

Is Scots Pine a Successful Invader in Contemporary Bog?

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Abstract. Scots pine (*Pinus sylvestris* L.) invading a floating bog (Wybunbury Moss National Nature Reserve, Cheshire, UK) was studied. Seed germination, establishment and tolerance to waterlogging were investigated. Vegetation type and topography were the most important factors dictating germination and seedling success. Six microhabitats of *Sphagnum*, *Sphagnum*-Ericaceae, *Sphagnum*-Cyperaceae, Ericaceae, Cyperaceae and bare peat formed 8, 15, 33, 17, 26 and 1%, respectively, of the central bog area. Germination was highest on *Sphagnum*-containing microhabitats. Seedling survival in each microhabitat was 2.1, 1.5, 1.6, 1.8, 1.9 and 0.5%, respectively. *Pinus sylvestris* seedlings have the capability to germinate and establish on the central bog at Wybunbury if they have a sufficient time of favourably unwaterlogged conditions in the first phases of germination.

Keywords: Scots pine, Peatland, Waterlogging, Topography, Germination, Seedlings.

1. Introduction

In Britain, Scots pine is one of a few common tree species to grow successfully in areas dominated by *Sphagnum* and many mature stands are recorded on bogs. Moreover, it has a long history in British bogs following post-glacial colonisation until climate changes ousted Scots pine from lowland bogs by c. 4000 BP [1]. Despite Scots pine is seen as an undesirable species in mires of high conservation interest since it overshadows and alters the bog communities through nutrient changes, the ability of Scots pine seedlings to invade bog areas has been largely unexamined [2].

It was noted that four factors were responsible for adverse conditions for vascular plants on bogs: low nutrient availability, anoxia due to the high water table, low temperature, and high acidity [3]. Also, it was concluded that water table was most important since for Scots pine a few dry years with a very low water table in slightly drier areas of woodland bogs has been seen to be sufficient for seedlings to establish [2]. Scots pine had the ability to form aerenchyma tissue in both stem and roots as a response to anoxic conditions [4]. But, *P. sylvestris* was classified as one of the species which had low flooding tolerance, ranking in the lowest of five levels [5]. Thus, there appears to be conflicting opinions about the tolerance to anoxic conditions in rooting zone of Scots pine.

It was found that *Sphagnum* at the top of actively growing hummocks can overtop vascular plants [3]. This interaction between Scots pine and *Sphagnum* is also influenced by seed predation, seeds becoming buried below the *Sphagnum* growth (light is needed for Scots pine germination), desiccation of young seedlings by drying of the loose moss mat, but most importantly by the seedlings becoming overgrown by *Sphagnum* because of a slower rate of height growth relative to *Sphagnum* [6]. However, if the Scots pine seedlings could grow fast enough to stay above the *Sphagnum* they have the chance to grow large enough to change the *Sphagnum*-dominated environment [2].

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Scots pine juveniles greater than 10 mm stem diameter have been shown to reduce the growth of *Sphagnum* [6], and thereby assisting other plants to establish on the bog surface. Furthermore, accumulation of pine litter can locally elevate nutrient availability reducing *Sphagnum* growth and rapidly changing the bog ecosystem [7].

Wybunbury Moss is a floating *schwingmoor* classified as a Grade 1 National Nature Reserve (NNR), notified as a Site of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC), and forms part of the Ramsar series of international wetlands. Its value lies in the range of mire and bog pool communities and associated invertebrate assemblages for which Wybunbury is internationally important. Scots pine was present on the site before the development of the floating bog but is unlikely to have been a natural component of these communities since the mid-Flandrian [8]. However, invasion of Scots pine seedlings and saplings onto the bog surface has an adverse effect on the mire communities, both for its shading and drying-out effects on the bog. Nevertheless, it is of conservation interest in its own right as habitat for rare beetles and so cannot be completely removed from the site. Management of the NNR currently involves both the removal of some mature Scots pine which have established through the twentieth century and the removal of seedlings and saplings which establish across much of the open mire communities. However, the removal is detrimental to the bog surface through disturbance, and is costly.

The aim of this study was to examine the ability of Scots pine at Wybunbury Moss to germinate and establish on different types of vegetation within the mosaic caused by varying topography. The specific aims were to: 1) determine the most favourable and unfavourable places (microhabitats defined by vegetation) for Scots pine seed germination and seedling survival; 2) determine the effect of surface topography (flooding level) on germination and seedling number.

2. Materials and Methods

2.1. Area of Study

Wybunbury Moss is a raft of floating *Sphagnum* peat (*Schwingmoor*) that lies in south Cheshire in the English Midlands [9] at latitude 53°02'N, longitude 2°27'W, 56 m asl. It is a deep basin bog, the surface is oval, 12 ha in area and the peat, at its maximum, is 4 m thick over up to 15 m of water [8]. The vegetation of the bog margins includes mixed woodland and reedswamp, pine woodland. The central *Sphagnum* lawn is 1.6 ha and dominated by 7 species of *Sphagnum* which are dominant on small hummocks (up to 18 cm high) and shallow depressions. Larger hummocks (>18 cm high) are gradually capped by *Aulacomnium palustre* and *Mylia anomala*. Scots pine was introduced to Wybunbury Moss in the late 1880s [10].

2.2. Experimental Design and Measurements

Extensive observations showed that the central part of the bog could be reliably divided into six types of vegetation microhabitats spread across four levels of topography. From random sampling of 10 x 2 m² plots, it was estimated that the central bog area was made up of the following microhabitats: 1) *Sphagnum* lawn (8% of the bog area), 2) *Sphagnum*-Ericaceae, containing *Calluna vulgaris*, *Erica tetralix*, *Vaccinium oxycoccus* and *Sphagnum* spp. (15%), 3) *Sphagnum*-Cyperaceae, dominated by *Sphagnum* spp., *Eriophorum angustifolium* and *E. vaginatum* (35%), 4) Ericaceae, containing *Calluna vulgaris*, *Erica tetralix* and *Vaccinium oxycoccus* (17%), 5) Cyperaceae, dominated by *Eriophorum angustifolium* and *E. vaginatum* (26%), and 6) bare peat (1%).

These six microhabitats were distributed over hummocks in the bog surface topography and so each could occur at varying heights above the water table. The hummocks were divided in four height classes, starting from the lowest point of the bare surface which in this floating bog represents the almost constant water table: 1) 0-6 cm, the depressions between hummocks which are commonly bare peat with remains of dead *Sphagnum* covered by water at all times, 2) 7-12 cm, uniform areas between the bare peat and the small hummocks (often up to 1m²) and most often dominated by *Sphagnum* and sometimes associated with Cyperaceae, 3) 13-18 cm, small hummocks with mixtures of the *Sphagnum*-containing microhabitats, and finally 4) the highest level >18 cm above the bare peat, large hummocks mostly dominated by either *Calluna vulgaris*, *Erica tetralix* or *Vaccinium oxycoccus* sometimes associated with *Sphagnum*.

Using a randomised block design, ten plots each 2 x 1 m were established on the central bog in April/May in each of the years 2008, 2009 and 2010 (i.e. 30 altogether). Each plot contained the 6 microhabitats but not consistently the 4 levels of topography. The highest hummock did not exceed 35 cm above the bare peat and so transitions between microhabitats were gradual rather than defined by abrupt changes in elevation. The size of microhabitat patches within each plot was normally between mostly 40 x 40 cm. Nine hundred Scots pine seeds were sown by scattering on the substrate surface from 1-2 cm height above the vegetation/substrate surface (to simulate natural seed fall) in each plot, 150 in each of the six microhabitat types. New seedlings were marked by plastic rings every two weeks during the first three months after seed sowing and once every 6 weeks thereafter. Percent germination of seeds sown, % mortality of germinated seeds and % survival of seeds sown were calculated. Seeds used in the first two seasons were commercially supplied from Carrbridge, Scotland. Seeds collected from Wybunbury Moss as part of this project were used only in the third season due to a lack in their availability. Seeds were stored in plastic bags at 5 °C before use. Germination capacity at the time of sowing, determined by germination trials in Petri dishes ($n = 200$), was 71% for the commercially sourced seed in both years and 64% for the Wybunbury Moss seed [11].

In August 2010, all surviving seedlings from all three sowings were gently removed from the substrate, and length and dry mass of shoot and root were measured. Root/shoot ratio was calculated afterwards. The total area of each microhabitat within the final 10 plots was sampled randomly and estimated using a 2 x 1 m wooden frame divided into 200 sections of 100 cm².

2.3. Statistical Analysis

All data was tested for normality and equal variance. One-way Analysis of Variance with blocks (habitats fixed, blocks random) was carried out on arcsine transformed data followed by Tukey's post hoc paired comparisons between means, to examine the differences in germination, survival and mortality. It was not possible to compare topography for the three variables because of non-orthogonality but orthogonal data was available for four microhabitats and three topography levels upon which a limited comparison was possible. A two-way ANOVA was used to compare these data between years. The proportions of surviving seedlings across habitats and topography were analysed by χ^2 and plant performance data were analysed by One-way ANOVA after log transformation for all the seedlings. Minitab® Version 16 (General Linear Model) was utilised for the analysis.

3. Results

3.1. Microhabitat, Germination and Seedling Survival

Germination percentage varied among microhabitats and between years, and the number of successful seedlings varied between years and among microhabitats. In 2008, when the seeds were sown in mid-May and left for 27 months, an overall significance was found with Tukey's paired comparison showing significantly higher germination and seedling survival on the pure *Sphagnum* microhabitat than in the other microhabitats (Table 1). The bare peat microhabitat showed no successful seedlings by the end of the period.

In 2009, germination continued for 16 months. Nevertheless, germination was low and there were no significant differences between microhabitats, but there were differences in seedling survival. The highest seedling survival in this year was found in *Sphagnum*/Ericaceae microhabitat at $7.0 \pm 1.51\%$ (Table 1).

In 2010, observations were only carried out for 4 months and with seeds from Wybunbury. Germination was again low and there were no significant differences between microhabitats in germination and seedling survival.

A comparison between the three years of total germination and seedling survival across all the microhabitats showed that total mean germination in the first year ($8.1 \pm 2.97\%$) was significantly higher than in the two other years ($F_{2,173} = 9.87$; $P < 0.01$). Seeds from Wybunbury, sown in the last year (2010), had the lowest total mean germination ($1.7 \pm 0.35\%$). Seedlings from the Scottish plantation seed, sown in the first year, had the highest total mean seedling survival at $4.1 \pm 2.23\%$ ($F_{2,173} = 6.40$; $P < 0.01$). Seeds from Wybunbury, again, showed the lowest total mean at $1.6 \pm 0.23\%$. Over the 3 years, mean germination

and survival was significantly higher in the *Sphagnum* microhabitat than Ericaceae, Cyperaceae and Bare peat microhabitats (Table 1).

3.2. Microhabitat and Seedling Performance

Seeds sown in 2008 produced seedlings 27 months old when harvested. These showed significant differences in shoot and root length between microhabitats (Table 2). The Cyperaceae microhabitat had some of the longest shoots and roots with means of 10.0 ± 0.64 cm and 10.7 ± 0.53 cm, respectively. Growth in the other microhabitats was varied. The Ericaceae and Sphagnum-Ericaceae microhabitats gave the shortest shoot and root length (Ericaceae 6.1 ± 0.33 and 7.6 ± 0.34 cm, respectively; Sphagnum-Ericaceae 6.6 ± 0.27 and 7.8 ± 0.43 cm, respectively). Shoot and root length in the Ericaceae microhabitat were significantly different from those in Sphagnum, Cyperaceae and Sphagnum-Cyperaceae microhabitats but not from Sphagnum-Ericaceae (Table 2). The Cyperaceae microhabitat was significantly the highest mean shoot dry mass (0.114 ± 0.0162 g) (Table 2). Mean root dry mass was significantly higher in the Cyperaceae microhabitat (0.034 ± 0.0035 g) than in all other microhabitats (Table 2). One-way ANOVA showed significant differences between microhabitats in the mass ratio of root/shoot (Table 2) where the *Sphagnum* microhabitat mean root/shoot ratio (0.332 ± 0.0073) was significantly lower than in the other microhabitats. The bare peat habitat was not included due to lack of seedlings.

For seeds sown in 2009, seedlings grew for 16 months. The Ericaceae microhabitat was significantly higher than the other microhabitats and produced the highest means of shoot and root length with 7.8 ± 0.52 and 10.9 ± 0.83 cm, respectively (Table 2). There were no significant differences in shoot and root dry mass nor root/shoot ratio between microhabitats. Seeds sown in 2010 were 4 months old at harvest. There were small differences between microhabitats in mean shoot and root length; wherever the *Sphagnum* occupied, the longest shoot and root were found, but these were not significantly different. There were significant differences in the root dry mass and root/shoot ratio with *Sphagnum*-Ericaceae higher than the rest.

3.3. Topography, Germination and Seedling Performance

Since the bog surface topography is formed of a mosaic of hummocks, each of the six identified microhabitats were found in one or more of the topographical height classes above the water table. This section investigates the effect of different levels of elevations on survival and seedling performance. Table 3 shows the percentage of Scots pine seedlings that germinated on different microhabitats and at different levels of elevation over each of the first two years.

In 2008, the highest germination percentages were found in the *Sphagnum* microhabitat at elevation levels 7-12 and 13-18 cm above the bare peat reference level at 22% and 25%, respectively (Table 3).

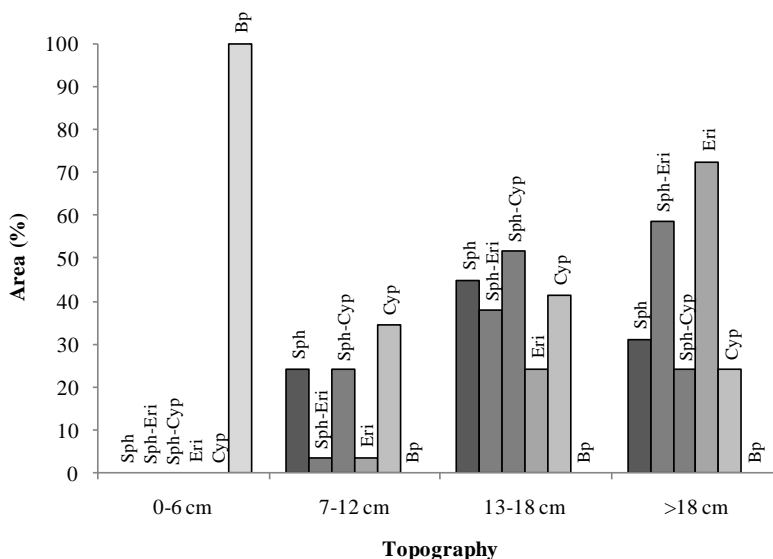


Fig. 1: The percentage area of the six microhabitat within each of 4 different levels of elevation in 29 plots, the bare peat only existed at 0-6 cm level above the ground (n = 174). Abbreviations: Sph = *Sphagnum*, Sph-Eri = *Sphagnum* + Ericaceae, Sph-Cyp = *Sphagnum* + Cyperaceae, Eri = Ericaceae, Cyp = Cyperaceae and Bp = Bare peat.

Table 1: Mean percent germination and seedling survival over three years (± 1 SE). 2008: seeds were sown in May 2008 and followed for 27 months; 2009, seeds sown in April 2009 and followed for 16 months; 2010 seeds sown April 2010 and followed for 4 months. The experiment ended in August 2010. Ten plots per used each year, each plot containing the 6 microhabitats. One plot in 2009 was lost 3 months after starting the experiment. Figures with the same letters within a variable are not significantly different (One-way ANOVA, $P < 0.05$).

Microhabitat	2008		2009		2010		Mean of the 3 years	
	Germination	Survival	Germination	Survival	Germination	Survival	Germination	Survival
<i>Sphagnum</i>	21.7 ^a \pm 7.85	16.7 ^a \pm 6.39	3.0 \pm 1.16	1.6 ^{ab} \pm 0.85	2.2 \pm 0.69	2.1 \pm 0.75	9.2 ^a \pm 3.17	6.6 ^a \pm 2.32
Sphagnum-Ericaceae	5.0 ^b \pm 1.95	4.0 ^{ab} \pm 1.41	4.4 \pm 1.75	7.0 ^a \pm 1.51	1.7 \pm 0.36	1.5 \pm 0.46	5.3 ^{ab} \pm 0.89	2.8 ^{ab} \pm 0.65
Sphagnum-Cyperaceae	10.4 ^{ab} \pm 4.37	5.4 ^{ab} \pm 2.25	3.7 \pm 1.09	2.0 ^{ab} \pm 1.13	1.7 \pm 0.60	1.6 \pm 0.84	3.6 ^{ab} \pm 1.66	2.4 ^{ab} \pm 0.79
Ericaceae	5.2 ^{ab} \pm 1.70	2.1 ^b \pm 1.09	0.8 \pm 0.36	0.8 ^{ab} \pm 0.75	1.0 \pm 0.40	1.8 \pm 0.64	2.5 ^b \pm 0.71	1.4 ^b \pm 0.41
Cyperaceae	2.3 ^b \pm 1.16	3.3 ^b \pm 2.36	2.3 \pm 0.88	1.3 ^b \pm 1.15	2.9 \pm 1.48	1.9 \pm 0.90	2.3 ^b \pm 0.69	1.3 ^b \pm 0.52
Bare Peat	3.5 ^b \pm 3.01	*	0.9 \pm 0.19	0.1 ^b \pm 0.07	0.5 \pm 0.28	0.5 \pm 0.22	1.7 ^b \pm 1.05	0.2 ^b \pm 0.09
F-value within years	F _{5,45} = 4.5; $P < 0.01$	F _{4,25} = 3.47; $P < 0.05$	ns	F _{5,23} = 3.90; $P = 0.01$	ns	ns	F _{2,173} = 3.34; $P < 0.01$	F _{2,173} = 4.09; $P < 0.01$

*Bare peat microhabitat was excluded because there were no survivors by the end of the period. ns: No significant differences were found.

Table 2: Seedling growth resulting from seeds sown in 3 different years on 5 different microhabitats Data are mean lengths (cm) of shoot (SL) and root (RL), dry mass (mg) of shoot (SDM) and root (RDM) and root/shoot ratio (R/S). Seedlings in the 2008 data were 29 months old using Scottish seeds, (n = 220, 46, 65, 27, and 19, respectively). Data from 2009 were 16 month old seedlings using Scottish plantation seeds, (n = 21, 60, 18, 7 and 12, respectively). Data from 2010 were four month old seedlings using seeds from Wybunbury (n = 30, 23, 24, 27 and 28 respectively). The bare peat microhabitat was excluded because there were no survivors by the end of the trial. Data are means ± 1 SE; Figures with the same letters within each data set are not significantly different (One-way ANOVA, $P < 0.05$).

Microhabitat	2008					2009					2010				
	SL	RL	SDM	RDM	R/S	SL	RL	SDM	RDM	R/S	SL	RL	SDM	RDM	R/S
<i>Sphagnum</i>	7.3 ^a \pm 0.12	9.6 ^a \pm 0.22	0.083 ^{ab} \pm 0.0032	0.025 ^{ab} \pm 0.0008	0.33 ^a \pm 0.007	5.0 ^a \pm 0.23	9.2 ^a \pm 0.50	0.048 \pm 0.0048	0.021 \pm 0.0018	0.48 \pm 0.027	4.7 \pm 0.16	8.2 \pm 0.46	0.028 \pm 0.0052	0.011 ^a \pm 0.0008	0.56 ^{ab} \pm 0.198
Sphagnum-Ericaceae	6.6 ^b \pm 0.27	7.8 ^b \pm 0.43	0.063 ^c \pm 0.0079	0.022 ^{bc} \pm 0.0021	0.39 ^b \pm 0.029	6.0 ^a \pm 0.22	9.5 ^a \pm 0.38	0.050 \pm 0.0040	0.019 \pm 0.0012	0.44 \pm 0.020	5.1 \pm 0.22	8.5 \pm 0.64	0.033 \pm 0.0041	0.013 ^b \pm 0.0010	0.40 ^a \pm 0.018
Sphagnum-Cyperaceae	7.7 ^a \pm 0.20	10.7 ^a \pm 0.40	0.072 ^{bc} \pm 0.0057	0.024 ^{ab} \pm 0.0014	0.38 ^b \pm 0.016	5.2 ^a \pm 0.23	8.4 ^a \pm 0.42	0.038 \pm 0.0031	0.017 \pm 0.0014	0.47 \pm 0.028	5.0 \pm 0.14	8.4 \pm 0.32	0.030 \pm 0.0026	0.009 ^a \pm 0.0008	0.31 ^b \pm 0.015
Ericaceae	6.1 ^b \pm 0.33	7.6 ^a \pm 0.34	0.055 ^c \pm 0.0060	0.018 ^c \pm 0.0019	0.36 ^b \pm 0.026	7.8 ^b \pm 0.52	10.9 ^a \pm 0.83	0.067 \pm 0.0109	0.021 \pm 0.0030	0.33 \pm 0.047	4.9 \pm 0.15	7.2 \pm 0.69	0.031 \pm 0.0060	0.009 ^b \pm 0.0006	0.30 ^b \pm 0.016
Cyperaceae	10.0 ^c \pm 0.64	10.7 ^a \pm 0.53	0.114 ^a \pm 0.0162	0.034 ^a \pm 0.0035	0.36 ^b \pm 0.059	5.3 ^a \pm 0.29	6.2 ^b \pm 0.58	0.050 \pm 0.0050	0.018 \pm 0.0050	0.36 \pm 0.023	4.7 \pm 0.14	8.0 \pm 0.48	0.031 \pm 0.0059	0.013 ^{ab} \pm 0.0030	0.48 ^{ab} \pm 0.143
F-value within years	F _{4,372} = 13.91; $P < 0.001$	F _{4,372} = 9.23; $P < 0.001$	F _{4,372} = 7.78; $P < 0.001$	F _{4,372} = 5.86; $P < 0.001$	F _{4,372} = 2.56; $P < 0.001$	F _{4,118} = 5.06; $P < 0.01$	F _{4,118} = 6.98; $P < 0.01$	ns	ns	ns	ns	ns	ns	F _{4,127} = 4.02; $P < 0.01$	F _{4,127} = 4.66; $P < 0.01$

ns: No significant differences were found.

Table 3: Mean germination percentage of Scots pine in 2008 (n = 377 over 10 plots) and 2009 (n = 124 over 9 plots) within six microhabitats examined at 4 levels of elevation each year.

Microhabitat	Germination (%) by year and elevation (cm)							
	2008				2009			
	0-6	7-12	13-18	>18	0-6	7-12	13-18	>18
<i>Sphagnum</i>	0	22	25	1	0	5	2	2
Sphagnum-Ericaceae	0	0	7	4	0	0	3	6
Sphagnum-Cyperaceae	0	20	4	0	0	6	3	0
Ericaceae	0	0	5	7	0	0	1	1
Cyperaceae	0	8	0	1	0	3	2	0
Bare Peat	4	0	0	0	1	0	0	0

Table 4: Seedling performance resulting from seeds sown in 3 different years on 3 different Topography. Data are mean lengths (cm) of shoot (SL) and root (RL), dry mass (mg) of shoot (SDM) and root (RDM) and root/shoot ratio (R/S).

Seedlings in the 2008 data were 29 months old using Scottish seeds, (n = 114, 224 and 39, respectively). Data from 2009 were 16 month old seedlings using Scottish plantation seeds, (n = 48, 50 and 25, respectively). Data from 2010 were four month old seedlings using seeds from Wybunbury (n = 15, 34 and 83 respectively). Data are means \pm 1 SE;

Figures with the same letters within each data set are not significantly different (One-way ANOVA, $P < 0.05$).

Topography	Year 2008					Year 2009					Year 2010				
	SL	RL	SDM	RDM	R/S	SL	RL	SDM	RDM	R/S	SL	RL	SDM	RDM	R/S
7 – 12 cm	7.5 ^a	9.9 ^a	0.072 ^a	0.024 ^a	0.38	5.5 ^a \pm 0.17	8.2 ^a \pm 0.32	0.051 ^b	0.021 ^a	0.44 ^a	4.9	8.4	0.032	0.012 ^a	0.40
	\pm	\pm	\pm	\pm	\pm			\pm	\pm	\pm	\pm	\pm	\pm	\pm	\pm
	0.22	0.27	0.0045	0.0011	0.015			0.0034	0.0011	0.019	0.12	0.74	0.0018	0.0009	0.028
13 – 18 cm	7.4 ^a	9.6 ^a	0.085 ^a	0.026 ^a	0.34	5.1 ^a \pm 0.17	8.6 ^a \pm 0.32	0.035 ^c	0.016 ^b	0.48 ^a	5.0	7.9	0.028	0.009 ^b	0.32
	\pm	\pm	\pm	\pm	\pm			\pm	\pm	\pm	\pm	\pm	\pm	\pm	\pm
	0.12	0.23	0.0031	0.0001	0.009			0.0024	0.0011	0.021	0.13	0.34	0.0014	0.0007	0.018
> 18 cm	6.4 ^b	7.8 ^b	0.038 ^b	0.019 ^b	0.35	7.5 ^b \pm 0.33	11.3 ^b	0.071 ^a	0.023 ^a	0.35 ^b	4.9	8.0	0.031	0.011 ^b	0.34
	\pm	\pm	\pm	\pm	\pm			\pm	\pm	\pm	\pm	\pm	\pm	\pm	\pm
	0.24	0.36	0.0061	0.0018	0.020			0.0071	0.0019	0.024	0.01	0.33	0.0011	0.0004	0.010
F-value within years	F _{2,374} = 5.91; $P < 0.01$	F _{2,374} = 5.98; $P < 0.01$	F _{2,374} = 11.16; $P < 0.001$	F _{2,374} = 9.66; $P < 0.001$	ns	F _{2,120} = 24.21; $P < 0.001$	F _{2,120} = 10.55; $P < 0.001$	F _{2,120} = 22.16; $P < 0.001$	F _{2,120} = 9.96; $P < 0.001$	F _{2,120} = 7.43; $P < 0.001$	ns	ns	ns	F _{2,129} = 4.48; $P < 0.05$	ns

ns: No significant differences were found.

Topography had a significant effect on the seedlings shoot and root length from the 2008 sowing (Table 4). Levels 7-12 and 13-18 cm above the bare peat had the highest mean shoot length (7.5 cm and 7.4 cm, respectively) and root length (9.9 cm and 9.6 cm, respectively). These were significantly higher than at level >18 cm which was mostly dominated by Ericaceae and *Sphagnum*-Ericaceae microhabitats. Two thirds of Cyperaceae microhabitat was located on levels 7-12 cm and 13-18 cm (Fig. 1). Level 0-6 cm was excluded due to the lack in survivors. Shoot and root dry mass were both significantly different between topographical height classes. Dry shoot and root mass at the >18cm level (0.038 g and 0.019 g, respectively) were significantly lower than at 7-12cm and 13-18cm which were not significantly different from each other. Topography did not affect the root/shoot ratio (Table 4).

In 2008, the total germination percentage was noticeably higher at levels of 7-12 and 13-18 cm (14 and 11%, respectively), particularly in *Sphagnum*-Ericaceae microhabitat which surprisingly showed the highest mean germination during this period (Table 3). Mean shoot (7.5 cm) and root (11.3 cm) length at >18 cm level were significantly longer than at 7-12 and 13-18, which were not significantly different from each other (Table 4). Seedlings >18 cm above the bare peat had significantly higher shoot and root dry mass compared to other levels with means of 0.071 and 0.023 g, respectively (Table 4). The resulting root/shoot ratios of seedlings >18 cm above the surface (0.351) was significantly lower than at other levels.

In 2010, there were no significant differences in shoot and root length and only root dry mass showed significant differences between topography (Table 4). Root dry mass at 7-12 cm (0.012 g) was significantly higher than at 13-18 cm (0.009 g).

3.4. Type of Vegetation and Topography

Within the 29 sampled plots, most microhabitats occurred in more than one topographical height class. The exception was bare peat which was only located at level 0-6 cm. The *Sphagnum* microhabitat was most widespread with 45% of its area in the 13-18 cm level, 31% at >18 cm and 24% within the 7-12 cm level (Fig. 1). Ericaceae and *Sphagnum*-Ericaceae microhabitats were mostly located on top of the hummocks, >18 cm above the bare peat, and rarely lower than 13 cm above the baseline.

3.5. Interactions Between Microhabitat and Topography

Since the microhabitat and topography data were not orthogonal, only 3 microhabitats and 2 levels of elevations could be included in a Two-way ANOVA. There were no significant differences in germination, surviving seedlings and mortality for either the microhabitats or topography.

Two-way ANOVA showed no significant interactions between microhabitat and topography in shoot length, but showed significant interactions between microhabitat and topography in shoot dry mass, root length and dry mass ($F_{2,67} = 8.91$, $P < 0.001$; $F_{2,67} = 6.46$, $P < 0.001$ and $F_{2,67} = 3.42$, $P < 0.05$, respectively). In shoot dry mass, there were significant interactions only between the lower mass in the *Sphagnum* habitat at >18 cm level and the *Sphagnum*-Cyperaceae at the same level. *Sphagnum*-Cyperaceae at >18 cm level exhibited higher shoot dry mass than lower levels. Root length in the Cyperaceae microhabitat at >18 cm level was significantly longer than those in the same microhabitat but at lower elevations. Also root length in the *Sphagnum* microhabitat at >18 cm level and the *Sphagnum*-Cyperaceae at 13-18 cm level were significantly longer than those in the Cyperaceae low elevation microhabitats. No significant interactions were shown in root/shoot ratio between microhabitat and topography.

4. Discussion

On this site, Scots pine trees produce heavy annual crops of low mass seeds [9]. Thus, the aim of this study was to investigate what aspect of the bog surface, formed of hummocks and hollows, and a mosaic of vegetation, would allow *significant* numbers of seed to germinate and survive.

The germination percentage was higher in 2008 than the other two years; 22% in the *Sphagnum* microhabitat, but only 4% and 2% in the next two years. The seed used in the first two years was from a Scottish plantation and in the third from Wybunbury Moss. Since germination capacity of the two seed sources was similar (71 and 64%, respectively), seed source is highly unlikely to be the cause of the germination variation. The only difference between the three years, apart from seed source was time of sowing and thus, associated weather. It is known that temperature has a significant effect on the germination of Scots pine [12]. The seeds were sown on 13 May 2008, 21 April 2009 and 20 April 2010 and the maximum temperature in these months was 17.1, 13.8 and 13.7 °C, respectively (data from Keele University, 8 km away). Records show higher temperatures in May than April in all three years, and since the optimum temperature for Scots pine germination is 21 °C this is an important factor in explaining germination differences between years [9]. A delay in germination due to colder conditions in the last two years may have allowed time for a greater predation of seeds.

Over the relatively long-term assessment periods of this study, it is clear that although germination was high on *Sphagnum*, mortality was also high. The main effect of *Sphagnum* was to bury young seedlings [6]. This undoubtedly explains why at an elevation of 13-18 cm, where distance above the water table slows moss growth and competition is reduced [6], germination and seedling survival was higher than the next lower level. Moreover, it is concluded that during warm springs the burial effect of *Sphagnum* is likely to be more pronounced due to increased height growth of the *Sphagnum* layer [6].

In hollows between hummocks, Scots pine seed showed very little germination in the bare peat microhabitat, undoubtedly due to waterlogging [6]. Seeds completely submerged in water appear incapable of germination, and even in aerated peat if within 1-1.5 cm of the water table [5].

Seedling performance varied between the microhabitats and topography. Seedlings germinating in the bare peat and between hummocks had less chance to grow and establish since flooding reduced the aboveground stem growth. Seedlings growing in both the Cyperaceae and the *Sphagnum* microhabitats at >18 cm produced longer roots than those seedlings germinating in the same microhabitats but at a lower level of elevation. This would appear to be related to the limited tolerance of coniferous roots to anoxia and thus poor growth and greater root decay under a shallower water table [13]. [14] The better aeration in the higher topographical levels would have provided more favourable condition for roots to grow, which agrees with that well-aerated peat of hummock tops allowed greater root growth as an aid to survival [6].

The results of this study suggest that *P. sylvestris* seedlings have the capability to germinate on a bog surface if they have favourable conditions during the early stages of establishment. It was found that seedling success of Scots pine on their uniform *Sphagnum* carpets was not affected by germination but by differential mortality affected by Microtopography [6]. At Wybunbury, however, with a greater diversity of plant species, both germination and survival were affected. Generally, over all years and microhabitats, the most successful germination was located 7-12 and 13-18 cm above the baseline, where the water table is deeper down. A

number of germinated seedlings were also found in level >18 cm but not under high density of Ericaceae and Cyperaceae. Similarly, seedling survival was greatest on the sides of hummocks.

Trees under stress channel a greater proportion of their energy into seed production [14] and Scots pine growing on marginal peat at Wybunbury produce an estimated 16 000 seeds that reach the central bog (1.6 ha) each year [9]. The six microhabitats of *Sphagnum*, *Sphagnum*-Ericaceae, *Sphagnum*-Cyperaceae, Ericaceae, Cyperaceae and bare peat formed 8, 15, 33, 17, 26 and 1%, respectively, of the central bog area; germination percentage in each microhabitat using data obtained from the 2010 trial was 2.2, 1.7, 1.7, 1.0, 2.9 and 0.5%, respectively. Seed from Wybunbury Moss has a mean viability of 64% [9]. Using these Figures, it can be calculated that on the central bog at Wybunbury these 16,000 seeds would be expected to produce just 145 new juveniles per year, a success rate of 0.91% of the seeds reaching the central surface every year. Regardless of the errors associated with this estimation, from a management viewpoint, this success rate is reassuringly low but still too high to meet management objectives [15] and represents a significant number of new Scots pine trees annually. It is not physically possible or economically viable to find all individual seedlings and cut or pull them from the surface; other management techniques are needed.

5. Conclusions

This study shows that bare peat is the worst microhabitat for Scots pine establishment and so increasing the area of peat scrapes (carried out as part of the management to foster early successional stages of bog development) would reduce the invasion of Scots pine. Alternatively, raising the water level of the central bog by manipulating drainage during seed shedding season (April and May) could help prevent new pine seedlings from establishing. This would work poorly at Wybunbury Moss given that the floating peat raft will tend to rise with any additional water but would be very feasible on more solid bogs. This work also suggests that drier bog surfaces in northern UK, predicted from current climate change scenarios [16], will lead to greater investigation of Scots pine into sensitive bog communities.

6. References

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