Does the restoration of shallow marginal peatlands alter the distribution or abundance of bog asphodel (*Narthecium ossifragum*)?

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SUMMARY

Bog asphodel, *Narthecium ossifragum*, is a flowering plant, commonly found in many wet acidic habitats, including upland blanket bogs where sheep and cattle grazing has been considered as the most feasible economic activity. It can be fatally toxic, especially to lambs, so there is concern that re-establishing blanket bog habitat will increase the distribution and abundance of bog asphodel and thus further threaten the marginal livelihoods of upland livestock farmers.

(1) Analysis of vegetation survey data collected pre- and post-restoration from 43 restored shallow peatland sites on Exmoor, an upland area on the northern coast of the UK's southwestern peninsula, showed only a small (4 %) increase in spatial distribution following restoration (rewetting). No increase in bog asphodel abundance was seen at six sites for which pre- and post-restoration percentage cover data were available. Moreover, bog asphodel did not appear post-restoration at any of the 21 sites (48 %) where it had not been recorded pre-restoration.

(2) A separate detailed study at one site demonstrated typical bog asphodel phenology and a life history strategy of growing and reproducing very slowly but persisting despite cold, wet and acidic conditions. Therefore, bog asphodel is ecologically unlikely to respond within a decade to any major change in its environment, such as rewetting of the peat. However, bog asphodel on Exmoor does show significant variability in size and in the proportion of plants that flower year on year.

(3) While the mechanisms by which bog asphodel exerts its toxic effect when ingested by ruminants have yet to be fully elucidated, the inconsistent pattern of toxicity seen in other parts of the UK and in northern Europe, where bog asphodel poisoning is reported to be a serious economic problem, may be driven by the influence of environmental factors on bog asphodel growth.

KEY WORDS: blanket bog, ditch blocking, Exmoor, life history strategy, phenology, toxicity

INTRODUCTION

The restoration of damaged peatland landscapes is a key element in climate change mitigation programmes because growing peatlands sequester atmospheric carbon, as well as providing a range of other ecosystem services (Joosten *et al.* 2016). An extensive programme of peatland restoration has begun in the United Kingdom (UK) where as much as 80 % of the peatlands are degraded (Bain *et al.* 2011), having been progressively damaged since the industrial revolution of the 19th century by peat extraction for agriculture, over-grazing, drainage, and industrially created atmospheric pollutants, e.g., sulphur dioxide, nitrous oxide, and heavy metals (Holden *et al.* 2007).

Upland peatland in the UK is mostly blanket bog in the west and north, a globally rare habitat found only in high latitude oceanic climates in both hemispheres. The UK has 13 % of the global blanket bog inventory and therefore peatland restoration programmes conserve this rare habitat as well as contributing to climate change mitigation (Humpenöder *et al*. 2020). Although much of the UK's blanket bog is over two metres in depth, the southwestern peatlands lie at the climatic limits of rainfall and temperature for peat formation and moreover some of the deposits are very shallow, often less than one metre in depth (Gallego-Sala & Prentice 2013, Grand-Clement *et al.* 2013, Gatis *et al.* 2019a). These peatlands are therefore especially susceptible to hydrological changes in a warming climate (Clark *et al.* 2010) which threatens not only their ability to sequester carbon but also the other goods a healthy peatland supplies such as flood alleviation, clean drinking water, biodiversity, food and fuel, recreational space and aesthetic qualities (Bonn *et al.* 2016). Exmoor is an upland area on the northern side of the UK's southwest peninsula bordering the Bristol Channel. The peatlands here have been overgrazed and drained since the 16th century (Grand-Clement *et al.* 2013, Bray 2015). Much of this landscape is dominated by purple moor grass (*Molinia caerulea*) which out-competes typical diverse bog vegetation when there is a widely fluctuating water table created by drainage ditches (Bunce & Barr 1988, Brys *et al.* 2005, Grand-Clement *et al.* 2015, Gatis *et al.* 2019b).

Bog asphodel (*Narthecium ossifragum* (L.) Huds) is a flowering plant common in wet acidic habitats. It is characterised by patches of shallow (< 15 cm) rhizomes from the nodes of which develop bright green curved sheathing leaves in spring, and tall yellow floral spikes in June and July (Summerfield 1974). The plant thrives in very wet and acidic conditions with low supply of solutes and is thus considered an indicator of healthy ombrotrophic blanket bog (JNCC 2006). However, when ingested the flowers and leaves can cause liver damage resulting in acute photosensitisation and renal failure (Strugnell 2014, Pollock *et al.* 2015). Young sheep and cattle with immature systems are particularly susceptible. The toxicity associated with bog asphodel presence has a variety of local names illustrating its range and importance: *yellowses* (Northumberland); *saut* (Cumbria); *plochteach* (Scotland); *hard lug* (Northern Ireland) and *alveld* or elf fire (Norway) (di Menna *et al.* 1992, Pollock *et al.* 2015). The mechanisms of its toxicity have yet to be fully elucidated, but the toxic effects of ingestion vary from year to year and between sites suggesting that variations in environmental factors may influence the extent of toxicity (Mysterud *et al.* 2016). Any increase in bog asphodel distribution and abundance could potentially affect the economics and viability of livestock farming - the predominant land use in these remote and difficult to farm landscapes (Mysterud *et al.* 2007, Pollock *et al.* 2015). This has been raised as a particular concern to farmers in peatland restoration areas - personal communications from Robin May (Exmoor), Lucy Porritt (Northumberland) - where moving the livestock to land without bog asphodel is not a practical option.

The Exmoor Mires Partnership (EMP, now the Southwest Peatland Partnership) has been restoring peatland on Exmoor since 1998, and to date has blocked ditches to rewet the peat over more than 1000 ha of degraded peatland. Since 2006 detailed vegetation surveys have been made at 43 restoration sites. Information from this large data set is used by Hand (2020) to assess the effects of the restoration of shallow peatlands on the distribution and abundance of bog asphodel (Hand 2020). An additional phenology study was designed to evaluate the growth characteristics of bog asphodel as an aid to predicting its likely response to acute environmental change.

This article addresses the following hypotheses in an area of shallow and climatically marginal peatland where the impacts of restoration on bog asphodel have yet to be studied:

(1) the rewetting of shallow marginal peatlands does not cause bog asphodel to expand its range or abundance;

(2) the ecology of bog asphodel predicts its response to rewetting; and

(3) variability in annual growth may explain the inconsistent toxic effects of grazing bog asphodel pastures.

METHODS

Peatlands region

Exmoor (51° 14′ N, 04° 02′ W to 51° 03′ N, 03° 18′ W) is an area of coastal uplands and deep wooded valleys bordering the Bristol Channel on the southwest peninsula of the UK (Figure 1). The uplands range in height from 300 to 500 m above sea level and are mostly covered in a thin (less than 1 m deep) layer of peat, over sandstone and shale (Bray 2015). Although there are areas of deeper (> 1 m) peat most of Exmoor's peat is less than 50 cm deep (Smith 2009). Mean monthly temperatures range from 1.1 °C in February to 18.6 °C in July and August (30-year mean 1981–2010 at nearby Liscombe (Met Office 2019)). Mean average annual rainfall over the same period was 1445 mm. Most of the area restored lies within the Exmoor Site of Special Scientific Interest (SSSI) and is therefore a priority area for restoration under the UK Biodiversity Action Plan (JNCC 1994).

Exmoor's peatlands have been degraded, mostly by overgrazing since the 16th century and by drainage from the 1850s. Drainage was often achieved by digging closely spaced shallow ditches across extensive areas of moorland (Grand-Clement *et al.* 2015, Luscombe *et al.* 2016, Gatis *et al.* 2019a). Pre-restoration, the most common type of vegetation found on Exmoor was *Molinia caerulea - Potentilla erecta* mire, M25 (Rodwell 1991), in which bog asphodel is an occasional component. The restoration works involved blocking the ditches every few metres with locally dug peat blocks, along with reprofiling to encourage the trapped rainwater to stay in the blocked ditches. Larger ditches were blocked

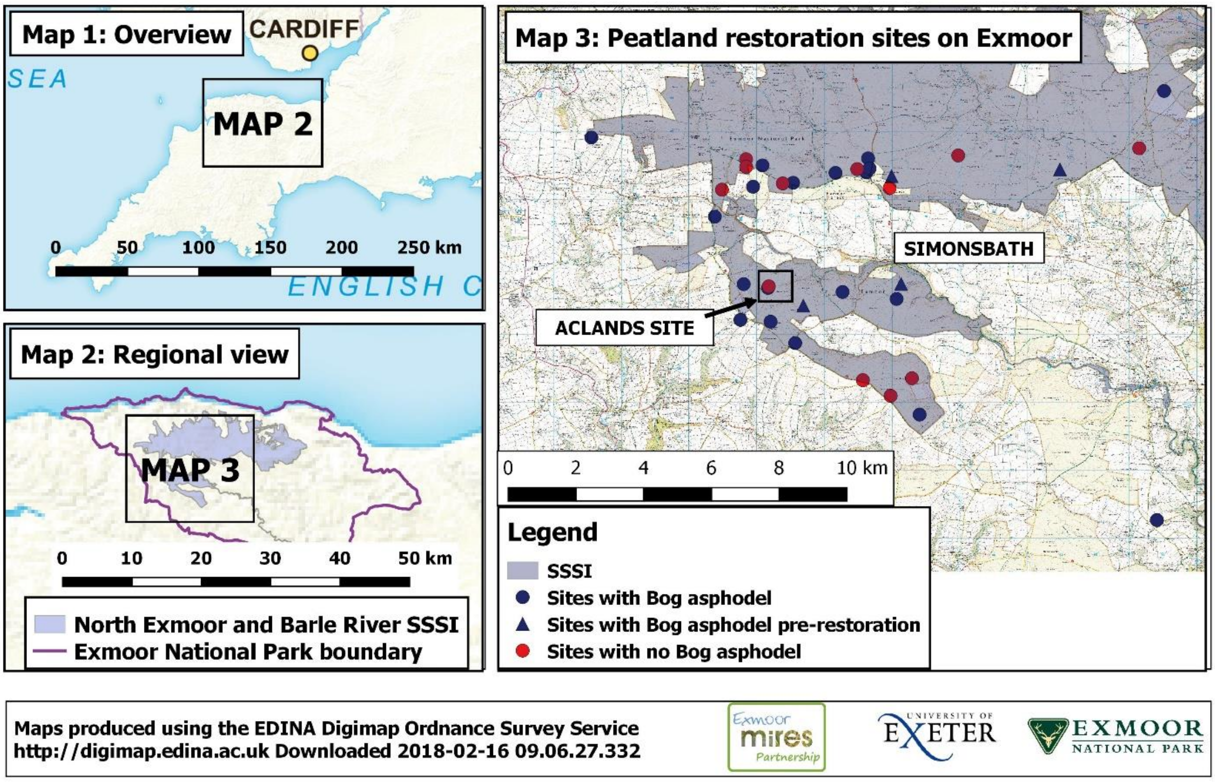

Figure 1. Map of Exmoor peatland restoration sites (n = 43) showing those with and without bog asphodel, including the Aclands site used in the separate phenology study.

with wooden dams, backed by peat and *Molinia* or sheep's wool bales (Brazier *et al.* 2020).

Thirteen-year distribution and abundance records

Data on bog asphodel presence were extracted from detailed Exmoor Mires Partnership (EMP) vegetation surveys made on 43 sites, all but six inside an area roughly 10 km square, pre- and post-restoration from 2006 to 2018 (Figure 1). The vegetation data had been collected from permanent transects established pre-restoration across one representative drainage ditch per site. The sites were restored between 2007 and 2014 and surveyed approximately every three years post-restoration. The transects were 30–50 m in length, and each comprised a continuous line of 1 m^2 quadrats, each divided into four 25 cm square sub-quadrats (120–400 sub-quadrats per transect). Recording methods changed from presence-absence scores in 2006–2010 to percentage cover scores from 2011. Percentage cover scores were estimated by eye, and the estimates were checked by the survey leader. Data were analysed to show changes in the presence of bog asphodel in each sub-quadrat over time, and the results presented as the change in the percentage of sub-quadrats occupied by bog asphodel. Changes in abundance were analysed at six sites for which pre- and post-restoration percentage cover data were available, and at another ten sites for which abundance data were available between subsequent post-restoration surveys. The results were presented as the change in total bog asphodel cover along each transect.

Two-year growth cycles

A two-year (2017–2018) phenology study of bog asphodel was also carried out at Aclands (51.134° N 03.811° W) (Figure 1), a site extensively studied by both EMP and the Universities of Exeter and Bristol (Grand-Clement *et al.* 2015, Luscombe *et al.* 2016, McAleer 2016, Freeman 2017, Gatis *et al.* 2020). Ten 1 m^2 'fixed' quadrats were established on two straight transects across the same restored ditch; five along a transect in a grazed area, and five along a transect in a fenced off area (Figure 2). In both summer seasons leaf and flower data were collected from each of the ten quadrats at approximately weekly intervals from May to August. Ten plants were randomly selected in each quadrat using random number tables at the beginning of the season and measured on each visit. The total number of flowers in each quadrat was recorded. Leaves and fruits were harvested in July–August and October for measurements of leaf mass, and seed mass and numbers, respectively. The data were used to compare the characteristics of bog

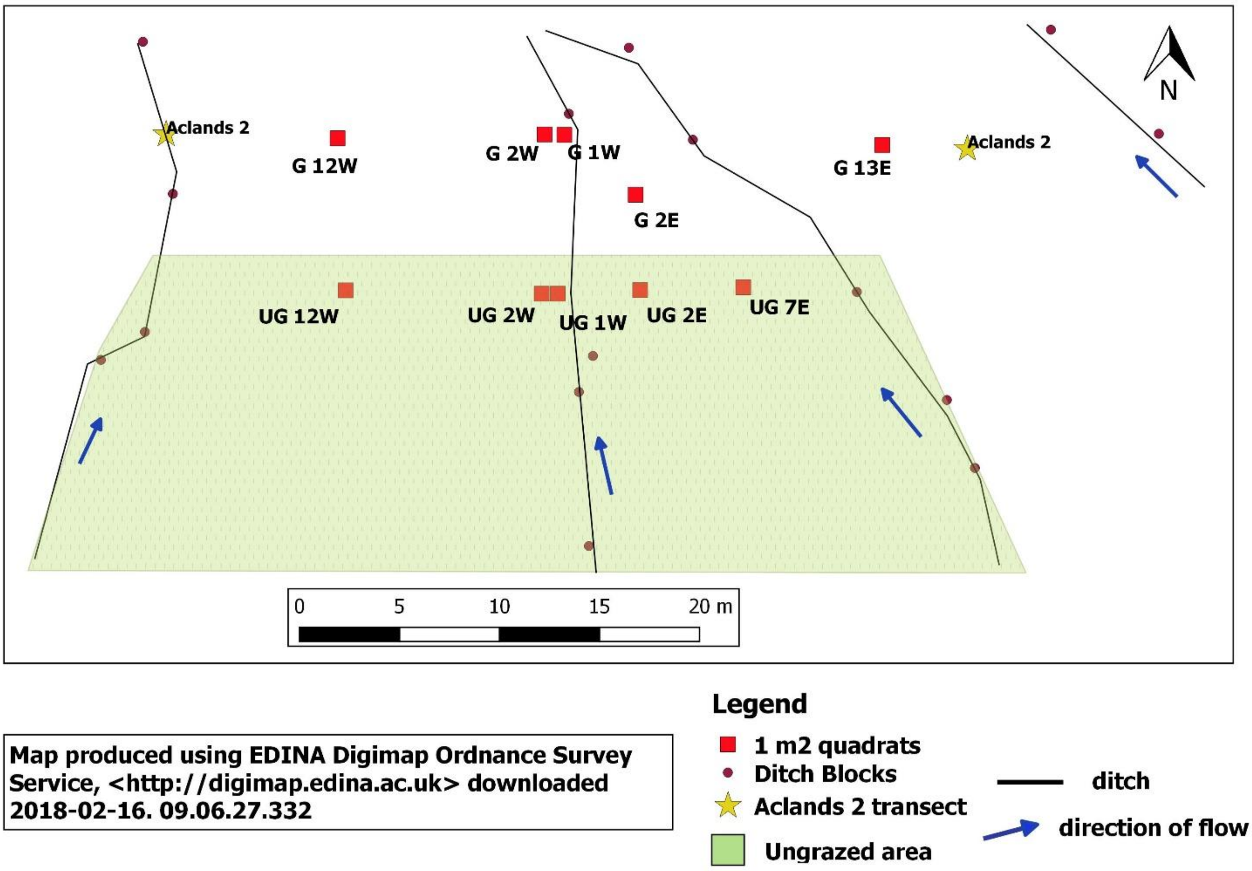

Figure 2. Diagram of the Aclands site used for the phenology study showing quadrat locations, ditches, grazed and ungrazed areas, and the ends of the Acland 2 transect included in the bog asphodel distribution and abundance analysis.

asphodel growing in the shallow marginal peatland of Exmoor with those recorded in the literature, and to compare growth in two consecutive growing seasons.

Water table depths (below ground surface) in plastic dipwells inserted beside each quadrat were recorded manually during each site visit (approximately 100 measurements in each year, see Table 2 later). Peat depth was recorded for each quadrat and water table depth presented as a proportion of the peat depth at each dipwell. The mean water table depth for the site (ten dipwells) was calculated for each site visit.

An additional subset of plants (16 in each quadrat) was monitored in 2018 to provide data to understand the plant's life history strategy in terms of the fundamental allocation of biomass between growth and reproduction (Grubb 1976, Grime 1979). An understanding of a plant's life history strategy allows its likely response to changing environmental conditions to be predicted. Grime's 'CSR' method uses maximum growth rate and a morphology index calculated from leaf size, litter accumulation and growth form to place plants on a spectrum of strategies between **C**ompetitive ability (larger, long-lived plants); **S**tress tolerance (surviving in very adverse conditions without achieving significant size or seed production); and **R**uderality (small plants that produce vast numbers of seeds). Leaf length and width were recorded for each plant at approximately weekly intervals during the growing season, and two plants from each quadrat were harvested for plant mass measurements on each visit to provide the necessary data.

Statistical analyses

The Welch two-sample *t*-test was used to test for variation between sets of normally distributed data, and the Wilcoxon rank sum test for data that were not always normally distributed. Pearson's Chi-squared test was used to test for homogeneity of variance, and the Shapiro-Wilk normality test for deviations from a normal distribution.

The online R Project for Statistical Computing programme (https://www.r-project.org/) was used for the *t*-tests and normality tests, and Microsoft Excel for testing homogeneity of variance.

RESULTS

Bog asphodel distribution and abundance changes following restoration

The analysis was based on 17 restoration sites on Exmoor at which bog asphodel was present and for which pre- and post-restoration survey data were available. For a further five sites with bog asphodel there were no post-restoration survey data, and at 21 sites (48 %) no bog asphodel was found pre- or post-restoration (Figure 1).

A small (< 1 %) increase in the spatial distribution of bog asphodel (mean 0 % ± 30 %) was found at 17 sites post-restoration which had taken place 2–11 years previously (Figure 3, column 3). There was wide variation in bog asphodel response between the sites. Both of the sites with exceptional bog asphodel responses (positive outliers in Figure 3) were valley mires where a more mesotrophic vegetation developed post-restoration. The negative outlier represents a site where ditch blocking had not resulted in rewetting of the peat.

Bog asphodel rhizomes typically grow in well-defined patches. At nine of the 17 sites it was possible to show that the bog asphodel patches did not expand post-restoration. As an example, Figure 4 shows that

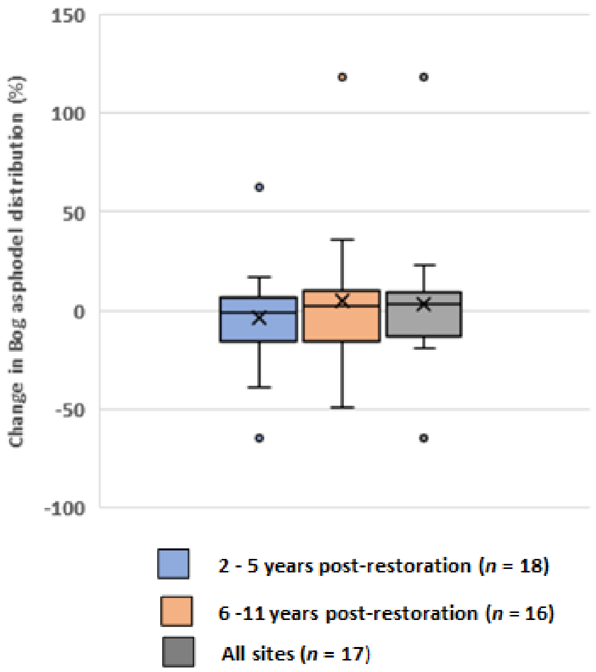

Figure 3. Relative changes in bog asphodel distribution post-restoration, shown as the change in % of sub-quadrats containing bog asphodel.

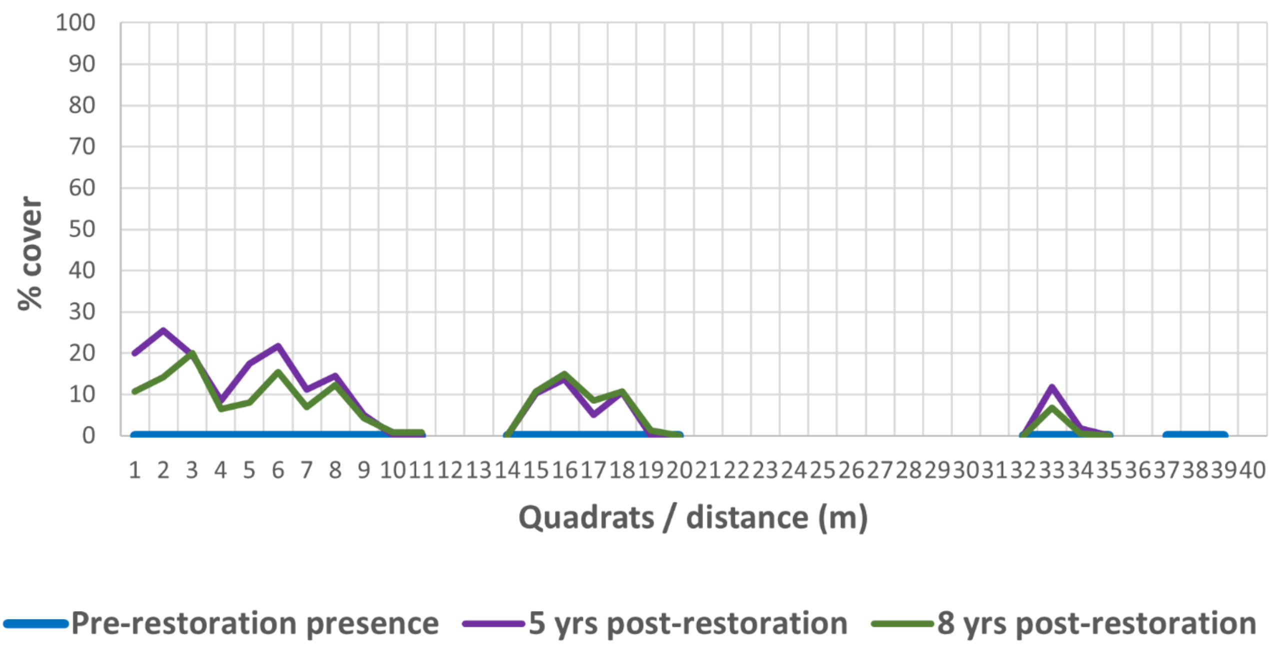

Figure 4. Bog asphodel distribution and cover at Vernies Allotment pre- and post-restoration. Blue line represents the pre-restoration presence of bog asphodel along the 40 m transect. Purple and green lines show % cover and distribution of bog asphodel along the transect 5 years and 8 years, respectively, post-restoration.

bog asphodel had not spread outside the original patches (defined by the blue lines indicating bog asphodel presence pre-restoration) at Vernies Allotment eight years post-restoration. This site was chosen to illustrate this point because it was one of the first sites to be restored (2008) and the boundaries of the bog asphodel patches remained static over eight years. The drainage ditch pattern on this site is also typical of Exmoor, a network of narrow shallow ditches close together. At the other eight sites the patch boundaries varied very slightly from year to year, both increasing and decreasing.

Both pre- and post-restoration abundance (% cover) data were available for six sites which have been restored since 2011. The mean change in spatial distribution was *10* ± 50 % and the mean change in abundance was -*30* ± 30 % (Figure 5). The apparent spread of bog asphodel at CH3 is anomalous as it represents an increase in presence from one to two sub-quadrats out of 120. Fewer plants were recorded, showing a reduction in abundance.

An inverse correlation between bog asphodel abundance and *Sphagnum* abundance may exist (Figure 6). The five sites (out of six) where there was a reduction in growth of bog asphodel post-restoration (Figure 5, blue bars) coincidentally showed an increase in *Sphagnum* growth (Figure 6, orange circles). An analysis of surveys providing abundance data at other sites showed a similar pattern at five of the ten sites. Of the 12 sites that demonstrated an increase in *Sphagnum* growth, ten (83 %) showed a corresponding reduction in bog asphodel growth. A non-significant negative correlation can be shown for the six sites (orange circles, Figure 6) where changes in growth were compared to baseline levels (Pearson's test, $r^2 = 0.46$).

Growth characteristics of bog asphodel

The phenology study carried out over two seasons at the Aclands site showed that bog asphodel growing on Exmoor is typical of the plants described by Summerfield (1974; Table 1). Some measurements namely leaf length, plant mass and inflorescence density showed significant differences between the two growing seasons. The mean water table depth was also significantly greater in 2018 (*40* ± 21 % of peat depth) compared to 2017 (*10* ± 15 % of peat depth; Wilcoxon rank sum test, $P < 0.0001$) (Table 2).

The bog asphodel phenology data were collected from two adjacent areas, one open to cattle grazing in the general area, and the other that had been fenced off for three years (Figure 2). The data were pooled for the results presented above. Although the leaves in the ungrazed area in 2017 were significantly longer than in the grazed area (mean length 270 ± 53 mm (ungrazed), 200 ± 56 mm (grazed), $P < 0.0001$, Welch two sample T test, $t = -6.31$), there was no significant difference in leaf length in the two areas in 2018. No other aspect of bog asphodel phenology was shown to vary significantly between the two areas.

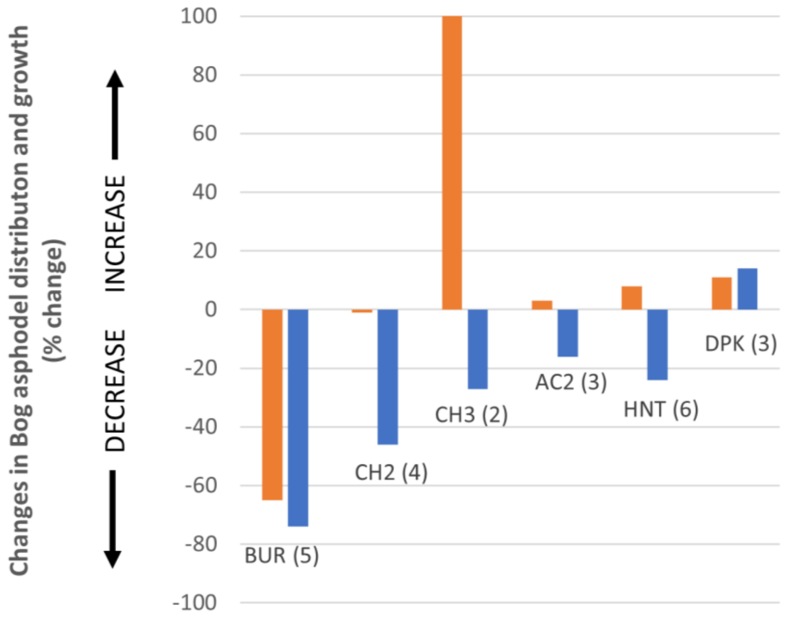

Figure 5. Changes in the distribution and abundance of bog asphodel at six Exmoor sites 2–6 years post-restoration. The name of each site is followed by the number of years since restoration in parentheses. Orange bars represent change in distribution as the relative change (%) of sub-quadrats containing bog asphodel. The blue bars represent the relative change in % cover of bog asphodel along the transect.

Bog asphodel phenology may be influenced by abiotic factors including climate and peat depth Water table depths were significantly different between years 2017 and 2018, both across the site and in the two areas (Table 2, Figure 7a). The peat was deeper in the ungrazed area (mean 43 cm versus 33 cm in the grazed area, Table 2), and this may influence the water table depth in very dry years. In the very dry summer of 2018 water table depth correlated with peat depth at Aclands (Figure 8). (Pearson's test r = -0.10, P > 0.05 (2017); r = -0.91, P < 0.01 (2018)).

The spring and summer temperatures and rainfall were significantly different in the two years (Figure 7b, Table 3). Spring 2018 was significantly colder and wetter than Spring 2017, whereas Summer 2018 was warmer and drier than the previous summer.

A separate investigation within the phenology study was undertaken in 2018 to establish bog asphodel's life history strategy. Grime (1979) recognised three main (CSR) contributions to a plant's life history strategy: **C**ompetitive ability (larger, long-lived plants); **S**tress tolerance (surviving in very adverse conditions without achieving significant size or seed production); and **R**uderality (small plants that produced vast numbers of seeds). For a large number of British species his data on growth rate and morphology could be plotted on a standard two-variable plot, on which it was possible to locate areas with high values for the C, S or R components. The results for bog asphodel from this study are shown (Figure 9), using a logarithmic scale on the horizontal growth axis to emphasise how slow growing bog asphodel is within a range of possible growth rates. The maximum growth rate (Rmax) was 0.26 g g^{-1} wk^{-1} and the Morphology index was 3 (Hand 2020). The Morphology index is calculated from the arbitrary classes to which leaf dimension, growth form and litter cover data are allocated (Grime 1979). Three other plants commonly found with bog asphodel on Exmoor, namely carnation sedge (*Carex panicea*), matt/mat grass (*Nardus*

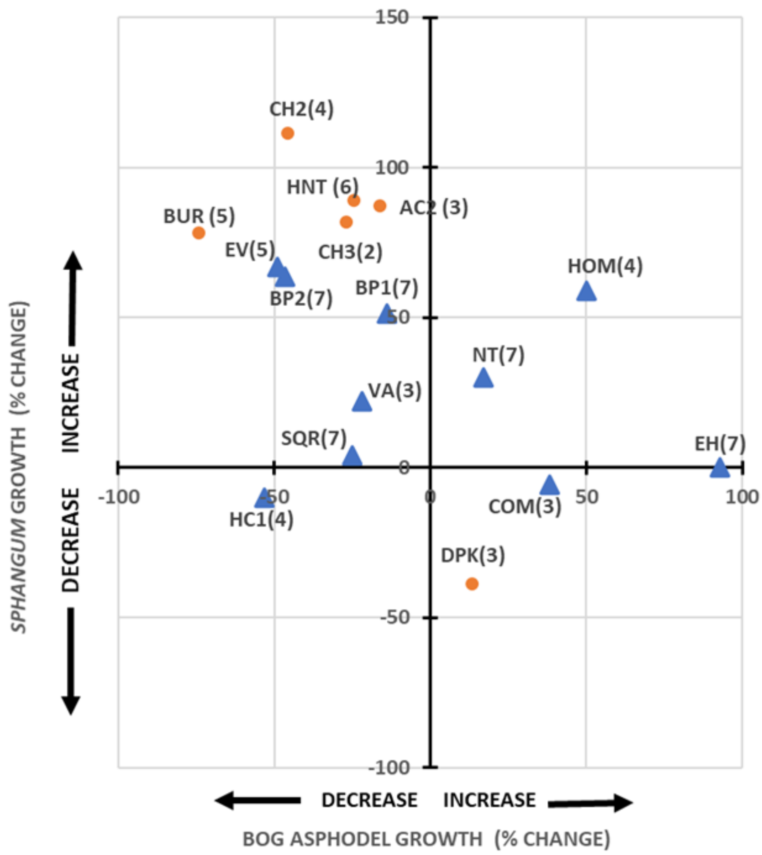

Figure 6. Relative changes in the abundance of bog asphodel and *Sphagnum* species at 16 Exmoor restoration sites. Abcissa: the relative change in % cover of bog asphodel (abundance) along the transect. Ordinate: the relative change in % cover of *Sphagnum* species (abundance) along the transect. Orange circles represent changes in abundance compared to pre-restoration levels. Blue triangles represent changes in abundance between two post-restoration surveys. For each point the time in years over which the change has taken place is given in parentheses.

stricta) and tormentil (*Potentilla erecta*) are also plotted (from Grime's data) to illustrate their similar strategies in this difficult habitat.

The growth curve of the plants used for the Grime calculations matched the growth curve of the plants being monitored for the plant's general growth characteristics (Table 1, 2018). Further analysis of the data showed that bog asphodel, in keeping with its conservative strategy, put only a small proportion of energy into seed production (Table 4). In 2017, 0.3 % of effort was directed to seed production. In 2018, with lower above ground productivity and more seed generation, the reproductive effort was still only 1 %.

Bog asphodel's life strategy is therefore one of high stress tolerance, with relatively slow growth, small size, and only moderately effective dispersal.

Table 1. Bog asphodel phenology on Exmoor 2017–2018 compared to reference data. Data are presented as the mean ± standard deviation (SD) where relevant. **Bold** type indicates statistically significant differences from reference data. Key: # indicates range over highland and lowland sites from Summerfield (1974); ## from *Ecological Flora of British Isles* http://ecoflora.org.uk/search_species2.php?plant_no=1830020010; [a] Welch two-sample t-test; [b] Wilcoxon rank sum test; ‡ July count; ‡‡ September count.

Characteristic	Reference data #	Aclands 2017	*n*	Aclands 2018	*n*	Significant differences 2017–2018
Leaf length (mm)	**50–400**	**230 ± 65**	**100**	**210 ± 60**	**187**	$P < 0.001$ [a]
Leaf width (mm)	2–5 ##	4.5 ± 0.9	100	5 ± 1	187	
Plant mass (g)		**0.2 ± 0.12**	**10**	**0.13 ± 0.02**	**10**	$P < 0.001$ [a]
Plant density (m^{-2})		300 ± 170	10	500 ± 250	10	
Aerial Productivity (mass x density) (g m^{-2})	20–200	80 ± 31	10	70 ± 35	10	
Inflorescence height (mm)	50–400	310 ± 51	21			
Inflorescences (% shoots)	**1.1–7.3**	**0.6 ± 0.4**	**10**	**3 ± 1.4**	**10**	$P < 0.01$ [a]
Inflorescences (m^{-2})		**2 ± 1.5**	**10**	**12 ± 6.7**	**10**	$P < 0.001$ [b]
Capsules per inflorescence	12.4–14.5	15 ± 4.1 ‡	21	16 ± 2.3 ‡‡	20	
Capsule length (mm)	≤ 12	6.6 ± 0.91	58			
Seeds per capsule	45–54	50 ± 14	56	50 ± 15	41	
Seed + wings length (mm)	7–9	4.3 ± 0.79	60	5.4 ± 0.73	60	
Seed length (mm)		1 ± 0.13	60	1.1 ± 0.19	60	
Seed mass (g x 10^{-4})	0.84–0.88	1.1 ± 0.67	13	0.7 ± 0.19	10	

Table 2. Water table depth below surface (as a proportion of peat depth) in 2017 and 2018, and peat depth, at Aclands; mean values ± SD are shown. [a] Welch two-sample t-test; [b] Wilcoxon rank sum test.

		2017	*n*	2018	*n*	Probability
Water table depth (as proportion of peat depth)	Aclands site	0.1 ± 0.15	110	0.4 ± 0.21	90	$P < 0.0001$ [b]
	Grazed area	0.1 ± 0.17	55	0.4 ± 0.21	45	$P < 0.01$ [b]
	Ungrazed area	0.1 ± 0.12	55	0.3 ± 0.18	45	$P < 0.0001$ [a]
		Grazed	*n*	Ungrazed	*n*	Probability
Peat depth (cm)		33 ± 1.6	5	43 ± 4.4	5	$P < 0.05$ [b]

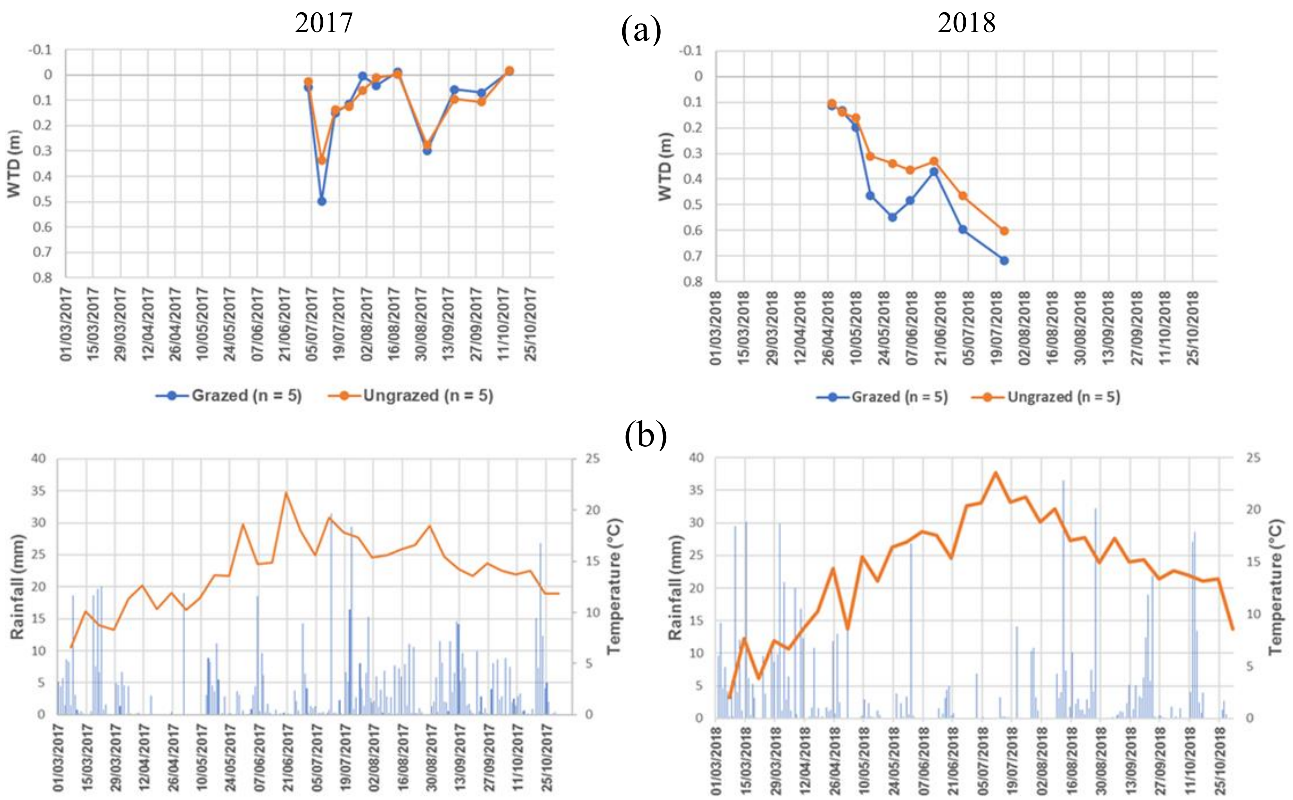

Figure 7. (a): water table depth (WTD) (m) at Aclands in 2017 and 2018. (b): daily rainfall at Hawkridge (blue bars, left hand vertical axis; Met Office 2021) and mean weekly temperature at Liscombe (orange line, right hand vertical axis; Met Office 2006), in 2017 and 2018.

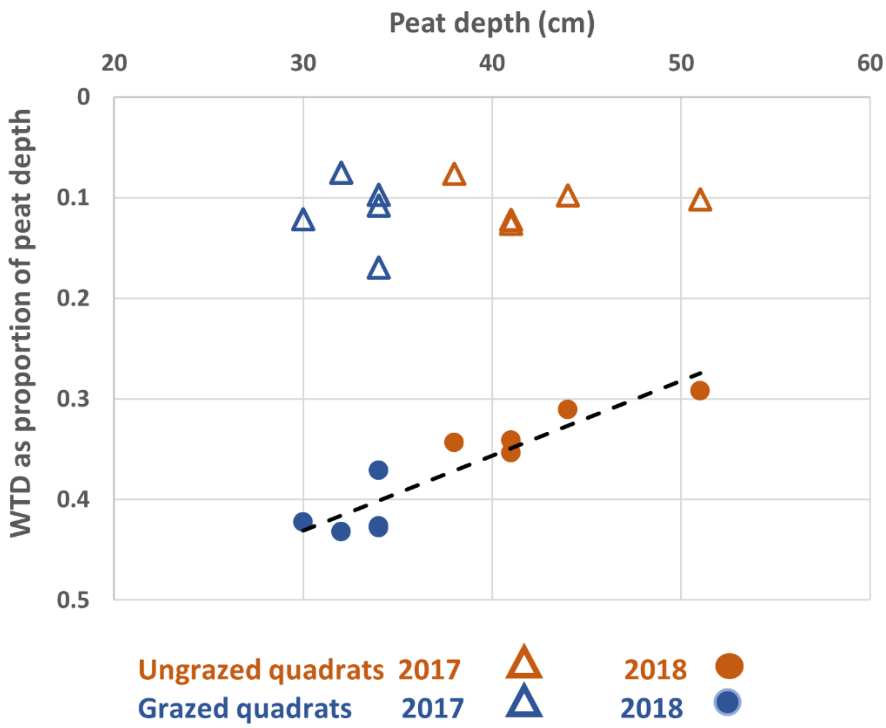

Figure 8. Correlation between water table depth (WTD) and peat depth at Aclands in 2017 and 2018. Triangles represent 2017 correlations, circles represent 2018 correlations, blue shapes represent the grazed quadrats, and orange shapes represent the ungrazed quadrats.

Table 3. Significant differences in mean daily temperature and mean daily rainfall on Exmoor in the spring and summer of 2017 and 2018 (Wilcoxon rank sum test).

Season	Mean daily temp. (°C ± SD) Liscombe	*n*	Probability *P*	Mean daily rainfall (mm ± SD) Hawkridge	*n*	Probability *P*
March–April 2017	10 ± 2.96	122	1.7e-6	3 ± 5.0	60	0.009
March–April 2018	8 ± 4.73	122		6 ± 7.7	60	
May–August 2017	16 ± 3.77	241	2.7e-7	3 ± 5.3	122	0.0002
May–August 2018	18 ± 4.11	241		2 ± 5.5	122	

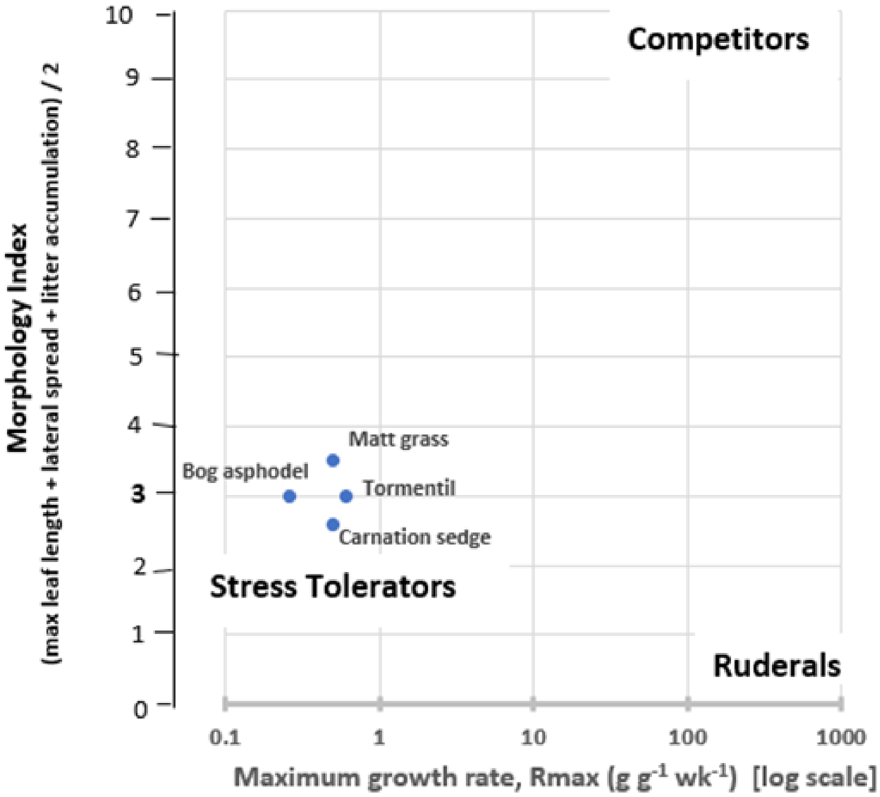

Figure 9. Maximum growth rate (g^{-1} g^{-1} wk^{-1}) and Morphology Index after Grime (1979) to demonstrate the life history strategy of bog asphodel (*Narthecium ossifragum*): very slow growth, small size and conservative form, i.e. stress toleration. Three other plants with similar strategies that are commonly found with bog asphodel on Exmoor are also shown: carnation sedge (*Carex panicea*), matt grass (*Nardus stricta*) and tormentil (*Potentilla erecta*).

DISCUSSION

The data from the 43 transects on Exmoor show that bog asphodel has increased its distribution very little post-restoration (Figures 3 and 4), nor has it appeared at the 21 sites from which it was absent pre-restoration (Figure 1). This behaviour is supported by the phenology study showing a plant with a very conservative growth and reproductive strategy (Figure 9, Table 4). In even more extreme conditions bog asphodel can exist in a state of biological inertia for years (Summerfield 1972). Grime's triangle is often quoted as a method to illustrate plant strategy allocation having been developed illogically from the two-variable plot by adding a third arbitrary axis in an arbitrary position to form a triangle (Grime 1979). However, not all plants, amongst them bog asphodel, can be accommodated within this triangle. A better

Table 4. Bog asphodel above ground and reproductive productivities in 2017 and 2018 at the Aclands site on Exmoor (mean values).

<table>
<tr><th colspan="2"></th><th>2017</th><th>2018</th></tr>
<tr><td rowspan="6">Variables</td><td>A. Plant mass (g) n = 10</td><td>0.2</td><td>0.13</td></tr>
<tr><td>B. Plant density (m^{-2}) n = 10</td><td>300</td><td>500</td></tr>
<tr><td>C. Inflorescence numbers (m^{-2}) n = 10</td><td>2</td><td>12</td></tr>
<tr><td>D. Capsules per inflorescence n > 20</td><td>15</td><td>16</td></tr>
<tr><td>E. Seeds per capsule n > 41</td><td>50</td><td>50</td></tr>
<tr><td>F. Seed mass ($g \times 10^{-4}$) n > 10</td><td>1.1</td><td>0.7</td></tr>
<tr><td rowspan="2">Productivity calculations</td><td>Aerial productivity ($g\ m^{-2}$) = A × B</td><td>60</td><td>65</td></tr>
<tr><td>Reproductive productivity ($g\ m^{-2}$) = C × D × E × F</td><td>0.165</td><td>0.672</td></tr>
<tr><td colspan="2">% effort directed to seed production</td><td>0.3</td><td>1</td></tr>
</table>

method (Pierce *et al*. 2017) that accommodates all plants uses three variables with fixed limits and a fixed sum that plot naturally in a triangle. The apices of the triangle are C, S and R strategies. However, the data necessary for this method to be applied were not generated for bog asphodel.

Two sites (data not included in these analyses) where there was evidence of significant bog asphodel expansion showed clear botanical evidence of mesotrophic conditions developing post-restoration. The possible link between *Sphagnum* growth and bog asphodel decline (Figure 6) might relate to water table depth. Many *Sphagnum* species thrive when the water table is near or at the surface whereas bog asphodel thrives best where there is water movement and a water table around 10 cm below the surface (Summerfield 1974). The evidence for bog asphodel's lack of response to peatland restoration, at least in the medium term, should alleviate the concerns of Exmoor land managers whose main land use is sheep and cattle farming.

There have, however, been a few reports of suspected bog asphodel poisoning in the Exmoor area (Robin May, personal communication). There is evidence that bog asphodel toxicity is mediated by co-factors in the substrate, although none has been definitively identified as yet (Mysterud *et al.* 2016, Barcelo *et al.* 2019). The damaged peat on Exmoor may not support bog asphodel's toxic potential. Indeed, some other changes which might result from peatland restoration, such as changes in greenhouse gas emissions and water quality, have yet to be demonstrated on Exmoor (Grand-Clement *et al.* 2014, Ritson *et al.* 2016, Green *et al.* 2018, Gatis *et al.* 2020). Exmoor's shallow peat may be slower to respond to rewetting because it does not have the same cushion of underlying intact peat as would be present in deeper peatlands, such as those of northern England, for example (Haapalehto *et al.* 2011, Luscombe *et al.* 2016, Urbanová & Bárta 2016, Green *et al.* 2017, Lundin *et al.* 2017). However, despite the shallow peatlands of Exmoor lying on the edge of the climatic envelope for blanket bog formation, and their being already threatened by climate warming (Gallego-Sala & Prentice 2013), these shallow peatlands can be successfully restored (Dixon *et al.* 2017, Lunt *et al.* 2019, Grobe *et al.* 2021).

The toxic effects of bog asphodel ingestion vary from year to year and from pasture to pasture (Mysterud *et al.* 2007, Ulvund 2012), and in this study the climate appeared to have a significant effect on bog asphodel leaf length and flower production, possibly mediated by variations in water table depth year on year. A comparison of rainfall and temperature patterns between Northumberland (where there are frequent reports of lambs being lost to bog asphodel poisoning) and Exmoor shows a greater increase since 2010 in rainfall and temperature in northern England than on Exmoor (Hand 2020).

Anecdotal reports (personal communications) of bog asphodel becoming more abundant when the Exmoor peatlands were rewetted coincided with Natural England restrictions on grazing (DEFRA 2005). Bog asphodel has a relatively high nutritional value in habitats often dominated by purple moor grass (*Molinia caerulea*) and bryophyte species (Hand 2020), and is readily grazed, especially the flowers (personal observation). The removal of grazing pressure is likely to have allowed existing plants to flower unhindered and thus appear more abundant. Conversely, bog asphodel plants in grazed and trampled areas tend to be smaller but more robust, a possible ecological response to the threat of predation (Whittaker 1975). This response can be exploited by using early season grazing to mitigate the toxic effects. Other mitigation strategies are to select less susceptible breeds of sheep and to have earlier lambing so that lambs are older and less susceptible to bog asphodel toxicity in early summer (Flåøyen 1991, Flåøyen & Jensen 1991).

In the short term, around a decade post-restoration, bog asphodel shows little response to the changed environmental conditions created by the rewetting of shallow marginal peatlands on Exmoor. It is therefore reasonable to conclude that neither the distribution nor the abundance of this potentially toxic plant would be affected by the restoration of shallow marginal peatlands in general.

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AUTHOR CONTRIBUTIONS

AH developed the research topic with MA. AH designed and carried out the experimental work and wrote the text. RB contributed to the discussions on peatland restoration and JC guided the ecology experimentation, content and presentation.

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