

Does the restoration of shallow marginal peatlands impact on the distribution and abundance of Bog Asphodel?

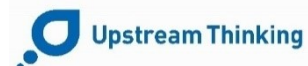
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Abstract

Healthy functional peatlands sequester carbon and are therefore important in the mitigation of climate change. In the United Kingdom 80% of peatland has been damaged by anthropogenic activities such as drainage and peat cutting. Most of the degraded peat is globally rare blanket bog found in upland regions, where the principal land use is livestock grazing.

Bog asphodel is a common British wildflower found on blanket bog and other very wet peatland habitats, which can also be fatally poisonous to grazing herbivores especially youngstock. Any increase could compromise the grazing in an already difficult environment.

This thesis investigated the growth and distribution of bog asphodel on shallow marginal restored peatlands on Exmoor in south-western United Kingdom, both in the field and from a vegetation survey database spanning 11 years from pre-restoration to present at 40 restored sites. The aims were to describe bog asphodel's phenology, and to assess its life history strategy and its contribution to sward quality in post-restoration habitats.

Bog asphodel's life history strategy is one of tolerating stress, rather than growing quickly or producing large numbers of seeds. This predicts that it will not respond rapidly to peatland restoration. On Exmoor, this prediction is confirmed by the historic data which show bog asphodel growing only slowly after restoration, and not spreading to other restored sites. Bog asphodel can contribute up to 20% of forage value in the transitional bog habitats that develop after rewetting, both in spring and autumn.

The implication for the restoration of shallow marginal peatlands is that bog asphodel persists post restoration but does not spread beyond pre-restoration patches or to other sites. Although it can contribute substantially to forage value in rewetted areas no significant injurious effects have been reported, either because more palatable and accessible grazing is available or because bog asphodel itself is less toxic on account of specific environmental conditions.

Table of Contents

Abstract.....	2
Table of Contents	3
List of Figures	4
List of Tables	6
Chapter 1. Introduction and literature review	7
1.1 Introduction	7
1.1.1 Peatland	7
1.1.2 Bog asphodel.....	9
1.1.3 Thesis aims and objectives.....	12
1.2 Peatlands literature review	13
1.2.1 Global peatlands.....	13
1.2.2 Peatland structure and vegetation	15
1.2.3 Peatlands and climate change.....	17
1.2.4 Peatlands and peatland restoration in the U.K.	19
1.2.5 Summary	23
1.3 Bog asphodel literature review	24
1.3.1 Ecological theory	24
1.3.2 The life form and life history attributes of bog asphodel.....	26
1.3.3 Community associations of bog asphodel	29
1.3.4 Bog asphodel toxicity.....	31
1.3.5 Summary	35
Chapter 2. Research into bog asphodel's relevance to peatland restoration	
36	
2.1 Bog asphodel's response to environmental change: life history	
attributes of plants as predictors of response to environmental change.	36
2.1.1 Introduction.....	36
2.1.2 Methodology	38
2.1.3 Results.....	45
2.1.4 Discussion	62
2.1.5 Conclusions	64
2.2 Bog asphodel's contribution to sward quality and grazing potential	66
2.2.1 Introduction.....	66
2.2.2 Methodology	69
2.2.3 Results.....	76
2.2.4 Discussion	93

2.2.5	Conclusions	95
Chapter 3.	Discussion	96
3.1	Bog asphodel ecology on Exmoor.....	96
3.2	Sward quality.....	99
3.3	Implications for peatland restoration	100
3.4	Limitations of the present study and suggestions for further work.....	101
3.5	Conclusions.....	102
	Acknowledgements	104
	Appendix: UK climate maps	105
	Glossary	107
	References	109

List of Figures

Figure 1:	Bog asphodel photographs.	11
Figure 2:	Global peatlands (Yu et al., 2010).....	14
Figure 3:	Peat structure	16
Figure 4:	Map showing U.K. peatlands, reproduced from (Bain et al., 2011) after (JNCC, 2011).	20
Figure 5:	Map of bog asphodel distribution in the United Kingdom (Summerfield, 1974)	27
Figure 6:	Location of bog asphodel demography experimental sites.....	39
Figure 7:	Experimental design for bog asphodel demography studies in 2017 and 2018	40
Figure 8:	Vegetation survey quadrat..	41
Figure 9:	Bog asphodel plant.....	42
Figure 10:	Growth of bog asphodel plants at Aclands in 2017 and 2018	47
Figure 11:	Ordination of bog asphodel (*) on Grime's Triangle.	48
Figure 12:	New growth from a bog asphodel rhizome 3rd May 2018.	50
Figure 13:	Bog asphodel distribution at Aclands pre- and post-restoration	51
Figure 14:	Bog asphodel distribution at Vernies Allotment pre- and post-restoration	51
Figure 15:	Bog asphodel distribution at Squallacombe pre- and post-restoration	52
Figure 16:	Changes in the distribution of bog asphodel at 18 restored sites on Exmoor.....	53
Figure 17:	Slope and altitude at the Aclands experimental site	54
Figure 18:	Water table depth (WTD) at the Aclands quadrats in 2017 and 2018 growing seasons	55
Figure 19:	Correlation between peat depth and water table depth (WTD) in the summer seasons of 2017 and 2018.	56
Figure 20:	Correlations between water table depth (WTD) and bog asphodel leaf height (A) and sward height (B) in 2018.	57

Figure 21: Correlations between peat depth and (A) maximum bog asphodel leaf height and (B) maximum sward height.	58
Figure 22: Maximum sward height in grazed and ungrazed areas in 2018.	59
Figure 23: Correlation between sward height and maximum bog asphodel leaf height in 2018.....	60
Figure 24: Relative changes in the abundance of bog asphodel and Sphagnum species at 16 Exmoor restoration sites.....	61
Figure 25: Growth of bog asphodel and Sphagnum species since restoration at six sites	61
Figure 26: Water table depth (WTD) at Aclands, and mean weekly temperature at Liscombe (UK Meteorological Office, 2019b) and daily rainfall at Hawkridge (UK Meteorological Office, 2019c) in 2017 and 2018.	65
Figure 27: Location of experimental sites within Exmoor National Park.	70
Figure 28: Experimental sites (A); habitat maps for Roosthitchen (B) and for Aclands (C).....	71
Figure 29: Photographs of the Aclands site.....	72
Figure 30: Photographs of the Roosthitchen site.....	73
Figure 31: Overall changes in five measures of forage value in Molinia-dominated (MD) and Transitional bog (TB) habitats on Exmoor.....	77
Figure 32: Changes in sward composition of Molinia-dominated habitat between spring (June) and autumn (September) at two sites.....	78
Figure 33: Changes in transitional bog sward composition between spring (June) and autumn (September) at two sites.....	79
Figure 34: Crude protein content and digestibility of 14 species in spring (blue) and autumn (orange).....	80
Figure 35: Changes in forage values between spring (blue) and autumn(orange) at Aclands.....	82
Figure 36: Changes in forage values between spring (blue) and autumn (orange) at Roosthitchen.	83
Figure 37: Contribution to the forage value of the individual species in Aclands Molinia-dominated habitat in Spring (blue) and Autumn (orange).	85
Figure 38: Contribution to the forage value of the 8 best individual species in Aclands transitional bog habitat in Spring (blue) and Autumn (orange).....	86
Figure 39: Contribution to the forage value of the 8 best individual species in Roosthitchen transitional bog habitat in Spring (Blue) and Autumn (orange). ...	87
Figure 40: Contribution of bog asphodel to forage quality at two transitional bog habitats on Exmoor.	90
Figure 41: Grazing patterns on Aclands (top) and Roosthitchen (lower) June - September 2018.....	92
Figure 42: Grazed bog asphodel (circled) Roosthitchen transitional bog September 2018.....	94

List of Tables

Table 1: Location and size of global peat deposits (after (Yu et al., 2010)).....	14
Table 2: National Vegetation Classifications in which bog asphodel is commonly represented (from (Rodwell, 1991)).....	30
Table 3: Species commonly associated with bog asphodel on Exmoor's peatlands (after Summerfield, 1974)	31
Table 4: Bog asphodel descriptive characteristics.....	45
Table 5: Comparison of key life history attributes of bog asphodel between 2017 and 2018.	46
Table 6: Calculations for Grime's Triangle ordination.....	47
Table 7: Bog asphodel above-ground productivity and seed production.	49
Table 8: Mean altitude and mean slope at the Aclands experimental site	54
Table 9: Statistical comparisons of temperature and rainfall in 2017 and 2018	63
Table 10: Common definitions of forage quality attributes and their measurement	68
Table 11: Species collected for forage analysis at Aclands and Roosthitchen in 2018 and 2019	75
Table 12: Statistical analysis of differences in forage values in spring and autumn at two sites.	81
Table 13: Bog asphodel forage values at two sites in spring and in autumn. ...	89

Chapter 1. Introduction and literature review

1.1 Introduction

Healthy functional peatlands are an important tool for the mitigation of climate change because of their value as carbon sinks (Joosten *et al.*, 2016). Restoration of damaged peatlands usually involves rapid rewetting and this environmental change is expected to impact vegetative structure. A study of the life strategies of peatland plants can predict temporal and spatial vegetation changes. Bog asphodel (*Narthecium ossifragum* (L.) Huds) is a common component of peatland habitats of interest because its leaves and flowers can be fatally toxic to grazing sheep and cattle. This thesis aims to investigate its life history from which to predict its likely response to the rewetting of the shallow marginal peatlands of south western United Kingdom (U.K.), and thus the wider implications for the management of restored peatlands.

1.1.1 Peatland

Peatland is a critically important ecosystem for the sequestration and storage of carbon (Joosten and Clarke, 2002; Lindsay, 2010). Peat is formed when dead organic matter accumulates because it is largely prevented from decomposing in saturated and therefore anaerobic conditions (Joosten and Clarke, 2002; Lindsay, 2010). Peatlands contain 20% of the world's carbon stores but only cover about 3% or 4 million km² of the world's surface (Bain *et al.*, 2011; Charman *et al.*, 2015; Joosten *et al.*, 2016). Most of the global peatlands lie in the northern hemisphere.

Most peat is formed from *Sphagnum* mosses which are uniquely structured to absorb and hold water, so that peatlands are globally important for both the water cycle and the carbon cycle. Besides their role in the cycling of carbon and water between land, water and the atmosphere, peatlands also provide goods such as fuel, fodder for livestock, timber, clean water and archaeological information, and contribute to cultural and aesthetic values (Billett *et al.*, 2010; Bonn *et al.*, 2016)

Since the industrial revolution of the 19th century peatlands in the United Kingdom (U.K.) have been progressively damaged by peat extraction for agriculture, by over-grazing, by drainage and by industrially created atmospheric pollutants like sulphur dioxide, nitrous oxide and heavy metals (Holden *et al.*, 2007). Damaged

peatlands become a source instead of a sink of atmospheric carbon as the peat decomposes on exposure to air, thus contributing to the increase in greenhouse gases (GHG), principally carbon dioxide (CO₂) and methane (CH₄), which is driving the recent rapid increase in average global surface temperature (Charman *et al.*, 2013; Collins *et al.*, 2013; Crowther *et al.*, 2016; IPCC, 2013.)

The realisation of the impact functioning peatlands could have on climate change mitigation is driving worldwide peatland conservation and restoration programmes, supported by the UN Conventions on Climate Change and on Biodiversity, and in Europe by directives on water and habitat (Bain *et al.*, 2011; Reed *et al.*, 2010).

In the U.K. peatland covers 9 – 15 % (46,000 – 77,000 km²) of the land and freshwater area (Bain *et al.*, 2011; Lindsay, 2010), a small proportion of the global peatland inventory of 4M km² (Yu *et al.*, 2010). However, because of the U.K.'s variable and temperate maritime climate, 90% of the U.K.'s peatland is blanket bog (Bain *et al.*, 2011; Billett *et al.*, 2010), and this represents 30% of a globally rare habitat found only in high-altitude oceanic fringes (Gallego-Sala *et al.*, 2010). These important blanket bog reserves are also particularly threatened by a globally warming climate because the U.K. lies at the southern climatic limit for such bogs in the northern hemisphere (Gallego-Sala and Prentice, 2013).

The U.K. has been at the forefront of peatland restoration since the 1990s, particularly the restoration of blanket bog which usually involved blocking the drainage structures to re-establish a permanently high water table (Andersen *et al.*, 2017; Grand-Clement *et al.*, 2015; Holden *et al.*, 2017; Parry *et al.*, 2014). Numerous studies have looked at the botanical and physical science of restoration (Bellamy *et al.*, 2012; Gatis *et al.*, 2016; Green *et al.*, 2017, 2018; Renou-Wilson *et al.*, 2018; Rey Benayas *et al.*, 2009). Water quality and hydrological changes associated with restoration are a major concern of water companies, who have supported research since restoration started in the U.K. because of their concern for watershed sustainability and management. The justification for carrying out large scale restoration of remote upland areas is however much debated, from both the economic and the political perspective (Bonn *et al.*, 2016; Grand-Clement *et al.*, 2013; Moxey and Moran, 2014; Stott *et al.*, 2012).

Exmoor is an area of coastal uplands in the South West peninsular of the U.K., in Somerset and Devon, lying on the very edge of the climate envelope suitable for the formation of blanket bog (Gallego-Sala *et al.*, 2010). For this reason the peat on Exmoor is shallow by U.K. standards, often less than 1m deep (Gallego-Sala and Prentice, 2013). Like much of the U.K's peatlands Exmoor's blanket bogs have become severely degraded by peat cutting, over-grazing, ploughing, burning and draining (Bain *et al.*, 2011; J Holden *et al.*, 2007; Grand-Clement *et al.*, 2015). Peatland restoration on Exmoor started in the 1990s and continued from 2006 when Exmoor Mires Partnership was formed to carry out a programme of mire restoration across Exmoor.

1.1.2 Bog asphodel

Bog asphodel (*Narthecium ossifragum*) is a typical component of the very wet, acidic and nutritionally poor environment found in healthy upland peatlands, along with *Sphagnum* mosses, cotton grasses and certain acid loving dwarf shrubs. It has fleshy curved bright green leaves which grow from persistent patches of rhizomes in spring and bright yellow spikey inflorescences in June and July (Summerfield, 1974)(Figure 1A,B,C). The flowers mature into shiny brown capsules (Figure 1D) which dehisce to release winged seeds (Figure 1E).

Bog asphodel is listed as an indicator for blanket bog and *Molinia* and rush pasture habitat under the Common Standards Monitoring scheme (JNCC, 2006). In other words, it indicates suitable abiotic conditions for these habitats, a very wet substrate that is acidic and nutritionally poor. Any changes in its distribution could be used as a proxy for monitoring environmental change such as that produced by peatland restoration works.

The *raison d'être* of all living organisms is to survive and reproduce, and to do this plant species have evolved a wide variety of life history strategies, which are intimately linked to their phenotypic life form (Grime, 1979; Grubb, 1976). These strategies utilise a plant's capacity to grow vegetatively and to produce seeds to differing degrees (Harper, 1977a). Understanding a plant's life history strategy allows its response to environmental change to be predicted, for example to the rapid hydrological changes wrought by blocking the ditches in drained peatland. This in turn will dictate if a plant will be an indicator of abiotic environmental conditions or a sentinel of ecosystem change involving complicated changes in vegetation assemblages and other abiotic and biotic systems.

Peatland restoration plans focus on a holistic approach, supporting all the benefits that accrue from healthy peatlands, for example flood alleviation and the provision of livestock fodder, as well as carbon sequestration (Aronson et al., 2006; Griscom et al., 2017). These plans can be informed by an understanding of the expected response of key plants e.g. *Sphagnum* species for re-establishing carbon sequestering function (González et al., 2014). Bog asphodel is notorious for the toxicity of its leaves and flowers for young grazing livestock (Mysterud et al., 2016; Pollock et al., 2015). Sheep farming is the main land use of the U.K's uplands so an understanding of how bog asphodel might react to peatland re-wetting is important for the sustainability of the restoration process, especially as it is a relatively nutritious and palatable plant in habitats which do not otherwise provide rich grazing (Pollock et al., 2007).

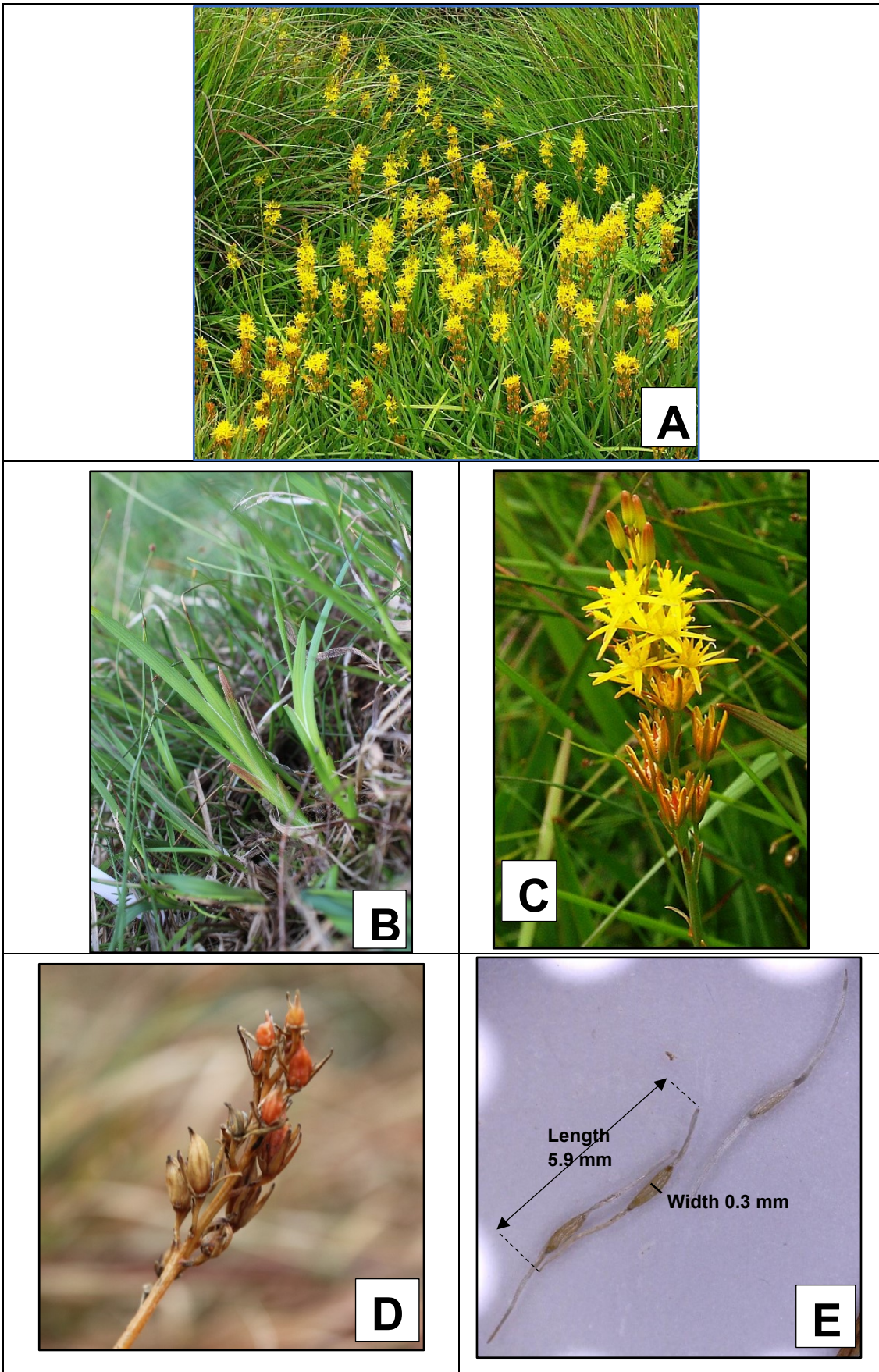


Figure 1: Bog asphodel photographs.

A: Bog asphodel patch(Eskdale, July 2004 © RWD; B: Bog asphodel leaves amongst purple moor grass (Exmoor, July 2017); C: Bog asphodel inflorescence (Duddon Valley September 2008 © RWD); D: Mature Bog asphodel inflorescence (Exmoor, October 2017); E: Bog asphodel seeds (Exmoor, October 2017)

1.1.3 Thesis aims and objectives

The aim of this thesis is to investigate the significance of bog asphodel for the restoration of shallow marginal peatlands in south-western U.K. In order to achieve this aim, the life history strategy of bog asphodel as a predictor of its response to environmental change will be investigated, and the consequences of this response for the management of restored shallow marginal peatlands assessed.

Specific objectives are to:

- Establish the life form attributes of bog asphodel growing on the shallow marginal peatlands of Exmoor;
- Establish the life history strategy of bog asphodel growing in the same shallow marginal peatland environment;
- Assess the impact of restoration on the distribution and abundance of bog asphodel on Exmoor;
- Assess the contribution bog asphodel makes to sward quality on Exmoor; and
- Assess the consequences for the management of shallow marginal peatlands.

1.2 Peatlands literature review

1.2.1 Global peatlands

Peatlands are the largest terrestrial stores of global carbon although they only occupy 3 – 5 % of global land mass (Joosten and Clarke, 2002; Page and Baird, 2016). Overall, global peatlands contain 20 % of global soil carbon, with an average of 1125 t C ha⁻¹ (Joosten *et al.*, 2016). Peatlands started to form first in tropical areas (defined as 30° N - 30° S) more than 20 ka (1 ka = 1000 cal yr BP), then in southern regions more than 15 ka and lastly in northern regions 11 – 9 ka (Loisel *et al.*, 2017; Macdonald *et al.*, 2006; Page *et al.*, 2004; Yu *et al.*, 2010) (Table 1). The peat deposits of the northern hemisphere are by far the most significant, stretching from Alaska and Canada, through northern Europe to Siberia, covering an area three times that of the tropical peatlands and containing ten times more carbon (Loisel *et al.*, 2017; Macdonald *et al.*, 2006) (Figure 2).

Peatland growth over millennia can be linked to climatic conditions (Yu *et al.*, 2009). Peat development did not start in the northern hemisphere until 11 ka as the region was still covered in retreating ice from the last ice age (Macdonald *et al.*, 2006). Since then, however, climatic conditions in the northern hemisphere have favoured peat formation with warm summers to maximise photosynthesis and carbon storage, and cold winters to minimize the loss of carbon through respiration (Yu *et al.*, 2010)

Early peatlands were warmer sedge-dominated CH₄ - emitting fens changing to *Sphagnum*-dominated ombrotrophic mires as the climate cooled (Beaulieu-Audy *et al.*, 2009; Charman *et al.*, 2015; Macdonald *et al.*, 2006; Nichols *et al.*, 2014). There is a general trend for higher latitude peatlands to accumulate carbon faster and to expand more geographically than the lower latitude peatlands where the balance between carbon sequestration and carbon emission through respiration and decomposition is tilted more towards carbon emission by the warmer climate. (Gallego-Sala *et al.*, 2018; Piilo *et al.*, 2019). Paleo-ecological reconstructions have shown that *Sphagnum* dominated habitats may also accumulate peat and carbon faster under suitable climatic conditions than sedge- dominated fens growing in warmer, drier conditions (Beaulieu-Audy *et al.*, 2009; Nichols *et al.*, 2014). The fine balance between carbon sequestration and emission is driven by

a series of complex ecohydrological feedbacks (Gatis *et al.*, 2016; Korrensalo *et al.*, 2017; Waddington *et al.*, 2015).

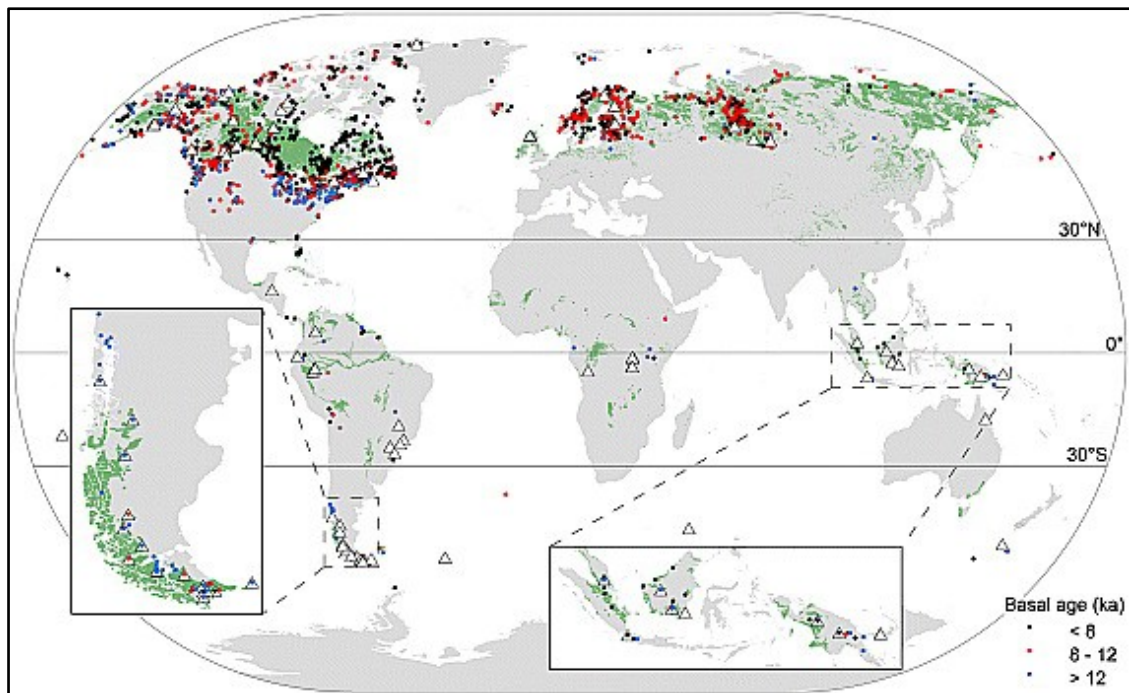


Figure 2: Global peatlands (Yu et al., 2010)
 Map showing that most carbon storing peatlands are located around the globe in the northern hemisphere with smaller fields in southern South America and on the Equator in Indonesia (inserts).

Geographical location	Initiation of peat formation	Present day area	C content	Mean rate of C accumulation 12 ka to present
Northern Hemisphere	11 – 9 ka	$4 \times 10^6 \text{ km}^2$	547 GtC	$18.6 \text{ gC m}^{-2} \text{ yr}^{-1}$
Tropical region	>20 ka	$368,500 \text{ km}^2$	50 GtC	$12.8 \text{ gC m}^{-2} \text{ yr}^{-1}$
Southern Hemisphere	>15 ka	$45,000 \text{ km}^2$	15 GtC	$22.0 \text{ gC m}^{-2} \text{ yr}^{-1}$

Table 1: Location and size of global peat deposits (after (Yu et al., 2010)).
 The table shows that the largest amounts of carbon are stored in the Northern Hemisphere. Carbon accumulated most quickly in the smallest area of peatland in Patagonia, Southern America.

There is now very little growth in peatland area around the world, but carbon continues to be accumulated, most rapidly in the northern peatlands. Although a warmer climate increases the productivity of peatlands, with peat occasionally being laid down at rates as high as $50 \text{ mm m}^{-2} \text{ yr}^{-1}$ against a global average of $3 \text{ mm m}^{-2} \text{ yr}^{-1}$ the sensitive balance between productivity, decomposition and climate suggests that peatlands are unlikely to remain carbon sinks beyond the present century (Gallego-Sala *et al.*, 2018; Piilo *et al.*, 2019). This has led to ‘eco-doom’ views being expressed by some commentators, fuelled by recent evidence that atmospheric carbon is still increasing (Allen *et al.*, 2018).

Definitions of peat and peatlands vary across institutions, disciplines and countries (Xu *et al.*, 2018). Peat can be defined as soil or substrate containing a minimum of 30% organic matter (Joosten and Clarke, 2002; Loisel *et al.*, 2014; Page and Baird, 2016) to at least 50% organic matter (Burton and Hodgson, 1987). However, organic soils or histosols containing at least 18 – 20% organic material, are usually regarded as the same as peat or peaty soils (Michéli *et al.*, 2006). Approximately half of the organic dry mass is carbon (Andrejko *et al.*, 1983). Peat is also defined by its thickness, the minimum varying from 10 – 100 cm across disciplines and countries (Bord na Móna, 1984; Joosten and Clarke, 2002; Michéli *et al.*, 2006). Shallow peat is defined as having a minimum depth of 10 - 40cm. Such a variety of definitions leads to a wide range of estimates of carbon reserves at global and national levels (Barthelmes *et al.*, 2009; Lindsay, 2010; Xu *et al.*, 2018). Yu *et al.* (Yu *et al.*, 2010) estimated the carbon content of global peatlands to be 612 GtC (Table 1).

1.2.2 Peatland structure and vegetation

Peat comprises two main layers, an upper acrotelm (10 – 25 cm thick) of actively growing plants with a variable water table, and a lower saturated catotelm (up to 10m thick) (Ivanov, 1981; Lindsay, 2010; Luscombe *et al.*, 2016) (Figure 3). The lower part of the acrotelm becomes increasingly anaerobic as oxygen is squeezed out by compacting plant material and water. *Sphagnum* species also create their own acidic environment which further slows decomposition (Clymo, 1994). The boundary between the acrotelm and catotelm marks the lowest level of the water table. The catotelm is anoxic and permanently saturated, consequentially there is very little water movement, decomposition or microbial activity. The dead plant material and its carbon content is thus preserved, essentially for ever unless the peat is dried out or physically damaged.

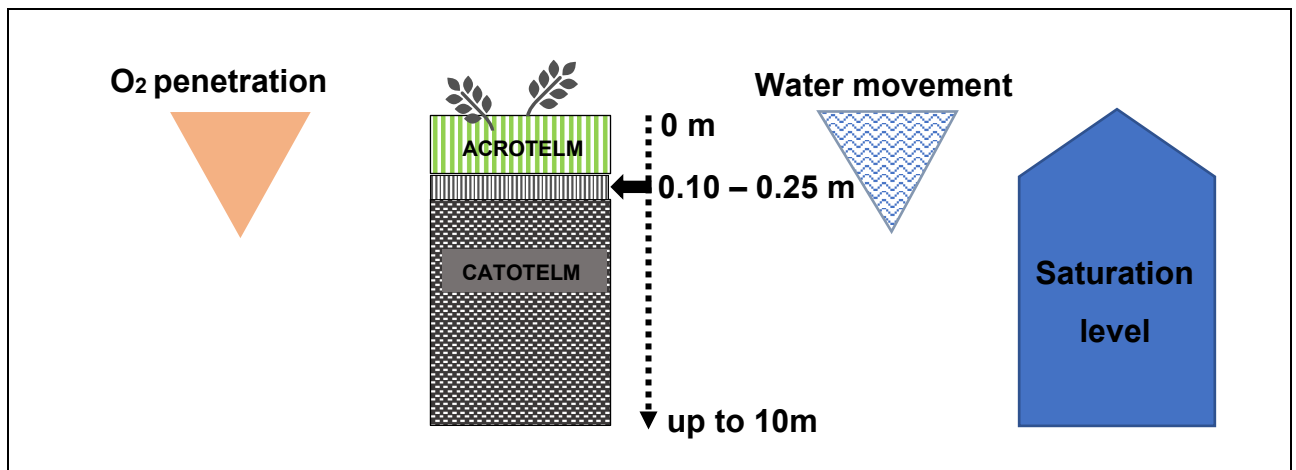


Figure 3: Peat structure

Diagram to show how oxygen penetration, water movement and saturation levels change between the acrotelm and catotelm (after Lindsay 2010)

Peatlands comprise many different types of habitat, dictated by their hydrology and thus the level of nutrients available. Each type has its characteristic vegetation; rain-fed (ombrotrophic) nutrient-poor bog vegetation is dominated by acid-forming *Sphagnum* (peat moss) species; groundwater- and rainwater-fed (minerotrophic) bog and fen vegetation is less acidic and comprises a much higher proportion of vascular species such as sedges and grasses (Lindsay, 2010; Rodwell, 1991). Intermediate poor fen or mesotrophic bog is typical of damaged peatlands and is dominated by *Molinia caerulea* (purple moor grass), which can tolerate the fluctuating water table levels. The *Sphagnum* mosses of ombrotrophic mires are associated with *Eriophorum* (cotton grass) species and dwarf shrubs, whereas minerotrophic mires (fens) support a variety of herb, grass and sedge species.

Species vary in the rate at which they decay and the slow decaying *Sphagnum* mosses contribute more to peat formation than the faster decaying herbs, sedges and grasses (Lindsay, 2010). However, a more stable carbon sink is created from assemblages offering a variety of photosynthesis rates, seasonal prominence and vegetation dominance (Korrensalo *et al.*, 2017). Moreover, changes in land use can shift the vegetation towards more vascular plants with a corresponding shift towards more carbon emissions (Veber *et al.*, 2018). Overall the rate of carbon accumulation (in dead organic matter) is determined by the balance (the net ecosystem exchange) between carbon sequestered during photosynthesis and carbon given off as carbon dioxide (CO₂) and methane (CH₄) in respiration and decomposition.

1.2.3 Peatlands and climate change

The anthropogenic release of carbon from the burning of fossil fuels and changes in land use as economic and population growth expanded rapidly with industrialisation from the 1850s has increased the concentrations of GHG, principally CO₂, CH₄ and nitrous oxide, in the atmosphere (IPCC, 2013). This in turn has driven a rapidly warming global climate (IPCC, 2014; Myhre *et al.*, 2013). Climate change refers to the various effects of global warming including increasing surface and ocean temperatures, sea level rise as ice melts and extreme weather events (Collins *et al.*, 2013). The knock-on effects of climate change phenomena are having profound and catastrophic effects on the natural environment and human populations, threatening global food and water security.

Peatlands have become a focus of attention for the mitigation of global warming, not least because they are uniquely sensitive to temperature change (Beaulieu-Audy *et al.*, 2009; Joosten and Clarke, 2002; Page and Baird, 2016; Waddington *et al.*, 2015). A warmer climate drives more primary productivity so that there is more plant material to be laid down as peat, but a higher rate of decomposition. For global warming the crucial point is whether primary production or decomposition dominates the carbon cycle. On the one hand Crowther (Crowther *et al.*, 2016) looked at emissions from soil at different levels of warming and found that the driver for soil emissions was the soil carbon stock. This suggests that the carbon rich northern peatlands where 80% of the global terrestrial carbon is stored would be particularly vulnerable to global warming. In addition, this net carbon emission would act as a positive feedback for further global warming by increasing the carbon levels in the atmosphere. On the other hand, Yu (Yu *et al.*, 2009) found peak levels of carbon accumulation (8.4 – 38g C m⁻² yr⁻¹ in Alaska) 11 – 8 ka in a period of warmer climate suggesting that productivity in this case was more dominant than decomposition. The frozen peatlands in the Arctic region only cover a relatively small area but contain a disproportionate amount of carbon (14% global stock) and therefore their fate is of critical importance to the global carbon balance (Bacon *et al.*, 2017; McGuire *et al.*, 2014; Swindles *et al.*, 2015). As they thaw inundated fens develop which act as small carbon sinks (< 0.8 Pg C yr⁻¹), supported by the high levels of saturation. However, the high levels of water also encourage the largely vascular vegetation to release more CH₄, thus creating a strong positive feedback on global warming (Christensen *et al.*, 2003).

It is uncertain whether global warming will drive these unfrozen peatlands to be net sinks or net sources of carbon (McGuire *et al.*, 2014). In support of a net sequestration of carbon Charman (Charman *et al.*, 2013) looked at carbon accumulation over the last 1000 years and demonstrated a linear relationship between photosynthesis and the length of the growing season and photosynthetically active radiation, suggesting that primary production is driving the carbon cycle, rather than decomposition. Functional peatlands are therefore expected to act as stronger carbon sinks in a warmer climate in the short term and at mid to higher latitudes but for this process to decline within 100 years as the climate warms even more, especially at lower latitudes (Gallego-Sala *et al.*, 2018; Lunt *et al.*, 2019).

Peatlands provide many other environmental and human benefits, or eco-system services, for example clean water, fuel, grazing, food and cultural and aesthetic value (Billett *et al.*, 2010; Bonn *et al.*, 2016; Grand-Clement *et al.*, 2013; Minayeva *et al.*, 2017; Swindles *et al.*, 2016). The archaeological record contained within peat as pollen and macrofossils provides invaluable evidence of past land use, cultures, climates and the reaction of peatlands to past climate change (Grand-Clement *et al.*, 2013; Swindles *et al.*, 2016). Given the rarity of peatlands worldwide, they support flora and fauna that are rare in global terms. Conversely, peatlands that have been degraded by drainage, over-grazing, burning, peat cutting and atmospheric pollution are net carbon emitters and cannot lay down peat, modulate rainfall runoff or support a healthy wildlife population (Grand-Clement *et al.*, 2014; Holden *et al.*, 2007).

Overall, peatlands feature strongly in the science of climate change and peatland conservation and restoration has become an international priority (Bonn *et al.*, 2014; Collins *et al.*, 2013; Froking *et al.*, 2011) despite a tendency to underestimate their potential for mitigation (Joosten *et al.*, 2016; Leifeld and Menichetti, 2018). Peatlands are afforded protection under the RAMSAR Convention (1971) which protects wetlands, the UN's Convention for Biodiversity and Framework Convention on Climate Change (1982), as well as the European Union's Water Framework Directive and Habitat and Species Directive (1992) (Page and Baird, 2016). These instruments along with non-governmental organisations e.g. the International Union for the Conservation of Nature, are

driving an extensive worldwide programme of peatland restoration and conservation.

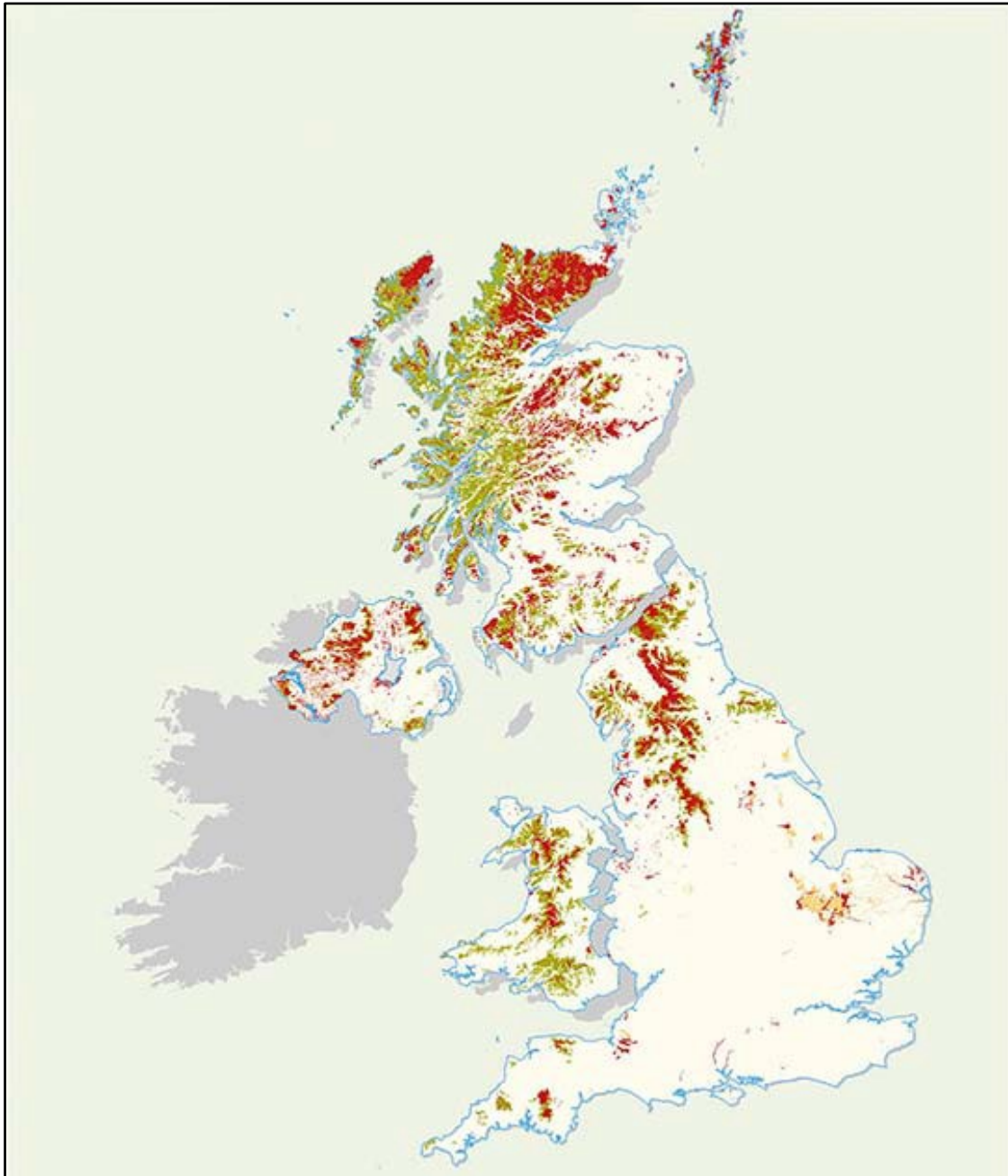
1.2.4 Peatlands and peatland restoration in the U.K.

The U.K. lies on the southern edge of the climatic envelope for the northern peatlands, strongly influenced by a wet oceanic climate (Gallego-Sala *et al.*, 2010). The U.K. has around 46,000 – 77,000 km² of peatland, approximately 1 % of global total and 9 – 15 % of the European peatlands (Bain *et al.*, 2011). The current estimate of the U.K.'s carbon inventory is at least 3.2 billion tonnes of carbon (Bain *et al.*, 2011).

Most of the U.K.'s peatland is blanket bog and raised bogs covering around 23,000 km² or 9.5 % of the U.K. land area, mostly in the uplands of Northern Ireland, Scotland, Wales, northern England and south-western England (Figure 4). As the U.K. holds 30 % of the global blanket bog inventory, it has international responsibility for its management and conservation (Bain *et al.*, 2011).

Blanket bog as its name suggests spreads over upland landscapes of varying topography. Most of blanket bog in England and Wales lies in National Parks and Areas of Outstanding Natural Beauty and therefore has an important role in landscape value for which these areas were designated (Shepherd *et al.*, 2013), as well as its roles in the carbon and water cycles. Blanket bog peat comprises 50 % carbon, ten times more carbon than is found in mineral soils, and in U.K. varies in depth from 30cm to as much as 12 m.

The cold, wet, low nutrient environment is inhabited by relatively few species such as the *Sphagnum* mosses, tiny insectivorous Sundews, the acid-loving bog asphodel, specialist insects like the Bog Hoover fly, and the birds and mammals that feed on them (Shepherd *et al.*, 2013). These specialist species are often rare elsewhere so blanket bog is important both for its geographical rarity and for the rarity of its inhabitants. In U.K. blanket bogs started to form 10 ka as the ice retreated and are a semi-natural habitat in that they started to form when the earlier woodlands were harvested (Bray, 2015).



Peat and peaty soils of the United Kingdom. Deep peat soils (dark brown), shallow peaty soils (green), wasted deep peat soils (light brown). Peat in South-East England is largely fen peat. Reproduction by permission of OS on behalf of HMSO@ Crown copyright and database Right 2010, MLURI 100019294, AFBI 1:50000 soil digital Data, National soil Maps @ Cranfield University, BGS 1:50000 digital data (license 2006/072)

Figure 4: Map showing U.K. peatlands, reproduced from (Bain et al., 2011) after (JNCC, 2011).

The U.K. in common with Western Europe has lost more than half its peatlands in the last 1000 years because of anthropogenic activities such as peat cutting, over-stocking and industrial pollution (Andersen *et al.*, 2017; Caporn and Emmett, 2009; JNCC, 2011; Smart *et al.*, 2010). 80 % of the U.K's remaining peatlands are damaged (Bain et al., 2011). The blanket bogs on, for example, the South Pennines and in the Peak District had become largely bare peat that had been

stripped of its vegetation by acid rain; whereas in other areas, the blanket bog was criss-crossed by shallow drainage ditches which had dried out the peat so much that purple moor grass and heather had replaced the peat-forming *Sphagnum* mosses (Gatis *et al.*, 2016; Grand-Clement *et al.*, 2015; Holden *et al.*, 2007, 2011; Wilson *et al.*, 2010). On Exmoor even before the enterprising Midlands businessman, John Knight, started a programme of extensive drainage in the 1830s, peat was cut extensively for domestic fuel and Exmoor provided summer grazing for huge numbers of animals. Drainage ditches continued to be cut all over Exmoor up until the 1980s (Mills *et al.*, 2010). As well as draining the peatlands, headage payments in 1960s and 1970s encouraged heavy grazing, although not as heavy as in the 16th and 17th centuries, and regular burning of large areas of heather moorland to encourage the more palatable grasses and younger heather shoots. The over-grazing and the burning only served to exacerbate the destruction of peatland habitat already stressed by drainage, peat cutting and pollution.

As well as international and European obligations to protect peatlands, there is economic benefit in both climate change mitigation and in all the other socio-economic benefits that accrue from healthy peatlands, like clean water, flood alleviation, biodiversity and landscape value (Moxey and Moran, 2014). There was a public perception that upland peatland is barren and useless, and that ecosystem services such as a clean and plentiful water supply were 'free' (Aronson *et al.*, 2006; Byg *et al.*, 2017). The socio-economic benefits of restoration are now better understood and accepted (Bonn *et al.*, 2014; Moxey and Moran, 2014).

Most of peatland restoration work in Europe is funded from EU funds such as the EU-LIFE Nature programme (Andersen *et al.*, 2017). However, NGOs and private companies with a vested interest in environmental conservation also contribute, as now does the Department for Farming and Rural Affairs (DEFRA). Southwest Water, for example, a private water company in South West England, largely funds the restoration work of the Exmoor Mires Partnership on Exmoor as part of their Upstream Thinking environmental management programme (EMP, 2019). Various levels of farming subsidies have encouraged more sustainable management of upland peatlands using CAP funding (Martin *et al.*, 2013). A system is also being developed to reward landowners for managing their land for the ecosystem services it can provide, the so-called Payment for Ecosystem

Services (PES) (Bonn *et al.*, 2014; Evans *et al.*, 2014; Glenk and Martin-Ortega, 2018).

Peatland restoration in the U.K. started in 1990s, and since then the U.K. has developed considerable expertise in the practice and science of restoration e.g. (Gatis, Luscombe, *et al.*, 2019; Holden *et al.*, 2017; Stephen *et al.*, 2011; Thom and Hinchley, 2019; Wilson *et al.*, 2010) backed by government legislation (DEFRA, 2007, 2009; Natural England, 2013).

Restoration strategies involve rewetting and revegetating damaged peatlands to re-establish, in the long-term, functional carbon sinks (Menberu *et al.*, 2016) as well as the many other ecosystem services that healthy peatlands provide (Bonn *et al.*, 2014; Grand-Clement *et al.*, 2013; Luscombe *et al.*, 2016; Ritson *et al.*, 2016). The rewetting is achieved by blocking drainage features with various materials according to the terrain, wooden or stone dams, peat or bales of sheep's wool, heather or *Molinia* (Armstrong *et al.*, 2009; Thom and Hinchley, 2019). The initial aim is to stabilise the water table at a higher level and alleviate flash flooding (Grand-Clement *et al.*, 2015; Holden *et al.*, 2017; Shuttleworth *et al.*, 2019; Wilson *et al.*, 2010). Emphasis is on minimal landscape impact using local materials whenever possible. Once rewetted, *Sphagnum* and other blanket bog species will regenerate or can be planted (Bellamy *et al.*, 2012; González *et al.*, 2014).

Blanket bog peat can vary in depth from 0.3 m to several metres, an important factor in predicting the response to ditch blocking. Very shallow damaged peatlands pose particular problems because there is no layer of intact wet peat above the underlying mineral substrate to slow the movement down-slope (Grand-Clement *et al.*, 2015). Where there is sufficient depth of peat rainfall trapped by ditch blocks can flow across the landscape, as would happen in a pristine peatland (Luscombe *et al.*, 2016).

The speed of spontaneous vegetation recovery is however very variable depending on the degree of peat degradation, peat depth, the effectiveness of re-wetting and the present and antecedent climate (Bellamy *et al.*, 2012; Grand-Clement *et al.*, 2014; Williamson *et al.*, 2017). Additional interventions such as *Sphagnum* re-introduction, *Molinia* mowing, landscape reprofiling or stabilising

bare peat with grasses and heather may be required (Lunt *et al.*, 2010; Rosenburgh, 2015; Thom and Hinchley, 2019).

There are, therefore, still many unknowns in peatland restoration, relating to the timescale of recovery, the most effective means of re-establishing peat forming vegetation and the effects of rewetting on peatland vegetation generally. Ditch-blocking and rewetting do not change GHG emissions in the short term (Gatis *et al.*, 2016; Green *et al.*, 2017) despite this being fundamental to peatland restoration. It is anticipated that this should change as *Sphagnum* cover is re-established but restored blanket bogs can go on emitting significant amounts of GHG even 30 years after restoration (Vanselow-Algan *et al.*, 2015). Recent research has focused on translating vegetation change and any related changes in GHG emissions from local to landscape scale to better understand the potential impact of restoration on climate change (Gatis *et al.*, 2017).

1.2.5 Summary

Peatlands are the most concentrated source of global carbon and thus critically important in the global carbon cycle and for mitigating the effects of climate change as driven by the ever-increasing levels of GHG in the atmosphere. Many of world's peatlands, including those in the U.K, have been severely damaged by inappropriate use and are the focus of restoration programmes enforced by national and international legislation. Peatland restoration in the U.K. has particular significance because the U.K. holds a third of the global inventory of rare blanket bog. Aside from their fundamental importance in the carbon cycle, healthy peatlands offer other goods and services, such as food, fuel, clean water, flood alleviation and cultural and aesthetic value. The restoration process is continually evolving as it is informed with experience and research on all levels, hydrology, vegetation, landscape impacts and land use issues. On vegetation, questions remain about the timescale of the desired changes, the direction of change and the impact of any changes in distribution of individual species, not only the peat forming plants and mosses but others, such as bog asphodel, that impact on land use and livelihoods in difficult upland areas.

1.3 Bog asphodel literature review

1.3.1 Ecological theory

Individual plants are typically sessile and therefore static within their environment, in contrast to the generally mobile individuals of the fauna. Plants species are commonly distinguished by the vegetative form of individuals. For example, giant long-lived oak trees clearly differ from tiny groundsel plants that produce thousands of airborne seeds, or from irises which shoot up each year from a persistent mat of rhizomes. Botanists have described in detail the diversity of physical structures of individual plant species e.g. (Perring and Walters, 1962; Rose, 2006). In the 1930s Raunkiær grouped plants according to the location of the bud in seasons of adverse conditions e.g. winter (Raunkiær, 1934). The small rapidly growing annuals that survive adverse conditions as seeds were 'therophytes', for example, and those with undergrown buds, whether bulbs or on a rhizome system were 'geophytes'. By the 1960s attention was being directed towards the connections between form and function. The life form of a plant can easily be described but more critical to the understanding of how plants thrive is the concept of life history strategy, the fundamental allocation of biomass (and therefore resources) between growth and reproduction (Grime, 1979; Grubb, 1976). The oak tree mentioned above allocates biomass first to growth then to reproduction, whereas the groundsel allocates most biomass to seed production and therefore remains a small plant. The allocation of biomass to growth confers size and thus the ability to compete for light and nutrients, whereas the allocation to reproduction confers the ability to disperse and avoid unsuitable conditions by colonising other more suitable sites.

Most plants reproduce by producing seeds, although there are common examples of vegetative reproduction like strawberry runners and onion bulbils. There is huge variety in the number of seeds produced by an individual organism, from 100 for *Alopecurus myosuroides* (an annual grass) to 10^{10} for a coastal redwood tree and this difference in reproductive capacity is related to the species' ability to produce the greatest number of dependents, independent of the hardships it faces or the availability of suitable habitat (Harper, 1977b). Seeds confer certain advantages over adult plants for species preservation. Their formation allows genetic variation, the mechanism underpinning natural selection

(Darwin, 1859). Seeds allow the genotype to survive adverse conditions and seasons and to disperse to other suitable habitats.

An understanding of a plant's life history strategy is therefore crucial for understanding how it survives and disperses, or does not, in changing environmental conditions. The physical environment is always changing, slowly or very rapidly, locally or globally. Examples of drivers of environmental change would be subtle or pronounced climate change, forest fires, ploughing for agriculture or by changing the hydrological regime e.g. by drainage.

Consider for example the effects of a forest fire, which creates an acute and abrupt change in the environment. The first plants to reappear in the burned area are the small annuals that have survived the fire as seeds which grow very rapidly on the bare ground with little competition for resources such as light and produce vast numbers of seeds which can then wait to germinate next time the conditions are right. They are followed by the plants that have survived the fire underground and other species whose seeds colonise the area, a process known as ecological succession. Eventually succession leads to a diverse vegetation community including plants (e.g. trees) that have succeeded in dominating the resources to grow to a large and stable size. While this might seem a static 'climatic' endpoint (Clements, 1916; Gleason, 1917), it is now thought that almost all plant communities are in a dynamic equilibrium constantly reacting to subtle biotic and abiotic changes (Bazzaz, 1996; Pickett *et al.*, 1987; Whittaker, 1953).

Ecological succession can be interpreted in terms of life history strategies of the community's constituent plants, with each species' participation in the succession process being dictated by its life history strategy. Several different classifications of strategies have been proposed to explain the process of ecological succession. MacArthur (MacArthur, 1962) proposed the r/K selection theory, whereby plants were either r-strategists allocating most of their biomass to reproduction, or K-strategists allocating their biomass mostly to growth. In succession the r-strategists arrive first as colonists, followed by the K-strategists. The Connell-Slatyer model uses the r-K continuum to suggest three possibilities for early succession: facilitation whereby plants create conditions that enable others to grow; toleration whereby plants establish independently of each other; or inhibition whereby once established plants inhibit the growth of other plants (Connell and Slatyer, 1977). Amongst other categories of life history strategy,

Grime (Grime, 1979) proposed three groups of strategy, ruderals (equivalent of r-strategists), competitors (equivalent of K-strategists) and stress tolerators to accommodate those plants that have neither r- nor K- strategies but do persist in conditions that are permanently adverse, such as cold, wet and acidic peatlands. Stress tolerator plant species do not allocate biomass quickly to either growth or reproduction. Neither the r-K nor the C-S-R theory accounts for the behaviour of all plants, and neither addresses the dominance of some plants over others (Grubb, 1976), but they capture and summarise a valuable set of covarying ecological attributes.

1.3.2 The life form and life history attributes of bog asphodel

Bog asphodel (*Narthecium ossifragum*) is one of the characteristic plants of blanket bog, and is listed as an indicator thereof under the Common Standard Monitoring scheme (JNCC, 2006). It is loosely related to the Liliaceae family (family Nartheciaceae) (Kelch, 2002; Strugnell, 2014), despite a superficial resemblance to an iris, and is a clonal perennial herb found on peatland. It is native to the British Isles. Although only found in wet acidic habitats such as mires and wet heathlands, bog asphodel is found throughout the north, west and south-west of the United Kingdom (U.K.) and Ireland (Figure 5), roughly following the distribution of peatland (Figure 4). It is common in lowland mires but is also found at altitudes of over 1000m e.g. at 1133m in Scotland (Summerfield, 1974). Bog asphodel is a globally rare plant in that its worldwide distribution is almost entirely limited to north-west Europe, from northern Scandinavia to Portugal (Hulten, 1950). One example of *Narthecium ossifragum* has been recorded in Japan, in North America the main species are *N. americanum* and *N. californicum*, and there is a record of a fourth species, *N. scardicum* Kusan., found only in Montenegro (Abrams, 1961; Bentham and Hooker, 1954; Summerfield, 1974; Willis, 1966).

It is locally abundant and easily recognised by the bright green fleshy shoots and bright yellow flower inflorescences that appear in June and July (Figure 1). It is still a common wildflower on uplands although it has been declining on lowland sites because of drainage or improvement since the 1960s (Preston *et al.*, 2002).

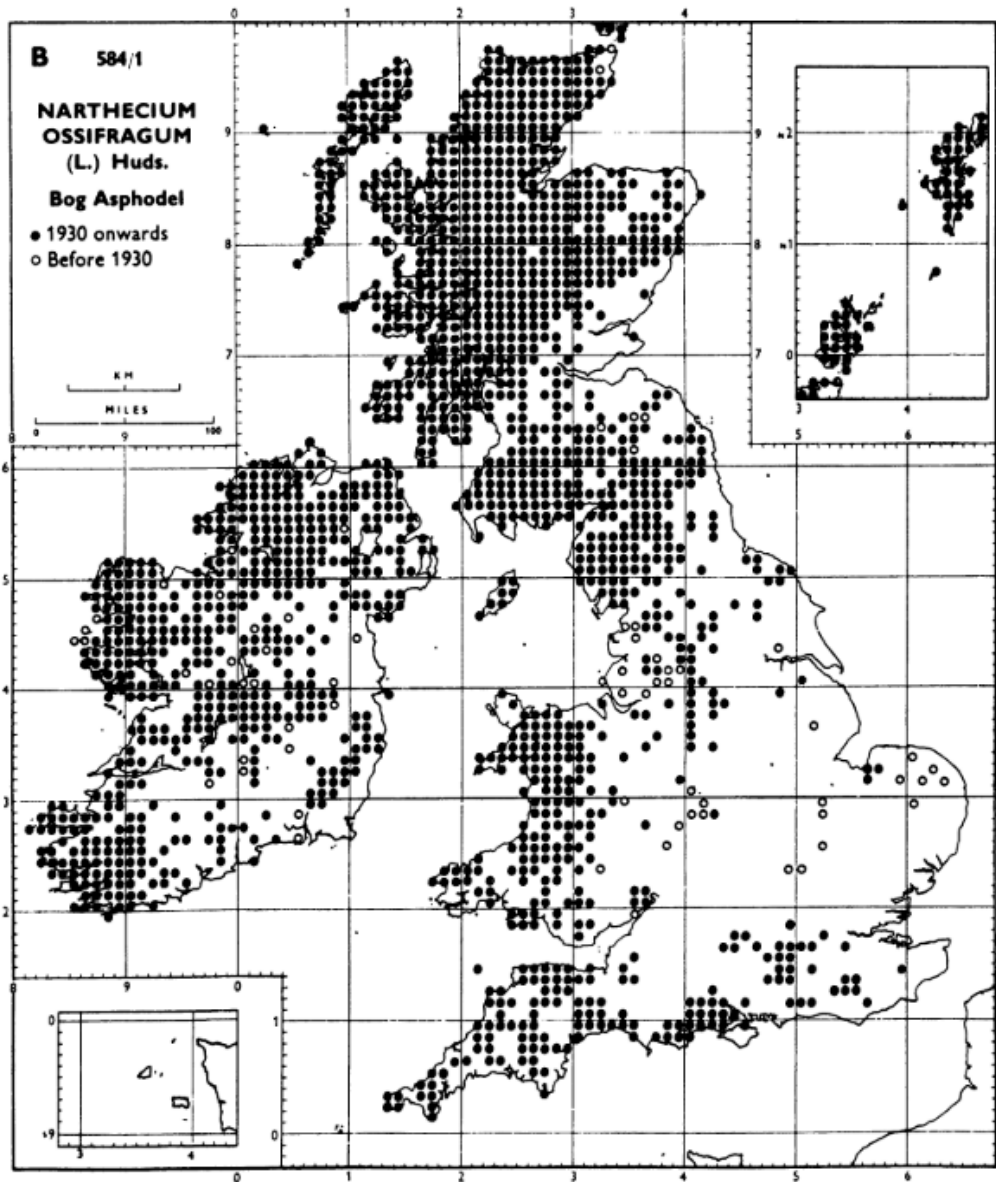


Figure 5: Map of bog asphodel distribution in the United Kingdom (Summerfield, 1974)

Summerfield (Summerfield, 1971, 1972, 1974) described the plant and its ecology in the 1970s. The following description of its structure and ecology is based on his work. Bog asphodel comprises rhizomes, 3-5mm in diameter, from which sterile leafy shoots grow from lateral and terminal nodes, and fertile shoots from terminal nodes. The rhizomes have a few primary roots and numerous smaller lateral roots (Heath *et al.*, 1938). The leafy shoots comprise four to six flattened sheathing curved bright green leaves 5 – 40 cm tall depending on conditions. The growing season is May to August, with flowering in June and July.

The fertile shoots comprise a few small basal leaves from which the inflorescence grows on an upright 10 – 30 cm stem. The flowers are bright yellow with

conspicuous brick-red anthers. No nectar is produced but the flowers emanate a strong carnation-like odour. Each inflorescence has on average 14 flowers which are pollinated by local insects (usually species of Diptera and Hymenoptera), presumably attracted by the colour and odour. The anthers and stigma ripen together but are sufficiently distanced to prevent self-pollination, although towards the end of the flowering season anthers dehisce to assist pollination of later opening lower flowers. The mature fruits are ridged and dark brown, and dehisce gently to release about 50 seeds each with two slender wings (Figure 1E, page 11). The inflorescence stems persist through the winter with some seeds still inside, whereas the leafy shoots turn a characteristic blotchy orange colour and die away. Only a small percentage (1 – 7 %) of the plant's above-ground production comprises fertile shoots, and very few seedlings survive in the field, although 90% of bog asphodel seeds will germinate in the laboratory (Summerfield, 1973). Germination under laboratory conditions is only restricted by water-logged conditions, low light levels and in temperatures above 31°C. Seeds that have been frozen for 11 weeks or more remain viable. Bog asphodel therefore produces a large proportion of viable seeds, but the seedlings do not persist in the field. They are fragile and succumb to freezing temperatures, water-logged conditions and especially being shaded out by other vegetation.

Bog asphodel is found on all types of peatland and it tolerates a wide range of soil pH but grows best where the pH is 4.5 – 5.5. It thrives in very wet conditions (Hill *et al.*, 2007), although less well in habitats where the water table remains within 10cm of the surface, and there is no surface water movement. Bog asphodel is extremely sensitive to shading and will gradually die out if its habitat is invading by *Molinia* or scrub vegetation. This may explain its disappearance since 1938 from eastern England, where peat cuttings have reverted to scrub (Figure 5). In lowland sites it grows luxuriously and forms dense fertile clonal patches, up to 2600 shoots m⁻². On exposed upland sites the plants are smaller, less densely packed (64-224 shoots m⁻²) and often infertile. Aerial productivity can be as little as 15 – 24 g dry weight m⁻² yr⁻¹, whereas in lowland mires productivity can be as high as 200 g dry weight m⁻² yr⁻¹. In Sweden productivity as high as 740 g dry weight m⁻² yr⁻¹ has even been recorded (Malmer, 1962).

1.3.3 Community associations of bog asphodel

Bog asphodel is a key species in several types of mire as described in the National Vegetation Classification (NVC) (Elkington *et al.*, 2001; Rodwell, 1991). It is significantly represented in seven NVC categories (Table 2). The term mire in this context refers to habitats that are permanently or periodically waterlogged by atmospheric precipitation, high ground water levels or lateral water flow (Rodwell, 1991). Wet heaths have an impermeable substrate layer to prevent water draining away or have a naturally high water table. M25 (*Molinia caerulea* – *Potentilla erecta* mire) is included because it is the most common designation for damaged upland peatlands, although bog asphodel is not commonly present. In south-west U.K. the only habitat with a constant component of bog asphodel which might appear following restoration of blanket bogs is M17 (*Trichophorum cespitosum* – *Eriophorum vaginatum* blanket mire). Other types of mire, such M1 (bog pools) and M4 (*Carex rostrata* mire) support little if any bog asphodel.



	Description	Sub-community	Frequency (Abundance)	UK distribution*
M6	<i>Carex echinata</i> – <i>Sphagnum fallax/auriculatum</i> mire	<i>Carex nigra</i> – <i>Nardus stricta</i> sub-community <i>Juncus acutiflorus</i> sub-community	III (2-3) IV (2-5)	N, Wales, SW
M14	<i>Schoenus nigricans</i> – <i>Narthecium ossifragum</i> mire		V (1 -4)	S, E coastal only
M15	<i>Trichophorum cespitosum</i> – <i>Erica tetralix</i> wet heath	<i>Carex panicea</i> sub-community General sub- community with no obvious sedge representation	V (1-4) V (1-6)	N, Wales, SW
M16	<i>Erica tetralix</i> – <i>Sphagnum compactum</i> wet heath	<i>Rhynchospora alba</i> – <i>Drosera intermedia</i> sub-community <i>Juncus squarrosus</i> – <i>Dicranium scoparium</i> sub-community	III (1-6) III (1-6)	NE, Wales, SW , SE
M17	<i>Trichophorum cespitosum</i> – <i>Eriophorum vaginatum</i> blanket mire		V (1-9)	NW, Wales, SW
M18	<i>Erica tetralix</i> – <i>Sphagnum papillosum</i> raised and blanket mire		III (1–7)	N, Wales
M21	<i>Narthecium ossifragum</i> – <i>Sphagnum papillosum</i> valley mire		V (1-8)	Wales, E, SW , S
	Commonly found on drained peatlands (included here for comparison)			
M25	<i>Molinia caerulea</i> – <i>Potentilla erecta</i> mire	<i>Erica tetralix</i> sub-community	II (1-7)	N, Wales, SW
Legend	Frequency (presence in samples): I - rare (1 – 20%) II - occasional (21 – 40%) III - common (41 – 60%) IV - constant (61 – 80%) V - <u>constant</u> (81 – 100%)	Abundance (no. plants in sample) <u>Domin</u> scores 1 = sparse (one or two plants) to 10 = densely packed in sample  Habitats found on <u>restored</u> peatlands in U.K.  Habitat commonly found on <u>drained</u> peatlands		* refers to England, Scotland and Wales.

Table 2: National Vegetation Classifications in which bog asphodel is commonly represented (from (Rodwell, 1991))

Bog asphodel is associated with certain blanket bog plants, particularly *Calluna vulgaris* (ling), *Erica tetralix* (cross-leaf heath) and *Eriophorum vaginatum* (Hare's tail cotton grass (Table 3). The table only includes those species regularly seen on Exmoor's mires.

Association Index	Species
>0.90	<i>Calluna vulgaris</i> , <i>Erica tetralix</i> , <i>Eriophorum vaginatum</i>
0.75 - 0.89	<i>Eriophorum angustifolium</i>
0.60 - 0.75	<i>Drosera rotundifolia</i> , <i>Trichophorum cespitosum</i>
0.50 - 0.59	<i>Sphagnum papillosum</i> , <i>S. tenellum</i> , <i>Molinia caerulea</i> ,
0.40 - 0.49	<i>Hypnum cupressiforme</i> , <i>Sphagnum cuspidatum</i>
0.30 - 0.39	<i>Potentilla erecta</i> , <i>Rhacomitrium lanuginosum</i>
0.20 - 0.29	<i>Vaccinium oxycoccus</i> , <i>Campylopus flexuosus</i>
0.10 - 0.19	<i>Campylopus atrovirens</i> , <i>Leucobryum glaucum</i> , <i>Pleurozium schreberi</i> , <i>Aulacomnium palustre</i> , <i>Dicranium scoparium</i>
<p>Association Index: 1 = always present with bog Asphodel; 0 = never found with bog asphodel. Index derived from historic data for over 40 mire communities across the UK (Summerfield, 1974)</p>	

Table 3: Species commonly associated with bog asphodel on Exmoor's peatlands (after Summerfield, 1974)

The boundaries between the association levels are not necessarily well defined and the level of association can vary with water table depth. In blanket bogs for example, bog asphodel can replace the hydrophilic *Eriophorum angustifolium* (bog cotton grass) in dominance as the water table falls from surface level, and then is itself replaced by *Eriophorum vaginatum* (hare's tail cotton grass) as the water table falls even lower, below 40 cm (Summerfield, 1974). Bog asphodel is found scattered through blanket bogs by growing up through the surface vegetation to avoid being permanently in standing water and is associated with shrubs and hummock-forming *Sphagnum* species. In raised bogs, bog asphodel flourishes when the water table sinks up to 40 cm below the surface, coinciding with *Sphagnum* regression (Sinker, 1962).

1.3.4 Bog asphodel toxicity

Bog asphodel has been recognised as poisonous to grazing livestock since the mid-20th century when its ingestion by lambs in Scotland and Norway was associated with hepatogenous photosensitisation (Ender, 1955; Ford, 1964). The condition is well known in Northern Europe as reflected by the various local names it goes under: *alveld* (elf fire) in Norway; *saut* in Cumbria; *yellowses* in Northumberland; *plochteach* in Scotland and *hard lug* in Northern Ireland. Even before the hepatogenous nature of the toxicity was recorded, bog asphodel (*Narthecium ossifragum* the bone breaker) was associated with a lack of condition and even the death of animals grazing pastures where it grew. However, as bog asphodel typically grows in low nutrient environments the general lack of nutritious forage, and specifically low calcium content, would contribute to poor condition (Strugnell, 2014). *Yellowses* will be used to refer to the photosensitising effects of bog asphodel ingestion forthwith, reflecting as it does the jaundice associated with liver damage.

The (secondary) photosensitisation occurs when a toxin causes liver malfunction so that phylloerythrin, a photodynamic metabolite of chlorophyll released by rumen microbes, accumulates and starts to circulate instead of being excreted by the liver (Strugnell, 2014). The phylloerythrin reacts with UV light reaching unprotected skin, mostly commonly on the ears, face and back to produce a violent inflammatory reaction, resulting in blistering and burning of the skin which subsequently becomes infected (Sargison, 2008; Ulvund, 2012). The most likely toxic agent associated with the photosensitisation effect of bog asphodel is saponin, a glycoside found in bog asphodel leaves and flowers, which is hydrolysed in the rumen to sapogenins which bind with glucuronic acid and are thought to block the excretion of phylloerythrin (Flåøyen, 2000). Lambs up to the age of five months are more severely affected than sheep, which are thought to develop some resistance to the toxic effects (Flåøyen *et al.*, 2001). The disease is at its peak in June and July when bog asphodel is in flower. As the saponin content of bog asphodel leaves remains the same throughout the season, this suggests that the young leaves and the flowers are especially toxic or at least more palatable.

There is a wide range of chemicals found in plants, bacteria and fungi which can cause photosensitisation if ingested, but those that affect grazing animals are predominantly of plant origin (Cheeke, 1995; Pollock *et al.*, 2015). St John's Wort (*Hypericum perforatum*) commonly found in lowland and improved pastures, contains the photodynamic compound, *hypericin*. The puncture vine (*Tribulus terrestris*) found in South Africa and Australia contains a steroidal saponin like bog asphodel and is associated with the photosensitisation condition of *Geeldikkop*.

Bog asphodel is also associated with nephrotoxicity in sheep and cattle (Angell and Ross, 2011; Flåøyen, Bratberg, *et al.*, 1995; Malone *et al.*, 1992; Wisløff, 2008) and other closely related plants (*Liliaceae*) are reported to cause nephrotoxicity in cats and dogs (Stokes and Forrester, 2004). However, the toxin is not thought to be saponin but rather another compound found in bog asphodel flowers, namely 3-hydroxy-2(5H)-furanone (Angell and Ross, 2011; Pollock *et al.*, 2015; Vu *et al.*, 2016), although Wisløff (Wisløff, 2008) recorded a case of severe renal toxicity in lambs when investigating saponin toxicity. On balance the evidence suggests that saponin is involved in hepatotoxicity in sheep and 3-hydroxy-2(5H)-furanone in the nephrotoxicity more often seen in cattle than sheep (Flåøyen and Wilkins, 1997; Li *et al.*, 1999). Renal damage is manifested as extensive renal necrosis and tubule damage, as well as liver damage (Angell and Ross, 2011; Carrick and Cowap, 2016; Strugnell, 2014).

A number of experimental studies have been carried out to try to determine the causative agents and to elucidate the toxic mechanisms. Ender (Ender, 1955) established that lambs only developed *yellowsees* if grazing on pastures containing bog asphodel. Ford (Ford, 1964) observed that lambs tended to graze the tips of bog asphodel leaves in which saponins are concentrated, but the disease is no more severe in Scotland than in Norway despite Scottish bog asphodel leaves containing higher levels of saponins (Wilkins *et al.*, 2004). Flåøyen and colleagues established that bog asphodel flowers can induce both liver and kidney toxicity in both sheep and cattle, whereas the leaves are only associated with liver damage (Flåøyen *et al.*, 1997; Flåøyen, Binde, *et al.*, 1995; Flåøyen, Bratberg, *et al.*, 1995). They also established on small numbers of animals that some breeds are less susceptible to bog asphodel toxicity than others (Flåøyen, 1991), and that adult sheep develop resistance to the toxic

effects of bog asphodel (Flåøyen *et al.*, 2001). However, many of these experiments found that large quantities of bog asphodel (40kg) were needed to extract enough saponins to reproduce clinical disease, and that feeding saponins directly did not always cause photosensitivity (Flåøyen *et al.*, 1991; Laksesvela and Dishington, 1983).

It is likely that other agents are involved in the aetiology of the diseases, the cofactor hypothesis, as bog asphodel ingestion does not consistently cause *yellowses* (Laksesvela and Dishington, 1983; Mysterud, 2001; Mysterud *et al.*, 2016; Pollock *et al.*, 2015). Soil bacteria were investigated back in the 1950s and no evidence for their involvement was found (Ender, 1955). Since the 1980s numerous bacteria and micro-fungi species have been found on bog asphodel roots and leaves but none has proved a convincing candidate for an injurious agent, either because they are not associated consistently with bog asphodel or they cannot be shown to cause photosensitisation in combination with saponins (Aas and Losvik, 1998; Flåøyen *et al.*, 1993; Mysterud *et al.*, 2016). Spores of *Pithomyces chartarum* cause facial eczema in New Zealand sheep (Bishop and Morris, 2007; Smith *et al.*, 1997). Facial eczema is exactly the same as the photosensitisation caused by bog asphodel ingestion except that the toxin that prevents the excretion of phylloerythrin is sporidesmin from the *P. chartarum* spores. However, *P. chartarum* is very rarely found on Bog asphodel in Northern Europe (Aas and Losvik, 1998). Spores of *Cladosporium* species are very common on vegetation, including bog asphodel and the ubiquitous *Molinia caerulea*, but are not consistently associated with bog asphodel in areas where *yellowses* is endemic (Mysterud *et al.*, 2016). Another candidate might be *Penicillium* species, famously effective against bacteria, some of which are known to cause nephrotoxicity (Mysterud *et al.*, 2016).

Mysterud (Mysterud *et al.*, 2016) found that the decomposition rate of bog asphodel leaves was much higher in pastures where *yellowses* was endemic than in pastures where it was absent. This suggests an association between microbial activity and bog asphodel toxicity. However, microbial activity is also significantly reduced in dry sunny weather (Sundin, 2002), suggesting that bog asphodel toxicity could be weather dependent.

None of the numerous bacteria and micro-fungi species found on bog asphodel roots and leaves has proved a convincing candidate for an injurious co-factor (Aas and Losvik, 1998; Flåøyen *et al.*, 1993; Mysterud *et al.*, 2016).

Bog asphodel's form and distribution are therefore thoroughly described but the mechanisms by which it exerts its toxic effects on herbivores have yet to be fully understood. An understanding of bog asphodel's life history strategy may be the key to managing its potential to poison grazing livestock on upland peatlands. The management of the uplands areas is however a balancing act between the conflicting demands of preserving healthy sustainable habitat, providing essential ecosystem services, supporting agriculture and providing a public amenity (Bonn *et al.*, 2014; Grand-Clement *et al.*, 2013).

Bog asphodel poisoning is a threat to the economics of sheep farming. In Norway 10-12% of ewes are lost to bog asphodel poisoning (Mysterud *et al.*, 2007; Pollock *et al.*, 2015) with lamb mortality rates even as high as 50%. In New Zealand facial eczema cost the equivalent of around £26 million p.a. in the 1980s and *geeldikkop* in South Africa an estimated equivalent of £650,000 in 1990s (Pollock *et al.*, 2015). In Cumbria farmers have reported losing up to 40% of their lambs to *yellowses*.

1.3.5 Summary

Bog asphodel is a common wildflower in upland peatland habitats in U.K. and Northern Europe. It has been shown to cause fatal renal or liver toxicity in several individual studies on sheep and cattle, but the causative agents and exact mechanisms remain to be determined. Its life history strategy appears to be one of tolerating the wet acidic conditions of upland peatlands. It does not produce masses of viable seedlings nor does it grow extravagantly, but it does survive at the limits of tolerable temperature, moisture and pH conditions.

Our understanding of its life history and ecology is incomplete in general and more specifically, it has not been studied in detail from the perspective of peatland restoration. Consequently, evaluating the life history strategy of bog asphodel and assessing its value as an indicator species for predicting and mapping habitat change has the potential to furnish key information for the management of restored peatlands.

Chapter 2. Research into bog asphodel's relevance to peatland restoration

2.1 Bog asphodel's response to environmental change: life history attributes of plants as predictors of response to environmental change.

2.1.1 Introduction

It is axiomatic in ecology that the life history characteristics of living organisms reflect and have developed from the environment in which they live, and thus all living organisms are to some extent habitat specialists. The reaction of organisms to changes in their habitat will alter distribution patterns. There are many examples of range shifts and distribution changes in response to the current global climate change: butterfly ranges moving northwards in U.K; polar bears struggling to survive as Arctic ice disappears (Chen *et al.*, 2011).

The extent to which a plant's distribution changes is a function of its demographic ability to survive, a combination of vegetative growth potential and seed dispersal (Harper, 1977a). Survival depends on relocating to a suitable environment or having the ability to survive in the changed environment. The capacity to survive changing environmental conditions is lodged in a species' life history strategy, which can be quantified in terms of growth rate and size (Grime, 1979). The significance of a plant's life history strategy is discussed in Chapter 1.3.1.

Bog asphodel is found in wet acidic environments including upland peatlands. The same anthropogenic drivers that are behind climate change have caused many peatlands to deteriorate so that their restoration has become a world-wide priority (Joosten *et al.*, 2016). The immediate aim of peatland restoration programmes is to rewet the peat by blocking drainage features across the landscape to restore and stabilise water table levels (Holden *et al.*, 2017). Such a fundamental and rapid change in environmental conditions is bound to affect the distribution of peatland plants, not only bog asphodel but also *Sphagnum* mosses whose presence is required to re-establish a functional peatland capable of carbon sequestration and water management (González *et al.*, 2014).

Peatlands are mostly found in the cool and wet higher latitudes (Chapter 1.2). The dominant land use is livestock grazing, which has prevented succession and created a mosaic of wet acidic habitats (in U.K.) ranging from blanket bog to

acidic grassland (Miles, 1987). Changes in plant distribution caused by habitat change will affect the grazing potential, especially if some plants are potentially hazardous. Mapping the progress of peatland restoration is an essential part of delivering sustainable outcomes for all stakeholders, including livestock farmers. Plants can be used as proxy measures of change both for specific abiotic factors (indicators) or for changes at community level (sentinels). Bog asphodel is listed as an indicator plant for blanket bog, as well as for *Molinia* or rush pasture (JNCC, 2006).

Here the potential of peatland restoration to change the local distribution and abundance of one specialist peatland plant, bog asphodel, is considered in the shallow marginal peatlands of south-western U.K.

Different rates of persistence and spread, survivorship, are predicted by a plant species' life history strategy (Grime, 1979). Grime devised a 'life history triangle' which is an ordination based on life form (growth rate and size). This quantitative method can be applied to all plant species to place them on a triangle whose apices are Grime's three extremes of life history strategy, competition, stress-tolerance and ruderal. The life history strategy of bog asphodel will be evaluated using the Grime's triangle method, in order to predict the likely response of its distribution to rewetting.

In summary the aim of this study is to undertake a demographic study to assess persistence, growth rate and reproductive allocation of bog asphodel in response to re-wetting. Specifically, the study had the following three objectives:

1. To describe the life form attributes of bog asphodel (*Narthecium ossifragum*) found on Exmoor;
2. To evaluate the life history strategy of bog asphodel after the method of Grime;
3. To evaluate the survivorship and likely distributional change of bog asphodel on restored peatland on Exmoor.

2.1.2 Methodology

Study system

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 peninsular of the U.K. (Figure 6). The uplands range in height from 300m – 500m above sea level and are mostly covered in a thin layer of peat, over sandstone and shale (Bray, 2015). Mean monthly temperatures range from 1.1 °C in February to 18.6 °C in July and August (30 year average 1981-2010 at nearby Liscombe (UK Meteorological Office, 2019a)). Mean average annual rainfall over the same period is 1445 mm. Although there are some areas of deeper peat (> 1 m), most of Exmoor's peat is around 0.3 m deep (Smith, 2009). Prior to restoration, the most common type of vegetation found on Exmoor was M25 (*Molinia caerulea-Potenilla erecta* mire (Rodwell, 1991), in which bog asphodel occasionally grows (Table 2).

The site at Aclands (51.134°N 03.811°W) (Figure 8) was chosen for the bog asphodel demography studies on Exmoor because it is a site with a wealth of past and present data from Exmoor Mires Partnership (EMP) vegetation studies and from scientific studies being carried out by the Universities of Exeter and Bristol (Freeman, 2017; Gatis *et al.*, 2016; Luscombe *et al.*, 2016). The wider Aclands area is grazed by a small herd of cattle (approximately 35 cows and a bull, and 36 calves) in the summer months and by a few ewes all year round.

In order to describe the characteristics of bog asphodel on restored peatland (Objective 1) two parallel sets of five 1 m² quadrats across a blocked drainage ditch were set up at 51.131°N, 03.811°W: one set (grazed series) in an area periodically grazed by cattle (and presumably deer) and along a vegetation survey transect set up by EMP; and the other (ungrazed series) in an area that had been fenced off for scientific experimental equipment for three years (Figure 7).

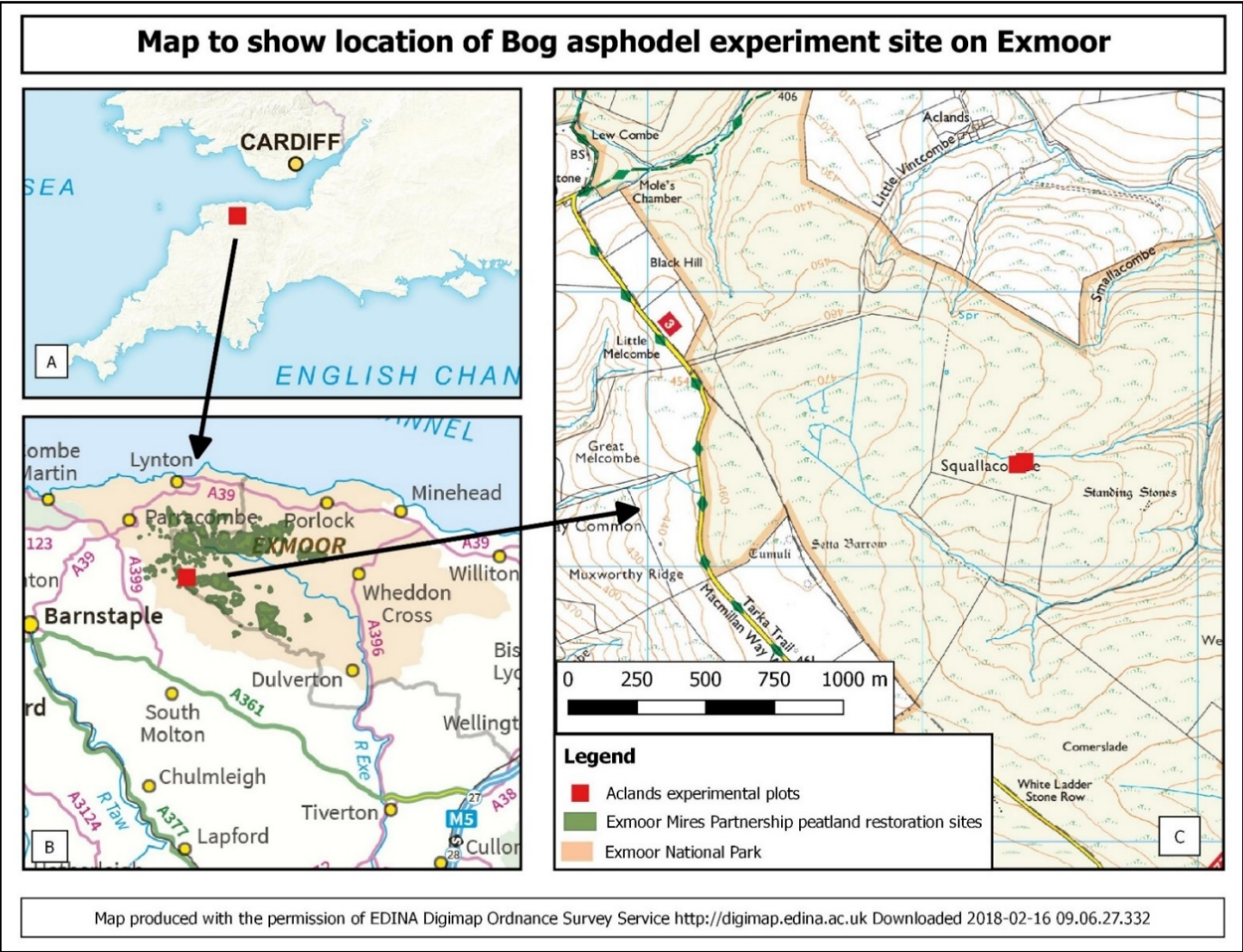


Figure 6: Location of bog asphodel demography experimental sites

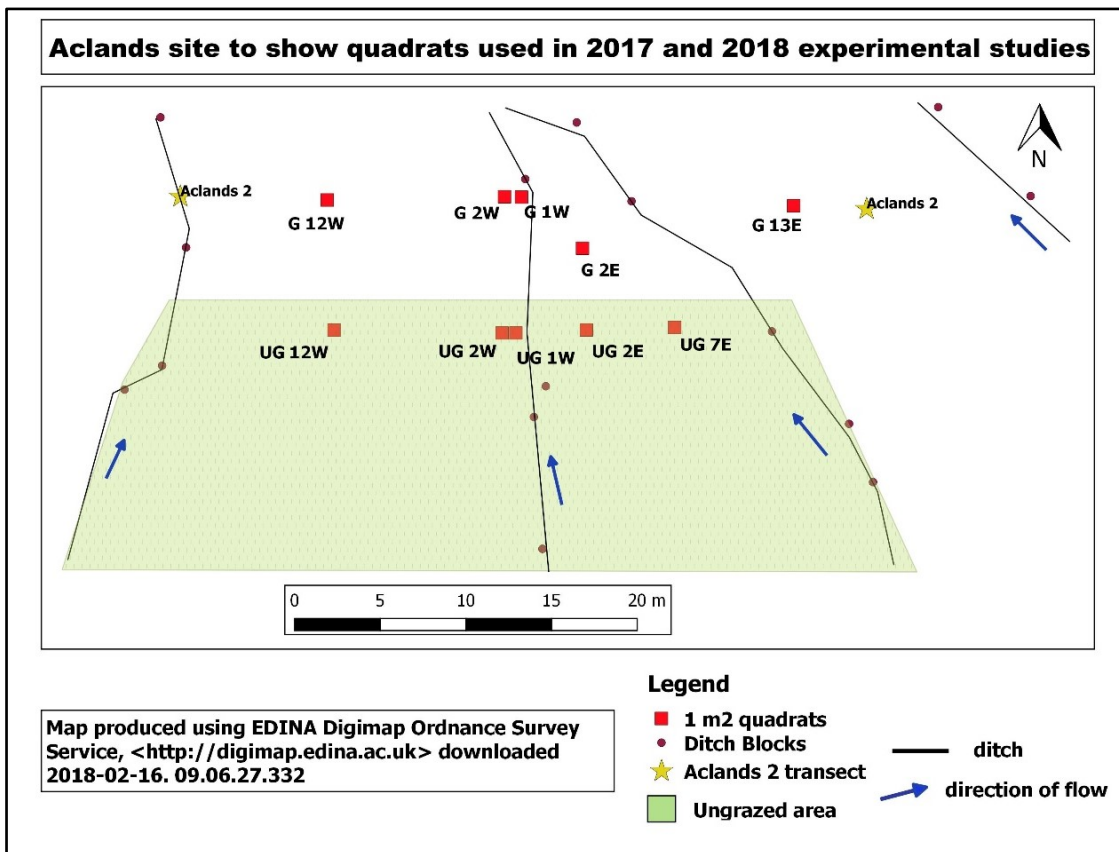


Figure 7: Experimental design for bog asphodel demography studies in 2017 and 2018

In order to measure the water table level a dipwell was inserted by each quadrat, and the distance to the central ditch recorded. Peat depth was measured at each quadrat using a 150 cm probe. A 1 m² plastic quadrat divided into 100 10 cm squares by elastic strings (Figure 8) was used to identify and return to study plants in each quadrat and to quantify the density of bog asphodel plants.

Quantification of the life history attributes of bog asphodel

In order to describe bog asphodel's life form characteristics the dimensions of individual bog asphodel plants were measured over two growing seasons (2017 and 2018) to produce a snapshot of the plant's variability and to compare the Exmoor bog asphodel to the definitive description of Summerfield (Summerfield, 1974) (Figure 9). The leaf and flowering data were collected from plants in the experimental quadrats (Figure 7) and the seed data from mature inflorescences collected from the general grazed and ungrazed areas near the quadrats.



Figure 8: Vegetation survey quadrat.

Quadrat in position at quadrat G1W with G2W beyond, 3rd June 2017. White plant labels mark plants to monitor. Yellow pegs ensure the quadrat is in exactly positioned on each visit

The Grime's triangle calculation for life history strategy (Objective 2) depends on measurements of maximum size and growth rate to ordinate on to the Grime's Triangle. In order to quantify maximum size, all the bog asphodel plants in ten randomly selected 10 cm squares in each of the ten quadrats were harvested (see Figure 7) after 12 weeks (27th July 2018). This time was selected based on the seasonal growth pattern recorded in 2017 (Figure 10). The width and height of all the leaves on each plant were measured, and all the plants were then frozen for dry mass measurements later.

In order to calculate the growth rate, 150 plants were randomly selected in early May 2018, 15 in each of the ten quadrats (the 'Grime' plants). Two of these plants were then randomly selected from each of the ten quadrats at regular intervals over the growing season. The plants were frozen and mean plant dry mass was calculated for each sampling day later. The heights of all the 'Grime' plants were recorded at each visit to provide a control for growth rate against a similar experiment in 2017 (see Figure 10).

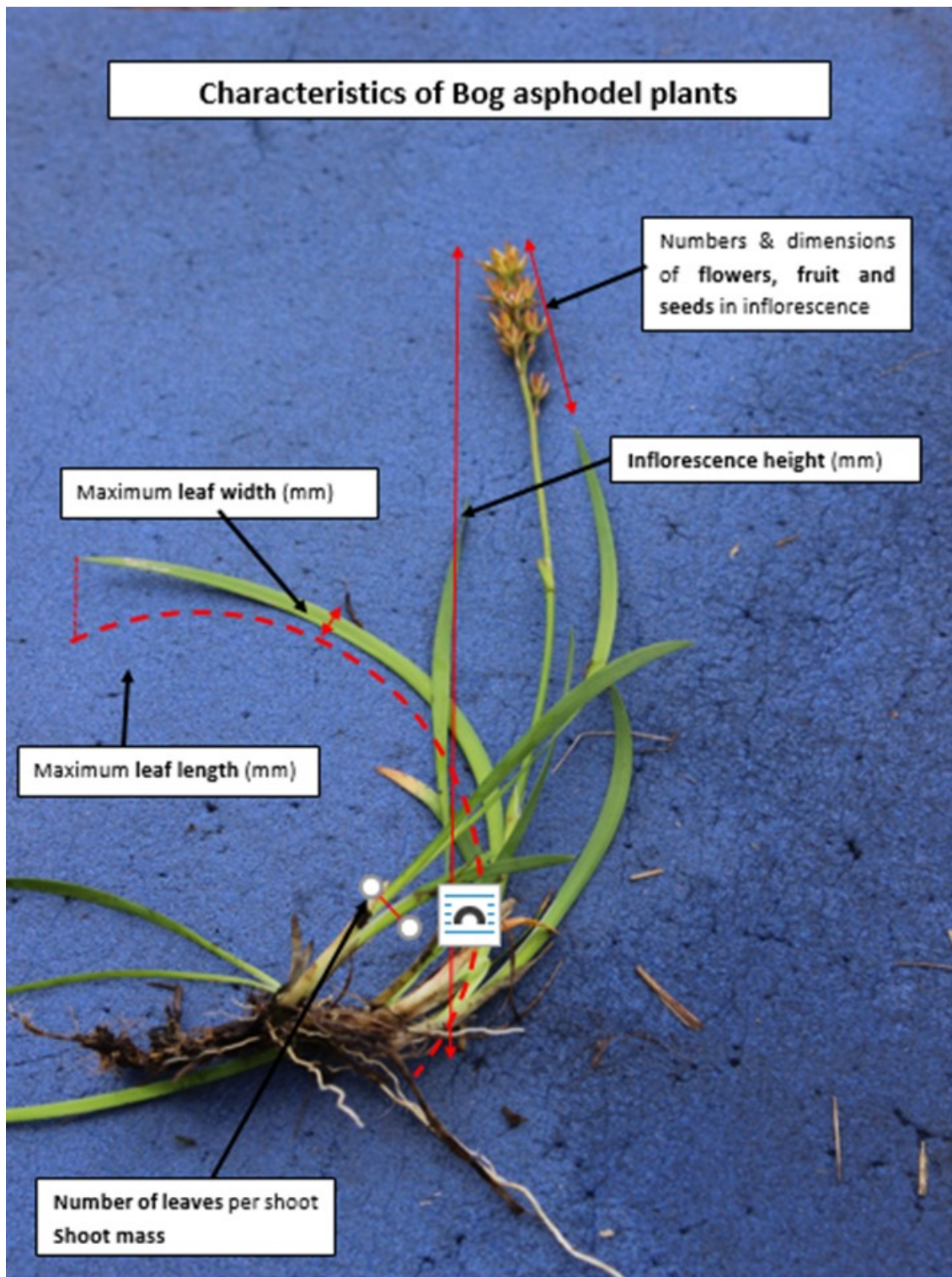


Figure 9: Bog asphodel plant
 A typical bog asphodel plant from Acland (July 2017) to show characteristic features and the dimensions measured.

In order to measure dry mass, the samples were weighed in plastic bags, before drying in a desiccator and re-weighing.

In order to evaluate bog asphodel's survivorship (Objective 3) on Exmoor's restored peatland its capacity to disperse seeds and its vegetative persistence were investigated.

Seed dispersal potential: Plant species can respond most rapidly to a changing environment by widely dispersing large numbers of seeds. Adaptive changes to vegetative means of distribution (e.g. rhizomes) take years. In order to quantify the relative importance of seed production to bog asphodel, all the flowers produced in each quadrat were monitored over two seasons, 2017 and 2018, to compare with the corresponding above-ground productivity. Mature flowers were collected from the general grazed and ungrazed areas near the quadrats in the autumn and dried. The number of ovaries per inflorescence and the number of seeds per ovary were counted. Individual seeds were measured and weighed.

In order to quantify above-ground productivity, the number of plants in each quadrat was estimated and multiplied by the mean biomass per quadrat. In 2017 the number of plants per quadrat was estimated by counting all the plants in the twenty 10 cm squares across the two diagonals of the 1 m² quadrat (Figure 8) and multiplying up. In 2018 the estimation was based on the counts in 10 randomly selected 10 cm squares within each 1 m² quadrat.

Survivorship and persistence: In order to evaluate survivorship ten bog asphodel shoots were selected in early June 2017 and tracked at intervals from June – August 2017 and again from May – July 2018. The position of each plant was marked with metal tent pegs and their position on the 1 m² grid recorded. The data on maximum leaf size collected from these plants can be compared to the same data collected from a second set of plants randomly selected in 2018 for the life history strategy study (the 'Grime' plants, Objective 2).

Bog asphodel characteristically grows in irregular patches with well-defined edges. In order to establish if there is year-on-year change in bog asphodel distribution following restoration the EMP's vegetation survey records for changes in bog asphodel distribution at restored sites across Exmoor were analysed. The relative changes in the distributions of bog asphodel and *Sphagnum* species were also analysed. This database spans 12 years, 2006 – 2018, and includes pre- and post-restoration data from over 40 sites.

The influence of water table depth (WTD), peat depth and sward height on bog asphodel growth. WTD was measured at each monitoring visit in 2017 and 2018. Peat depth and altitude at each quadrat was established at set up in 2017. In 2018 sward height was measured periodically at each quadrat.

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 normal distribution.

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

2.1.3 Results

Description of bog asphodel's natural history

The natural history of bog asphodel plants on Exmoor broadly matches the definitive data reported by Summerfield for the species over a range of habitats (Summerfield, 1974) (Table 4). There is considerable variation in the mean values for leaf height and plant mass and in the proportion of sterile to fertile shoots between the two years. These attributes are also towards the lower end of the reference ranges, compatible with growing at an approximate altitude of 444m. The variation in capsule numbers is most likely because capsule numbers were counted at different times in the two seasons.

Characteristic	Summerfield 1974 #	Aclands 2017	Aclands 2018
Leaf height (mm)	50 - 400	233.1	205.7
Leaf width (mm)	2 - 5 *	4.5	4.6
Plant mass (g)		0.242	0.126
Plant density (m ⁻²)		340	491
Productivity (g/m ²)	20 - 200	82.14	61.87
Inflorescence height (mm)	50 - 400	299	
Inflorescence % **	1.1 - 7.3	0.58	2.73
Capsules per inflorescence	12.4 - 14.5	14.9‡	16.3‡‡
Capsule length (mm)	≤ 12	6.6	
Seeds per capsule	45 - 54	50	52
Seed + wings length (mm)	7 - 9	4.3	5.4
Seed length (mm)		1	1.1
Seed mass (g x 10 ⁻⁴)	0.84 - 0.88	1.08	0.68
# range over highland and lowland sites			
* Ecological Flora of British Isles			
**% of fertile /sterile shoots			
‡ July count; ‡‡ September count			

Table 4: Bog asphodel descriptive characteristics
Descriptive characteristics of bog asphodel plants harvested on Exmoor in 2017 and 2018, compared to reference data (Summerfield, 1974).

According to Summerfield (Summerfield, 1974) the season of maximum leaf growth for bog asphodel is generally mid-June to mid-July, with flower production starting 2 -3 weeks later. In 2018 on Aclands flowers appeared over a 10-day period starting on 6th June with maximum growth mid-May – mid-June (Figure 10). Recording started later in 2017 but extrapolating the growth curve backwards suggests maximum growth in the same period. Flowering started on 25th June in 2017.

A more detailed analysis of the variation between 2017 and 2018 shows some significant differences (Table 5).

Characteristic	Aclands 2017	Aclands 2018	Significant differences	n	Statistical test
Max leaf height (mm)	233.08 ± 64.5	205.68 ± 57.7	p < 0.001	n = 100 - 187	Welch two-sample t-test
Plant mass (g)	0.242 ± 0.12	0.126 ± 0.02	p < 0.001	n = 10	Welch two-sample t-test
Plant density (m ⁻²)	340 ± 167	511 ± 247	ns	n = 10	Welch two-sample t-test
Productivity (g/m ²)	76.62 ± 30.8	65.28 ± 34.7	ns	n = 10	Welch two-sample t-test
Inflorescences (m ⁻²)	2.1 ± 1.5	11.6 ± 6.7	p < 0.001	n = 10	Wilcoxon rank sum test
WTD (normalised)	0.110 ± 0.03	0.372 ± 0.05	p < 0.001	n = 10	Wilcoxon rank sum test

Table 5: Comparison of key life history attributes of bog asphodel between 2017 and 2018.

The maximum leaf height measurements are based on 10 or more plants from each quadrat, whereas the other five measures are based on a mean measurement for each of the 10 quadrats.

Water table height (WTD) is included here as the most obvious difference between the two seasons was the difference in rainfall both during the growing seasons and in the intervening winter. However, no significant difference in productivity is seen; the plants in 2018 were smaller but there were more of them. The marked difference in the number of inflorescences may have significance for the reported variability in the toxicity of bog asphodel pastures year on year (Pollock *et al.*, 2015).

Evaluation of bog asphodel's life strategy

The time scale for maximum growth rate and height of the 'Grime' plants (black line and squares) is comparable to that of other plants in the same area (Figure 10). Bog asphodel sits firmly in the stress-tolerator corner of Grime's Triangle (Table 6, Figure 11). Three other herbaceous species found with bog asphodel on Exmoor which have similar coordinates and would therefore appear to adopt a similar survival strategy are also plotted on Grime's triangle, namely *Nardus stricta* (Ns), *Potentilla erecta* (Pe) and *Carex panicea* (Cp)(Figure 11)(Grime, 1979).

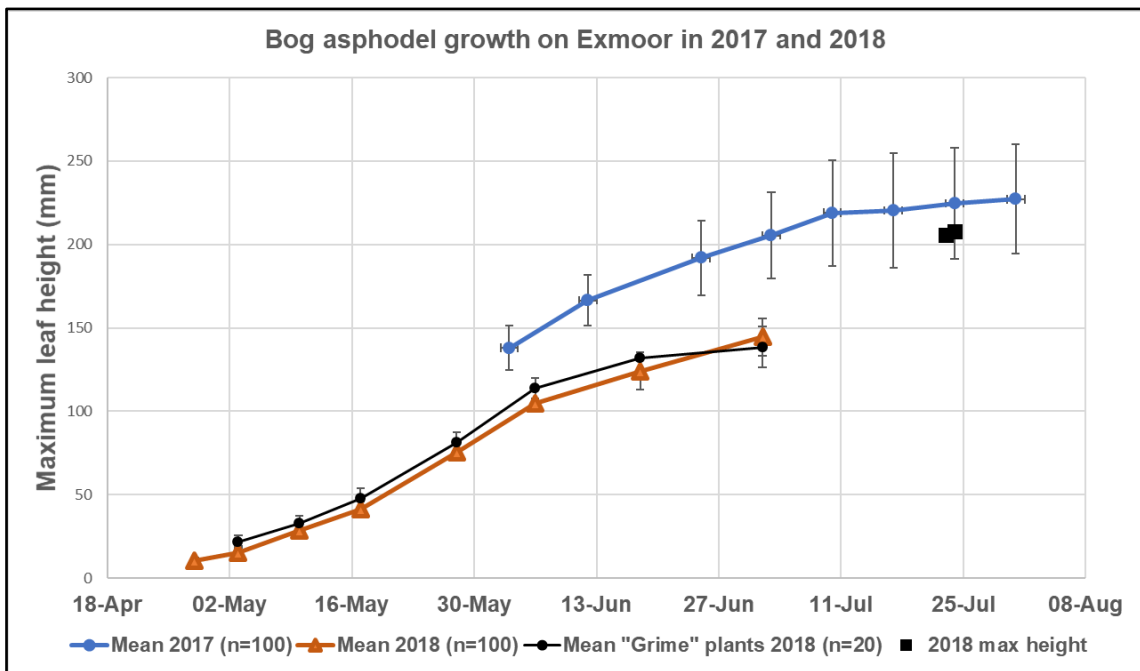


Figure 10: Growth of bog asphodel plants at Aclands in 2017 and 2018
 Significant difference in maximum height of bog asphodel plants at Aclands in 2017 and 2018. Blue dots: max height of 100 plants through 2017 season. Orange triangles: max height of 100 plants through 2018 season. Black dots: max height of plants selected for Grime's calculation through 2018 season. Black squares: max ht achieved by 100+ plants in 2018 season.

Date	mean mass (n = 20)	R_{max} (g g ⁻¹ wk ⁻¹)
28-May	0.04	
06-Jun	0.05	0.222
18-Jun	0.08	0.258
02-Jul	0.10	0.155

$\log R_{max} = 0.589$

Morphology calculation (Grime, 1974)		
$M = (a + b + c) / 2$	Bog asphodel	Description
a = max leaf height	2	120-240 mm
b = lateral spread, ie leaf width	3	perennials with compact unbranched rhizome or forming small tussock 10cm
c = litter accumulation	1	thin discontinuous cover of persistent litter

M = 3

Table 6: Calculations for Grime's Triangle ordination
 Calculation of maximum growth rate (R_{max}) and Morphology index (M) for bog asphodel after Grime 1979 (Grime, 1979). The data were collected from plants harvested between 2 May and 25 July 2018 (black line and squares (Figure 12)).

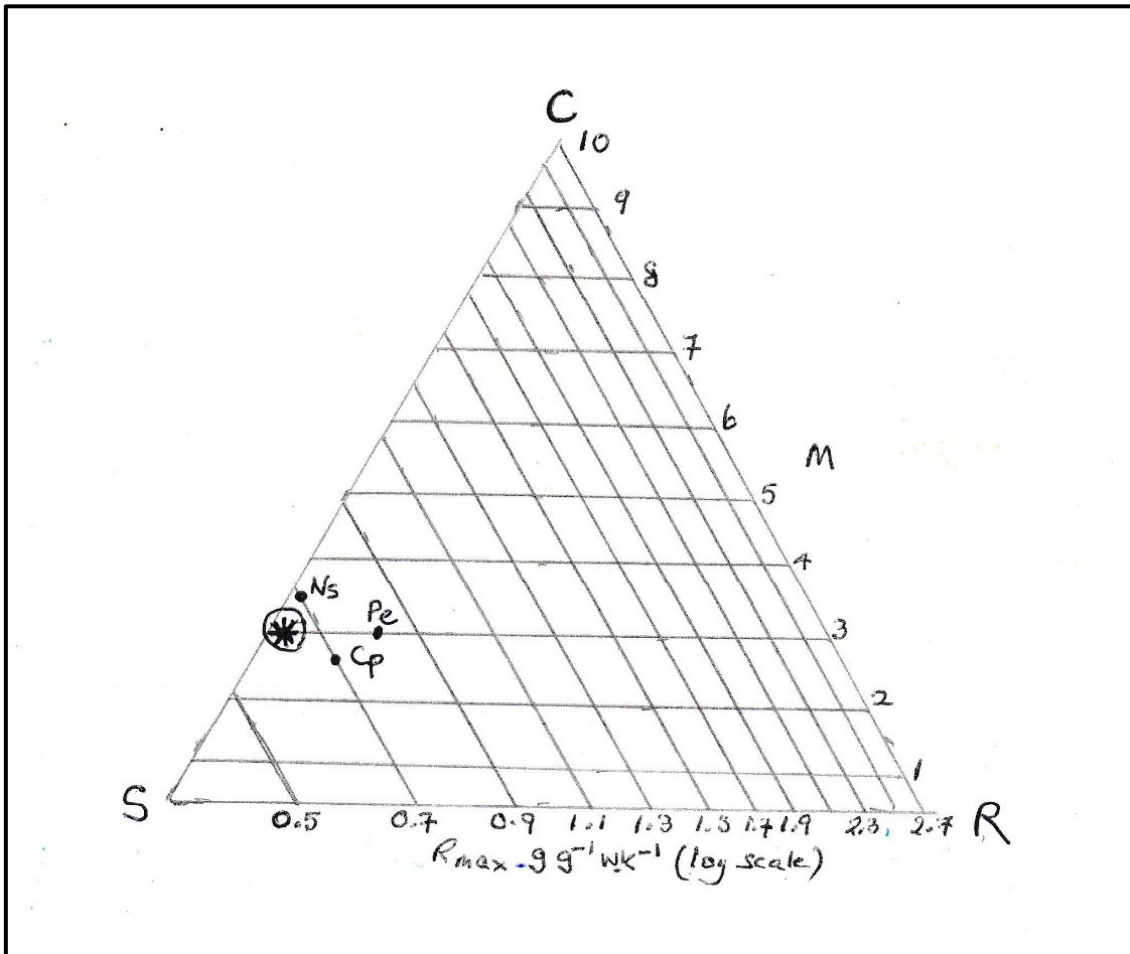


Figure 11 Ordination of bog asphodel (*) on Grime's Triangle.

The computation of values for maximum growth rate (R_{max}) and morphology index (M) are shown in Table 6. R_{max} is plotted on a log scale. (Cp *Carex panicea*, Ns *Nardus stricta*, Pe *Potentilla erecta*. C competition life strategy, S stress toleration life strategy, R ruderal life strategy.

Evaluation of bog asphodel's survivorship and persistence on Exmoor

a) Reproductive allocation for seed dispersal

The ratio of above-ground productivity, i.e. total leaf mass (m^{-2}) to total seed mass (m^{-2}) gives a measure of the relative importance of the two for a species' life history strategy. Bog asphodel on Exmoor puts only 0.2 – 1% of effort into generating seeds (Table 7). The strategic effort for bog asphodel is therefore strongly directed towards vegetative growth. It is noticeable from these data that there is considerable year-on-year variation in all the parameters measured except for capsule and seed numbers.

Characteristic (mean values)	Aclands 2017	Aclands 2018
A. Plant mass (g)	0.242	0.126
B. Plant density (m ⁻²)	340	491
Above-ground productivity (g/m²) A x B	82.28	61.87
C. Inflorescence numbers (m ⁻²)	2.1	11.6
D. Capsules per inflorescence	14.9	16.3
E. Seeds per capsule	50	52
F. Seed mass (g x 10 ⁻⁴)	1.08	0.68
Reproductive productivity (g/m²) C x D x E x F	0.169	0.669
% effort directed to seed production	0.002	0.011

Table 7: Bog asphodel above-ground productivity and seed production. Above-ground productivity is mean max plant mass (A) x mean quadrat plant density (B). Reproductive productivity is mean no. inflorescences (C) x mean no. capsules per inflorescence (D) x mean no. seeds per capsule (E) x mean seed mass (F).

b) Vegetative growth

New growth was evident in May 2018 where plants had been marked the previous year (Figure 12). New growth appeared in the same position for all 100 of the 2017 plants, but 80% of the shoots were shorter in 2018 than in 2017 (Tables 4 – 5, Figure 10).

During the growing season the rhizomes appear to grow a few centimetres, so that a ramet that starts off in one 10 cm square may end up in an adjacent one, evidence of lateral spread within a patch of bog asphodel. However, in two quadrats where the bog asphodel patch ended halfway across the 1 m² quadrat this boundary did not move between 2017 and 2018, evidence of persistence but not growth in the short term.



Figure 12: New growth from a bog asphodel rhizome 3rd May 2018.

Four of the quadrats lie along an EMP vegetation survey transect on the same site (Aclands 2 stars on Figure 7). Along the whole transect, there was a small increase in distribution three years after restoration, 61.25 % of 160 sub-quadrats contained bog asphodel after restoration compared to 59.38 % pre-restoration (Welch two sample t-test, $t = -0.34$, $p = 0.73$). However, there was an insignificant reduction in the mean cover of bog asphodel from 14.06 % to 11.88 % after restoration (Welch two sample t-test, $t = 0.70536$, $p = 0.48$) (Figure 13). At the four experimental quadrats along this transect, three showed an increase in cover three years after restoration ranging from 0.25 % to 2.5 % but at the quadrat next to the ditch (G1W, q20 on Figure 13) there was a 20% drop in cover after restoration.

Analysis of the vegetation survey data for Vernies Allotment (Figure 14) shows almost no change in distribution since restoration, mean percentage of sub-quadrats occupied before restoration was 36.88 % and eight years after restoration 38.13 % (Welch two sample t-test, $t = -0.23$, $p = 0.82$). There was a slight reduction in mean sub-quadrat cover between five years (4.93 %) and eight years (3.84 %) after restoration (Welch two sample t-test, $t = 1.26$, $p = 0.21$).

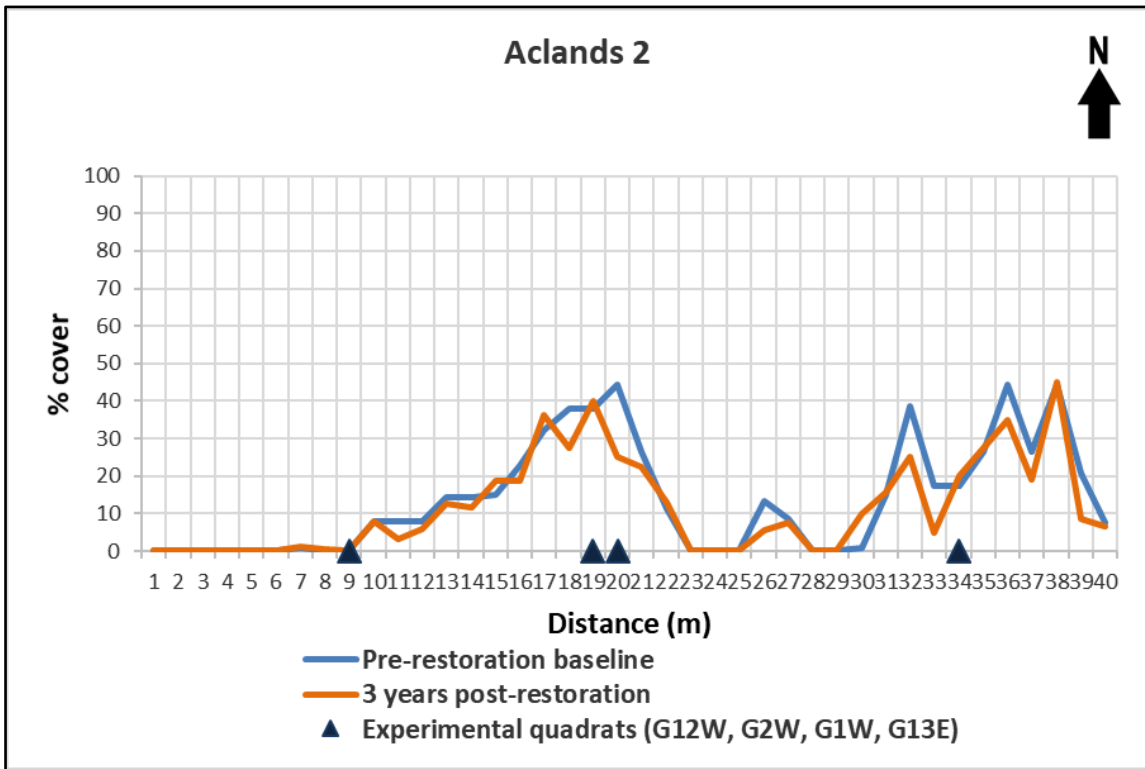


Figure 13: Bog asphodel distribution at Aclands pre- and post-restoration
Shifts in bog asphodel distribution (x-axis) and % cover (y-axis) at the Aclands experimental site post restoration

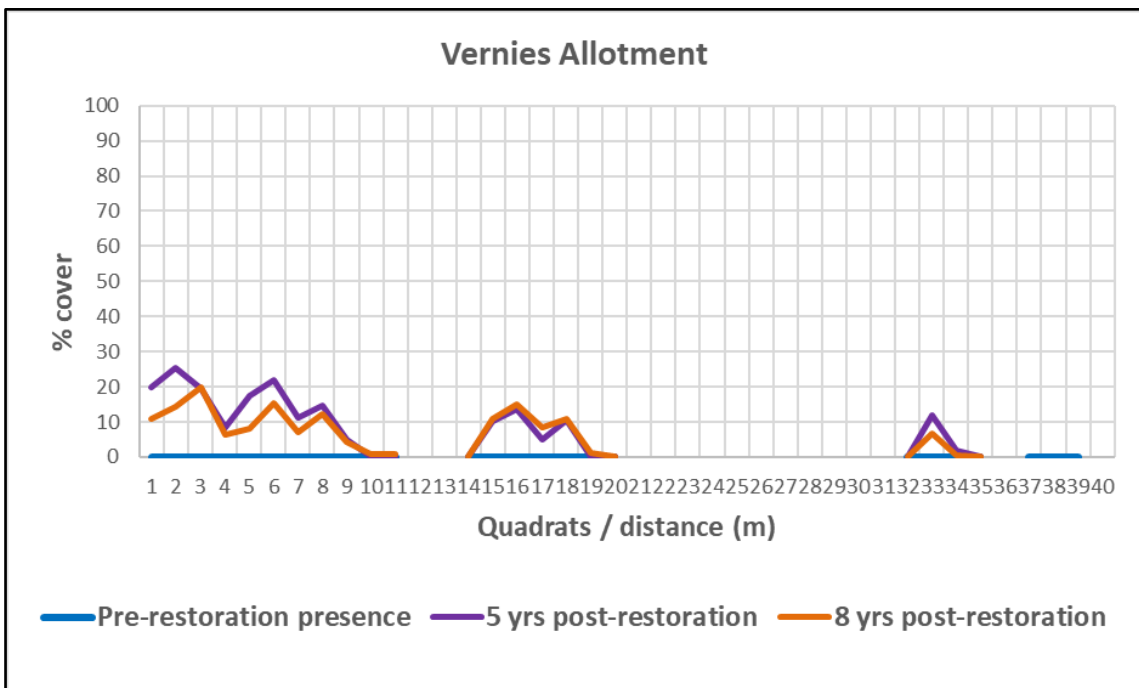


Figure 14: Bog asphodel distribution at Vernies Allotment pre- and post-restoration
Shifts in bog asphodel distribution (x-axis) before and after restoration, and in % cover (y-axis)(post-restoration only) at Vernies Allotment. NOTE: Blue lines indicate only the presence of bog asphodel before restoration, not % cover.

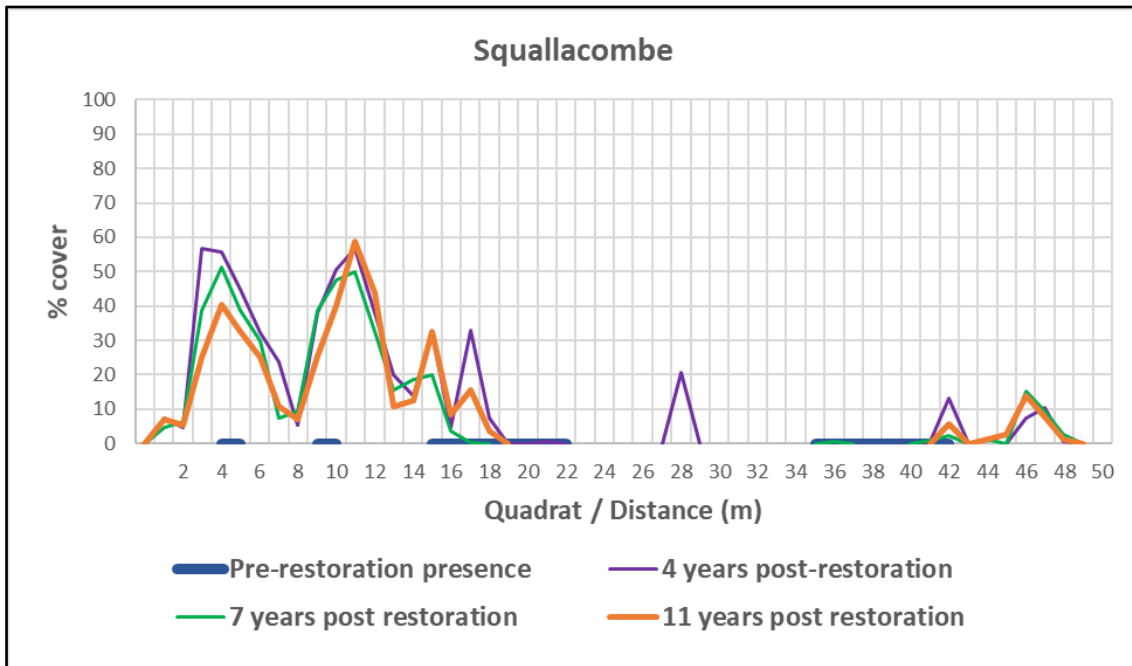


Figure 15: Bog asphodel distribution at Squallacombe pre- and post-restoration. Shifts in bog asphodel distribution (x-axis) before and after restoration, and in % cover (y-axis) (post-restoration only) at Squallacombe. NOTE: Blue lines indicate only the presence of bog asphodel before restoration, not % cover.

At the Squallacombe transect (Figure 15) there is again only a very small increase in occupied sub-quadrats, 37 % before restoration and 39.5 % eleven years after restoration (Welch two sample t-test, $t = -0.51$, $p = 0.61$) although there appears to be consolidation of the bog asphodel population at the start of the transect. This transect, originally across a large ditch/gully, has largely filled with water since restoration (Q20 – 40). Bog asphodel cover is starting to reduce from a mean sub-quadrat cover of 11.59 % four years after restoration (purple line) to 8.73 % 11 years after restoration (orange line) (Welch two sample t-test, $t = 1.63$, $p = 0.10$).

Analysis of the most recent vegetation surveys at 18 sites on Exmoor shows a small increase in bog asphodel distribution since restoration of 3 % (mean change 0.03 ± 0.33) (Figure 16). The surveys carried out within five years of restoration show a reduction in bog asphodel distribution (mean change -0.05 ± 0.29) and probably reflect more the effects of restoration disturbance than ecological change. The mean level after the initial disturbance, i.e. 6 – 11 years after restoration is for an increase in bog asphodel distribution of 4 % (mean change

0.04 +/- 0.34). Although the mean increase following restoration for all sites is 3%, a comparison of distribution site by site reveals a small drop in bog asphodel

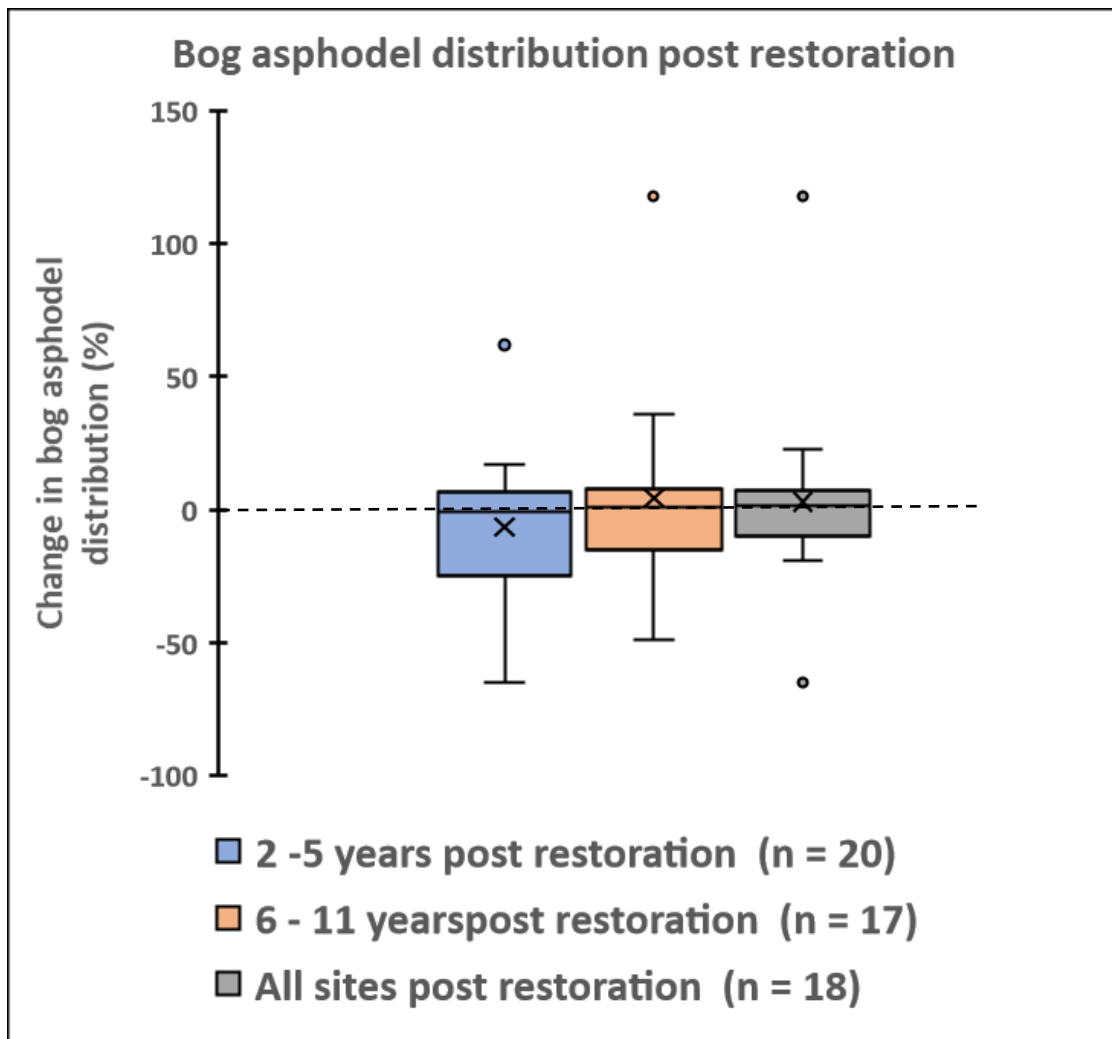


Figure 16: Changes in the distribution of bog asphodel at 18 restored sites on Exmoor. Zero represents no change in bog asphodel distribution.

distribution across all sites with bog asphodel occupying a mean 39.05 % of sub-quadrats before restoration and 38.95 % after restoration (Paired t-test, $t = 0.053$, $p = 0.95$).

This is evidence on a landscape scale that bog asphodel expands its range only slowly in the short term (< 11 years) after restoration, if at all.

c) Other factors influencing bog asphodel growth

Other factors that may influence the above-ground productivity of bog asphodel include WTD, peat depth and sward height. Water table depth (WTD) was the most obvious abiotic variation between 2017 and 2018 which could have influenced bog asphodel growth (Figure 18).

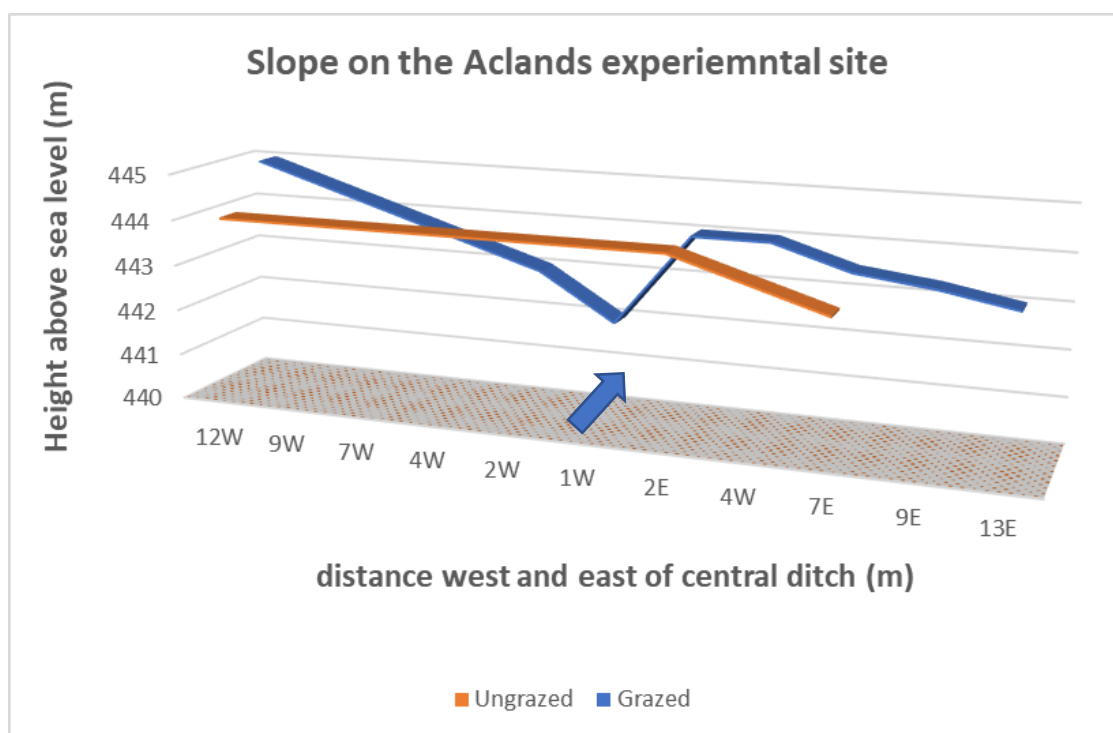


Figure 17: Slope and altitude at the Aclands experimental site

Diagram showing the slope on the Aclands experimental site from west to east. Orange line: ungrazed quadrats from (l-r) 12W to 7E. Blue line: grazed quadrats from (l-r) 12W to 13E. Blue arrow indicates position and direction of flow of the central ditch (see Figure 7).

	Mean altitude (m asl)	Mean slope (m m ⁻¹)
Ungrazed	444	0.05
Grazed	443.4	0.08

Table 8: Mean altitude and mean slope at the Aclands experimental site

Mean altitude and mean slope on the ungrazed (orange) and grazed (blue) sections of the Aclands experimental site (see Figure 17 above)

The site slopes from west to east and the ungrazed area is on average 0.6m higher than the more northerly grazed area (Figure 17, Table 8). The two areas also have different topologies and there are more ditch blocks in the upper ungrazed area (orange). However there were insufficient data to determine if slope or the position of the main ditch influenced the behaviour of the water table (Luscombe *et al.*, 2016).

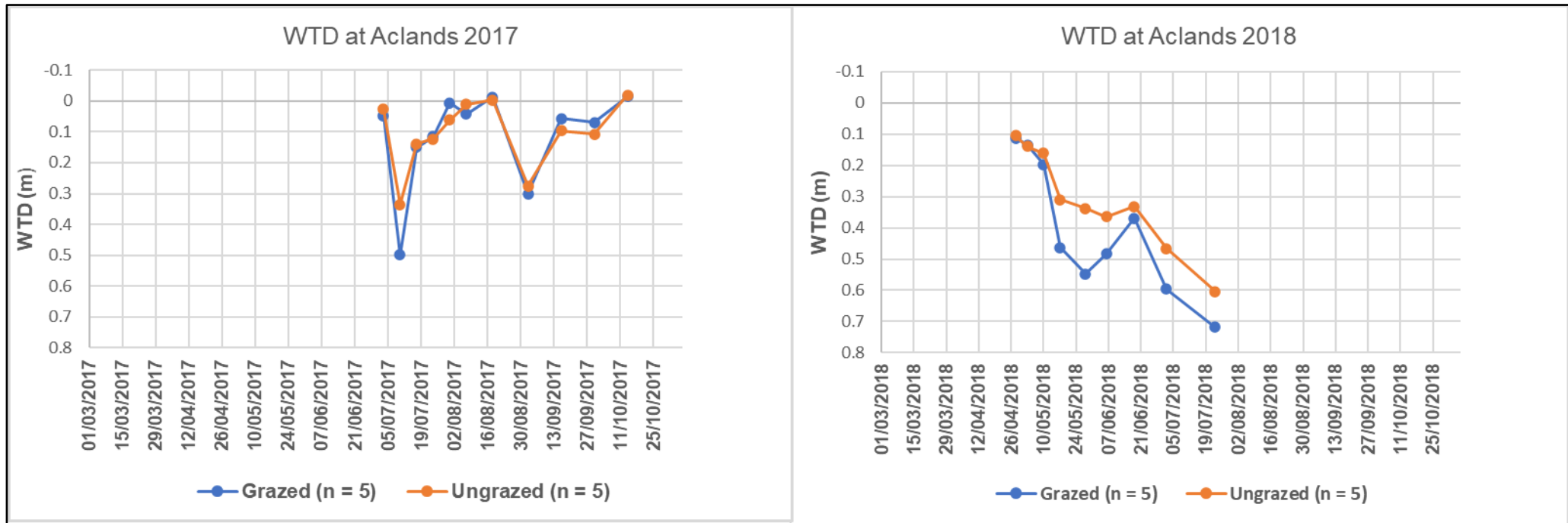


Figure 18: Water table depth (WTD) at the Aclands quadrats in 2017 and 2018 growing seasons

The data only show the mean seasonal WTD for each of the 10 dipwells. Mean seasonal WTD correlated with peat depth in 2018 but not in 2017 (Figure 19) (Pearson's test $r = -0.10$, $p > 0.05$ (2017); $r = -0.91$, $p < 0.01$ (2018)). In the very dry conditions of 2018 the water table was higher in the ungrazed area, where the peat is deeper but not significantly so. Mean peat depth in the ungrazed area was $43\text{cm} \pm 4.4\text{cm}$, and in the grazed area $32.8\text{cm} \pm 1.6\text{cm}$ (t-test, $t = 0.02$, $p > 0.05$).

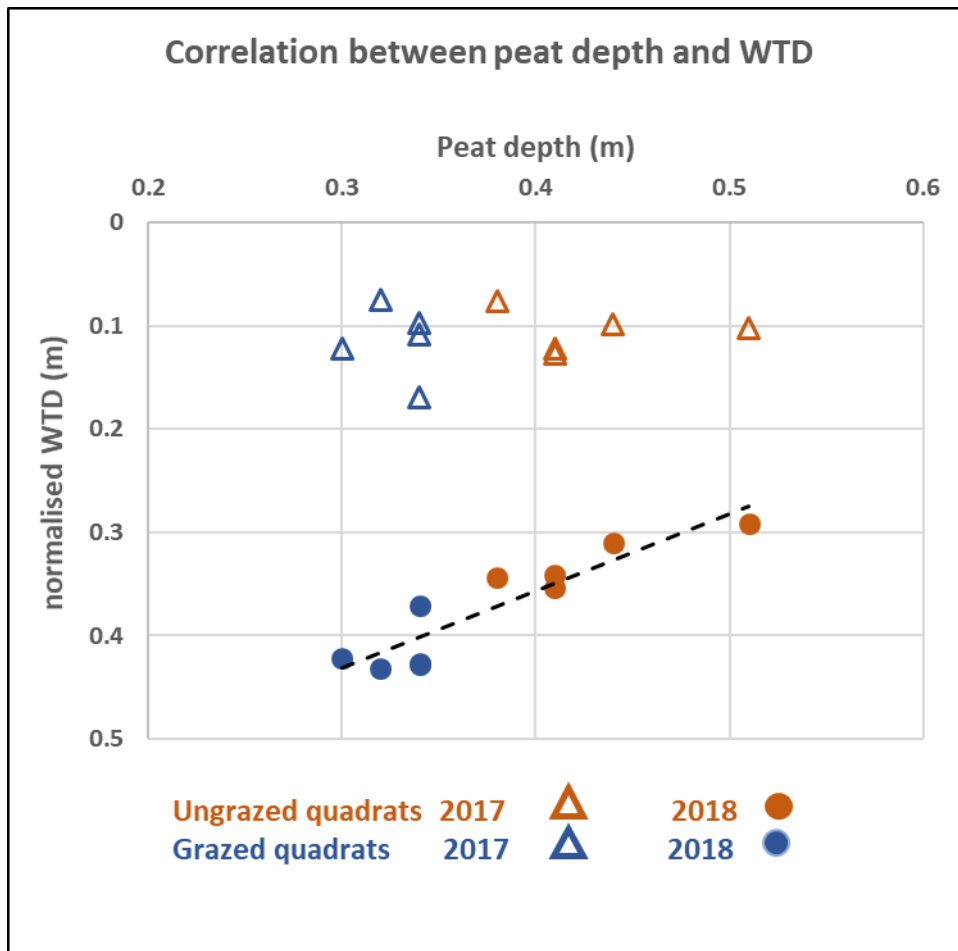


Figure 19: Correlation between peat depth and water table depth (WTD) in the summer seasons of 2017 and 2018.

Orange triangles and dots: ungrazed quadrats; blue triangles and dots: grazed quadrats. Dotted line: trendline for 2018 series.

There was no correlation between WTD and maximum height of the bog asphodel leaves in 2018 (Figure 20A) (Pearson's test, $r = -0.39$, $p > 0.05$). WTD did however appear to correlate with the general sward height in 2018 (Figure 20B) (Pearson's test, $r = -0.67$, $p < 0.05$).

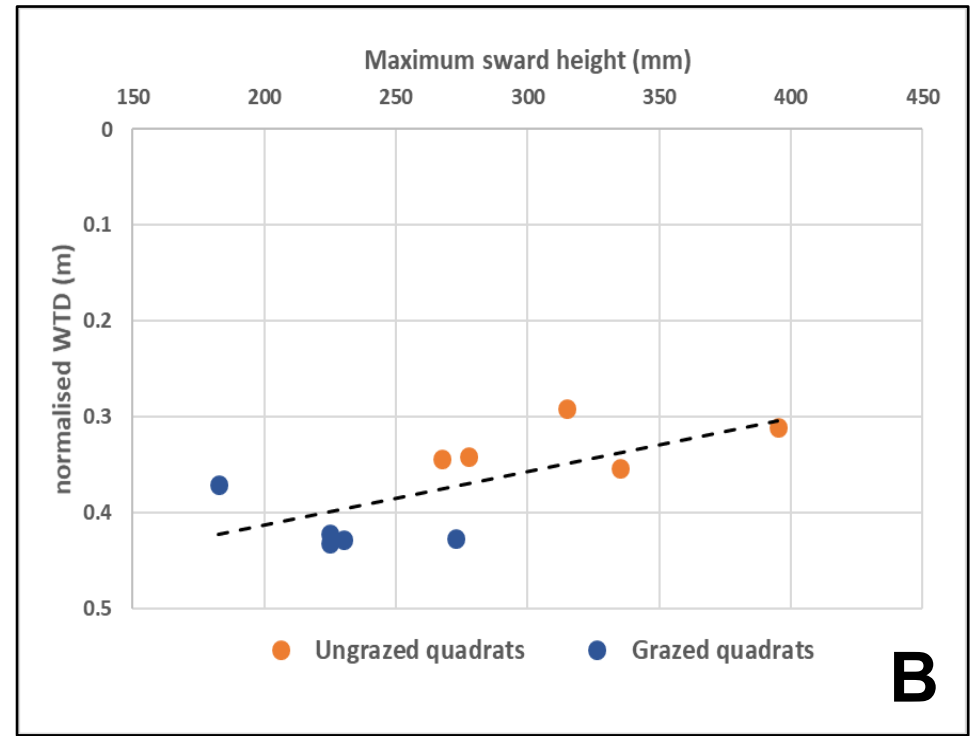
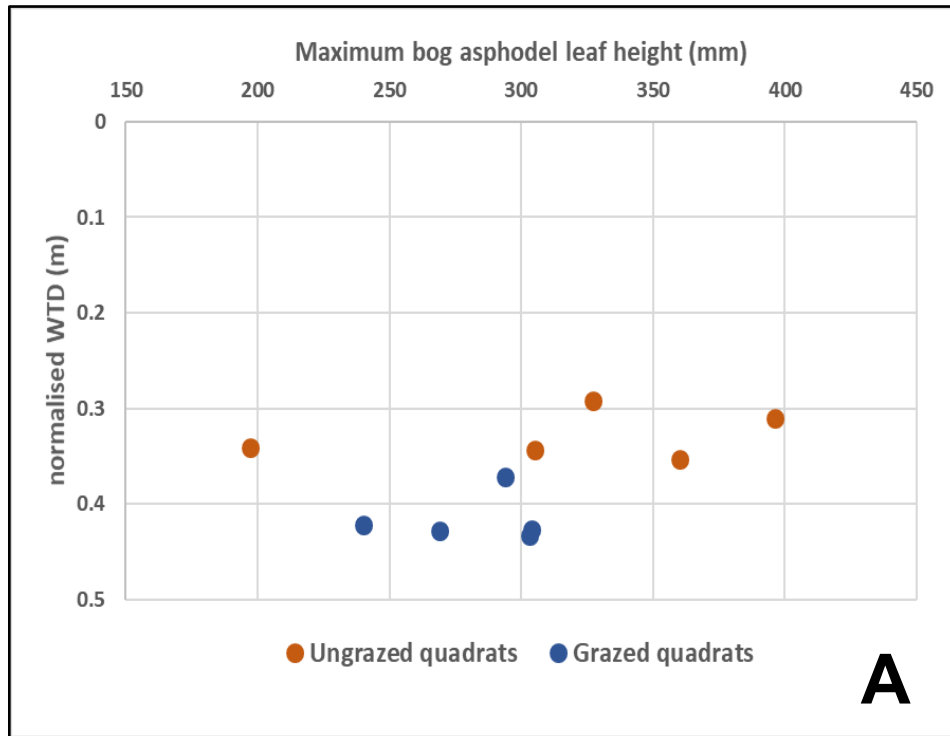


Figure 20: Correlations between water table depth (WTD) and bog asphodel leaf height (A) and sward height (B) in 2018. Dashed line = trendline for significant correlation between WTD and sward height.

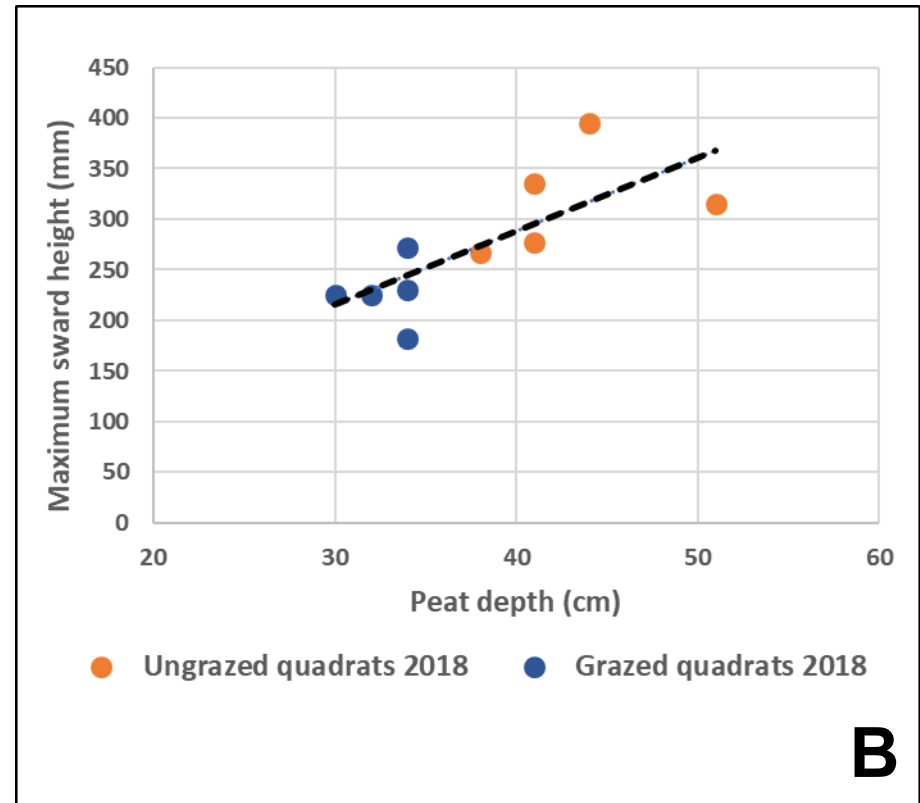
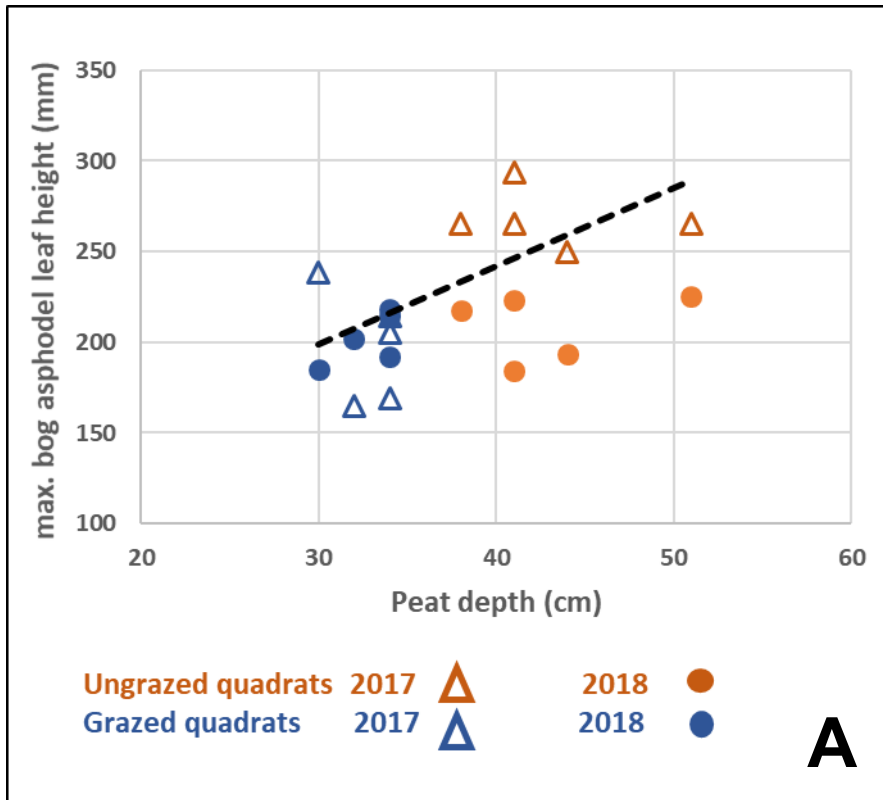


Figure 21: Correlations between peat depth and (A) maximum bog asphodel leaf height and (B) maximum sward height. Dashed line = trendlines for significant correlations between peat depth and maximum bog asphodel leaf height in 2017, and between peat depth and sward height in 2018.

General sward height also correlated with peat depth in 2018 (Figure 21B) (Pearson's test, $r = 0.74$, $p < 0.01$). Maximum bog asphodel leaf height only correlated with peat depth in 2017 (Pearson's test, $r = 0.64$, $p < 0.05$), not in 2018 (Pearson's test, $r = 0.35$, $p > 0.05$) (Figure 21A).

The sward in the ungrazed area was taller (mean $318 \text{ mm} \pm 46 \text{ mm}$) than in the ungrazed area ($227 \text{ mm} \pm 29 \text{ mm}$) (Figure 22) as might be expected, but the difference was not significant (T-test, $t = 0.2$, $p > 0.05$). There was however a correlation between sward height and maximum bog asphodel leaf height (Pearson's test, $r = 0.65$, $p < 0.05$) (Figure 23).

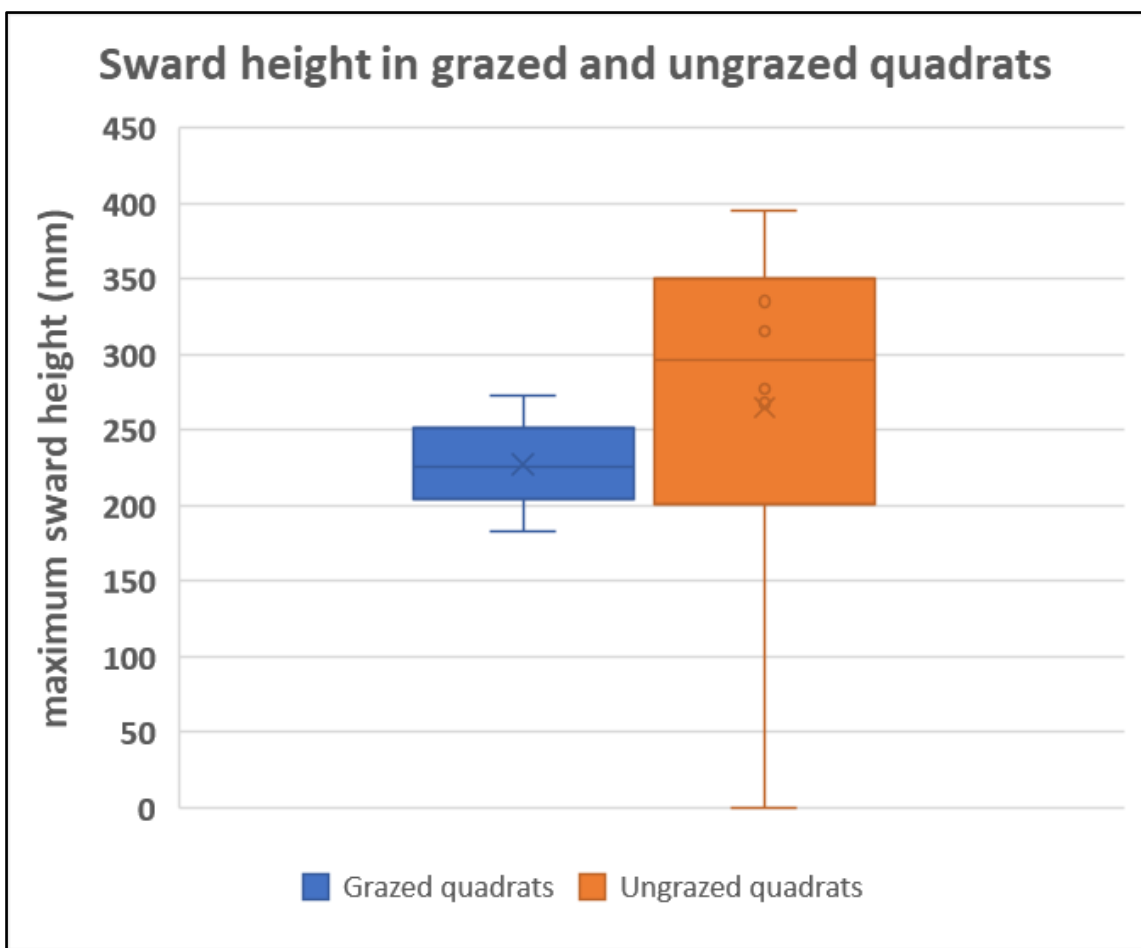


Figure 22: Maximum sward height in grazed and ungrazed areas in 2018.

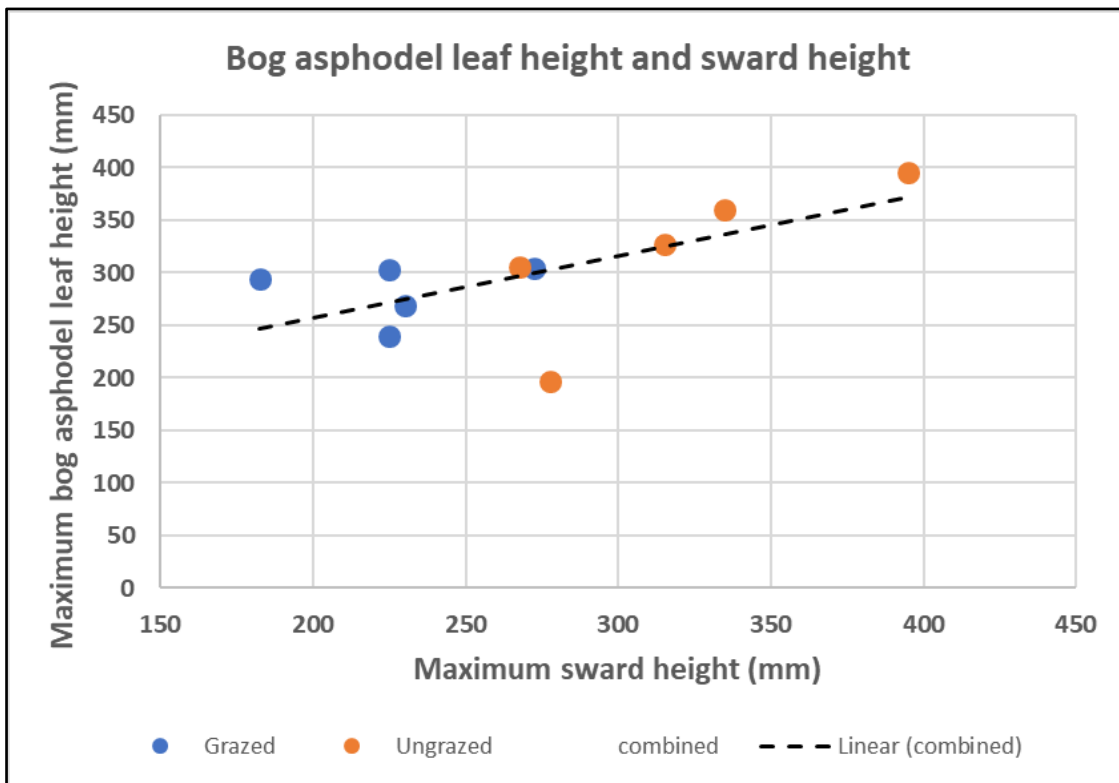


Figure 23: Correlation between sward height and maximum bog asphodel leaf height in 2018

Dashed line = trendline for significant correlation between sward height and leaf height

From the EMP vegetation survey records it was possible to compare changes in bog asphodel growth to changes in *Sphagnum* growth (all species) over the same period (Figure 24). In half the cases bog asphodel was declining as *Sphagnum* cover was increasing (Figure 24, top left quarter). The number in parentheses refers to the number of years over which the change occurred. Only those points marked with # indicate a change since restoration, i.e. compared to baseline data. Overall there is no correlation between changes in bog asphodel growth and changes in *Sphagnum* growth (Pearson's test, $r = 0.22$, $p > 0.05$)

For six sites for which cover data from before restoration is available (#) there appears to be a relationship between the growth of two species (Pearson's test, $r = 0.93$, $p < 0.01$) (Figure 25). The cover of bog asphodel is tied to *Sphagnum* cover even when this is in decline, perhaps because of deteriorating environmental conditions. The sites where both *Sphagnum* and bog asphodel are in decline are where restoration as in ditch blocking has had no effect as yet.

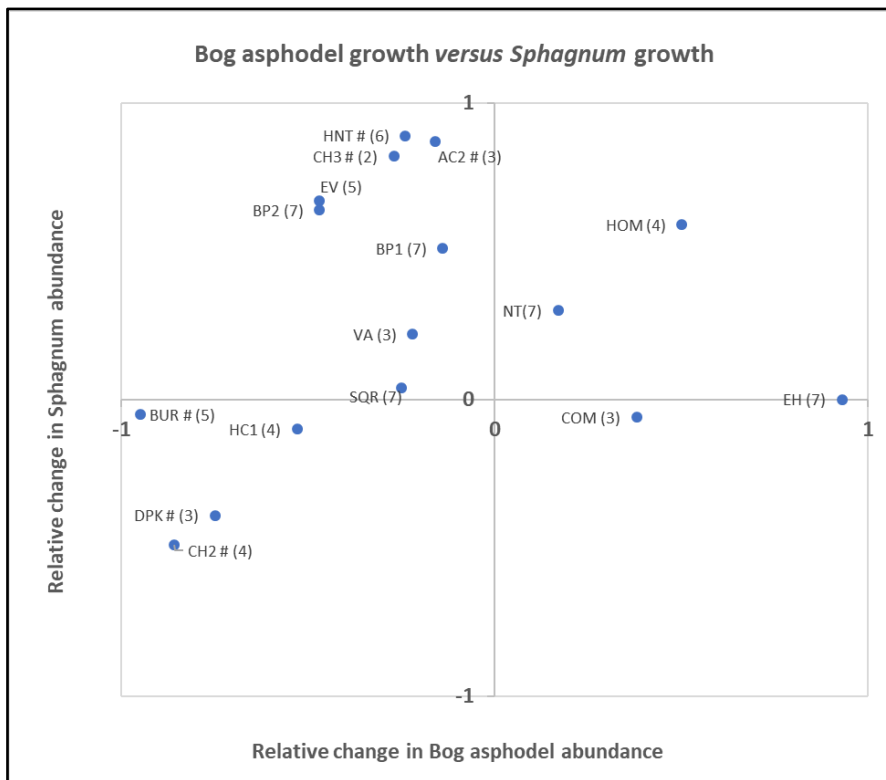


Figure 24: Relative changes in the abundance of bog asphodel and Sphagnum species at 16 Exmoor restoration sites. Abscissa = bog asphodel growth, -1 = halving, +1 = doubling. Ordinate = Sphagnum growth, -1 = halving, +1 = doubling. 0 = no change. # changes from pre-restoration baseline.

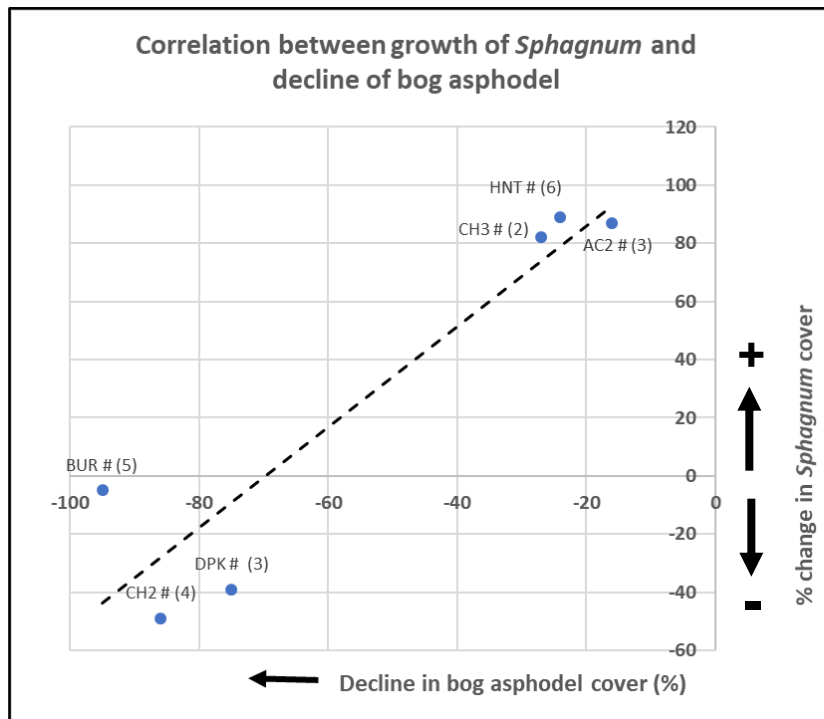


Figure 25: Growth of bog asphodel and Sphagnum species since restoration at six sites. Abscissa; % decline in bog asphodel, Ordinate: % change in Sphagnum cover from a decline of 60% to an increase of 120%

2.1.4 Discussion

Life form attributes and life history strategy of bog asphodel

The life form attributes of selected bog asphodel plants recorded over two seasons showed considerable variation from year to year (Table 4), suggesting some plasticity in above-ground phenotype (e.g. plant height). However, the plant is known to be very sensitive to light conditions (Summerfield, 1974) and it is possible that the disturbance to the sward by repeat measurements in 2017 created a less dense sward in 2018 with correspondingly more light penetration and less etiolation of bog asphodel leaves

Bog asphodel grows in well-defined patches which do not appear to expand following restoration in the short term (Figures 13 and 14) and it does not expend much effort in producing seeds to widen its range (Table 7). Its fundamental attributes are therefore highly conservative, offering a suitable strategy for tolerating environmental conditions which are unfavourable for many plants. The results of the Grime's Triangle analysis show bog asphodel having a typical stress tolerating life history strategy (Figure 11), in keeping with its behaviour when the peatland in which it is growing is rewetted (Figure 16). It persists with minor changes to its local growth pattern year on year but does not expand its range significantly. Two of the other plants with a similar life history strategy shown on Figure 11 are associated with bog asphodel (Table 3), namely *Carex panicea* and *Potentilla erecta*.

Survivorship of bog asphodel in restored shallow marginal peatlands

While the desk-top study appears to show a slight increase in bog asphodel distribution at restored sites, this trend is not consistent (Figure 16). The sites are re-surveyed only every three years so the vegetation survey results for a particular site will vary according to the years (and their climate) in which it is surveyed (Gatis *et al.*, 2019), and the experimental studies show that bog asphodel does not grow consistently from year to year (Table 4).

The outliers on Figure 16 represent three unusual restored sites. The lower ones indicating a marked decline in bog asphodel presence are from a site where ditch blocking has not achieved rewetting. The outliers representing a marked increase in bog asphodel distribution are from two sites with vegetation characteristic of mesotrophic conditions, suggesting springs and groundwater may play a

significant role in their hydrology. Most restoration sites on Exmoor are however ombrotrophic.

The analyses of possible correlations between bog asphodel growth and WTD, peat depth and sward height suggest abiotic and biotic factors may influence how bog asphodel reacts to a changing environment (Figures 19-23), but there were too many dependent variables for any reliable conclusions to be drawn. The possible correlation with *Sphagnum* cover is intriguing, suggesting that bog asphodel cover decreases as *Sphagnum* cover increases (Figures 24-25). This is most likely to reflect an underlying change in water table as *Sphagnum* species, especially the peat-forming ones require a high and stable water table (Sinker, 1962; Straková *et al.*, 2012). Plants, especially perennials, are known to occupy hydrological niches (Bartelheimer *et al.*, 2010; García-Baquero *et al.*, 2016). There is, for example, a clear differentiation in growth of the two *Eriophorum* species and bog asphodel depending on WTD

Climate generally may also influence the growth of bog asphodel year on year. Analysis of temperature and rainfall from March to October in 2017 and 2018 shows significant differences during the spring and summer of both years (Table 9). These differences are reflected in the corresponding WTD records, as reported above (Figures 18). Figure 26 shows both these WTD records and the corresponding temperature and rainfall records. Spring 2018 was significantly colder and wetter than the Spring 2017, whereas Summer 2018 was warmer and drier than Summer 2017 (Table 9) (UK Meteorological Office, 2019b, 2019c).

	Daily temp. (°C) Liscombe	*	Daily rainfall (mm) Hawkridge	*	Total rainfall (mm)
Mean Mar - April 2017	9.96	p = 1.73 e-06	2.72	p = 0.009	166
Mean Mar - April 2018	7.63		5.60		341.6
Mean May - August 2017	16.21	p = 2.67 e-07	3.10	p = 0.0002	380.9
Mean May - August 2018	17.96		2.09		256.5
* Wilcoxon rank sum test					

Table 9: Statistical comparisons of temperature and rainfall in 2017 and 2018

The effect of either or both of these seasonal differences may have stimulated bog asphodel to produce shorter leaves but more shoots and flowers in 2018 (Table 4). Intuitively the spring climate (Mar-Apr) might be expected to influence early summer growth more than the summer climate (May – October), although WTD fell steeply in May 2018 (Figure 26) which could have influenced plant

growth. In 2017 with a consistent WTD around 10cm below the surface (Figure 19), plants were taller than in 2018 when the water table went much lower (Table 4).

2.1.5 Conclusions

My work suggests that peatland restoration *per se* does not impact significantly on the distribution of bog asphodel. The determination of the life history strategies of the dominant components of the vegetation can predict their likely long-term responses to environmental change. This in turn can be used to inform management strategies following landscape scale habitat restoration.

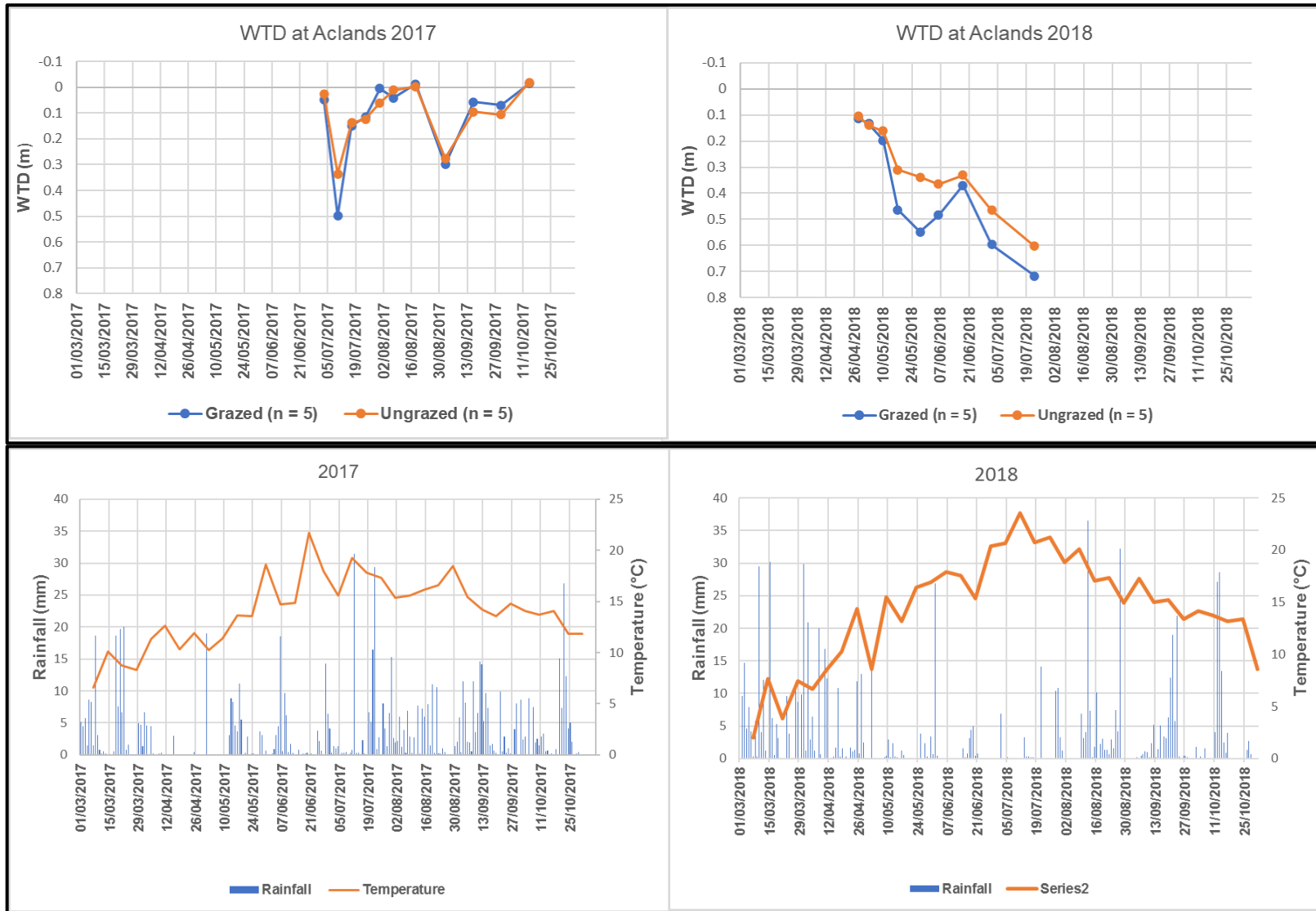


Figure 26: Water table depth (WTD) at Aclands, and mean weekly temperature at Liscombe (UK Meteorological Office, 2019b) and daily rainfall at Hawkridge (UK Meteorological Office, 2019c) in 2017 and 2018.

2.2 Bog asphodel's contribution to sward quality and grazing potential

Bog asphodel is a common component of peatland vegetation and its leaves and flowers can be toxic to grazing livestock. The aim of this section is to assess the contribution bog asphodel makes to the quality of transitional bog and what implications this has for management of such restored peatlands.

2.2.1 Introduction

Current concerns over global warming and the vulnerability of planetary resources have focused attention on the potential of peatlands to act as carbon sinks and sources of environmental goods (Bain *et al.*; Bonn *et al.*, 2014). Much of the UK's peatland is blanket bog and 80% of this is in poor condition as the result of more than 200 years of damage inflicted by drainage, over-grazing, burning and atmospheric pollution (Andersen *et al.*, 2017; Holden *et al.*, 2007). International and national drivers (e.g. IPCC (IPCC, 2014), UK Biodiversity Action Plan (JNCC, 1994)) require such habitats to be returned to favourable condition (Bonn *et al.*, 2016). Healthy functional peatlands are an important tool for the mitigation of climate change. The U.K. lies on the south-western edge of the climatic envelope for northern peatlands and peat formation is therefore particularly at risk from the warming climate, especially the peatlands of the South-West, some of which are also very shallow (Gallego-Sala and Prentice, 2013). However, so far the U.K.'s south-western peatlands have continued to act as carbon sinks in the warming climate (Lunt *et al.*, 2019), and elsewhere restoration efforts on climatically marginal peatlands have been shown to increase the likelihood of increasing carbon sink capacity (Dixon *et al.*, 2014).

Most peatland restoration projects aim to rewet the peat by blocking up drainage features (Armstrong *et al.*, 2009; EMP, 2019). The blocks prevent the water running off the peatland and create a higher and more stable water table (Holden *et al.*, 2011; Luscombe *et al.*, 2016). This change in hydrological environment aims to encourage a different vegetation to that found on drained peatlands where the water table fluctuates widely between precipitation events (Bellamy *et al.*, 2012; González *et al.*, 2014; Grand-Clement *et al.*, 2015). Healthy blanket bog vegetation is dominated by *Sphagnum* mosses and associated vascular plants and bryophytes which thrive in a cool, constantly wet, acidic and

nutritionally poor environment (Rodwell, 1991). Bog asphodel is one such vascular plant, thriving best when the water table is stable around 10cm below the surface with surface water movement (Summerfield, 1974).

Upland land use in the UK is dominated by livestock farming and peatland restoration has to take into account farmers' needs as well as those of other stakeholders (Aronson *et al.*, 2006; Bonn *et al.*, 2016; Byg *et al.*, 2017; Griscom *et al.*, 2017). A legitimate concern for farmers is how the rewetting will affect the quality and quantity of land they have available for grazing, and thus profitability.

Semi-natural grasslands as found on upland farms may not offer the same level of nutrition as intensively managed and improved lowland grassland but enough for stock to thrive and put on weight (Common *et al.*, 1991; Fraser *et al.*, 2013). *Molinia* is relatively high in crude protein, and the spring growth of most moorland plants is digestible and provides acceptable levels of nutritional quality (Critchley *et al.*, 2008; Freeman, 2017).

Exmoor's moorlands are a mosaic of vegetation types, from dry acid grassland, through wetter *Molinia*- and rush-dominated heathland to very wet valley mires and blanket bog (Freeman, 2017). The aim of restoration is to convert the pervasive *Molinia*-dominated wet heath to transitional bog in the short term and blanket bog in the longer term. *Molinia caerulea* (purple moor grass) is a robust tussock grass which outcompetes most other flora, including bog asphodel, to create a monoculture across large areas of drained peatland. Transitional bog species include *Sphagnum*, dwarf shrubs such as *Erica tetralix*, *Eriophorum* species and herbs such as bog asphodel, as well as *Molinia*. Blanket bog is dominated by *Sphagnum* species with dwarf shrubs, *Eriophorum* species and herbs such as *Drosera* (Sundew), *Vaccinium oxycoccus* (Cranberry) and bog asphodel (Freeman, 2017; Rodwell, 1991). Raising the water table has been shown to facilitate vegetation change, even where the original mire vegetation has been very badly eroded or even destroyed (Bellamy *et al.*, 2012; Menberu *et al.*, 2016).

The main forage attributes that contribute to quality are given in Table 10.

Attribute	Unit	Explanation	Laboratory analysis	Effect on forage quality
Dry matter (DM)	g/kg	All non-water components of the forage / sample, measured as the total weight of the sample with water removed	Sample dried and reweighed.	Contribution to forage quality inversely related to % of NDF in DM
Crude protein (CP)	g/kg	The total nitrogen in the forage / sample, including both true protein and non-protein nitrogen	Dry sample digested in acid and distilled to release ammonia. N in ammonia measured, x 6.25 to reflect average N in biological protein	Main contributor to weight gain
Neutral detergent fibre (NDF)	g/kg	A measure of plant cell wall components and total fibre constituents, including cellulose, hemicellulose, lignin, silica, tannins and cutins.	Dry sample dissolved in detergent to remove non-fibrous material. Residue weighed as fibre content .	High levels reduce forage quality because highly indigestible
Digestibility (D)	%	The extent to which the forage / sample is absorbed by the animal as it passes through the digestive system	Dry sample digested <i>in vitro</i> and result compared with forage samples of known <i>in vivo</i> digestibility levels.	Directly contributes to forage quality, closely related to ME
Metabolisable energy (ME)	MJ/kg	The gross energy in the forage / sample minus the energy lost through excretion	Standard calculation of 0.16 x digestibility %	Energy available from digested proportion of DM
Best quality forage has high levels of CP and D, low values of NDF				

Table 10: Common definitions of forage quality attributes and their measurement (after Freeman 2017))(Freeman, 2017; Mariotti et al., 2008; Thomas, 1990)

The quality of a sward varies with vegetative composition, seasons, grazing pressure, climate and topography, and is compromised if it contains plants such as bog asphodel which has potent toxins in its leaves and flowers (Pollock *et al.*, 2015). Grazing animals themselves also affect the sward by opening it up and thereby encouraging biodiversity, by preferentially grazing different areas and by causing eutrophication by defecation (Adler *et al.*, 2001; Anderson *et al.*, 2016).

Freeman (Freeman, 2017) studied the grazing patterns of cattle and the variations in forage quality between habitats and in different seasons, at a restored site (Aclands) on Exmoor. A similar methodology was used to assess the contribution of bog asphodel to the swards of *Molinia*-dominated wet heath and transitional bog, as examples respectively of pre- and post-restoration habitat, and thus their grazing potential and management. The studies were carried out at two contrasting peatland restoration sites on Exmoor.

Specifically, the study had three objectives:

1. To evaluate differences in sward quality of *Molinia*-dominated habitat and transitional bog habitat in spring and autumn;
2. To evaluate bog asphodel's contribution to sward quality on restored shallow peatlands; and
3. To assess habitat grazing preferences of cattle on two restored peatland sites on Exmoor.

2.2.2 Methodology

Sites

Two sites were used for this research, Roosthitchen (RST) (51.149°N 3.833°W) and Aclands (AC) (51.134°N 03.811°W) which is part of the larger Squallacombe site (Figure 27). The annual rainfall at nearby Liscombe (51.087°N 3.608°W) is 1445mm, and the annual temperature range is 5.8 – 12.1 °C (1981-2010 30 year average (UK Meteorological Office, 2019a). Both sites are in the River Barle catchment, and both are grazed seasonally by cattle and intermittently by deer. The two sites have different ditch patterns with a few deep ditches at Roosthitchen and an extensive pattern of shallow criss-crossing ditches at Aclands (Figure 28A). The Roosthitchen site is north facing whereas the Aclands site faces south.

The Aclands site (Figure 29) ranges in height from 440 – 460 m a.s.l. and is grazed in summer by 30 Devon cows, 31 calves and one Charolais bull. There were also a few ewes on the site all year.

The Roosthitchen site (Figure 30) is much wetter than Aclands with a different habitat mosaic (Figure 28 B/C). The site is 400 – 440 m a.s.l. Roosthitchen and the adjacent site are grazed by around 50 head of cattle in the summer season.

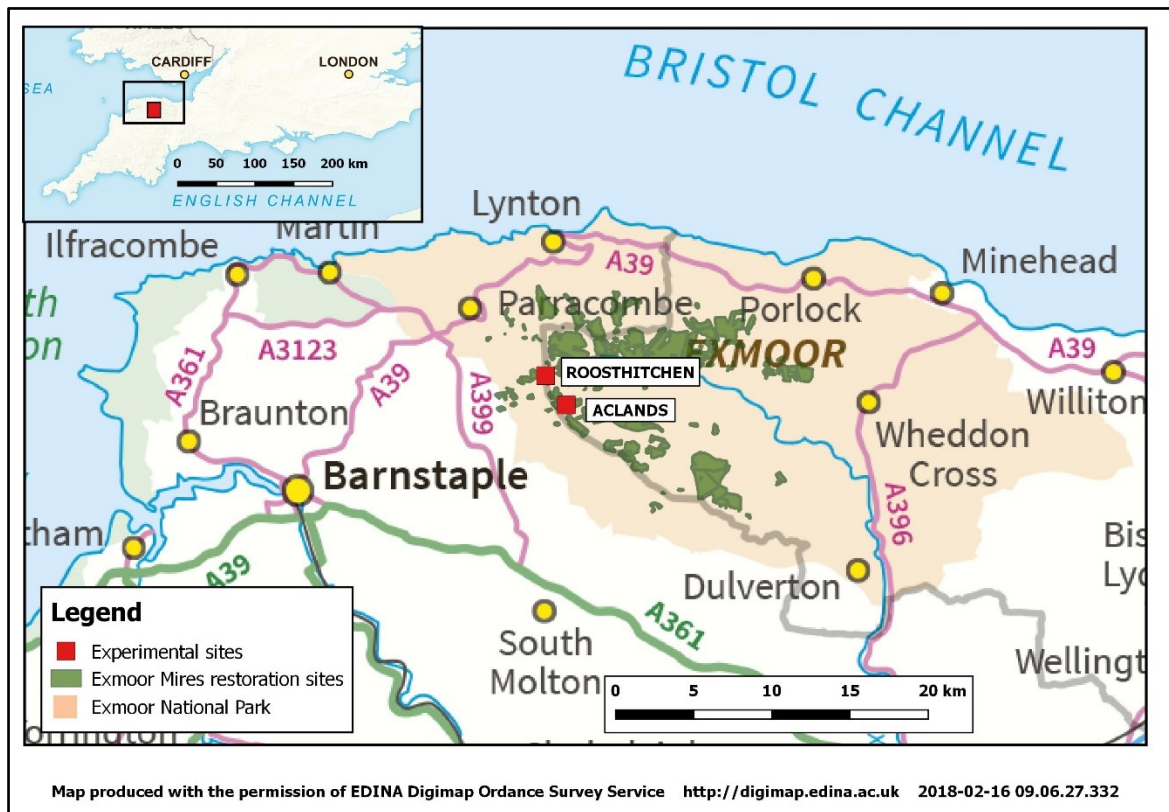


Figure 27: Location of experimental sites within Exmoor National Park.

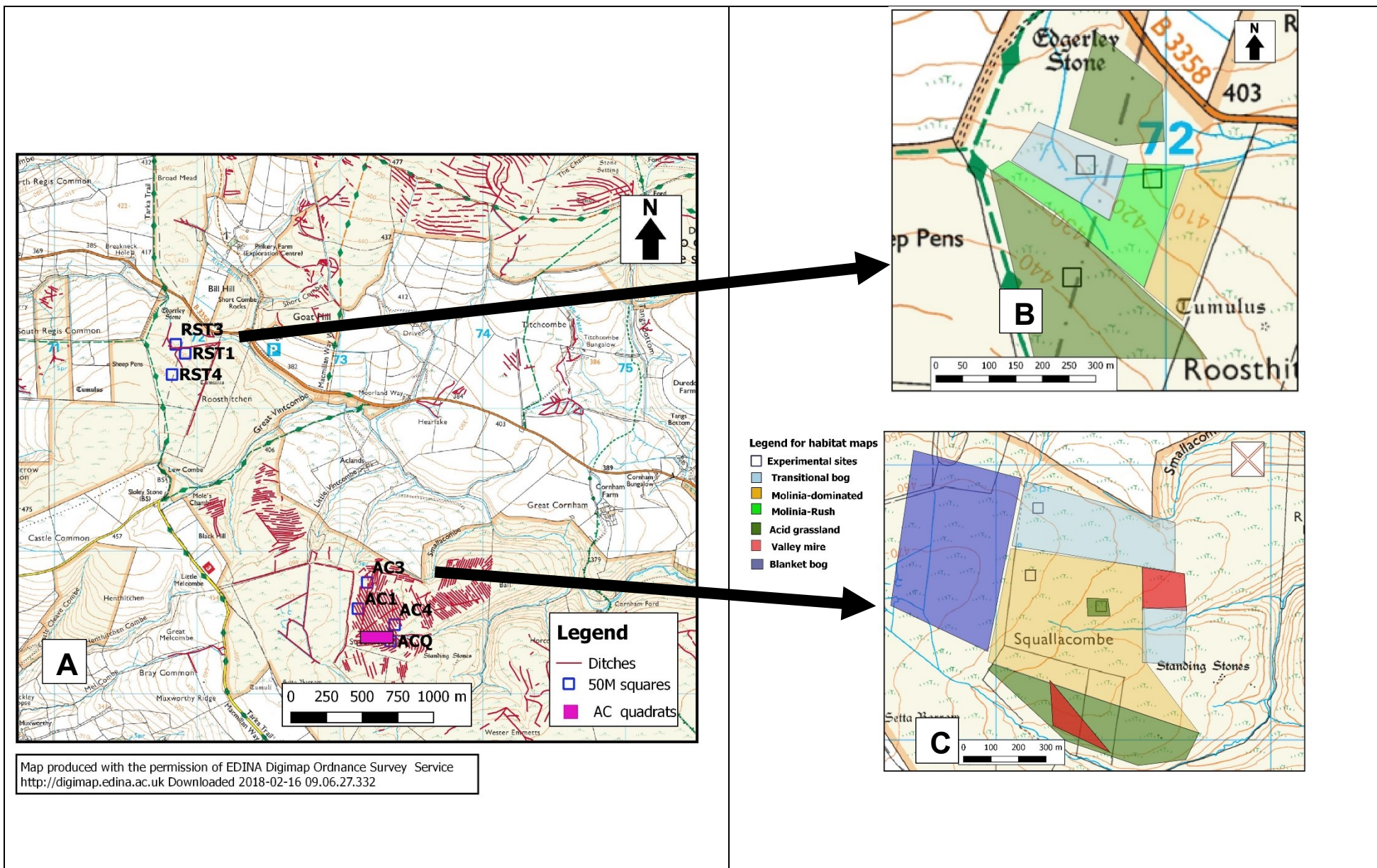


Figure 28: Experimental sites (A); habitat maps for Roosthitchen (B) and for Aclands (C)

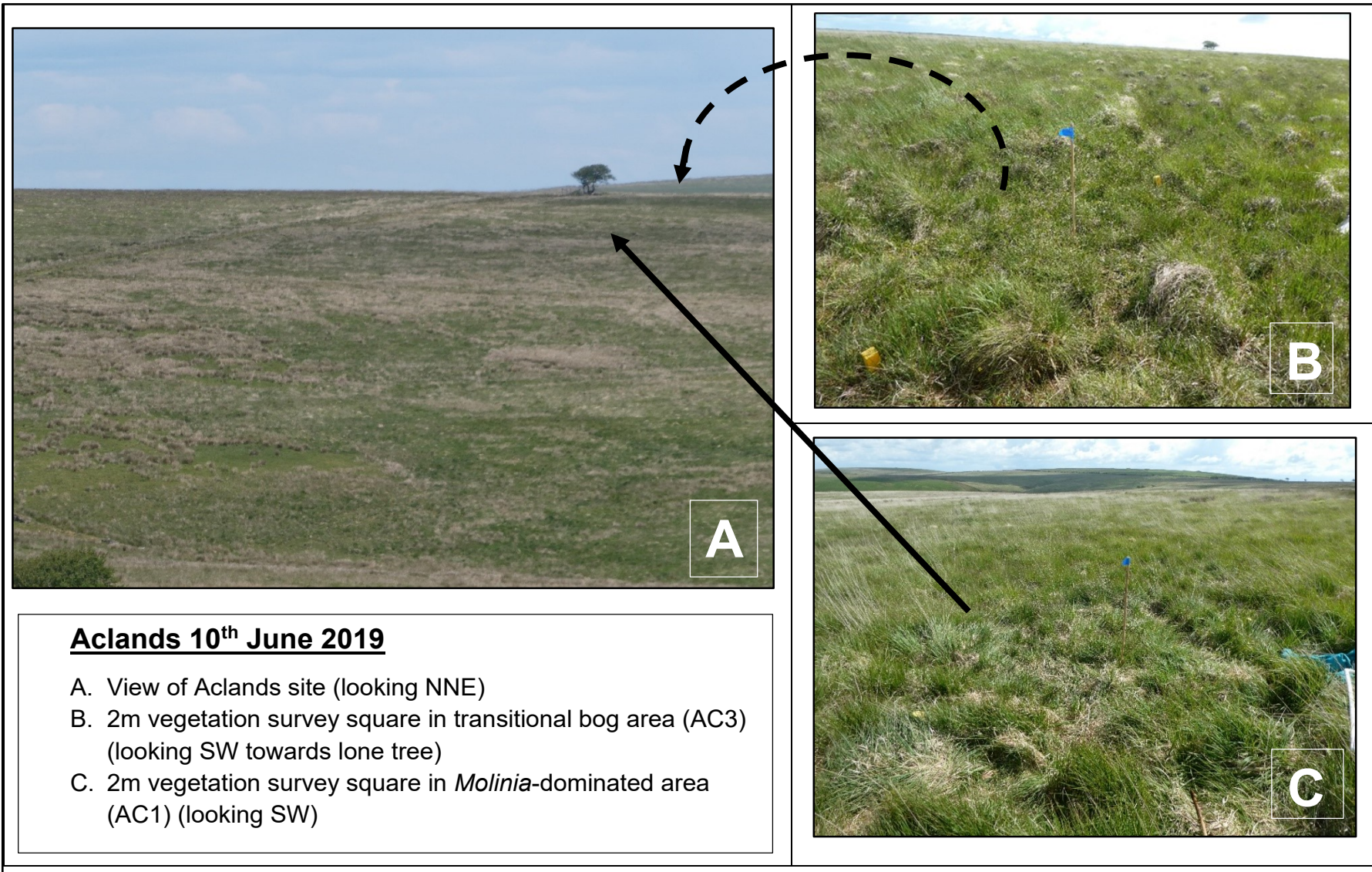


Figure 29: Photographs of the Aclands site.

6th June 2019
Roosthichen site



A. Roosthichen site looking south



B: Molinia-rush dominated habitat (RST1)



C: Transitional bog habitat (RST3)



D: Close-up of transitional bog vegetation

Figure 30: Photographs of the Roosthichen site

At each site 50m squares were set up in *Molinia*-dominated habitat (AC1 and RST1), transitional bog (AC3, RST3) and dry grassland (AC4 and RST4) for dung counts (Figure 28A). Vegetation studies were conducted within the *Molinia*-dominated (MD) and transitional bog (TB) squares only.

Sward quality investigation

The sward quality studies were based on the methodology used by Guy Freeman (Freeman, 2017). The vegetation analysis carried out on 1 m² plots in 2018 was a pilot study for vegetation surveys in 2 x 2 m plots in 2019. In 2019 a 2 x 2 m plot was set up in the MD and TB squares at each site for vegetation analysis. The cover of individual species was estimating in each 1 m² by recording the number of 10 cm squares in the quadrat (Figure 8) that they occupied. 14 species samples were sent for forage analysis in June and September 2019 (Table 11). The samples (of individual species or species groups such as fine grasses) were collected from a variety of habitats within each site to give samples representative of the quality in the general area, and each sample comprised leaves, fruits, flowers and stems according to season. Samples were analysed at Yara Analytical Laboratories in Pocklington, Yorkshire, using their LC4 fresh grass forage analysis (<https://www.yara.co.uk/crop-nutrition/farmers-toolbox/other-analyses/>). This analysis gives dry weight, crude protein, neutral detergent fibre, digestibility, metabolisable energy and other values for each species sample (Table 10). These figures can then be used to calculate comparable values for each habitat type in each season by using the percentage contribution of each species to the different habitats.

Grazing studies

Dung counts were carried out on each 50m square monthly from June to September 2018. Each pile of cattle dung was marked with the month's colour using stock spray paint and its position recorded.

	Species	Common name	<i>Molinia</i> -dominated		Transitional bog	
			AC1	RST1	AC3	RST3
Herbs	<i>Calluna vulgaris</i>	Ling	√	√ ‡	√	√ ‡
	<i>Erica tetralix</i>	Cross leaf heath	√*	√ ‡	√*	√ ‡
	<i>Gallium saxatile</i>	Heath bedstraw	√	√ ‡	√	√ ‡
	<i>Narcethium ossifragum</i>	Bog asphodel	√	√	√	√
	<i>Potentilla erecta</i> #	Tormentil	√	√ ‡	√	√ ‡
	<i>Vaccinium myrtillus</i>	Bilberry	√	√ ‡	√	√ ‡
Grasses	Fine grass species		√	√ ‡	√	√ ‡
	<i>Molinia caerulea</i>	Purple moor grass	√	√	√	√
Rushes	<i>Juncus</i> species	Rush species	√	√	√	√
Sedges	<i>Carex</i> species	Sedge species	√	√	√	√
	<i>Eriophorum angustifolium</i>	Bog cottongrass	√	√ ‡	√	√ ‡
	<i>Eriophorum vaginatum</i>	Hair tail cottongrass	√	√ ‡	√	√ ‡
Mosses	<i>Spagnum</i> species	peat moss species	√	√ ‡	√	√ ‡
	Turf moss species	other bryophyte species	√	√ ‡	√	√ ‡

‡ not sampled in 2018

* not sampled in June 2018

only sampled at RST in Sept 2019

Carex species	<i>Carex binervis</i> , <i>C. demissa</i> , <i>C. echinata</i> , <i>C. nigra</i> , <i>C. panicea</i> .
Fine grass species	<i>Agrostis</i> sp., <i>Anthoxanum oderatum</i> , <i>Deschampsia flexuosa</i> , <i>Festuca</i> sp., <i>Holcus lanatus</i> .
Juncus species	<i>Juncus acutiflorus</i> , <i>J. effusus</i> .
Sphagnum species	<i>Sphagnum capillifolium</i> , <i>S. cuspidatum</i> , <i>S. denticulatum</i> , <i>S. fallax</i> , <i>S. palustre</i> , <i>S. papillosum</i> , <i>S. subnitens</i> , <i>S. tenellum</i> .
Turf moss species	<i>Aulacomnium palustre</i> , <i>Hypnum jutlandicum</i> , <i>Pleurozium schreberi</i> , <i>Polytrichum commune</i> , <i>Pseudoscleropodium purum</i> , <i>Rhytidiadelphus squarosus</i> .

Table 11: Species collected for forage analysis at Aclands and Roosthitchen in 2018 and 2019

2.2.3 Results

Sward quality

Transitional bog (TB) habitat at both sites has a higher sward quality than *Molinia*-dominated (MD) habitat (at Aclands), across all five measures of quality and in both seasons (Figure 31). Each bar represents the sum of the contributions of the species present in the habitat. The vegetation structure of both habitats at the two sites is shown in Figures 32 - 33. It is immediately apparent that the Roosthitchen "MD" site is too species rich to be a typical *Molinia*-dominated habitat and it has not therefore been considered further in these analyses. The poorer sward quality of MD habitat is a direct function of its poverty of species.

The fourteen species include all those that occupied more than 1% of cover in the two habitats. The two TB sites have similar vegetation, the main differences being that *Eriophorum vaginatum* and turf mosses are well represented in Aclands TB whereas these two are replaced by *Carex* species and *Juncus* species in Roosthitchen TB (Figure 33 A/B). In the autumn there were small changes in the proportional presentation of species at both sites, notably a larger proportion of *Carex* species at Roosthitchen.

The quality of individual species (as measured by their crude protein (CP) and digestibility (D) values) changes from spring to autumn (Figure 34). The species from the two sites have approximately the same ranges of digestibility and crude protein in spring and autumn. Within each cluster the species in the top right segment are the most nutritious. *Carex* species and turf mosses retain their relative position into autumn but others, e.g. *Vaccinium myrtillus*, are markedly less nutritious in the autumn. Bog asphodel (solid arrows in Figure 33) retains its position as a moderately nutritious species at Aclands, but not at Roosthitchen.

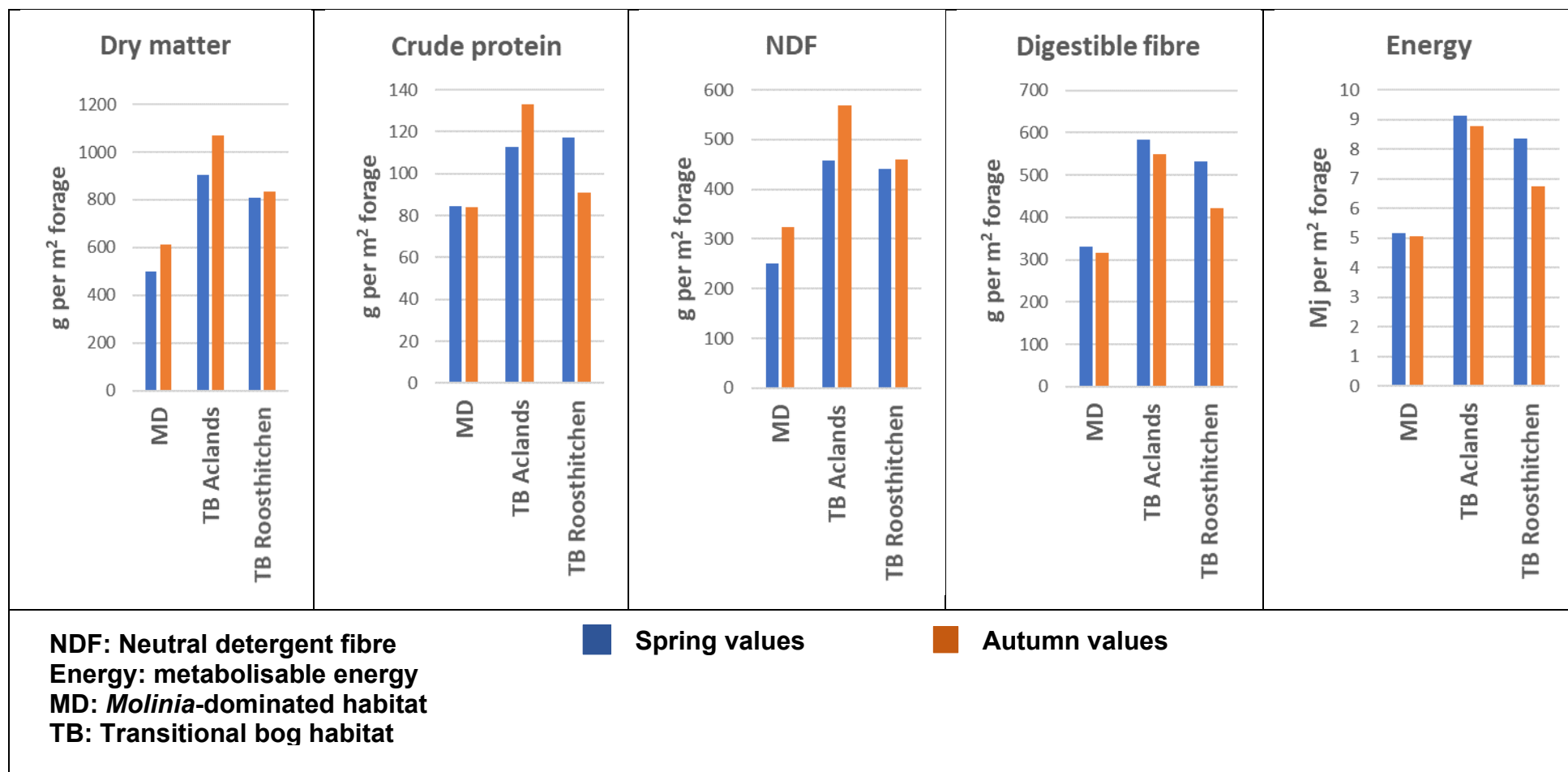


Figure 31: Overall changes in five measures of forage value in *Molinia*-dominated (MD) and Transitional bog (TB) habitats on Exmoor.

Each bar represents the sum of the contributions of the species present. A species' contribution is its value for that forage quality multiplied by its representation (%) in the vegetation. MD vegetation surveyed at square AC1, TB Aclands vegetation surveyed at square AC3, TB Roosthitchen vegetation surveyed at square RST3.

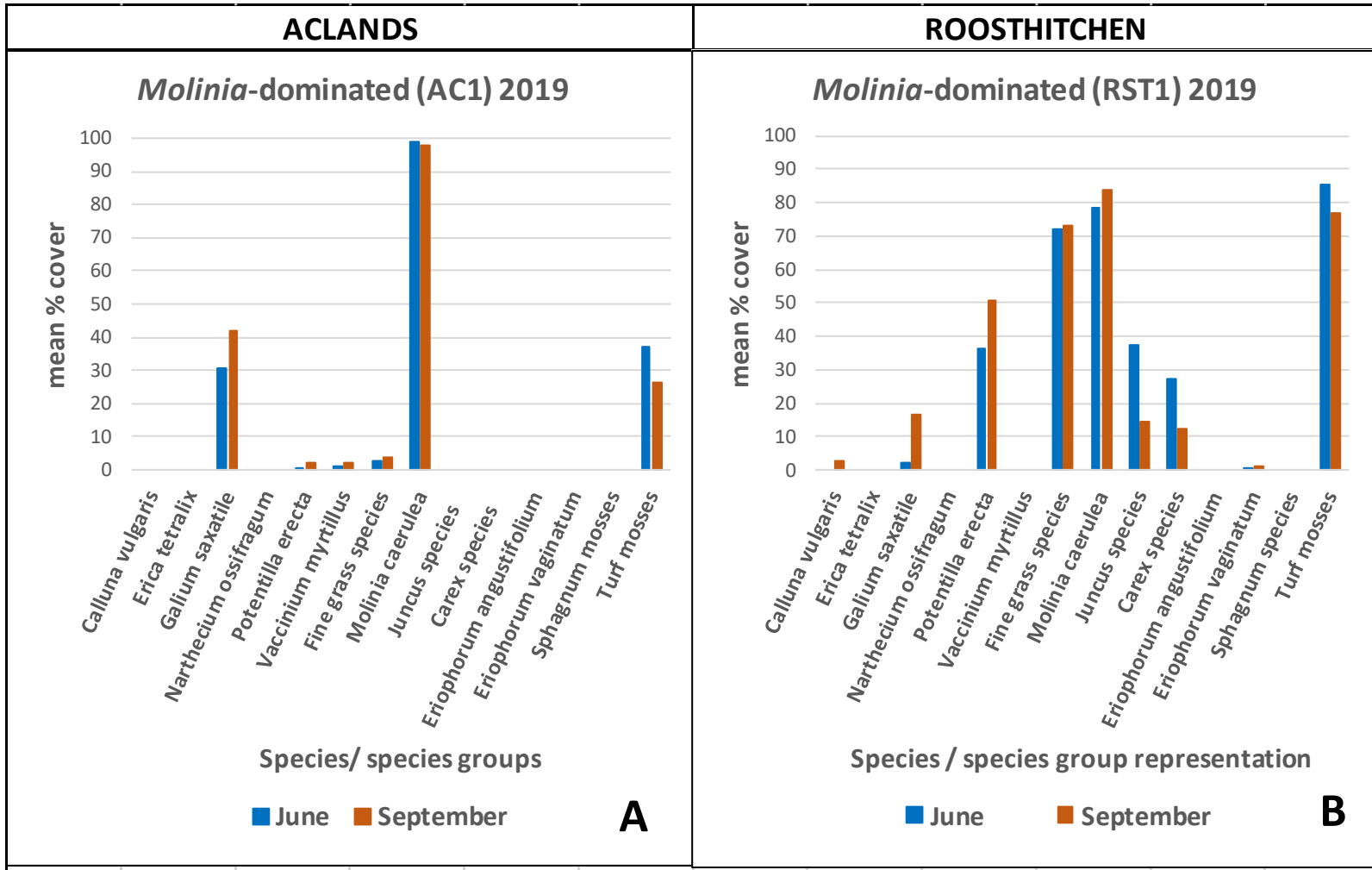


Figure 32: Changes in sward composition of *Molinia*-dominated habitat between spring (June) and autumn (September) at two sites
 A = Aclands ; B = Roosthitchen

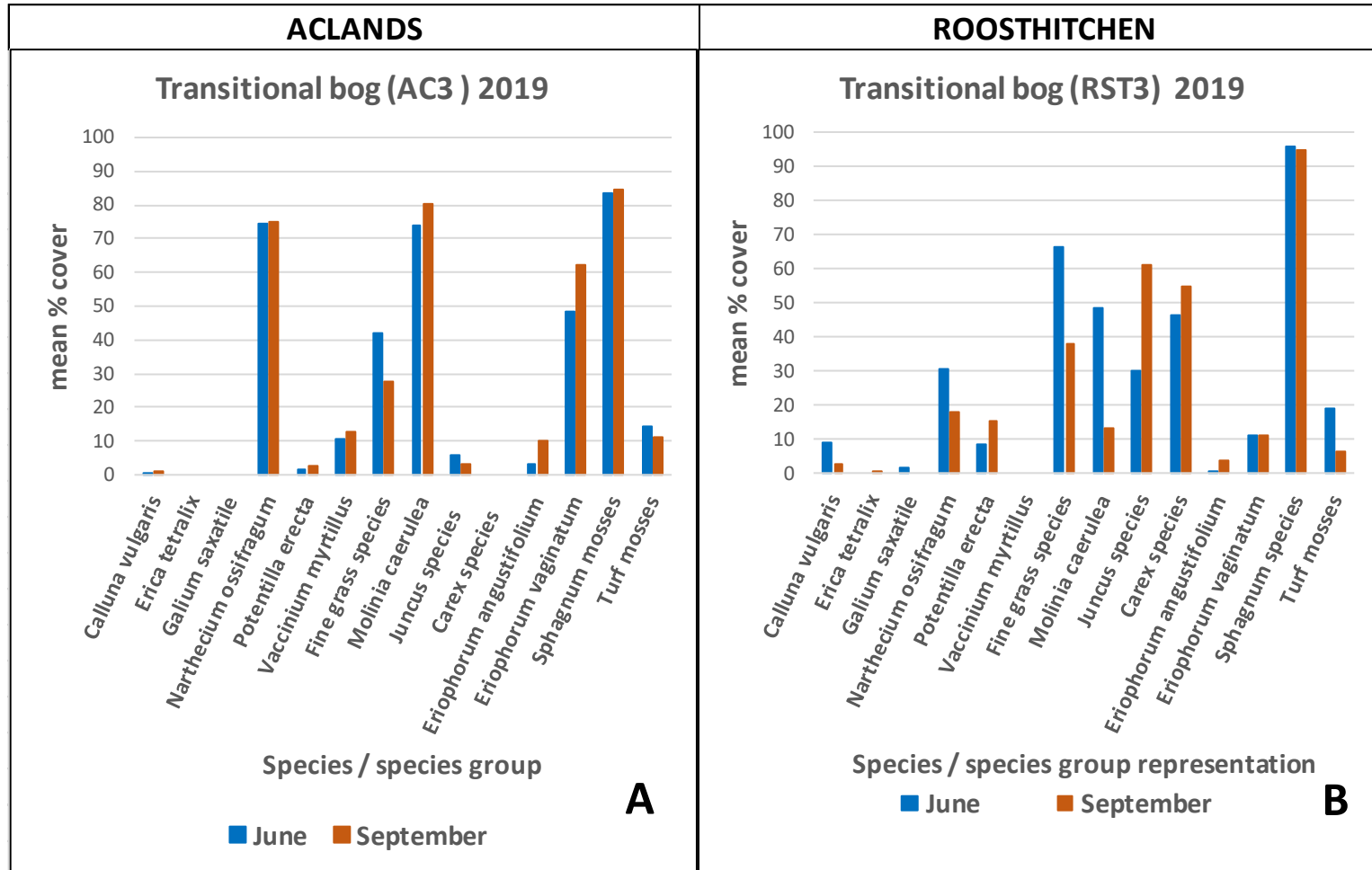


Figure 33: Changes in transitional bog sward composition between spring (June) and autumn (September) at two sites.

A = Aclands, B = Roosthitchen

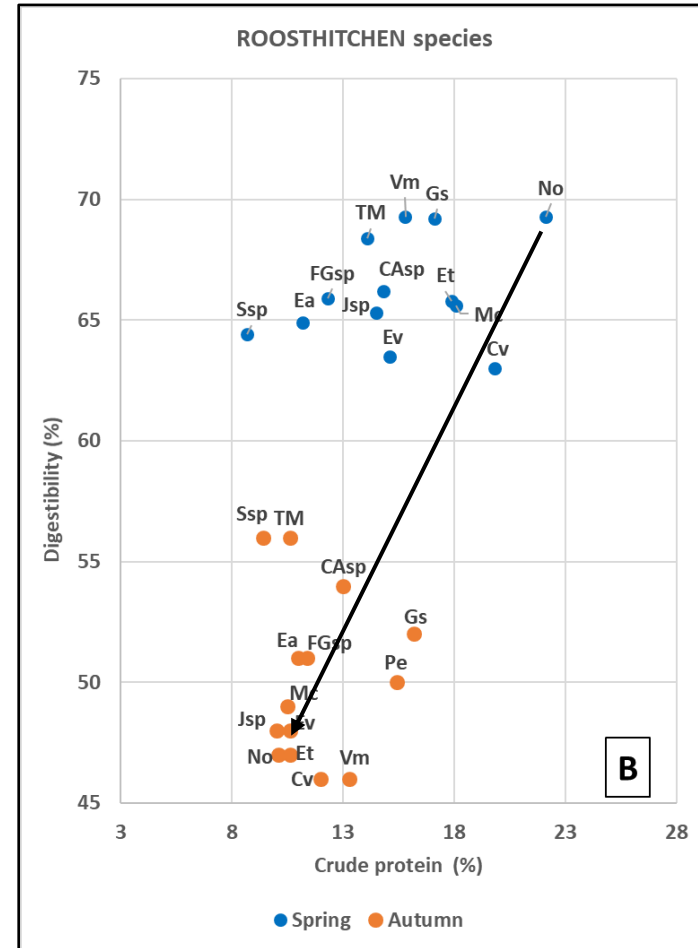
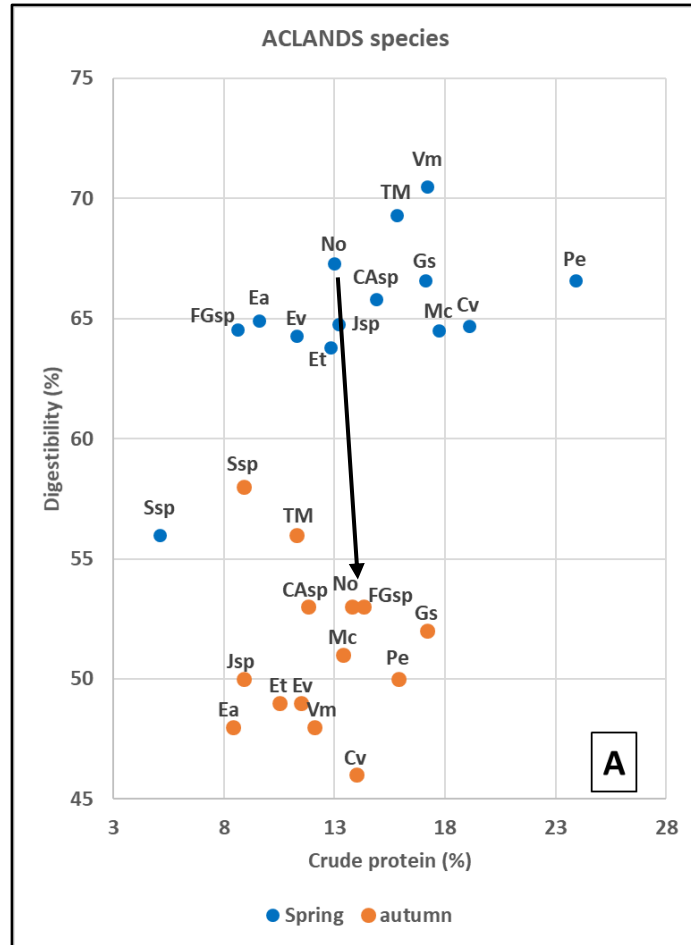


Figure 34: Crude protein content and digestibility of 14 species in spring (blue) and autumn (orange)
 A = Aclands and B= Roosthitchen. (CAsp Carex species, Cv Calluna vulgaris, Ea Eriophorum angustifolium, Et Erica tetralix, Ev Eriophorum vaginatum, FGsp Fine grass species, Gs Galium saxatile, Jsp Juncus species, Mc Molinia caerulea, No Narthecium ossifragum (Bog asphodel), Pe Potentilla erecta, Ssp Sphagnum species, TM turf moss species, Vm Vaccinium myrtillus.

→ Changes in Bog asphodel forage value between seasons.

There were increases in dry matter and neutral detergent fibre (NDF) for the suite of species at both sites in autumn, and decreases in CP, D and metabolisable energy (ME) (Figures 35 - 36). The ME value is calculated from digestibility and these two measures therefore vary in tandem (Table 10). At both sites the reduction in D and ME was significant (Table 12). Only at Roosthitchen was there a significant drop in CP levels.

	ACLANDS		
MEAN % of 14 species	spring	autumn	Wilcoxon rank sum test
Dry matter (%)	29.55	34.71	ns
Crude Protein (%)	14.21	12.29	ns
Neutral detergent fibre (%)	47.18	50.65	ns
Digestibility (%)	65.44	51.14	w=194.5, p = 1.00e-05
Metabolisable energy (MJ/100g)	1.03	0.82	w=194, p = 1.13e-05
	ROOSTHITCHEN		
MEAN % of 13 species	spring *	autumn	Wilcoxon rank sum test
Dry matter (%)	29.84	34.44	ns
Crude Protein (%)	15.50	11.44	w=143, p = 0.003
Neutral detergent fibre (%)	50.73	52.68	ns
Digestibility (%)	66.22	50.08	w=169, p = 1.62e-05
Metabolisable energy (MJ/100g)	1.04	0.80	w=169, p = 1.56e-05
* only 13 species were sampled at Roosthitchen in the spring			

Table 12: Statistical analysis of differences in forage values in spring and autumn at two sites.

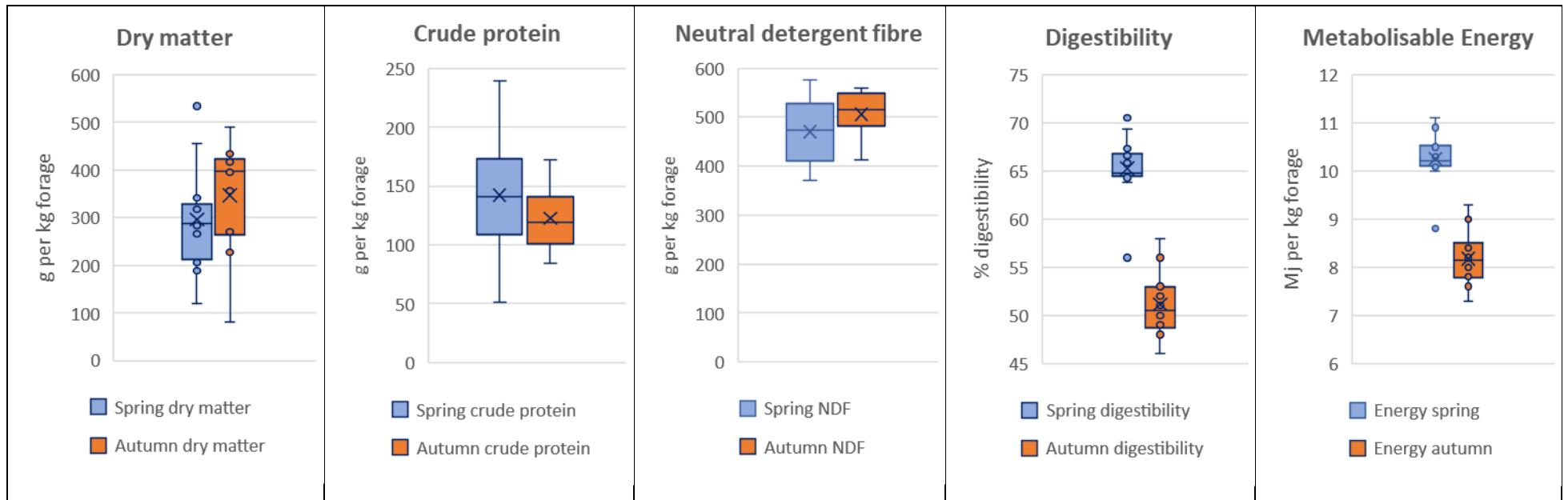


Figure 35: Changes in forage values between spring (blue) and autumn(orange) at Aclands

Each plot represents the mean of 14 species commonly found in transitional bog habitat

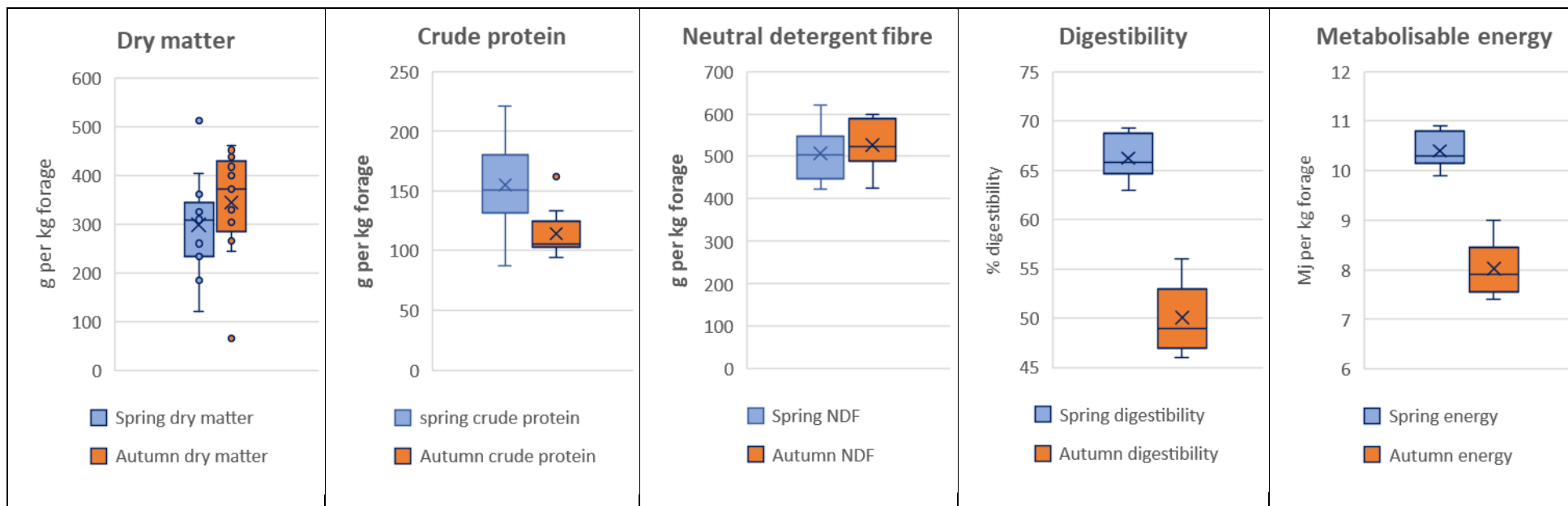


Figure 36: Changes in forage values between spring (blue) and autumn (orange) at Roosthitchen.

Each plot represents the mean of 13 species commonly found in transitional bog habitat.

The above results show that there is little difference in forage values of typical moorland species generally between the two sites. However, at habitat level sward structure and quality can be dominated by individual species (Figures 37 – 39).

In a typical *Molinia*-dominated sward at Aclands three species (out of six), *Galium saxatile*, *Molinia (caerulea)* and turf mosses, provide almost all the forage value under the five measures considered in this paper (Figure 37). The other three species make little contribution to forage value. *Molinia* contributes the most value in all five measures and in both seasons. This contrasts to the trends seen generally (Figures 35 - 36) where only dry mass and NDF consistently increase in autumn.

The analysis of forage value of the two TB swards focused on the eight species making the most contribution (out of 14 at Aclands and 13 at Roosthitchen). The most striking observation about the forage quality of the two transitional bog habitats (Figures 38 - 39) is that *Molinia* provides most forage quality in both seasons with the autumn values being higher for all five measures compared to the spring. At Aclands the three species providing the most forage value in both seasons are *Molinia*, *Eriophorum vaginatum* and bog asphodel, although *Sphagnum* mosses make up a greater proportion of the vegetation cover (Figure 33). All three provide more dry matter, CP and NDF in the autumn, but unlike *Molinia*, bog asphodel and *E.vaginatum* have lower levels of digestibility (and energy) in the autumn.

At the Roosthitchen transitional bog habitat, the spring forage quality (all five measures) is provided by fine grass species, *Molinia* and *Carex* species (Figure 39). In autumn the three top species for forage quality are *Molinia*, *Juncus* species and *Carex* species. There was less bog asphodel at Roosthitchen than at Aclands which would explain the smaller contribution to sward quality.

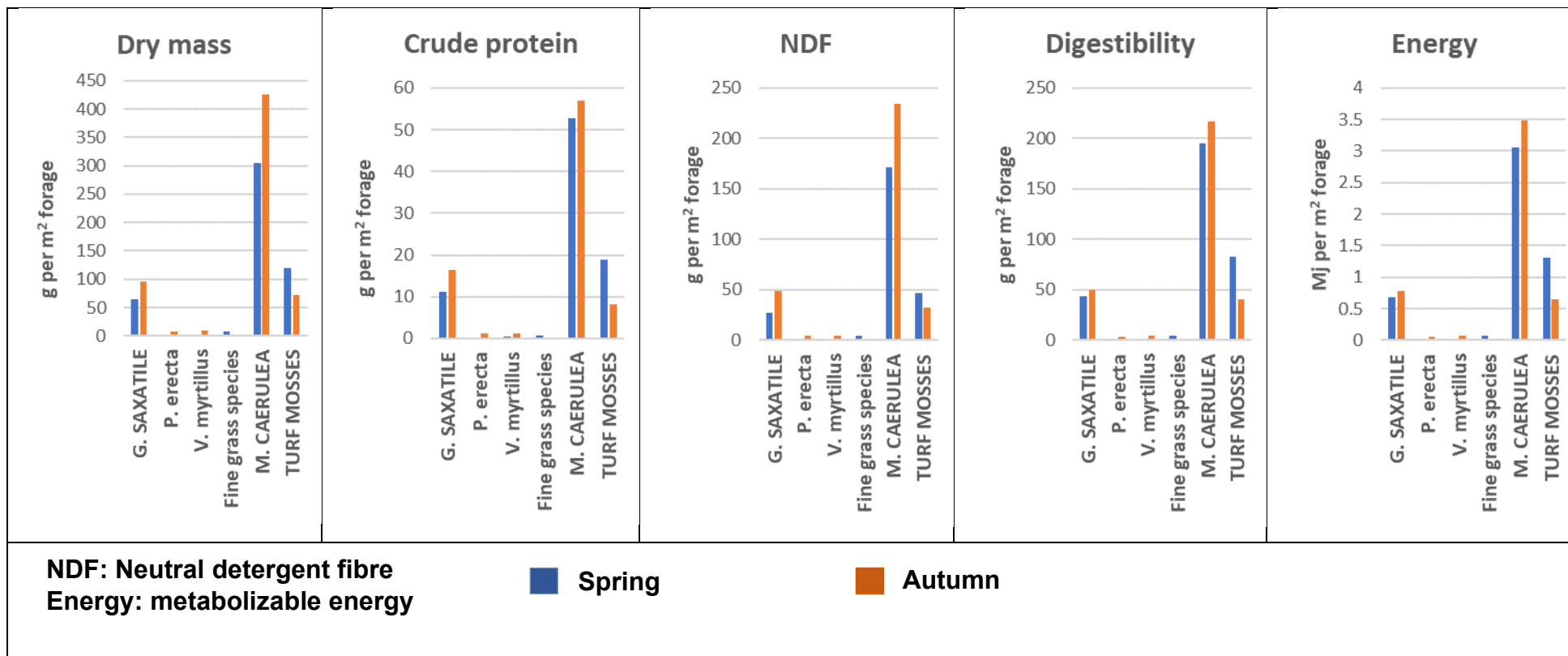


Figure 37: Contribution to the forage value of the individual species in Aclands Molinia-dominated habitat in Spring (blue) and Autumn (orange).

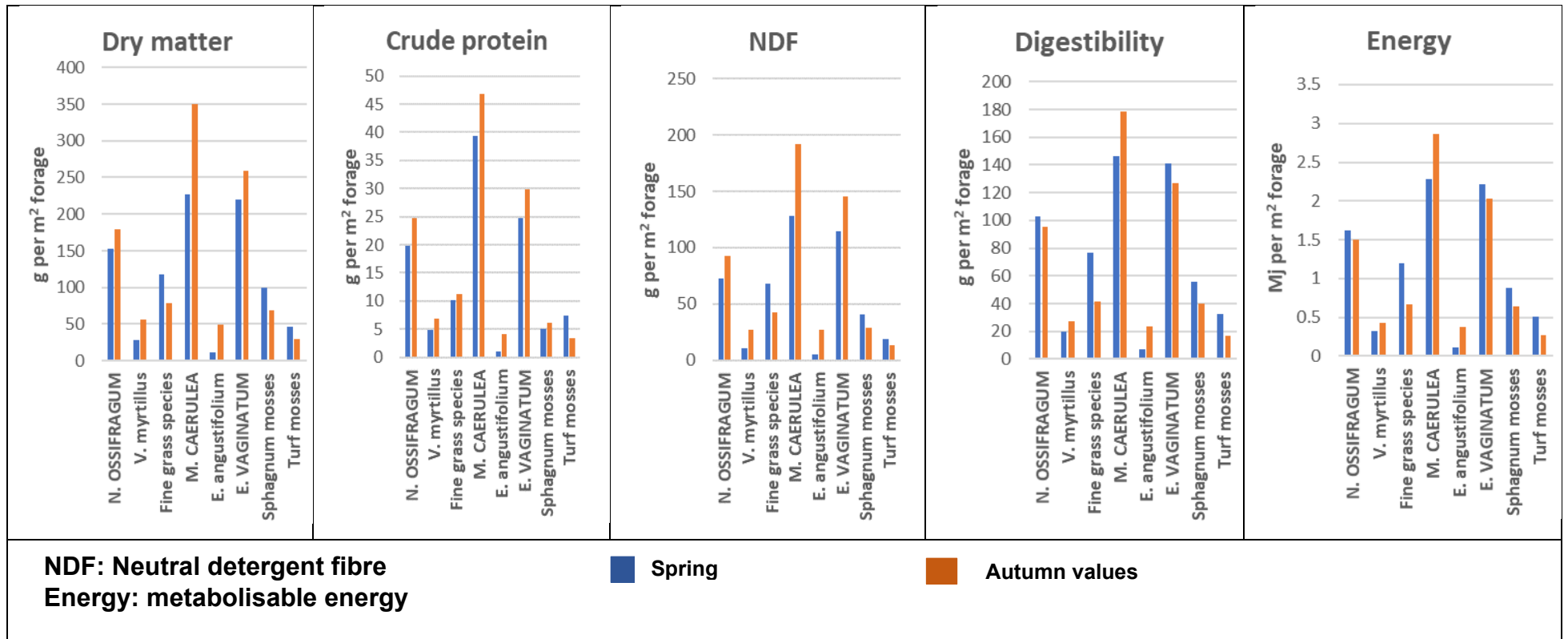


Figure 38: Contribution to the forage value of the 8 best individual species in Aclands transitional bog habitat in Spring (blue) and Autumn (orange).

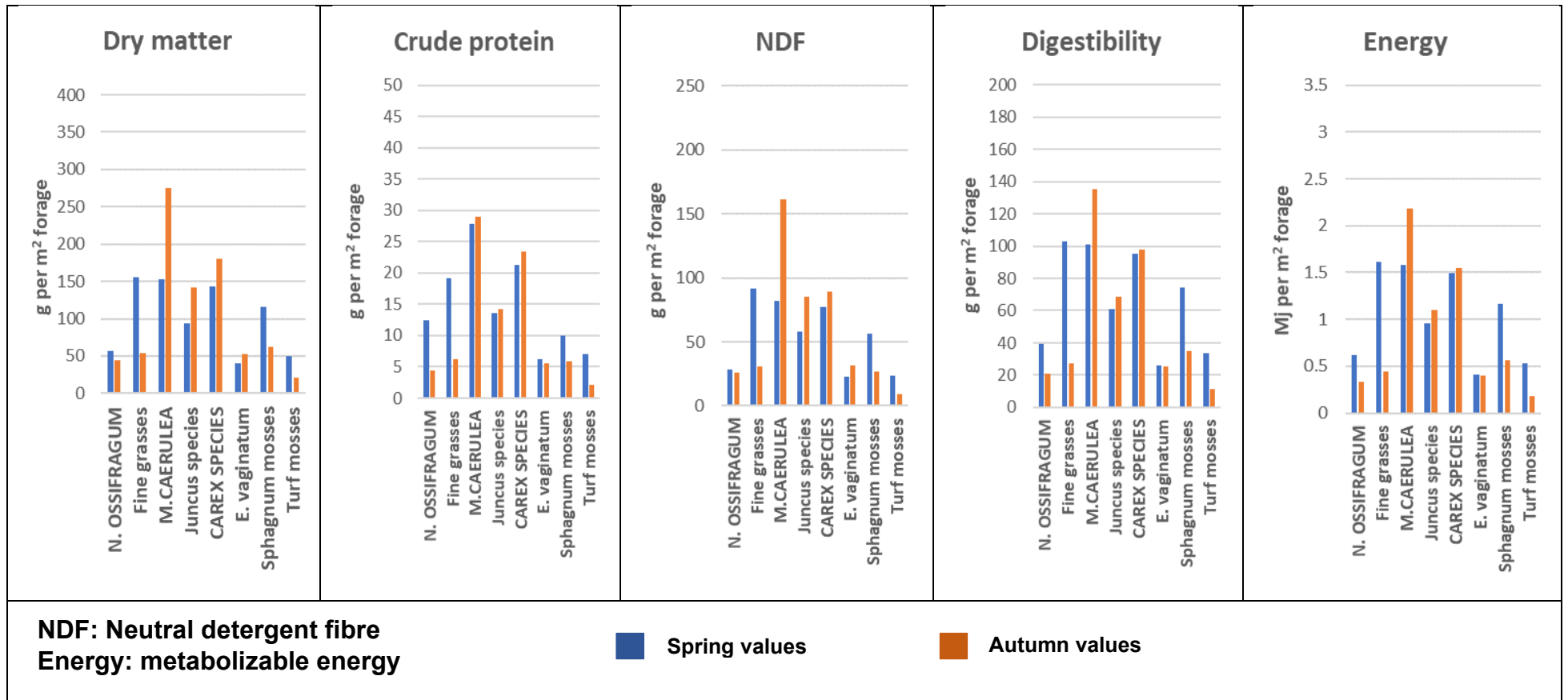


Figure 39: Contribution to the forage value of the 8 best individual species in Roosthitchen transitional bog habitat in Spring (Blue) and Autumn (orange).

To summarise, there is a marked difference in structure and forage quality between *Molinia*-dominated habitat (typical of damaged peatlands) and transitional bog habitat which appears when peatlands are rewetted. Generally, all habitats have more dry matter and fibre in autumn than in spring, and less digestible matter and energy, although protein levels may increase in transitional bog habitat in the autumn and thus contribute to its autumnal sward quality. *Sphagnum* species add little to forage quality despite dominating the vegetational composition of transitional bog.

Bog asphodel's contribution to sward quality

Bog asphodel is represented in both TB habitats in spring and autumn, at Aclands 75.25 % and 75.75 %, respectively, and at Roosthitchen 30.75 % and 18 %, respectively. It was not found in the Aclands MD habitat, but some was seen in the vicinity of the atypical Roosthitchen 'MD' square (RST1).

Bog asphodel makes a substantive contribution to Aclands TB sward quality (Figure 40A). In spring bog asphodel contributes a mean forage value across the five measures of quality of 17.17 ± 0.7 % at Aclands (Figure 40A) and in autumn 17.22 ± 0.8 %, with an increase in crude protein contributing to the slight increase in autumnal value. At Roosthitchen (Figure 40B) the spring contribution is 7.77 ± 1.5 % with a drop to 5.13 ± 0.3 % in autumn. This difference reflects subtle differences in bog asphodel forage values between the two sites (Table 13), and the fact that less bog asphodel was recorded at Roosthitchen in the autumn survey. The site has been trampled and was exceptionally wet in September making the survey very taxing.

The forage values for Bog asphodel at both sites mirror the changes from spring to autumn seen in the general suite of moorland species, except for CP at Aclands which increases in autumn (highlighted in Table 13). This might explain why the combined species autumn CP value does not decrease in autumn as much at Aclands (where there is more bog asphodel) as at Roosthitchen (Figures 35 - 36).

	Aclands spring	Aclands autumn	Roosthitchen spring	Roosthitchen autumn
Dry mass (g/kg)	206	240	184	244
Crude protein (g/kg)	130	138	221	101
Neutral detergent fibre (g/kg)	477	517	504	592
Digestibility (%)	67.3	53	69.3	47
Metabolisable energy (Mj/kg)	10.6	8.4	10.9	7.6

Table 13: Bog asphodel forage values at two sites in spring and in autumn.

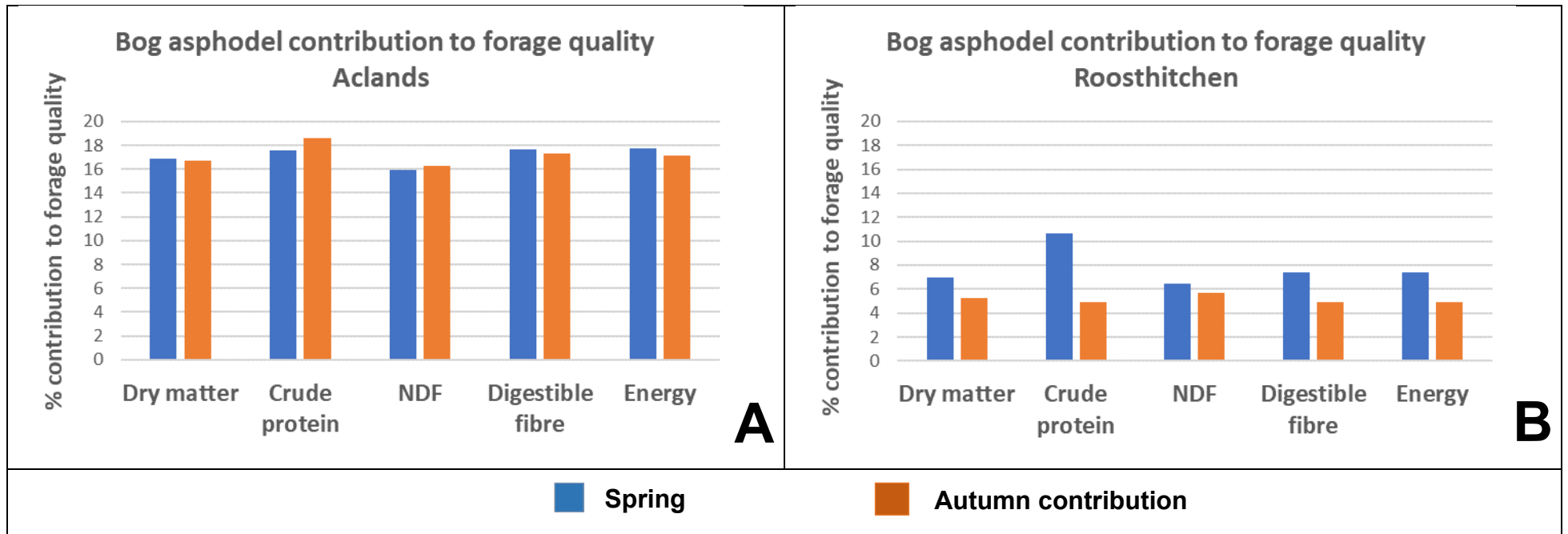


Figure 40: Contribution of bog asphodel to forage quality at two transitional bog habitats on Exmoor.

Grazing potential

The *Molinia*-dominated and transitional bog habitats at the two sites were only grazed occasionally, if at all, during the summer of 2018 (Figure 41), suggesting that cattle do not intentionally graze areas of either *Molinia*-dominated or transitional bog sward. The three 50 m squares set up at each site were monitored in June, July, August and September 2018 for grazing by counting dung heaps.

On Aclands, only the MD habitat (AC1) had evidence of grazing by cattle (*Molinia*, soft rush, fine grasses and *Eriophorum* species) (Figure 41, top). Although some of the vegetation (*Molinia* and bog asphodel) had been grazed in the TB habitat (AC3, grey squares) no dung was found in the immediate vicinity. In the dry grassland square (AC4) there was no evidence of grazing although cattle have congregated in this isolated patch of dry grassland in previous years (N. Gatis, personal communication).

On Roosthitchen all three squares were grazed (Figure 41, lower). The atypical “MD” habitat was grazed throughout the season, probably reflecting the species richness. The TB habitat was only grazed lightly, most likely by cattle *en route* to other areas, whereas the dry grassland square was heavily grazed but not until September.

Young soft rush and *Molinia* were preferentially grazed in the “MD” habitat early in the season. Bog asphodel, *Molina* and heath bedstraw were grazed later in the season. Although bog asphodel was not recorded in the vegetation squares used in 2019, it was found in the wider 50 m square. *Molinia* and bog asphodel were grazed in the TB square, although there was no evidence that this was specifically by cattle

The grazing study supports the hypothesis that cattle do not preferentially graze areas rich in bog asphodel.

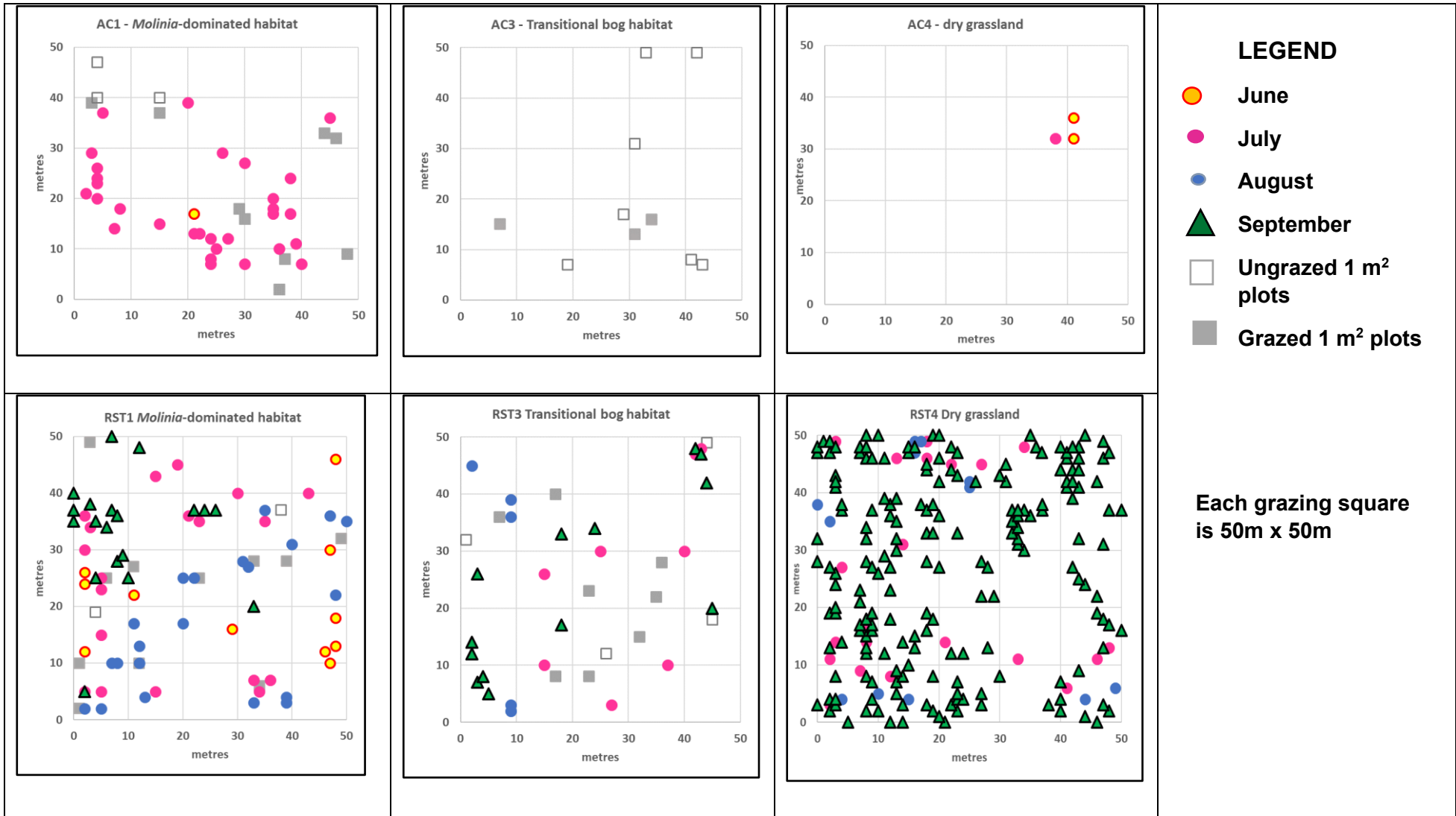


Figure 41: Grazing patterns on Aclands (top) and Roosthitchen (lower) June - September 2018.

Each coloured shape indicates cattle dung found in June (yellow circle), July (pink circle), August (blue circle) and September (green triangle)

2.2.4 Discussion

Sward quality at restoration sites on Exmoor

The TB habitat which typically appears in the vicinity of ditch blocks on restored peatland is of higher forage value than the *Molinia*-dominated swards that cover much of shallow drained peatlands. This increase in forage value is driven by an increase in species, a result of rewetting drained peatlands (Bellamy *et al.*, 2012; Komulainen *et al.*, 1999). The two sites studied on Exmoor contrasted in both the nature of their drainage (Figure 26) and in the type of basic vegetation. Aclands is essentially an ombrotrophic site whereas the Roosthitchen vegetation displays mesotrophic characteristics. *Cirsium palustre* (marsh thistle) and *Pedicularis sylvatica* (lousewort) were recorded there, both species that favour a less acid and more nutrient-rich environment than bog asphodel (Hill *et al.*, 2007). Both TB habitats provided similar levels of forage value in spring and autumn but from subtly different vegetative composition, specifically relating to *Eriophorum vaginatum* (Aclands) and *Carex* species (Roosthitchen) (Figure 33). Freeman (Freeman, 2017) established for *Molinia caerulea* that samples from different habitats did not have significantly different forage values, so it is reasonable to assume that the two sets of samples were comparable although those from Aclands were collected from a wider sample of habitats. Limiting the samples to 14 species kept the cost of the analyses within limits, and still included all species that covered more than 1% of the sample vegetation. *Sphagnum* mosses (and other bryophytes) dominate transitional bog vegetation and their re-establishment is an aim of peatland restoration, but they cannot be grazed by cattle and would not be grazed by sheep given their low nutritional values (Grant *et al.*, 1987) so arguably they do not contribute to sward quality. The theoretical contribution of *Sphagnum* species to sward quality was approximately 10 % across the five measures of sward quality in spring and 6% in autumn on Exmoor.

The reason for conducting spring and autumn sampling was to investigate if the type of habitat being created by rewetting might be favoured in one season. At Roosthitchen *Carex* species increased their forage value in the autumn and made the second largest contribution to forage value after *Molinia* (Figure 39). They contributed 15 % of forage value in spring and 19 % in autumn, despite an overall drop in forage value in autumn (Figure 31). At Aclands *Carex* species were not

significantly represented but *Eriophorum vaginatum* provided 20% of forage value in both spring and autumn (Figure 38).

Bog asphodel is more likely to be foraged in the spring (by cattle) when the leaves and flowers are succulent and easily grazed in the sward, compared to autumn when its leaves are dying off. However, at Aclands bog asphodel, including mature fruits, was marginally more nutritious in autumn, whereas at Roosthitchen it appeared to lose nutritional value although it was evidently grazed along the sides of tracks (Figure 42).



Figure 42: Grazed bog asphodel (circled) Roosthitchen transitional bog September 2018

Grazing potential

Upland land use in the U.K. is dominated by livestock farming. The ability of the sward to nurture livestock is crucial to the profitability of farming in these remote areas. Peatland restoration appears to be adding to sward quality by encouraging increases in biodiversity and consequently forage value near the ditch blocks. It has been shown that cattle preferentially graze grassland areas (Pratt *et al.*, 1986) and earlier evidence from the wider Aclands area suggests that cattle do not graze either MD or TB habitats there if there is other high quality sward available e.g. dry grassland (Freeman, 2017). Moreover, current agri-environmental schemes designed to reverse the effects of over-grazing and permit vegetation recovery allow grazing only during the summer season and at low stockage level (Natural England, 2013). My data show the same pattern.

2.2.5 Conclusions

Restored shallow marginal peatlands can provide good quality forage in autumn as well as spring. *Molinia* provides the most nutritional value in transitional bog, and bog asphodel can also make a significant contribution. However, these areas are rarely grazed if adequate good quality grazing is available elsewhere, which will remain the situation while stocking levels are low.

Chapter 3. Discussion

3.1 Bog asphodel ecology on Exmoor.

Bog asphodel is an example of a plant that grows in infertile, i.e. nutrient deficient, soil. Such plants have several characteristics in common including a reduced herbaceous form and an inherently slow growth rate (Grime, 1979). Narrow leaved tussock-forming grasses and ericaceous species e.g. *Nardus stricta* and *Calluna vulgaris* are common on ombrotrophic sites and display conservative growth forms, very narrow or tiny leaves. Kruckeberg (Kruckeberg, 1954) noticed that plants growing very slowly in infertile soil did not grow more quickly in fertile soil. This observation has been extended to typical moorland grasses, such as *Festuca ovina* and *Agrostis tenuis* (Bradshaw *et al.*, 1964; Jowett, 1964) and subsequently inherently low growth rate was shown to correlate strongly with tolerance of mineral nutrient deficiencies e.g. (Grime and Hunt, 1975; Hackett, 1965). Bradshaw (Bradshaw *et al.*, 1964) also showed that these grass species which had evolved to make low demands on nutrients would never compete for yield with fertile soil species, such as *Lolium perenne* even in reduced nitrate conditions. Another consequence for slow-growing stress-tolerating plants is that they are particularly vulnerable to physical damage such as predation (Whittaker, 1975) and have evolved methods of resistance, such as unpalatability. Bog asphodel is obviously palatable but its reduction in growth when grazed may allow it to reduce predation and rely for survival on its underground rhizome system.

My calculations put bog asphodel firmly in the stress-tolerating corner of Grime's Triangle (Chapter 2.1). However, my study was carried out in an area of the Aclands site (ACQ, Figure 28A) where extensively studies of WTD, water chemistry and gas fluxes before and since restoration six years ago have yet to demonstrate consistent change. The peak flows off the site have reduced and background flow is steadier, but there have been no consistent changes in WTD or water quality and very little increase in biodiversity (Gatis *et al.*, n.d.; Gatis *et al.*, 2019; Grand-Clement *et al.*, 2014). It is possible that the site has yet to react to the rewetting (Green *et al.*, 2017; Haapalehto *et al.*, 2011; Lundin *et al.*, 2017; Urbanová and Bárta, 2016), suggesting that bog asphodel growth may not have been influenced by as rapid a change in environment as expected. Nevertheless, evidence from the historic vegetation data show that bog asphodel does not

spread rapidly following rewetting of ombrotrophic sites on Exmoor, and this agrees with knowledge about this species in general.

Despite being constrained by its life history strategy, bog asphodel does appear to spread, albeit within a localised area, if rewetting results in an increase in nutrients, as may be the case at Roosthitchen. Minerotrophic sites have been shown to react much more quickly to rewetting than ombrotrophic sites (Komulainen *et al.*, 1999; Tuittila *et al.*, 2000). Roosthitchen is an example of the former and Aclands of the latter. At the Roosthitchen site bog asphodel has increased its distribution since restoration, as represented by the upper outlier on Figure 16. However, there is no evidence that the plant grows any more robustly in these conditions.

Bog asphodel growth on Exmoor is typical of the plant growing at altitudes around 400 m a.s.l., smaller and less dense than plants found in lowland habitats but still fertile (Summerfield, 1972). It is known to be sensitive to light levels (Summerfield, 1971) and sward height appears to influence the form of the plant, being taller in high swards and much shorter and more robust where the vegetation is grazed or trampled e.g. on the edge of tracks. It appears to flower more freely in areas where grazing is excluded (Rawes, 1983) but flowers were grazed preferentially by cattle on Exmoor (personal observation) so it is possible that flowers have been eaten rather than that there were fewer of them in grazed areas.

Although fairly high levels of bog asphodel cover in discrete transitional bog plots were recorded, the pilot vegetation survey project in 2018 (not reported above) which used ten randomised 1 m² quadrats gave mean bog asphodel cover in transitional bog areas of 12 % (Aclands) and 14 % (Roosthitchen), and in *Molinia*-dominated areas of 2 % (Aclands) and 4 % (Roosthitchen). This agrees with an mean cover of 12% across the wider Aclands site (Freeman, 2017), and 8 % of mire vegetation in Scotland (Boatman and Armstrong, 1968) and illustrates the ability of bog asphodel to persist in a variety of wet acidic environments as expected of a species utilising a 'stress tolerator' strategy. Bog asphodel has only been recorded before or after restoration on half of the Exmoor Mires Partnership restoration sites transects, which suggests that there could be suitable habitat for it to increase its distribution but that it would only do so very slowly.

The shallowness of the Exmoor peat may also influence how bog asphodel grows, as a function of water table behaviour. Bog asphodel grows best when WTD is 10 cm or more below the surface and where there is lateral water movement and some oxidation (Boatman and Armstrong, 1968; Summerfield, 1971).

A greater proportion of the peat will be damaged when drainage ditches are cut into shallow peat and this affects the hydrological response to rewetting and rainfall events (Luscombe *et al.*, 2016). Some correlations were seen between WTD, which could reflect peat moisture and oxygen levels, and the height of bog asphodel plants and the general sward in shallow restored peatland. This supports the proposition that bog asphodel is capable of responding to habitat changes caused by peatland restoration. However no studies have yet compared bog asphodel growth on shallow and deep peat.

The year-on-year variation in bog asphodel growth may link to its potential to cause toxic effects which can occur when the leaves and particularly the flowers are ingested by grazing herbivores (Pollock *et al.*, 2015; Ulvund, 2012). The effects of ingesting bog asphodel leaves and flowers vary between pastures, from year to year and in UK between northern England and south-western England. A possible link was shown between bog asphodel growth and flowering and climate in shallow south-western peatlands (Chapter 2.1). Barcelo (Barcelo *et al.*, 2019) has shown that mycorrhizal activity, a possible co-factor in the aetiology of bog asphodel toxicity (di Menna *et al.*, 1992; Mysterud *et al.*, 2016), is temperature dependent. In Northumberland, lamb mortality from bog asphodel poisoning has increased in the last ten years, more so at farms in the western part of the Northumberland National Park where the rainfall is higher (Abi Mansley, personal communication). Although peatland restoration has been going on there during this period, annual rainfall in 2017 in Northumberland was 105-125 % of the 1981-2010 average, whereas the corresponding figure for Exmoor was 95-105 % ((UK Meteorological Office, 2020) (Appendix 1A). Similarly, temperatures in Northumberland were 0.5 – 1.0 °C above the historic average in 2017, whereas on Exmoor the corresponding increase was 0.2 – 1.0 °C (Appendix 1B).

It is possible that the condition of the peat also influences the presence or activity of organisms that might facilitate the toxic effects of bog asphodel ingestion. For example, mycorrhizal activity can be impaired in highly acidic soil (Hewitt, 1952).

It is known that some bog asphodel pastures are less toxic than others (Laksesvela and Dishington, 1983). Bog asphodel-related poisoning of livestock is rare on Exmoor, so it could be possible that Exmoor's shallow peat does not facilitate bog asphodel's toxic potential. Conversations with Exmoor landowners and graziers for whom bog asphodel poisoning might be an issue reveal that they are aware of the problem but only occasionally does a lamb succumb to possible but unproven bog asphodel poisoning. This could be a conservative estimate because lambs dying on remote moorland pastures can be picked off by scavengers. Conversations with local vets suggests that most cases of photosensitization are seen in animals grazing in-by land where bog asphodel would not be found. Natural England staff who monitor the management of peatland habitats across the region (Exmoor, Dartmoor and Bodmin Moor) have no reports of bog asphodel posing a problem for graziers (personal communications). Overall, this suggests that distribution changes of bog asphodel on Exmoor, and possibly in the South West in general, do not pose a serious threat to livestock.

3.2 Sward quality

Bog asphodel is a relatively nutritious plant in moorland assemblages, rated 4th – 6th most palatable among peatland plant species (Pollock, *et al.*, 2007). Herbivores select habitat and the species therein according to their forage requirements which vary with species, breed and season, and in line with the availability of different plants (Anderson *et al.*, 2016; Bele *et al.*, 2015; Mancinelli *et al.*, 2015; Williams *et al.*, 2012). Cattle, by virtue of their size, range widely in order to find enough forage, quantity being as important as quality (Critchley *et al.*, 2008; Kaufmann *et al.*, 2013). They may therefore graze bog asphodel leaves or flowers growing amongst *Molinia* but not the shorter leaves in closer swards. Sheep are able to graze the sward much closer and much more selectively (Williams *et al.*, 2010). My findings about bog asphodel's contribution to sward quality suggest that it may enhance autumn grazing on restored peatland, perhaps in part because the mature seed heads persist into the winter, although these may contain additional toxic chemicals (Vu *et al.*, 2016).

Climate can also influence the nutritional value of vegetation within and between years as wetter and warmer conditions encourage plants to mature and thus lose digestibility more quickly (Buxton, 1996). However, my findings indicate that bog

asphodel retains much of its forage value into the autumn, at least at Aclands in a relatively wet year (2019) when rainfall in south-western UK was 105-115 % over the historic average (Appendix 1C).

3.3 Implications for peatland restoration

By re-establishing a higher and more stable water table peatland restoration has supported an increase in biodiversity on Exmoor. At the older restoration sites the floral diversity has increased by 30 – 40 % in a few years (EMP, 2019), with the maximum number of species seen at ombrotrophic sites being around 40. These changes in vegetation increase the nutritional value of the sward (Chapter 2.2). The distribution of bog asphodel however has remained fairly constant, continuing at sites where it was recorded before restoration and spreading very little since restoration. This is in accordance with its life history strategy, which predicts that bog asphodel will persist in adverse conditions, such as fluctuating moisture levels and high acidity, but that its distribution will increase relatively slowly with the change to a more stable environment because of its inherent low growth rate and low allocation to seed dispersal. Consequently, the distribution of bog asphodel does not map restoration progress, it only indicates the presence of roughly suitable environmental conditions.

Toxicities in livestock caused by bog asphodel ingestion are most common in June and July when the leaves are succulent, and the plant is flowering. This coincides with natural weaning of lambs who are particularly susceptible to the effects of ingesting bog asphodel (Flåøyen and Jensen, 1991). Draining moorland and adding lime were traditional methods used both to improve fodder quality and remove bog asphodel. Such methods are no longer compatible with management practices to promote environmental protection, so bog asphodel is present in many upland pastures where the principle land use is sheep grazing, and this must be factored into management practices. Upland farming is dependent for viability on agri-environmental subsidies which impose controls on stocking levels and seasonal grazing (Martin *et al.*, 2013; Natural England, 2013). However, there are still measures that can be taken to reduce the injurious effects of bog asphodel ingestion. Bog asphodel appears to grow more conservatively in well-trodden habitats, so counter-intuitively grazing might inhibit the prevalence of bog asphodel. Winter grazing also appears to keep bog asphodel in check, and there were anecdotal reports of profuse flowering when grazing was stopped

during the Foot and Mouth outbreak of 2002. Lambs can be removed from open moorland in June and July although many upland farms do not have suitable in-bye land on which to put them (David Martin, personal communication). Lambing can be brought forward so that lambs are more mature during the bog asphodel flowering season and potentially less susceptible to the effects of bog asphodel ingestion. Some breeds of sheep may also be less susceptible (Flåøyen, 1991), as suggested by the genetic link to resistance to facial eczema in New Zealand sheep, an identical condition to *yellowsoes* (Bishop and Morris, 2007). Cattle can also be affected, although more often by renal toxicity (Malone *et al.*, 1992). The wettest areas can be fenced off to guard against liver fluke as well as bog asphodel ingestion (Abi Mansley, personal communication), but such capital investment is often not possible on hill farms that struggle to be viable concerns. This intervention might be reserved for spring-fed or valley mire sites where bog asphodel might spread more than on ombrotrophic sites.

3.4 Limitations of the present study and suggestions for further work

The two sites were chosen as contrasting examples of the effects of restoration on Exmoor. It might have been expedient to have included at least one site grazed extensively by sheep as lambs are particularly susceptible to the injurious effects of bog asphodel.

The experimental squares on Roosthitchen could have been better placed to compare the *Molinia*-dominated and transitional bog habitats.

This study suggests further investigations to:

1. tease out the relationships between water table depth, peat depth, sward height and the growth of bog asphodel;
2. to determine the role of peat condition and depth in the manifestation of bog asphodel's toxic effects; and
3. to examine the effects of climate change, specifically temperature and rainfall, on the growth of bog asphodel.

3.5 Conclusions

1. Bog asphodel remains after the restoration of shallow marginal peatlands but does not spread substantially, as predicted by its life history strategy
2. Bog asphodel is a relatively palatable and nutritious plant in habitat typical of recently restored shallow marginal peatlands. It is therefore likely to be ingested by livestock if they graze rewetted areas where it exists, and the potential exists for it to cause injurious effects.
3. However, there are no consistent reports of bog asphodel induced toxicity in south-western U.K. (Exmoor, Dartmoor and Bodmin Moor) either before or since peatland restoration programmes commenced. This may be because forage of sufficient quality is readily available elsewhere so that the rewetted areas are not grazed to any extent. Other explanations are that peat condition or the climate in south-western England does not facilitate the toxic effects of bog asphodel ingestion as seen for example in northern England. Climatic variation might also explain year on year differences in bog asphodel growth and ability to cause injurious effects.
4. Implications for the management of shallow marginal peatlands:
 - a. Bog asphodel will be eaten if accessible or if stocking levels increase, and it provides forage value possibly more so in autumn. However, there is no evidence that it is more widely distributed after restoration implying that there is no increased likelihood of injurious effects of ingestion;
 - b. Lambing could be brought forward so that lambs are older and less susceptible in the crucial June – July period;
 - c. Sheep and cattle breeds could be selected for resistance to bog asphodel toxicities;
 - d. Areas where there are springs could be fenced off as there is some evidence that bog asphodel may spread in such areas.
 - e. Bog asphodel pastures could be grazed during the winter and early spring to keep the plant in check.

The restoration of shallow marginal peatlands *per se* does not impact the distribution and abundance of bog asphodel in the short term. A warmer and wetter climate in future decades might encourage a greater abundance of bog asphodel at restored sites. However, the threat of an increase in bog

asphodel poisoning on the shallow marginal peatlands of South West England is currently low and the other benefits accruing to the establishment of healthy sustainable peatland landscapes are of paramount importance for developing resilience in the face of climate change.

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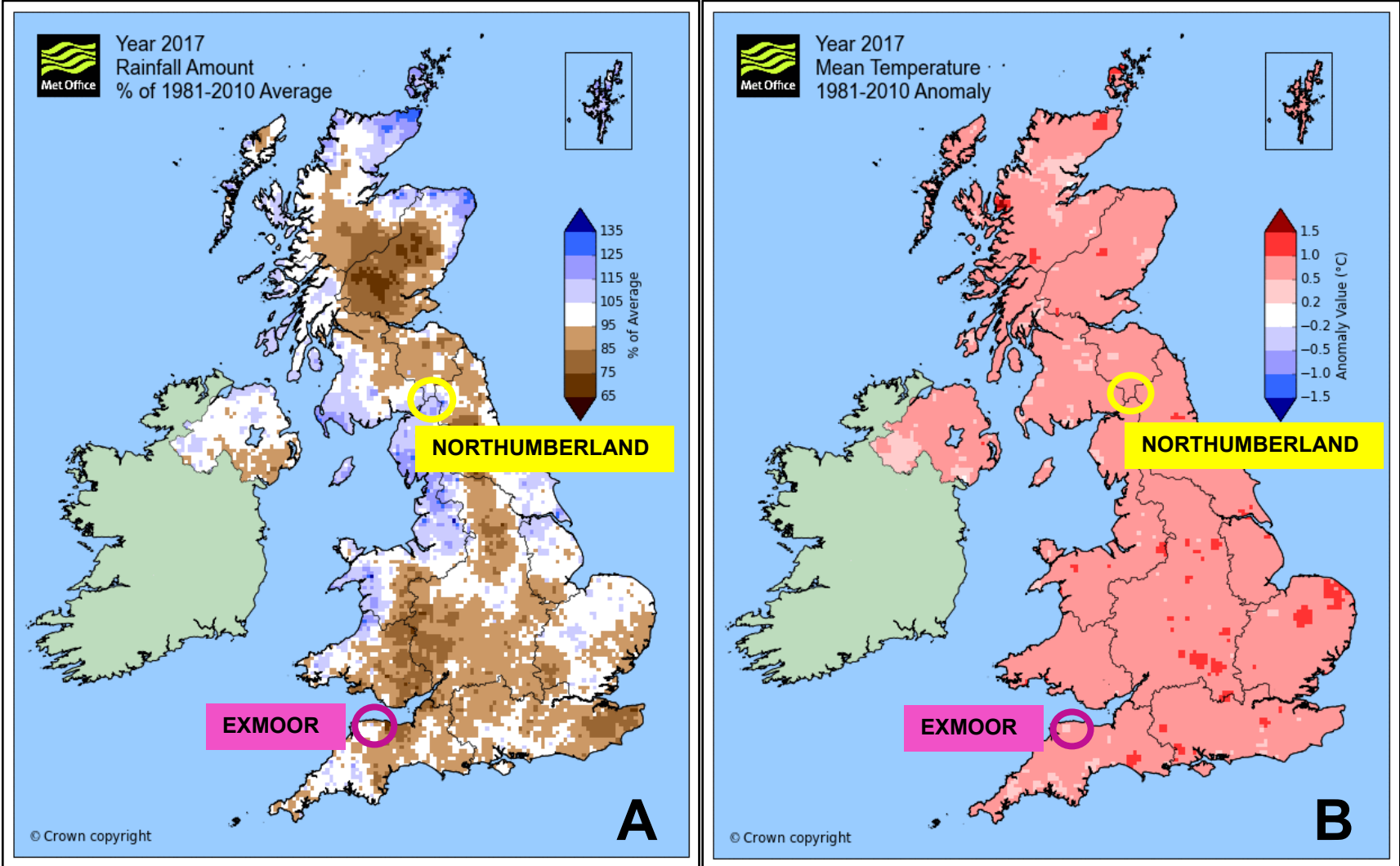
I would like to thank Robin May (Aclands) and the Woolhanger Estate (Roosthitchen) for allowing me to carry out fieldwork on their land, and for taking an interest in my work.

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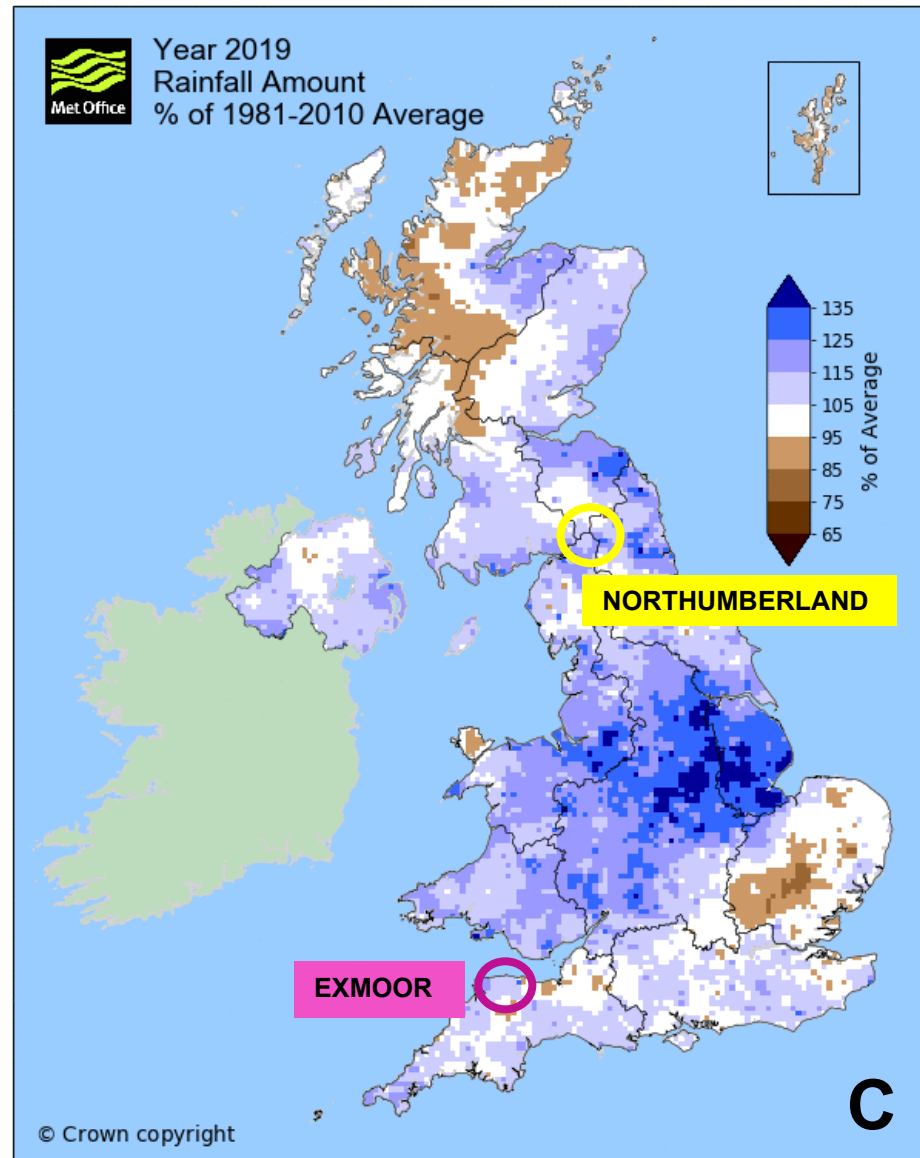
I am very grateful to Neville England of the Geography Technical Department at the University of Exeter for interpreting my drawings to produce a robust and transportable quadrat for the fieldwork, and for the support of the laboratory staff to prepare, weigh and measure all the bog asphodel samples.

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Appendix: UK climate maps



Downloaded from UK Meteorological Office website 14/01/2020 (UK Meteorological Office, 2020)



Downloaded from UK Meteorological Office website 14/01/2020 (UK Meteorological Office, 2020)

Glossary

Acid grassland: grassland growing on acidic soils, such as those in moorlands and heathlands, also referred to as Dry grassland

Agrostis: species of grass known as bents, characteristic of semi-improved upland pastures.

Anthropogenic: originating in human activity.

a.s.l.: above sea level

Assemblage: all of the species within a particular habitat.

Blanket bog: a peat-forming ombrotrophic mire, usually in upland areas.

Bryophyte: non-vascular plants, including mosses and liverworts.

CAP: Common Agriculture Policy (European Union)

CH₄: Methane, a greenhouse gas

CO₂: Carbon dioxide, a greenhouse gas

DEFRA: Department for the Environment, Farming and Rural Affairs.

Dry grassland: see Acid grassland

Dwarf shrub: a short woody plant, typically referring to species in the Ericaceae (heather) family.

Ecosystem: a biological community of interacting organisms and their physical environment.

EMP: Exmoor Mires Partnership – the consortium of stakeholders in the programme to restore damaged peatland on Exmoor

GHG: greenhouse gases

IPCC: Inter-governmental Panel on Climate Change

ka: 1000 calendar years before present

MD: *Molinia caerulea*-dominated habitat

Minerotrophic: soils with higher nutrient levels and lower levels of acidity.

Mire: peatland where peat is actively being laid down.

Mesotrophic: having a moderate amount of dissolved nutrients

***Molinia*:** here refers to purple moor grass *Molinia caerulea*, a robust, tussock forming grass species characteristic of acidic soils.

Moorland: extensive areas of rough grassland or heathland.

NVC – National Vegetation Classification

Ombrotrophic: rain-fed only, from clouds

Peatland: land consisting of peat soils or peat bogs.

PES: Payment for Ecosystem Services

Ruderal: a plant that develops strategies to combat periodic partial or complete destruction

Sphagnum: bog moss species, important in the formation of peat in blanket bogs.

TB: transitional bog habitat

Vascular plant: plants containing lignified tissues allowing the transport of water and minerals.

WTD: water table depth, normalised relative to peat depth

Yellowses: photosensitivity disease caused by ingesting bog asphodel. Also known as *Plochteach*, *saut*, *hard lug*, *alveld*.

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