Lycopodiella inundata in British plant communities and reasons for its decline

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ABSTRACT

We investigated the community context of *Lycopodiella inundata* (Lycopodiaceae) in ten representative sites in England and Scotland. Vegetation classification (TWINSPAN), detrended correspondence analysis and indicator species analysis were used to derive community types and to reveal the phytosociological position of this scarce and threatened species. In the study sites *L. inundata* mostly occurs on very acidic, oligotrophic, moist to wet soils in fully exposed situations in wet heaths and along lake margins. The classification resulted in four vegetation units: a *Drosera intermedia–Sphagnum tenellum* community in England, and three community types in Scotland, viz. a *Drosera anglica–Myrica gale* community, an *Eleocharis multicaulis–Narthecium ossifragum* community and a *Hydrocotyle vulgaris–Leontodon autumnalis* community. The ecological differences between the communities in England and Scotland were mostly related to soil reaction, and the English sites were probably the most acidic. *L. inundata* seems to tolerate a wide range of soil pH and levels of soil moisture, whereas it seems to be intolerant to shading or eutrophication. Eutrophication may be partly responsible for the species' general decline across Europe. The scope for future conservation of this species is discussed.

KEYWORDS: classification, indicator analysis, lake margin, niche width, ordination, wet heath.

INTRODUCTION

Lycopodiella inundata (L) Holub, the Marsh Clubmoss, is a homosporous perennial pteridophyte within the *Lycopodiaceae* (Holub 1964). It is a small, bright green, creeping, moss-like plant producing 2–3 cm tall cones with weakly differentiated sporophylls in the autumn. The species has an amphi-atlantic distribution, occurring in Japan, North America, central and northern Europe, but it is absent from the central parts of Russia (Hultén & Fries 1986). In England it is mainly found on wet heaths (Rhynchosporion), often on bare peaty or occasionally sandy soils. It favours areas which are inundated in the winter and spring, kept open by occasional disturbance (Tansley 1953; Rodwell 1991). The species has also been found as a pioneer in disused sand and gravel pits (Petch 1980; Pickering & Wigston 1990), whilst in Scotland it mostly grows in the inundation zone along the edges of oligotrophic lakes on organic silt (Stewart *et al*. 2000).

Lycopodiella inundata is a stress tolerator according to the Grime strategy system, as indicated by its low biomass and low potential growth rate, little vertical growth, and rapid reproduction in autumn (Hodgson *et al.* 1999). The species often occurs as a pioneer and may easily be excluded if succession proceeds, as evidenced in Norfolk (Petch 1980). *L. inundata* is therefore only found where the vegetation is recently cleared or is constantly kept open. In England human disturbance such as foot paths, tracks and abandoned quarries seem to be necessary to maintain suitable habitats, which may indicate a lack of fully natural habitats for the species. It is possible that the

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species has never been a part of the natural flora in southern England, but invaded at the same time as heathlands spread, as Wiinstedt (1953) suggested for *L. inundata* in Denmark. One of the natural habitats for *L. inundata* is probably more like the one encountered around lochs in Scotland, where a fluctuating water level and ice movements in the winter maintain an open vegetation. The margins around salt marshes in Massachusetts, USA, are also reported to provide the essential disturbance and acidity for the occurrence of *L. inundata* (Wherry 1920).

It seems that human destruction of wetlands, in combination with eutrophication and changed management, have caused the decline of *L. inundata* in most of Europe (Denmark, Pihl *et al*. 2000). *L. inundata* is associated with the Habitat Action Plans for lowland heathland and purple moor grass and rush pastures and is included in the Annex V of the Habitats Directive (1992). In Britain, *L. inundata* has disappeared mainly from the central and northern English localities, probably due to the loss of habitat through drainage, lack of grazing and pollution (Stewart *et al*. 2000). It is considered “nationally scarce” and is identified as a priority species under the U.K. government’s Biodiversity Action Plan. Conservation of *L. inundata* is, however, difficult since little is known about its ecology, including potential reasons for decline and response to environmental change (Stewart *et al*. 2000).

The aim of the present study is 1) to classify the vegetation associated with *L. inundata* in Britain, 2) to describe the habitats of *L. inundata* by ordination and indicator analysis, and 3) to discuss the present and future status of *L. inundata* in Britain. We especially want to address the question whether it is possible to plan conservation actions for a species like *L. inundata*, which relies in certain instances on recurring disturbances, which for other reasons may not be desirable.

METHODS

STUDY AREA

In England five representative sites (Table 1, Figure 1) of *L. inundata* were selected in Surrey and Hampshire. The sites represent most of the types of habitats where *L. inundata* is known to occur in England (Stewart *et al*. 2000). In all of the study sites the soil was firm with a rather open vegetation. Water levels were high enough to keep the area moist in summer and wet or flooded in winter and spring. The bare ground was often covered by mats of the purple alga, *Zygogonium ericetorum*, which forms a crusty cover during dry weather and keeps the soil moist underneath. *L. inundata* is often the first coloniser of patches of bare soil, as for example on Chobham Common where it was growing on the edges of small holes left after peat digging. A similar case was observed on Elstead Common where it seemed to be spreading down a new footpath crossing the original track.

In Scotland sites along five different lakes (lochs/lochans) were studied (Table 1, Figure 1). Despite grazing in the Scottish Highlands, the main disturbance factor in the study habitats were water table fluctuations and moving ice at the shoreline, especially since the vegetation of the study habitats was sparse and much less palatable to livestock and deer than the surrounding heath vegetation.

DATA COLLECTION

Patches of vegetation with *L. inundata* were sampled according to the Braun-Blanquet method (Dierschke 1994), using 4–15 quadrats each of 4 m^2 and placed systematically to cover the variation within the area. The percentage cover of each species of vascular plant and bryophyte was estimated by eye and assumed reliable to the nearest five percent. One percent was the lowest possible score. The survey was undertaken in June and July 2000. The percentage cover values were transformed into the Domin scale to make the data comparable with the British National Vegetation Classification (NVC) (Rodwell 1991). In addition, the per cent cover of bare soil was recorded.

VEGETATION CLASSIFICATION

Clustering of the entire community dataset was performed with the programme TWINSPAN (Hill 1979). The cut levels 0, 2, 5, 10 and 20 were used, and no quadrats or species were omitted. Three levels of divisions were chosen, otherwise the default options were applied. Clusters resulting from

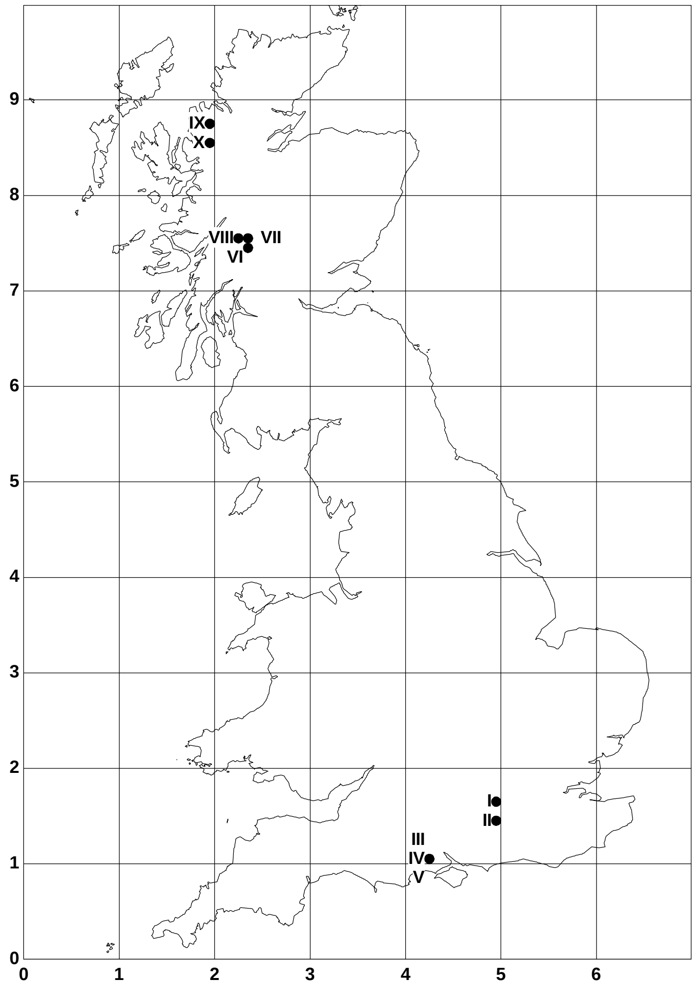

FIGURE 1: Map of the ten locations surveyed for habitats with *L. inundata* (Roman numbers correspond to sites described in Table 1).

TABLE 1. SITES SURVEYED IN BRITAIN

Site no.	No. of quadrats	Site name	County	National grid ref.
		ENGLAND		
I	9	Chobham Common	Surrey	SU965655
II	15	Elstead Common	Surrey	SU900400
III	5	Station Road Holmsley, New Forest	Hampshire	SU231009
IV	10	Holmsley ridge, New Forest	Hampshire	SU217011
V	4	Duckhole Bottom, New Forest	Hampshire	SU253019
		SCOTLAND		
VI	10	Lochan na h-Achlaise	Main Argyll	NN312480
VII	10	Loch Ba	Main Argyll	NN320520
VIII	10	Dubh Lochan	Main Argyll	NN274537
IX	11	Loch Maree Islands	West Ross	NG9172
X	6	Loch Bharranch	West Ross	NG979576

TABLE 2. SYNOPTIC TABLE OF THE FOUR DESCRIBED COMMUNITIES

			SCOTLAND	
	ENGLAND	Scotland	Loch Maree	Loch Maree
Community	1	2	3	4
Number of quadrats	42	37	6	4
Number of species	38	48	27	18
Agrostis stolonifera		5(1)		
Betula pubescens (s)	41(1)			
Breutelia chrysocoma		14(1)		
Calluna vulgaris	95(1–10)	86(1–12)	67(1–5)	75(1)
Campylopus atrovirens		22(1)	17(1)	
Campylopus introflexus	19(1–5)			
Carex cf. *viridula*	5(1)			
Carex echinata		46(1)	67(1–5)	
Carex nigra		76(1–10)	67(1–5)	100(20–25)
Carex panicea	21(1)	81(1)	100(1–10)	100(5–10)
Carex viridula ssp. *oedocarpa*		70(1–5)	100(1–10)	100(5–10)
Dicranella palustris		5(1)		
Drosera anglica		86(1–5)	50(1)	
Drosera intermedia	86(1)			
Drosera rotundifolia	64(1)	76(1)	100(1)	100(1)
Drosera × *obovata*		27(1)	17(1)	
Eleocharis multicaulis	19(1–5)	11(1)	100(1–20)	100(1–5)
Equisetum fluvatile		5(1)		
Erica tetralix	100(1–15)	65(1–5)	33(1–5)	
Eriophorum angustifolium	31(1)	51(1)	50(1)	
Festuca ovina	2(1)	3(5)	100(1–5)	100(15–25)
Hydrocotyle vulgaris			33(1)	100(1)
Juncus acutiflorus	19(1)	46(1–5)	33(1)	
Juncus bulbosus	52(1)	100(1)	83(1)	
Juncus conglomeratus		16(1)		
Juncus effusus	12(1)			
Juncus squarrosus	43(1–5)	49(1–25)		
Jungermannia sp.	2(1)	11(1)		
Leontodon autumnalis				100(1)
Littorella uniflora				25(1)
Lobelia dortmanna		22(1)	17(1)	100(1)
Lycopodiella inundata	**76(1)**	**97(1)**	**100(1)**	**100(1–5)**
Molinia caerulea	100(1–25)	100(1–25)	100(5–15)	100(1–5)
Myrica gale		59(1–10)		
Nardus stricta		68(1–10)		50(1)
Narthecium ossifragum	19(1–10)	76(1–5)	100(1)	
Pedicularis sylvatica	19(1)	19(1)	33(1)	
Pellia epiphylla		38(1)		
Pinguicula vulgaris		51(1)	33(1)	
Pinus sylvestris	57(1)	3(1)	50(1)	75(1)
Pleurozia purpurea		11(1)		
Polygala serpyllifolia		27(1)		
Polytrichum commune	2(1)	11(1)		
Potentilla erecta	10(1)	51(1)		
Racomitrium lanuginosum		19(1)		
Ranunculus flammula		65(1)	33(1)	100(1)
Rhynchospora alba	24(1)	3(1)	50(1)	
Rhynchospora fusca	12(1)			
Salix cf. *cinerea*	7(1)			
Salix repens	7(1)			
Sphagnum compactum	62(1–60)	100(1–30)	100(1–5)	
Sphagnum papillosum	2(1)	35(1–5)		
Sphagnum tenellum	60(1–34)			
Succisa pratensis		46(1)		25(1)
Trichophorum cespitosum	62(1–20)	35(1–5)	100(1–5)	50(1)

1, *Drosera intermedia–Sphagnum tenellum* community; 2, *Drosera anglica–Myrica gale* community; 3, *Eleocharis multicaulis–Narthecium ossifragum* community; and 4, *Hydrocotyle vulgaris–Leontodon autumnalis* community. Frequency (%) of species in quadrats is shown together with the percentage cover range in brackets, when the frequency is above 5% in any one community. (s) denotes seedling.

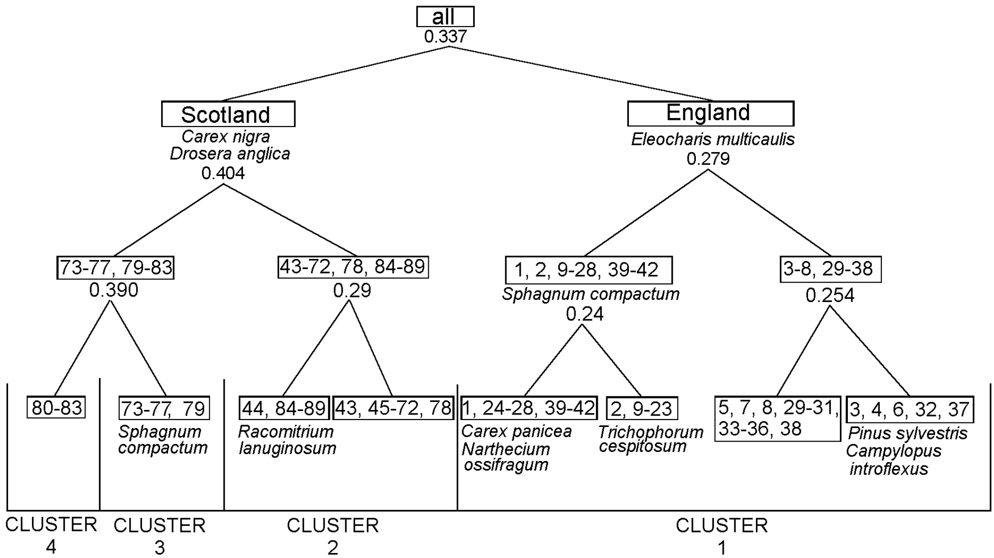

FIGURE 2: TWINSPAN dendrogram for the whole data set. Eigenvalues, quadrat numbers and indicator species are given.

divisions with eigenvalues higher than 0·3 are treated as final clusters, which, however, do not necessarily constitute communities. The resulting vegetation units are named informally as communities after the most characteristic species.

In order to compare our results with the British National Vegetation Classification (NVC) (Rodwell 1991) the Domin-transformed cover values at each site were compared with the NVC data using the computer program MATCH (Malloch 1997). The similarity coefficients of the quadrat data for each site were compared with the descriptions in Rodwell (1991).

INDIRECT GRADIENT ANALYSIS

The floristic variation within the English and Scottish subsets of data, as well as the entire data set, were assessed with the computer program CANOCO, version 4.0 (ter Braak & Smilauer 1998). We used detrended correspondence analysis (DCA) with standard options to extract the primary ordination axes. The correlation of sample scores on the four axes with percentage bare soil and Ellenberg's indicator values were tested with Pearson correlation coefficient assuming a linear relationship.

Because the sites and quadrats were selected in places where *L. inundata* is known to occur, this species is certainly over-represented within the dataset. However, making the species "passive" did not change the result of the analysis and no down weighing was done in the results presented.

INDICATOR SPECIES ANALYSIS

The only environmental variable obtained in the field was percent bare soil, and the method of "bio-indication" is thus used to give an indication of the general habitat quality. The species indicator system of central Europe (Ellenberg *et al*. 1991), that has been calibrated to British conditions (Hill *et al*. 1999, 2000) was used to derive average bio-indicator scores for each quadrat. The extension of the Ellenberg indicator values to geographical areas outside central Europe has previously been successful, both in comparison of vegetation clusters and in connection with ordination (Diekmann & Lawesson 1999; Lawesson & Mark 2000).

For each quadrat a weighted average of the Ellenberg indicator values of each species for light (L), soil moisture (F), soil reaction (pH) (R), and nitrogen (N) was calculated with species cover as weights (Diekmann 1995). Note that the N-value probably indicates general soil fertility rather than availability of nitrogen. The median indicator value was used for each variable to characterise the habitats of *L. inundata* in the described communities and in England and Scotland, respectively. Differences were tested with the non-parametric Mann-Whitney test.

RESULTS

VEGETATION CLASSIFICATION

The entire dataset contained 89 quadrats from 10 sites with a total of 69 plant species. The TWINSPAN analysis resulted in four final clusters (Figure 2). The first division of the dataset separated the Scottish from the English quadrats. All quadrats from England were placed in one vegetation unit as the subsequent divisions had low eigenvalues. The Scottish quadrats were more heterogeneous and split up into three final clusters. In general, the Scottish quadrats contained more species (51 compared to 39 from England); some of the most common species included *Ranunculus flammula*, *Succisa pratensis*, *Lobelia dortmanna*, *Carex echinata*, *Drosera* × *obovata* and *Pellia epiphylla*. The quadrats from Loch Maree Islands were all different from the remaining Scottish quadrats and were further divided into two clusters, although containing only a few quadrats. The synoptic table list the species with a frequency >5% in at least one of the four final clusters or communities (Table 2).

1. *DROSERA INTERMEDIA–SPHAGNUM TENELLUM* COMMUNITY

This community was observed in the south of England and, besides *Lycopodiella,* it was characterised by the presence of *Rhynchospora alba*, *R. fusca*, *Campylopus introflexus* and *Drosera rotundifolia*. It was found in wet heath intermediate between wet hollows and the drier plateau, and had the (significantly) lowest indicator value for soil reaction and also a very low N-value, indicating that this habitat was strongly acidic and nutrient poor (Table 3).

2. *DROSERA ANGLICA–MYRICA GALE* COMMUNITY

This community was characterised by the presence of *Breutelia chrysocoma*, *Juncus conglomeratus*, *Pellia epiphylla*, *Pleurozia purpurea* and *Polygala serpyllifolia*. It was the most species-rich community studied, and occurred around lakes in sheltered areas allowing deposition of a thin layer of organic silt. The littoral zone was between 0·3 and 3 m wide or completely absent depending on the slope between the surrounding heath and the lake. Soil reaction was the only indicator value differing significantly from all the other communities, and with a median Ellenberg value of 3·00 the habitat of this community was mostly found on acidic soils.

3. *ELEOCHARIS MULTICAULIS–NARTHECIUM OSSIFRAGUM* COMMUNITY

Here a high frequency of *Eleocharis multicaulis*, *Carex viridula* ssp. *oedocarpa* and *C. panicea* was characteristic. Compared to the closely related *Drosera anglica–Myrica gale* community, fewer species were found, but this may partly be due to the low number of quadrats. The habitat was a sheltered inundation zone around lakes, as described for the previous community. This community was found on a (significantly) slightly more neutral substrate than the two previous, and the soil had the same low nutrient status as the *Drosera intermedia–Sphagnum tenellum* community.

TABLE 3. MEDIAN OF WEIGHTED AVERAGES OF ELLENBERG'S INDICATOR VALUES FOR THE FOUR COMMUNITIES, THE ENGLISH AND SCOTTISH SUBSETS AND THE ENTIRE DATASET

	Ecological indicator variables				
Vegetation unit	L	F	R	N	% BS
1	7·6	7·9	2·5	1·6	60
2	7·4	8·0	3·0	1·9	60
3	7·6	8·1	3·4	1·6	45
4	7·4	7·3	3·9	1·9	30
England	7·6	7·8	2·5	1·6	60
Scotland	7·4	8·0	3·1	1·9	50
total data set	7·5	7·9	2·8	1·7	55
Total range	7·1–8·0	7·0–8·7	2·0–4·0	1·2–2·1	5–95

The ecological variables are: light (L), soil moisture (F), soil reaction (R), soil fertility (N) and percent bare soil (BS).

TABLE 4. PEARSON CORRELATION COEFFICIENTS BETWEEN DCA AXES AND ELLENBERG'S INDICATOR VALUES AND PERCENTAGE BARE SOIL (% BS) AS EXPLANATORY VARIABLES

Data set	Variable	DCA axis 1		DCA axis 2		DCA axis 3		DCA axis 4	
Entire	Light	-0·190	n.s.	**-0·823**	***	**-0·823**	***	0·041	n.s.
	Moisture	-0·057	n.s.	0·577	***	-0·456	***	-0·054	n.s.
	Reaction	**0·857**	***	0·37	***	0·043	n.s.	0·032	n.s.
	Fertility	0·425	***	-0·124	n.s.	0·739	***	0·113	n.s.
	%BS	0·017	n.s.	-0·505	***	0·036	n.s.	**-0·226**	*
England	Light	**0·773**	***	-0·403	**	0·195	n.s.	-0·025	n.s.
	Moisture	0·691	***	0·025	n.s.	0·258	n.s.	-0·546	***
	Reaction	0·171	n.s.	0·399	**	0·415	**	**-0·643**	***
	Fertility	-0·738	***	**0·441**	**	0·005	n.s.	-0·153	n.s.
	%BS	-0·713	***	0·262	n.s.	**0·433**	**	-0·016	n.s.
Scotland	Light	0·342	*	**0·746**	***	**-0·328**	*	0·28	n.s.
	Moisture	-0·194	n.s.	0·727	***	0·035	n.s.	0·265	n.s.
	Reaction	**0·714**	***	-0·072	n.s.	-0·23	n.s.	-0·224	n.s.
	Fertility	-0·318	*	-0·635	***	-0·124	n.s.	**-0·511**	***
	%BS	-0·222	n.s.	0·169	n.s.	-0·253	n.s.	0·136	n.s.

Significance levels given as *** P<0·001; ** P<0·01; * P<0·05; ns P>0·05. The highest value for each axis and dataset is in bold type.

4. *HYDROCOTYLE VULGARIS–LEONTODON AUTUMNALIS* COMMUNITY

Littorella uniflora and a high abundance of *Carex nigra* were characteristic of this community, which was found only on the Loch Maree Islands. Here it occurred on soil several centimetres deep and inundated from winter to spring. In July *L. inundata* was found about 3 m from the shore line, growing well above water-level. The impression of the vegetation was more like a grassy sward and, in addition to the species mentioned in Table 2, the rare *Deschampsia setacea* was also growing here (P. Lusby, pers. comm.). The quadrats representing this community had (significantly) the lowest indicator value for moisture (F) and the highest for soil reaction (R) (Table 3). This suggests that the soil was drier and less acidic than in any of the other communities.

ORDINATION AND CORRELATION

The first axis extracted by DCA showed that a unimodal model described the species response curves well since the length of the axis is 3·4 SD. As the quadrats from England and Scotland occurred at opposite ends of the first axis it confirms that there were major differences in species composition between the two countries. The amount of variation explained by axes 2, 3 and 4 (Eigenvalues 0·24–0·22) was substantially lower than the first (EV=0·55), and the lengths of axes 2, 3 and 4 were also rather short (2–2·5 SD). These axes described collectively the pattern within England and Scotland, respectively, and separate analyses were therefore carried out for these regions, while only axis 1 was meaningful for the entire dataset. Correlation analysis revealed that Ellenberg's indicator value for reaction was responsible for most of the variation in species composition between the English and the Scottish quadrats (Table 4), but the value for nitrogen also contributed significantly to the underlying gradient of axis 1.

The DCA analysis for the English data produced overall a lower level of significance with lower eigenvalues (0·40–0·06) and shorter axes. It was difficult to see a pattern in the distribution of the quadrats in the output, and this suggests that all quadrats should be classified into one vegetation unit. Ordination of the Scottish dataset produced a first axis that explained about half of the variation in species composition (EV=0·54). The length of axis 1 was 2·9 SD and it mainly described the separation between quadrats 80–83 and the rest. The underlying gradient for this axis correlated best with the indicator value for soil reaction but light and soil fertility also contributed significantly (Table 4). The succeeding axes reflected gradients in the vegetation that had little significance since the eigenvalues were very low (EV=0·13–0·05).

The Ellenberg indicator values for soil reaction and soil fertility were the only variables with a significant ($P<0{\cdot}001$) difference between England and Scotland (Table 3). The weighted averages were also slightly different for light, but there were no significant difference in percentage bare soil cover or soil moisture between England and Scotland.

DISCUSSION

HABITAT CONDITIONS OF *LYCOPODIELLA INUNDATA*

This study shows that the habitats of *L. inundata* are clearly different between England and Scotland in some respects, but for other variables no difference between the two countries could be detected. In terms of soil reaction the English habitats are probably more acidic whereas the substratum in the Scottish habitats, surprisingly, could be close to neutral according to the indicator value of the species present. Soil reaction has been measured to be about pH 4·5 in a *L. inundata* population in England (Pickering & Wigston 1990). For the remaining three indicator values and percentage bare soil there were no significant differences between the two countries, and the habitats can be characterised as exposed sites with constantly moist, very infertile soil, with about 50% of bare soil. Pickering & Wigston (1990) found an increase in total nitrogen content in the soil immediately around *L. inundata* compared to the surroundings, and they suggested a causal relationship between *L. inundata* and *Drosera rotundifolia*, the latter supplying nitrogen leaking from its insectivorous activity. From the present survey such a relationship was not obvious, as *L. inundata* was just as frequently found without *Drosera* plants in its immediate vicinity. The species presumably survives the infertile site conditions by having a slow growth rate and perhaps in association with mycorrhiza.

COMMUNITY TYPES WITH *LYCOPODIELLA INUNDATA*

The NVC communities with highest similarity to the vegetation of the ten locations of this study are listed in Table 5. The *Drosera intermedia–Sphagnum tenellum* community resembles the *Erica tetralix–Sphagnum compactum* wet heath (M16). This is a community of the British lowlands and it is found on shallow, seasonally inundated peat too dry or too freely drained for the development of Sphagnetalia vegetation and too wet for Calluno–Ulicetalia heaths (Rodwell 1991). *L. inundata* is only mentioned in connection with the *Rhynchospora alba–Drosera intermedia* sub-community, but according to the present study the species is also found in the drier typical sub-community. The *Drosera intermedia–Sphagnum tenellum* community also resembles the Sphagno tenelli–Rhynchosporetum albae of continental NW-Europe and Scandinavia (Dierβen 1982), where *L. inundata* is characteristic of the wetter parts. It thus seems that this is a favoured vegetation for *L. inundata* throughout its European range.

For the Scottish quadrats the concordance with NVC units is ambiguous (see below). Different quadrats with the same similarity coefficients for different NVC units occurred at the same locality and, referring to the NVC community descriptions, both M16a and M17a are very unlikely to correspond to any of the recorded quadrats (Rodwell 1991). The *Scirpus cespitosus–Erica tetralix* wet heath, *Carex panicea* sub-community (M15a) is the best match to both the *Drosera anglica–Myrica gale* community and the *Eleocharis multicaulis–Narthecium ossifragum* community.

For the quadrats from Loch Maree the similarity coefficient is particularly low and the MATCH output for the site reveals a separation of the quadrats into two groups. The first group is a mixture of mire communities similar to M15a, whereas quadrats 73 and 79–83 best match the *Hypericum elodes–Potamogeton polygonifolius* soakway (M29). This community is characteristic of shallow pools in peats and peaty mineral soil with periodic inundation. Neither *Hypericum elodes* nor *Potamogeton polygonifolius* were seen during the survey, but many of the associated species mentioned in the description were found. The community is stated to occur on the beginning of a transition to truly aquatic vegetation in lakes, so it is likely that the *Hydrocotyle vulgaris–Leontodon autumnalis* community is at least related to this NVC community.

According to the continuum concept, a low similarity is to be expected for matching sampled vegetation stands with previous community descriptions (Økland 1990; Wilson & Chiarucci 2000). This theory views the vegetation community as an artificial unit, since species are believed to react to environmental heterogeneity on all scales creating a continuous gradient in vegetation

TABLE 5. RESULTS OF COMPARING THE STUDY QUADRATS FROM THE TEN LOCATIONS WITH THE NVC SYSTEM

Site no.	Best matching NVC community	Community code	Similarity coefficient (%)
I	*Erica tetralix–Sphagnum compactum* wet heath, typical sub-community	M16a	58·6
II	*Erica tetralix–Sphagnum compactum* wet heath, typical sub-community	M16a	63·6
III	*Erica tetralix–Sphagnum compactum* wet heath, typical sub-community	M16a	45·5
IV	*Erica tetralix–Sphagnum compactum* wet heath, *Rhynchospora alba–Drosera intermedia* sub-community	M16c	59·0
V	*Erica tetralix–Sphagnum compactum* wet heath, *Rhynchospora alba–Drosera intermedia* sub-community	M16c	63·0
VI	*Scirpus cespitosus–Erica tetralix* wet heath, *Carex panicea* sub-community	M15a	53·4
VII	*Erica tetralix–Sphagnum compactum* wet heath, typical sub-community	M16a	54·5
VIII	*Scirpus cespitosus–Erica tetralix* wet heath, *Carex panicea* sub-community	M15a	53·3
IX	*Scirpus cespitosus–Erica tetralix* wet heath, *Carex panicea* sub-community	M15a	44·9
X	*Scirpus cespitosus–Eriophorum vaginatum* blanket mire, *Drosera rotundifolia–Sphagnum* spp. sub-community	M17a	52·6

types. Using relevés to classify vegetation will thus always be a more-or-less inaccurate procedure depending on the degree of homogeneity of a particular stand of vegetation. Poor similarity between the Scottish quadrats and the NVC may thus be due to under-representation of Scottish sites in the NVC survey, where either a new community has been missed or some of the variation within the M15 is not covered.

ECOLOGY OF *LYCOPODIELLA INUNDATA*

Since all the sampled localities contain *L. inundata*, the range of indicator values for light, moisture, reaction and fertility can be used to model the niche of *L. inundata* in Britain. The estimated range for light and nitrogen was very narrow implying that *L. inundata* is intolerant of shading and occurs on very infertile soils. This corresponds well with the species being a poor competitor for light and a stress tolerator, in this case stress by lack of nutrients and high soil moisture. Regarding soil moisture and soil reaction the range is a little wider. From observations on the habitats in Britain it seems that they are all under water in winter and spring, but only moist in summer and a wide moisture amplitude is thus experienced every year. However, species often have differing ecological requirements across their range, and in Scandinavia *L. inundata* also grows in places which range from moist to dry during the year and which are protected by a cover of litter and mosses during winter (Øllgaard & Tind 1993).

Despite the described type of habitat being fairly common in Britain, *L. inundata* is decreasing. Øllgaard (1985) proposes a highly efficient spore dispersal for *L. inundata* and it seems that it is the establishing phase that is critical for the colonisation of new areas. Gametophyte development is reported from Denmark, where maturity was reached within a couple of years, and germination from dormant spores is reported in Britain (Stewart *et al*. 2000), though vegetative spread is considered most important in already established populations. We thus believe that certain micro-environmental factors are limiting the establishment of *L. inundata*, but more research is needed in order to determine exactly which factors. From this study light and soil fertility are the best candidates, but measurements at a smaller scale are needed to verify this. Pollutants in rain water have been suggested to have a negative effect on *L. inundata* (Stewart *et al*. 2000) and the deposition of nutrients over Europe is resulting in dramatic changes in heathland vegetation (Bobbink 1998; Berendse *et al*. 1993).

Lycopodiella inundata is the subject of conservation initiatives in Britain and Europe such as protection of habitat, management and restoration (Stewart *et al*. 2000). We would like to question the efficiency of these measures, as in our view it is doubtful whether a relatively ephemeral species such as *L. inundata* can be protected in this way. The overall factor important for the occurrence of this species is suitability of habitats. But as most heathland is semi-natural and drastic management is needed to continuously provide suitable habitat for *L. inundata* here, we suggest that focus is instead placed on protection of the natural habitat, which seems to be the margins of oligotrophic lakes. Management of heathland for *L. inundata* is for many reasons undesirable and could eventually destroy the natural habitat for other protected organisms.

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