditions (*D. rotundifolia*: Est.  $0.64 \pm 0.26^{***}$ ,  $0.25 \pm 0.20^*$ , *E. vaginatum*: Est (light).  $0.76 \pm 0.43^{***}$ , Table 6). Traits of *V. oxycoccos* were independent of the abiotic variables in the field (Table 6).

#### 3.2.4. Trait sensitivity to greenhouse treatments

Water level and peat provenance, which were experimentally varied in the greenhouse, showed significant impacts on the growth of *E. vaginatum*, while only affecting the survival of *D. rotundifolia* and *V. oxycoccos* (Table 7). The survival of *D. rotundifolia* significantly increased with higher water levels in interaction with peat provenance ( $p < 0.05$ , Table 7, Fig. D.1). The diameter of *E. vaginatum* significantly increased with a higher water table ( $p < 0.05$ , Table 7, Fig. D.2), whereas its biomass was jointly affected by water level and peat provenance ( $p < 0.05$ ). The survival of *V. oxycoccos* was enhanced by the water table treatment ( $p < 0.05$ , Table 7). All in all, the reproduction traits were independent of greenhouse treatments (Table 7).

## 4. Discussion

### 4.1. Species-specific differences and species selection

We selected plant species that provide information on the phenomenon of interest, i.e. are adapted to wet, acidic and nutrient-poor conditions (Wein, 1973, Jacquemart, 1997, Nordbakken et al., 2004). Nevertheless, the three species differed in their survival rate and in reproductive output in both field and greenhouse, and showed considerable growth variability in response to environmental conditions.

While under field conditions almost all *E. vaginatum* and more than half of *D. rotundifolia* survived, only slightly more than a third of all *V. oxycoccos* plants had re-sprouted. *E. vaginatum* was the least sensitive of the three selected species: It supports different conditions ranging from desiccation to waterlogging (Bragazza and Gerdol, 1996), and is one of the first colonisers after peatland rewetting (Gorham and Rochefort, 2003). A similar high survival rate for this species was reported by Bennington et al. (2012) in a reciprocal transplant experiment. As the species was not present in all sites, we assume dispersal or establishment limitation to occur. The same holds for *D. rotundifolia*, as its survival was higher than expected; no natural populations were occurring in the study area. However, it was not true for those sites, where high mortality suggested habitat conditions to be insufficient. Our results highlight the importance of the upper peat layer for the species, as shown in the field (i.e. positive influence of increased water holding capacity, negative of potassium content) and supported by the greenhouse experiment (significant interaction of peat provenance and water). The species has shallow roots and does not tolerate prolonged drought (Crowder et al., 1990), which is more likely to occur in a peat substrate with low water holding capacity. This can also explain the interrelation of water level and peat provenance in the greenhouse: We suppose that *D. rotundifolia* can survive on degraded peat if the water level is high enough. As the survival of *V. oxycoccos* was twice as high in sites with naturally occurring populations of the species, we conclude that site limitation is the main cause for its poor performance. Based on the results of the greenhouse experiment (i.e. significant increase in survival with higher water levels), we presume that water levels were too low in these sites. However, there must be other reasons for the

poor re-sprouting of *V. oxycoccos*, since some individuals also died in occupied sites. One possible explanation is that transplant shock is important for the largest of the three planted species; and Burney and Burney (2016) also reported a high proportion of transplant shock in their experiment. Besides, we need to consider that the biomass of all individuals had been harvested for a preliminary analysis and *Vaccinium* species are generally not adapted to the cutting of tillers (Nestby et al., 2014).

The growth of the three species cannot be directly compared, as they have different growth forms and traits showed different responses to field and greenhouse conditions. While in the field the growth of *D. rotundifolia* was only influenced by canopy shading, *E. vaginatum* also responded to pH and water holding capacity. This indicates that once *D. rotundifolia* survived, it depended less on peat characteristics, while light still influenced its growth. The species is known to be critically threatened by canopy shading (Crowder et al., 1990). By contrast, our results suggest that the growth of *E. vaginatum* changes in line with improved water holding capacity and pH, considering that peat provenance might be interdependent with water level, as shown in the greenhouse experiment. Bennington et al. (2012) demonstrated that the species' size is highly plastic in response to site conditions, thus making it a useful indicator in phytometer experiments. Though, its growth has to be analysed carefully, and Fetcher and Shaver (1983) indicated that the species can switch growth and survival strategies in order to adjust to changed conditions. *V. oxycoccos* did not show any significant response in growth under field conditions, most likely because of missing data due to poor survival. This is supported by significant results in the greenhouse, where more data on its growth could be gathered and a relation with the water table treatment was found.

While more than half of *D. rotundifolia* individuals produced capsules, and more than a third of *E. vaginatum* individuals had inflorescences in the field, no *V. oxycoccos* flowered. As we had cut the plants the year before measurement, apparently the time was insufficient for this species to reproduce. It needs to form buds in the first year before flowering in the second year (Yudina and Maksimova, 2005). For *E. vaginatum*, flower production even increased in unoccupied sites, supporting the assumption that this species is not site-limited. In general, the reproduction of *D. rotundifolia* and *E. vaginatum* was influenced by similar abiotic conditions: negatively by phosphate (both spp.), potassium (*D. rotundifolia*) and pH (*E. vaginatum*), and positively by light (both) and water holding capacity (*D. rotundifolia*).

Thus, apart from reproductive output, the species did not show a complementary response to site conditions: They were more or less sensitive (cf. Bakker et al., 2006) or indicated different microhabitats of peatlands. Like Landenberger and Ostergren (2002) and Dietrich et al. (2013), we conclude that the use of several species leads to more detailed information, particularly when using species of different growth forms and resource acquisition strategies. Following the attributes of bioindicators of Burger (2006), a good strategy would be to choose species with different degrees of sensitivity to the specified stressor. In our case, *D. rotundifolia* could not survive under too low of levels of water holding capacity, while *E. vaginatum* was able to adjust its size in response to environmental stress. Another strategy would be to use different life stages as suggested by Dietrich et al. (2013). We only used adult plants, but for more exhaustive studies, seeds and seedlings can complement results, as site and establishment limitations occur at different phases of a plant's lifecycle (Clark et al., 2007). If funding is limited, one might also use fewer or only one species, but then a careful selection based on the specific study questions is even more important. For example, when disentangling site or dispersal limitation, only the species of interest are reasonable phytometers, while a larger range of species can be used when site quality alone is to be assessed.

### 4.2. Trait comparison and selection

A review by Younginger et al. (2017) revealed that most studies



measure fecundity-related metrics and biomass or size, while only few use survival as an estimate of plant fitness. Growth or performance are the most commonly used parameters in phytometer experiments (Dietrich et al., 2013), and there are many examples of seed-sowing experiments using survival as an important explanatory variable (e.g. Egawa and Tsuyuzaki, 2015; Bourgeois et al., 2016). Among all possibilities, those traits should be chosen that not only respond to crucial site conditions, but are accurate, precise and easy to measure (Gibson, 2002; Landenberger and Ostergren, 2002; Lindborg et al., 2005; Burger, 2006).

*Survival* is a straightforward indicator for site limitation, as species disappear promptly when habitat quality deteriorates (Lindborg et al., 2005). In our study, survival generally responded to important environmental conditions in restored peatlands, which is peat, especially nutrient availability, and water (Nordbakken et al., 2004); but, as shown above, responses depended on the species. Using survival alone only provides a limited perspective on the studied questions in many cases. First, it cannot be used as an indicator of fitness alone, as it is not able to predict reproduction, as shown by the fact that not all surviving individuals flowered (Table 2). Second, at the beginning of a phytometer experiment, transplant shocks might occur due to root damage or insufficient moisture during transportation; therefore, care has to be taken when drawing conclusions on site limitation in early experiment phases. Third, the measurement of survival seems unambiguous and easy at first glance, but can be challenging to determine, especially for cryptophytes and hemicryptophytes. For example, during our experiments, some individuals of *D. rotundifolia* that had lost all leaves were still able to build new rosettes within the same growing season. Most importantly, survival is a naturally dichotomous variable and cannot be used for measuring different levels of a specific stressor. As mentioned above, in our study, water holding capacity, for example, was reflected by the survival of *D. rotundifolia*, but its different expressions were better visible via growth of *E. vaginatum*. Nevertheless, survival is a fast measure and can easily complement the survey of other traits to provide essential information for the most sensitive species.

*Growth* can be estimated in numerous ways, albeit being most commonly based on the determination of dry mass (Tracey et al., 2016). Our results point out that vegetative as well as total dry biomass are the most variable traits and thus theoretically most suitable to detect differences in site conditions. However, significant responses to abiotic conditions could only be detected for *E. vaginatum*. Its biomass was increased under high light and water availability in the field. In the greenhouse, the dry mass of *E. vaginatum* was able to detect a joint effect of water level and peat provenance, while its diameter only significantly responded to the water treatment. Besides supporting the indication strength of biomass compared to diameter, this finding highlights that plasticity not only depends on traits and species but also on the controlling factors, and interactions might exist (cf. Moor et al., 2017). For example, Ordoñez et al. (2010) explain their contrasting effects of water supply on leaf traits (leaf nitrogen and phosphorus concentration) through a decrease of nitrogen availability with wetness under long-term anoxic conditions. The measurement of biomass itself is accurate and easy to do. Yet, for the determination of plant dry mass, the individual has to be harvested, which is limited to the end of an experiment or to species that are adapted to damages similar to cutting. Tracey et al. (2016) also argued that measures of ‘space-occupancy’ might be more representative of what a plant experiences in its lifetime than dry mass. Similarly, we found a strong correlation of biomass with other growth metrics like *height*, *tussock diameter* or *length of shoots*, and those traits responded to comparable site conditions like biomass. For example, the tussock diameter of *E. vaginatum* also indicated light conditions and water holding capacity, and, for *V. oxycoccus*, phosphate was the only explanatory variable remaining in the model for biomass and *shoot length*. This suggests that these traits are interchangeable with biomass, while they have the advantage of being non-destructive. They can therefore be used for long-term monitoring with repeated

measurements, whose importance has long been acknowledged in plant population ecology (Gibson, 2002). Furthermore, these non-destructive measurements also allow for the analysis of relative growth (difference of final and initial size), which has been done in former studies, e.g. Baeten et al. (2010). It is not necessary for small initial size, like in *D. rotundifolia*, where final *rosette diameter* as well as *leaf number* were highly correlated with the relative increase of those parameters. This is an important result in order to simplify phytometer studies. Besides, the rosette diameter and leaf number of *D. rotundifolia* were not useful in our study, as they did not respond to any of the measured environmental conditions, neither in the field nor in the greenhouse. The same applies to the shoot length of *V. oxycoccus*. While growth is less important for long lifecycle species like *V. oxycoccus*, the fitness of *D. rotundifolia* as a hemicryptophyte with fast growth highly depends on it (Adler et al., 2014). Yet, its rosette diameter and leaf number could not be explained via measured abiotic variables. SLA was less variable than other growth traits in our experiments, although other studies found a high intraspecific variability in this trait (e.g. Poorter et al., 2009; Scheepens et al., 2010). Like many other results of our study, the correlation of SLA with other growth traits was species-dependent. The low variability and relationship of SLA to growth traits of *E. vaginatum* can be explained by difficulties in its measurement for a grass with needle-like leaves. SLA of *V. oxycoccus*, however, was significantly correlated with shoot length, as expected. In general, the variability of growth seemed to be more species- than trait-specific, highlighting that measures of space-occupancy have to be chosen according to life and growth form.

Quantifying *reproductive output* is probably the most intuitive method of determining fitness (Harper, 1977). We measured the capsule or inflorescence number and weight per inflorescence, which showed high plasticity. This is different from seed mass, which is known to have a low intraspecific variability (Violle et al., 2009), and therefore was not measured in this study. The reproductive output of *D. rotundifolia* as well as of *E. vaginatum* responded to many different field parameters, but not to greenhouse treatments. This might partially be explained by the fact that an important driver of reproductive output, i.e. light (Heger, 2016), was not manipulated in the greenhouse. In the field, however, not only light, but peat nutrient content (phosphate and potassium for *D. rotundifolia*, phosphate alone for *E. vaginatum*) as well as water holding capacity (both spp.) and pH (*E. vaginatum*) influenced the capsule or inflorescence number, respectively. Therefore, it remains unclear why reproduction traits did not respond to water level and peat provenance in the greenhouse. Possible explanations for peat provenance being a poor predictor of trait plasticity in the greenhouse include: (i) peat provenance effects were overlaid by stronger impacts of water level, or (ii) nutrients in substrate are depleted and peat becomes increasingly decomposed after longer periods. Theoretically, more than the capsule or inflorescence number, the most accurate way of measuring fitness would be to determine the number of sexually and asexually produced progeny (Younginger et al., 2017), knowing that the number of seeds alone does not necessarily imply a large number of descendants (Harper, 1977). As this approach is time-consuming and involves molecular techniques, most studies use seed-related metrics as well as flowers or fruits (Younginger et al., 2017). The capsule and inflorescence number were highly correlated with growth traits in our study as well as in many other cases (Younginger et al., 2017). However, as mentioned above, reproductive output only provides limited data in phytometer studies in which not all individuals flower and not all species reproduce every year. Therefore, we suggest that growth traits would be sufficient for studying phytometer performance when time and resources are limited.

## 5. Conclusion

In our study, most responses of species to environmental conditions were species-dependent, which is related to the use of contrasting

growth forms (rosette-forming hemicryptophyte, tussock-grass forming hemicryptophyte and evergreen chamaephyte). Therefore, our first conclusion is that the use of several species supplies more information, especially when using species that differ in their sensitivity to the stressor of interest. However, this also implies that our results can hardly be generalised and do not allow for universal recommendations in restoration projects. They rather point out the crucial importance of carefully pre-selecting species based on ecosystems and study questions (e.g. assessment of site quality, dispersal limitation).

The selection of traits should follow in a second step and be based on the growth form of the respective species, as they also were species-specific. While for more robust, fast-growing species (*E. vaginatum*), individual growth and reproduction are the most important performance traits, long-lived species (*V. oxycoccus*) depend mostly on survival, and very sensitive species (*D. rotundifolia*) on survival or fast reproduction. This should be considered when selecting traits. Generally, when resources within the monitoring project are limited, we suggest survival and growth as indicators of phytometer performance. While survival guarantees a minimum amount of sufficient data under largely unsuitable conditions that cause the mortality of the most sensitive species, growth is more variable, providing a more detailed picture of site conditions. For selecting among a large variety of growth traits (e.g. height, diameter, biomass), we recommend using those that are most easy and accurate to measure, as generally many correlations exist, and variability is more species- than trait-specific. When resources are sufficient, measuring a larger number of traits in a preliminary investigation and a subsequent analysis of correlation and variability like in our study are helpful tools.

Overall, phytometer experiments provide a profound understanding of environmental factors driving restored ecosystems and should be more commonly used by practitioners as well as scientists. They can inform practitioners whether active reintroduction is meaningful for specific sites or species. Their broader application in scientific studies will help advance and standardise the approach.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2017.12.018>.

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