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Succession of a degraded bog in NE Denmark over 164 years – monitoring one of the earliest restoration experiments

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Abstract

We present the results of a unique study of long-term succession in a former raised bog after intensive peat cutting. As probably one of the first restoration experiments the study site 'Gammelmose' (22 ha) in NE Zealand, Denmark, was in 1844 protected from any further human usage. Since then several surveys of water level, peat re-growth and vegetation change were carried out in 18 permanent plots. The vegetation data from 1861, 1885, 1963, 1981 and 2005 were analysed with DCA and correlated with selected environmental variables. The peat layer increased in thickness by <1 m within the period 1859–2005, and the bog surface became slightly convex; the water level was at 10–20 cm belowground in 2005. The vegetation developed from an open wetland with a number of fen species over a phase with locally dominant *Phragmites australis* to a half-open birch-pine forest with abundant *Sphagnum*-mosses. The increasing frequency of woody species was reflected by lower Ellenberg indicator values for light and soil moisture. The first DCA axis was correlated with succession time and frequency of woody species, and negatively with the two Ellenberg indicator values. The second DCA axis was also correlated with time and woody species, but negatively with Ellenberg values of soil nutrients and soil reaction. In the period 1861–2005, several fen species with relatively high demands for light and nutrients disappeared (e.g. *Peucedanum palustre, Stellaria palustris, Viola palustris*), while most bog species continued (e.g. *Andromeda polifolia, Vaccinium oxycoccos, V. uliginosum*), and new plant species – mainly naturalised from gardens – immigrated (e.g. *Spiraea alba* var. *latifolia, Picea glauca, Prunus padus*). In 2005, the vitality and growth of many trees in the bog looked reduced, and some of the taller individuals began to sink into the peat layer. Thus, in future the half-open bog forest may show some natural dynamics allowing survival of bog species in a mosaic of changing microhabitats.

Zusammenfassung: Sukzession eines abgetorften Hochmoores in Nordost-Dänemark über 164 Jahre – Monitoring eines der ältesten Renaturierungsexperimente

Wir stellen einen einzigartigen Datensatz vor zur unbeeinflussten Sukzession eines abgetorften Hochmoores in NO-Seeland, Dänemark. Das Untersuchungsgebiet ‚Gammelmose' (22 ha) wurde durch königliches Dekret 1844 unter Totalschutz gestellt und seit dieser Zeit mehrfach bezüglich Torfmächtigkeit, Wasserstand und Vegetation untersucht, letzteres in 18 Dauerflächen. Die Vegetationsdaten von 1861, 1885, 1963, 1981 und 2005 wurden mit einer DCA ausgewertet und mit ausgewählten Umweltvariablen korreliert. Die Torfmächtigkeit wuchs mit <1 m von 1859 bis 2005; die Mooroberfläche ist nun leicht konvex und der Wasserstand 10–20 cm unter Flur. Die Vegetation veränderte sich von einem gehölzfreien Feuchtgebiet mit einer Reihe von Niedermoorarten über eine Phase mit stellenweise dominantem *Phragmites australis* zu einem Birken-Kiefernwald mit hoher *Sphagnum*-Deckung in der Moosschicht. Die zunehmende Häufigkeit der Gehölze spiegelte sich in abnehmenden Ellenberg-Indikatorwerten für Licht und Bodenfeuchte wider. Die erste DCA-Achse war mit der Sukzessionszeit und der Häufigkeit der Gehölze korreliert sowie negativ mit den genannten Ellenberg-Werten. Die zweite DCA-Achse war ebenfalls mit der Zeit und dem Gehölzaufkommen korreliert, aber negativ mit den Ellenberg-Werten für Boden-Nährstoffe und -reaktion. Von 1861 bis 2005 verschwanden verschiedene Niedermoorarten mit relativ hohen Licht- und Nährstoffansprüchen (u. a. *Peucedanum palustre, Stellaria palustris, Viola palustris*), während einige Hochmoorarten aushielten (u. a. *Andromeda polifolia, Vaccinium oxycoccos, V. uliginosum*), und neue Arten – größtenteils verwildert aus Gärten – einwanderten (u. a. *Spiraea alba* var. *latifolia, Picea glauca, Prunus padus*). Die Vitalität und das Wachstum vieler Bäume waren 2005 reduziert, und besonders die großen Individuen begannen in die Torfdecke einzusinken. Zukünftig könnte sich ein halboffenes Waldmoor entwickeln, das aufgrund interner Dynamik das Überleben von Hochmoorarten in einem Mosaik wechselnder Kleinstandorte erlauben würde.

Keywords: autogenic succession, bog regeneration, fen-bog transition, peat layer, tree invasion, water table.

1. Introduction

Restoration ecology is a relatively recent discipline within vegetation science. It is fostered by an increasing understanding of ecosystem processes and vegetation dynamics, and it is necessary as a proactive way of landscape planning and species conservation in regions and sites where anthropogenic impacts have been particularly negative (VAN ANDEL & ARONSON 2012). Restoration of wetlands has been a focus for some decades (WHEELER & SHAW 1995), and although a number of successful examples exist on restoring of fens and bogs (EIGNER & SCHMATZLER 1980, GROOTJANS et al. 1998), the restoration of the later is still problematic due to inappropriate water levels and widespread atmospheric nitrogen deposition. A limitation for new restoration measures in degraded bogs is the lack of long-term data from historical surveys, and thus many projects are done on a trial and error basis without sufficient scientific background and with no monitoring of succession in permanent plots.

Raised bogs are the result of long-term autogenic succession in various forms of wetlands, and in NW Europe bogs were often formed in shallow post-glacial lakes where organic material gradually replaced the water body, and dynamic peat growth slowly raised the surface of the bog above the groundwater level (DIERßEN 1996, ELLENBERG & LEUSCHNER 2010). However, this succession also depends on allogenic factors, especially on a nutrient-poor landscape and a cool moist climate as recorded for the subatlantic climatic period since about 2500 BP. In the past centuries human interference, such as drainage, peat cutting and fertilisation, have had considerable negative effects on ecosystem properties and vegetation characteristics of bogs in NW Europe (DIERßEN 1996). More recently, studies have shown that bogs are changing worldwide, and especially invasion of woody species has been reported from Chile, Canada and several parts of Europe (LINDERHOLM & LEINE 2004, LACHANCE et al. 2005). An appropriate hydrological regime is the main precondition for this ombrotrophic ecosystem (BRIDGHAM & RICHARDSON 1993), and decreased precipitation or increased temperatures have negative effects on bogs (WELTZIN et al. 1993). Climate change has therefore been suggested as a factor facilitating tree invasion, although several studies have demonstrated that anthropogenic impacts such as draining and peat cutting are still most significant (PFADENHAUER & KLÖTZLI 1996, LINDERHOLM & LEINE 2004).

Most bogs in Europe were heavily exploited during the past two centuries, and many different actions have been applied to save the remaining near-natural bogs as well as to restore fragmented and degraded ones (PFADENHAUER & KLÖTZLI 1996). Today bog restoration is even required in areas protected, e.g. as ‘habitat area’ according to the EEC Habitat Directive (EEC 1992). Various methods have been developed for bog restoration, but still it is a difficult and expensive task to restore near-natural conditions (GROOTJANS et al. 2006). Could free secondary succession be a successful option for bog restoration as suggested by LAVOIE et al. (2003)?

Here we present a unique study of a cutover bog in NE Denmark where vegetation development and site conditions have been monitored since 1844, which is far longer than most other studies, for example HANSEN & MADSEN (1984) in SW Jutland (Gråbjerg Mose, 1957–1981) or 30 years of vegetation change described for valley mires in Suffolk (FOJT & HARDING 1995). From the present study we can learn what might happen if a degraded bog is left to regenerate by itself.

The objectives of the study were (1) to describe historical changes in bog surface, peat layer and hydrological conditions, (2) to analyse a long-term set of vegetation data based on permanent plots, and (3) to discuss the results with respect to recommendations for future bog restoration projects.

2. Study site and methods

2.1. Bogs in Denmark

Southern Scandinavia is situated in the main zone of raised bogs in Europe (DIERßEN 1996). In NE Denmark the last glaciation created a diverse landscape relief with numerous small depressions (VESTERGAARD 2007). Here the humid and cool climate facilitated the development of a diversity of swamps, fens and bogs, but industrialisation and agricultural intensification have markedly reduced wetlands in this part of Denmark. Peat was cut extensively in the past centuries, particularly during World Wars I and II, and today most bogs are drained, cultivated or surrounded by urban expansion (FRITZBØGER 2004). As a result, the remaining bogs are isolated and affected by various anthropogenic impacts such as lowered water table, increased disturbance and eutrophication. In the early 20th century Denmark was still covered by 20–25% wetlands, but these had decreased to about 4.5% by the end of the 20th century (VESTERGAARD 2007). As a consequence, raised bogs have become very rare in Denmark, and there are today probably only 20 near-natural bogs left in the country, compared with 668 bogs in 1919.

2.2. Study site

The study site 'Gammelmose' is a former raised bog, situated about 10 km north of the centre of Copenhagen, the capital of Denmark (+55°75′43.85″, +12°50′38.50″, 28 m a.s.l.; Fig. 1). It developed in a circular depression (most likely a kettle hole) within sandy moraines from the last glaciation. Its size (22 ha) is quite modest, but still larger than most fens and bogs in NE Zealand, where the average area was 1.5 ha for about 450 of these fens and bogs in the 19th century (KOCK-JENSEN 2009). The climate in that region is temperate and subatlantic with relatively moist cool summer and mild winter. The mean annual temperature is 8.0 °C, annual precipitation 613 mm (1961–1990; DANMARKS METEOROLOGISKE INSTITUT 2009). No groundwater-abstraction facilities are known from the surroundings of Gammelmose.

The area north of Copenhagen was rich in bogs before the 19th century, but due to marked population growth and urbanisation most have been drained and used for urban expansion (KOCK-JENSEN 2009). In the early 19th century the population and industry in Copenhagen were growing which caused an increasing demand for fuel. Since the country was already more or less deforested at that time (VESTERGAARD 2007), peat was the most important energy source but also disappearing fast. The study site Gammelmose, for example, had been exploited intensively in most parts leaving only a relatively thin layer of peat and a system of drainage ditches in 1844. At that time the principles in regeneration of bog ecosystems were more or less unknown (VAUPELL 1862). Thus, as a kind of early restoration project King Christian 8th decided to protect Gammelmose by law from any human usage, including drainage, peat cutting, berry collection or animal grazing (NIELSEN 1970). The early abandonment of grazing is remarkable, because grazing of wetlands has a long tradition in Denmark. This strict protection was confirmed by modern nature conservation laws in the 20th century. Since then, scientists have studied the development of the bog to detect long-term changes in peat thickness, water level and vegetation.

We know of no other study on free succession in a raised bog left untouched for more than 150 years. However, the surroundings of Gammelmose have changed markedly, from an open agricultural landscape to dense suburban housing and industry. The bog is today surrounded by gardens and roads, and thus completely isolated from other near-natural habitats. This has some direct and indirect effects on the bog ecosystem, for example diffuse drainage and a high number of naturalised ornamental species from near-by gardens (KOLLMANN et al. 2006). First results on vegetation change in Gammelmose were published by HANSEN et al. (1978), albeit without statistical analyses.

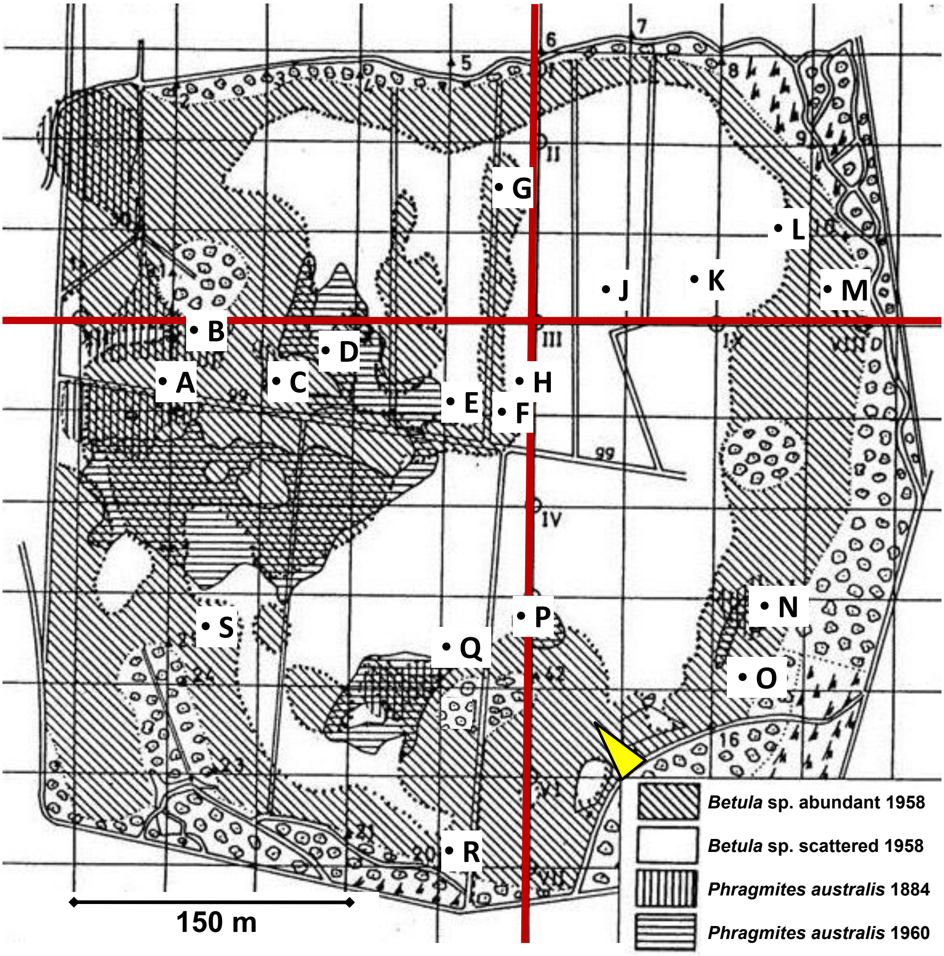

Fig. 1: Map of the study site 'Gammelmose' in 1958/60 (NE Zealand, Denmark; modified after Hansen et al. 1978). At that time the regenerating bog was already more or less covered by a sparse birch forest, and *Phragmites australis* had markedly increased in abundance compared to 1884. Around the bog and on three 'islands' with mineral soil a mixed hardwood forest had developed (*Fagus sylvatica, Quercus robur, Betula pubescens, Acer pseudoplatanus*). The red lines indicate two transects used for surveying peat depth and water level (I–XVI); the letters (A–S) represent the 18 permanent plots surveyed since 1843. Double lines within the bog are former drainage ditches, or foot paths around the bog. The yellow arrow indicates the direction of the historical photos shown in Fig. 2.

Abb. 1: Karte des Untersuchungsgebietes ‚Gammelmose' aus den Jahren 1958/60 (NO-Seeland, Dänemark; verändert nach Hansen et al. 1978). Ende der 1950er Jahre war das regenerierende Hochmoor schon weitgehend von einem schütteren Birkenwald besiedelt, während die Deckung von *Phragmites australis* deutlich vergrößert war, verglichen mit 1884. Am Rand des Moores und auf ‚Inseln' mit Mineralboden stockte Mischwald (*Fagus sylvatica, Quercus robur, Betula pubescens, Acer pseudoplatanus*). In Rot die beiden Transekte, entlang derer Torfmächtigkeit und Wasserstand gemessen wurden (I–XVI); die Buchstaben (A–S) bezeichnen die 18 Dauerflächen, in denen die Moorvegetation seit 1843 untersucht wurde. Doppellinien im Moor sind ehemalige Dränagegräben; außerhalb des Moores Fußwege. Der gelbe Pfeil zeigt die Blickrichtung der drei historischen Photos der Abb. 2 an.

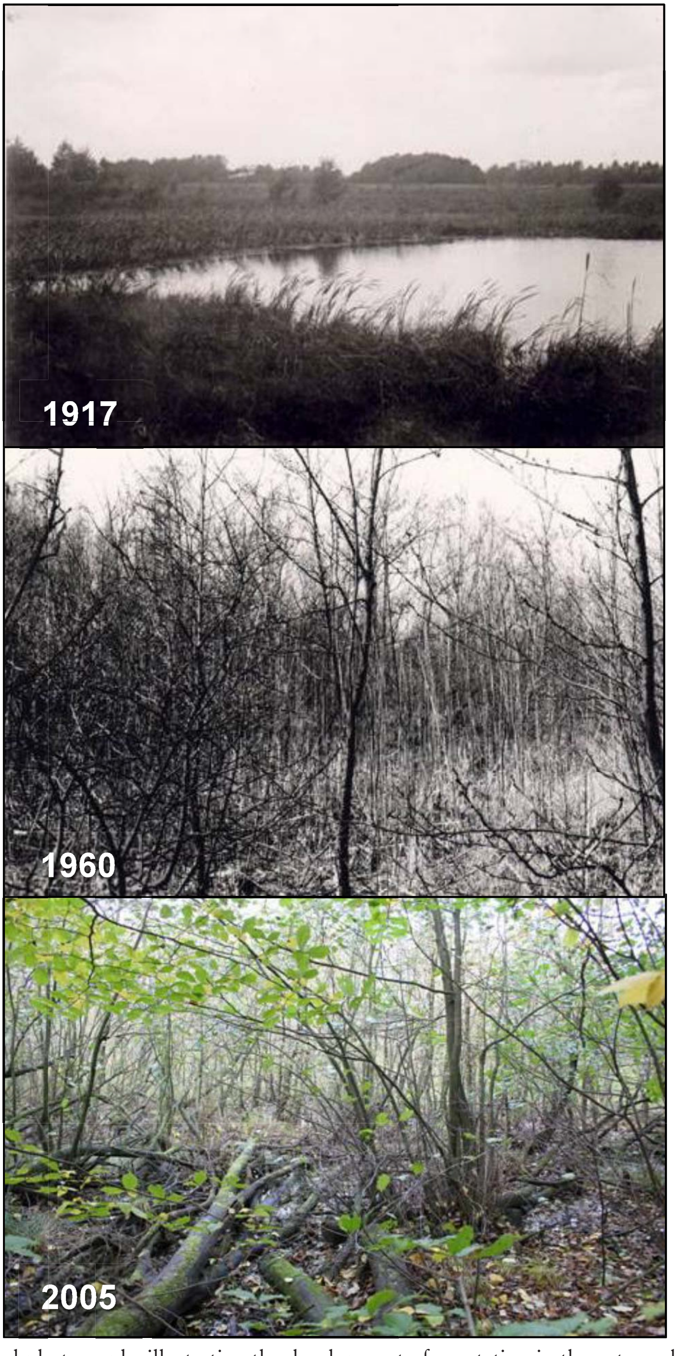

Fig. 2: Historical photographs illustrating the development of vegetation in the cutover bog 'Gammelmose' in the period 1917–2005. They are taken from the same point at the former lagg zone of the bog (cf. Fig. 1) which now has developed into a near-natural *Alnus glutinosa* forest.

Abb. 2: Historische Photographien, die die Vegetationsentwicklung des abgetorften ‚Gammelmose' von 1917 bis 2005 zeigen. Die Photos sind vom südöstlichen Moorrand aus aufgenommen, mit der Lagg-Zone im Vordergrund (s. Abb. 1), die sich in jüngster Zeit zu einem naturnahen Erlenwald entwickelt hat.

2.3. Measuring peat thickness and water table

The original objective with the protection of Gammelmosen was to study the regeneration of peat, and thus peat cores were measured along two transects crossing the bog from N–S and E–W in 1859, 1971 and 2005 (Fig. 1). However, the surveys followed not precisely the same transects, and there were some differences in peat classification methods (HANSEN et al. 1978). Thus, the results cannot be statistically compared.

In 1970 and 2005, the height of the water table was followed by monthly measurements for one year. For this purpose perforated plastic pipes with 4 cm diameter were established down to the mineral soil, and the bog surface was levelled relative to a standard outside Gammelmose. The difference in water table between each month and the annual averages 2005 were compared with HANSEN et al. (1978).

2.4. Vegetation monitoring and analysis

In 1844, 18 circular plots with a radius of 6 m (113 m^2) were installed within Gammelmose and permanently labelled with thick oak poles (Fig. 1). The location of the plots was haphazardly chosen covering all major parts of the bog. In the permanent plots the vegetation was registered six times (1844, 1861, 1885, 1963, 1981, 2005); coverage of vascular plants was recorded on a percentage scale, while the historical records on mosses were less reliable and thus could not be included in the analyses. However, a detailed survey of mosses was done in 2005, with six systematically placed frequency frames of (25 grid cells per frame) in each of the 18 permanent plots. Tree age and growth were investigated in May 2006 with increment corers in a number of systematically chosen individuals of *Betula pubescens* and *Pinus sylvestris* (details in ROELSGAARD 2006). The presence of naturalised ornamentals was surveyed along 10-m spaced transects in June 2005 (see KOLLMANN et al. 2006).

The historical and the recent vegetation data were entered into the program TURBOVEG (HENNEKENS & SCHAMINEE 2001); nomenclature followed OBERDORFER (2001) for vascular plants and FRAHM & FREY (2004) for mosses. Ellenberg indicator values were calculated as estimators for soil reaction (R), moisture (F), nutrient content (N) and light (L) (ELLENBERG et al. 1991). To study the change in vegetation composition, detrended correspondence analysis (MCCUNE & MEFFORD 1999) was performed on the 18 plots from all surveys, and the main coenoclines were extracted and represented as axes which were correlated with time, frequency of woody species, species numbers and Ellenberg indicator values (Spearman rank correlation).

3. Results

3.1. Changes in topographic and hydrological conditions

While in 1959 large parts of the bog were covered by water with a thin floating *Sphagnum* layer and some undisturbed peat left at greater depth, in 2005 all water bodies were filled with peat and the old drainage channels were hardly visible any longer (Fig. 2). The maximum peat depth in 1859 was 3.5 m, while in 2005 it was 4.5 m. However, in most parts of the two transects peat depth was only 1–2 m, and here little peat increment or even a slight reduction in the peat layer were observed (Fig. 3).

Looking at the macro- as well as the micro-topography of the bog (Fig. 4) the surface became slightly convex in 1971 and 2005 as characteristic for a raised bog. The micro-topography was, however, not typical for a raised bog since few hummocks existed in 2005, mostly formed by *Sphagnum palustre*, and hollows were mostly found around trees sunken into the peat, thus creating small water holes around the trunks. The dominating mosses *S. fallax* and *S. fimbriatum* both tended to form a rather flat micro-relief.

In 2005, the water table followed roughly the bog surface at a depth of 10–20 cm, although there were some wetter parts in the bog margin and a slightly drier bog centre, a difference which was most marked in spring (Fig. 4). The wettest month in 2005 was April and the driest July. At no time in that particular year the water table was more than 70 cm below the bog surface, and the average distance was 16.9 cm.

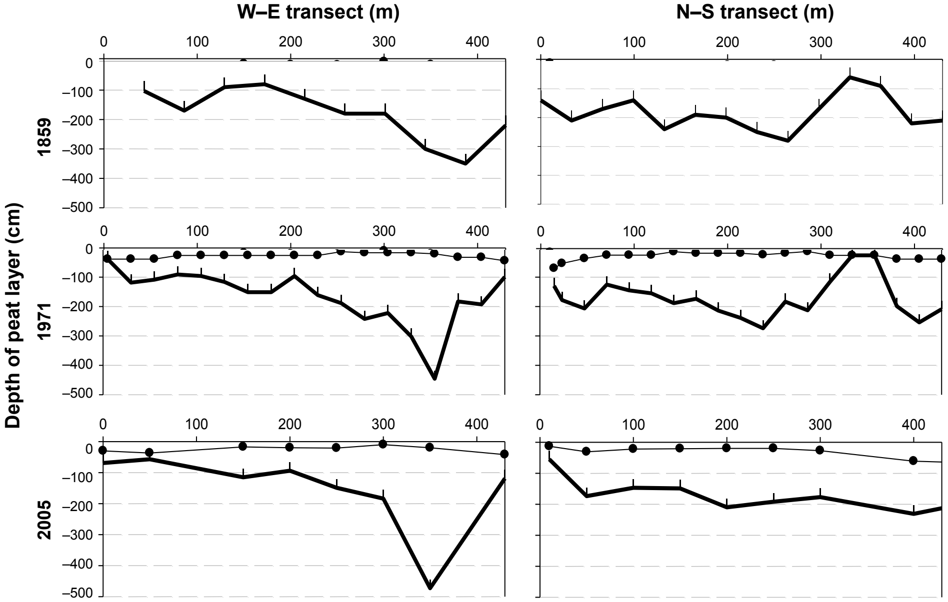

Fig. 3: Depth of the peat layer (bold line) of the study site 'Gammelmose' in the years 1859, 1971 and 2005. For 1971 and 2005 depth is indicated in relation to the bog surface (dotted line), while for 1859 the bog surface was set to zero. In 2005, the island with mineral soil on the southern part of the N–S transect was not surveyed.

Abb. 3: Torfmächtigkeit (fette Linie) des ‚Gammelmose' in den Jahren 1859, 1971 und 2005. Für 1971 und 2005 ist die Tiefe angegeben im Verhältnis zur Mooroberfläche (punktierte Linie), während für 1859 die Mooroberfläche gleich Null gesetzt wurde. Die Mineralbodeninsel im südlichen Teil des N–S-Transektes wurde 2005 nicht untersucht.

3.2. Vegetation change

There was a clear development in the vegetation of the regenerating bog over the 164 years of the study. The number of woody species per plot (without chamaephytes) significantly increased during that time period (Fig. 5), while light intensity and soil moisture, as calculated from the Ellenberg indicator values, decreased. The total number of species in the permanent plots fluctuated between 18 and 50, with no clear trend over the five survey periods.

In the DCA analysis time of succession had the highest correlation with ordination axis one (Fig. 6, Table 1). Synchronous to time the number of woody species (and the total number of species) per plot were also negatively correlated with the first DCA axis, while there was no corresponding correlation with the number of herbaceous species and dwarf shrubs. The mean Ellenberg indicator values for light and soil moisture were positively correlated with this axis, and so did the Ellenberg indicators for soil nutrients and soil reaction, albeit less significant than with the second DCA axis. The latter mainly separated the more nutrient-rich plots with a higher pH and higher numbers of herbaceous species from the more acidic plots, which were also experiencing less light. Focusing at the 2005 survey shows that the vegetation transformed into a forest bog, divided in an acidic and nutrient-poor part and lightly more nutrient-rich parts. The latter plots (top of DCA axis 2) were close to the lagg zone where mineral soil and groundwater were available, and where leaves from *Alnus glutinosa* added some extra nutrients to the poor *Sphagnum* blanket.

Species composition followed the change of the local environment with time (Table 2), while especially the woody species influenced the abiotic conditions. After drainage of the bog and removal of the original peat layer in the early 19th century, trees from the surround-

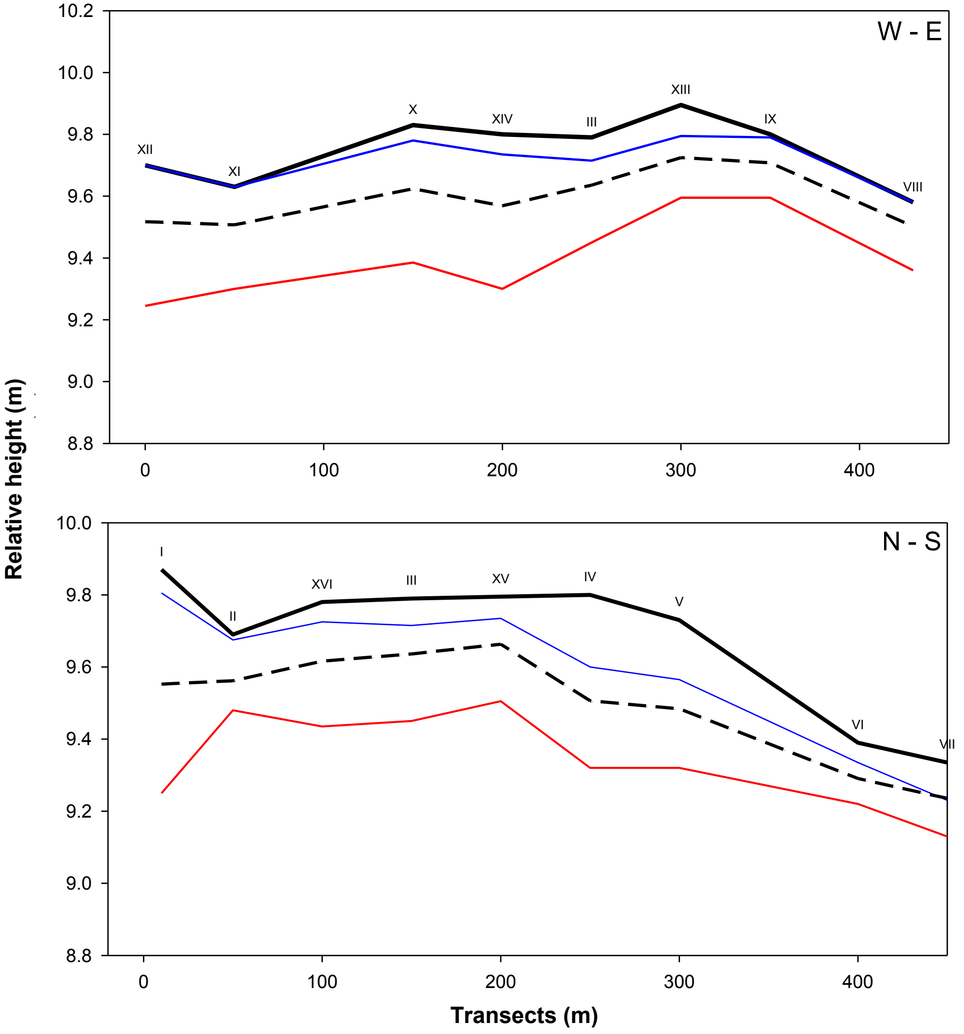

Fig. 4: Water level measured over one year along two transects crossing the regenerating bog 'Gammelmose', including the sites used for measurements (Roman numbers in Fig. 1). The thick line shows the bog surface, the broken line the mean water level for 2005, while the blue and red lines are the water level in April and July 2005, respectively.

Abb. 4: Wasserstand des regenerierenden Moors ‚Gammelmose' entlang zweier Transekte; die römischen Ziffern weisen auf die in Abb. 1 dargestellten Untersuchungspunkte hin. Die durchgezogene schwarze Linie entspricht der Mooroberfläche, die gestrichelte Linie dem mittleren Wasserstand im Jahre 2005, und die blaue und rote Linie den Verhältnissen im April und Juli 2005.

ing forest began to colonise the regenerating bog. There were probably also some facilitating effects of the drainage ditches, diffuse atmospheric nutrient input and garden plantings around Gammelmose. An overview of this succession 1861–2005 can be seen in Fig. 7 showing the species distribution in the ordination space. Some specialists with high light demands became extinct (e.g. *Drosera rotundifolia*, *Equisetum fluviatile*, *Utricularia vulgaris* agg.), while others spread into the bog during the last survey period (1981–2005; e.g. *Acer pseudoplatanus*, *Fraxinus excelsior*, *Spiraea alba* var. *latifolia*). In 2005, species with higher nutrient demands were restricted to the marginal parts of the bog (*Calla palustris*, *Eriophorum angustifolium*, *Menyanthes trifoliata*, *Molinia caerulea*, *Phragmites australis*). In general,

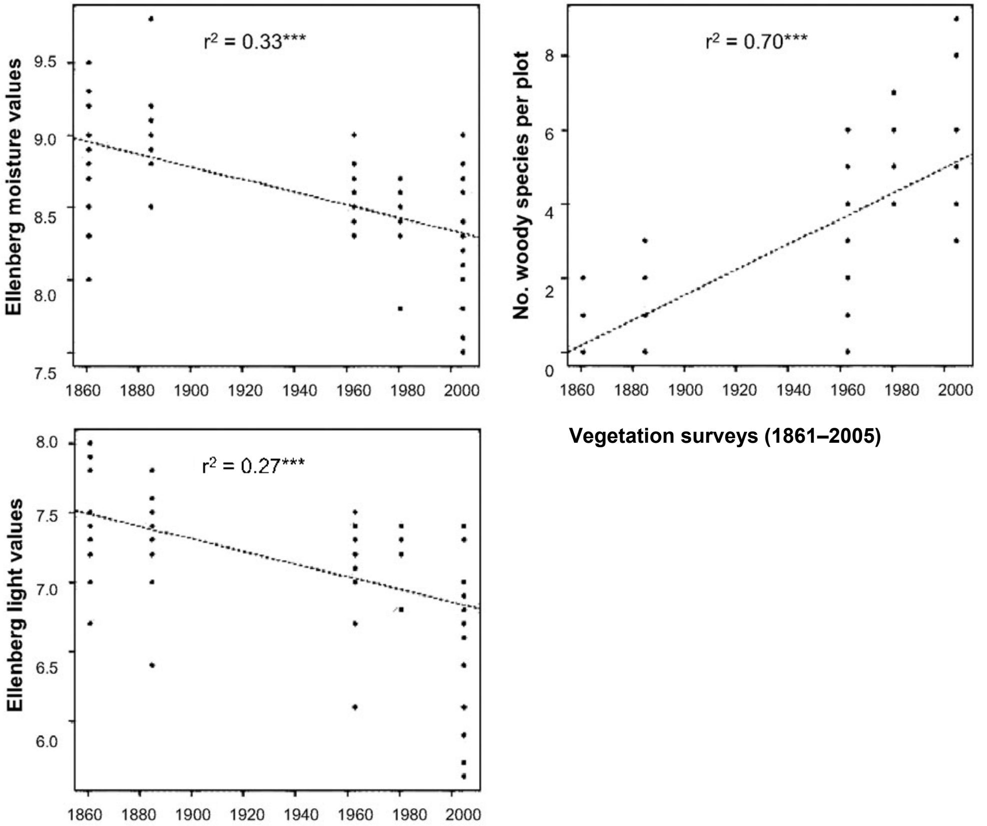

Fig. 5: Development of site conditions in the regenerating bog 'Gammelmose' during the survey period (1861–2005), as estimated by the number of woody species in 18 permanent plots, and mean Ellenberg indicator values for soil moisture and light (linear regressions, n = 74, *** P < 0.001).

Abb. 5: Entwicklung der Standortsverhältnisse in dem regenerierenden Moor ‚Gammelmose' von 1861 bis 2005 anhand von Angaben zur Gehölzartenzahl in den 18 Dauerflächen sowie mittleren Ellenberg-Zeigerwerten für Bodenfeuchte und Licht (lineare Regression, n = 74, *** P < 0.001).

species typical for open and rather wet conditions disappeared and more shade-tolerant plants and woody species established, while the ground vegetation in 2005 still was dominated by mosses and dwarf shrubs of the Ericaceae (mainly *Andromeda polifolia, Calluna vulgaris*, *Vaccinium oxycoccus* and *V. uliginosum*).

The survey of mosses in 2005 revealed that *Sphagnum fallax* was the most common species with a mean frequency of 13.9% within 25 grid cells of the 0.25-m^2 frames, followed by *Aulacomnium palustre* (2.9%; Table 3). Comparing the previous survey period (Hansen et al. 1978) with the 2005 results some characteristic mosses of raised bogs had disappeared (e.g. *Sphagnum magellanicum*, *S. papillosum* and *S. teres*) as well as species typical for acid fens, such as *Drepanocladus aduncus* and *D. fluitans*. However, the field layer of the bog was still largely covered by mosses, and in particular by *Sphagnum* spp. The more shade-tolerant *S. fallax* and *S. fimbriatum* were dominating with patches of *S. palustre* and *S. squarrosum* in between, and also *Polytrichum commune* and *P. strictum* increased in the drier parts.

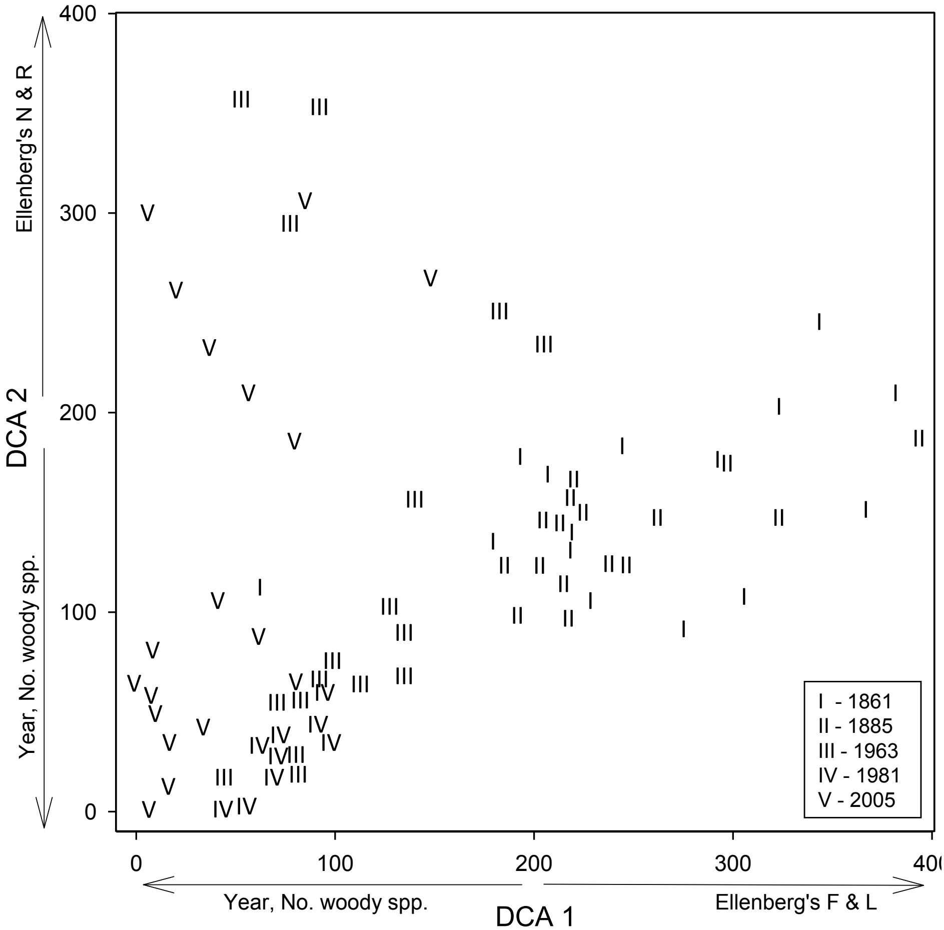

Fig. 6: DCA ordination plot of the vegetation development in 18 plots in the regenerating bog 'Gammelmose' over five surveys (Roman numbers). The explanatory factors with highest correlation to the axes are indicated with arrows showing the direction of the correlation (cf. Table 1).

Abb. 6: DCA-Ordinationsplot der Vegetationsentwicklung auf 18 Dauerflächen des regenerierenden Moores ‚Gammelmose' von 1861 bis 2005 (römische Ziffern). Die erklärenden Variablen mit stärkster Korrelation mit den Achsen sind angegeben (statistische Ergebnisse in Tabelle 1).

3.3. Tree establishment and exotic plant invasion

In 2005, *Betula pubescens* trees were evenly distributed all over the study site, while *Pinus sylvestris* was most common in the centre of the bog. The age of the *Betula pubescens* trees was 26–80 years (n = 488). *Pinus sylvestris* trees were just about 35 years, and the oldest individuals were 40 years (n = 106). There was a clear indication for poor tree growth in most parts of the bog; several trees were thrown over or sunken into the wet peat layer, and no seedlings or young saplings were observed (J. KOLLMANN, unpubl. data).

In total 29 species non-native to Denmark were recorded in Gammelmose, with three dispersal syndromes: Most trees were wind-dispersed, the shrubs bird-dispersed, and bulbous and corm plants were probably introduced as garden waste from surrounding housing. Most of the introduced species were found in the forest on mineral soil, while the two *Spiraea* species were clonally invading from the lagg zone, locally out-competing most other species.

Table 1: Spearman correlation between the main DCA axes and ecological explanatory factors in the regenerating bog (only significant correlations are shown).

Tabelle 1: Spearman-Korrelation zwischen den DCA-Hauptachsen und ausgewählten ökologischen Variablen des regenerierenden Moores (nur signifikante Korrelationen).

	DCA 1		DCA 2	
Year	–0.84	<0.0001	–0.31	0.007
No. woody spp.	–0.76	<0.0001	–0.31	0.007
Ellenberg F	0.66	<0.0001		
Ellenberg L	0.43	0.0001	–0.25	0.03
Ellenberg N	0.36	0.002	0.84	<0.0001
No. spp.	–0.29	0.013		
Ellenberg R	0.24	0.049	0.79	<0.0001
No. herb spp.			0.24	0.041

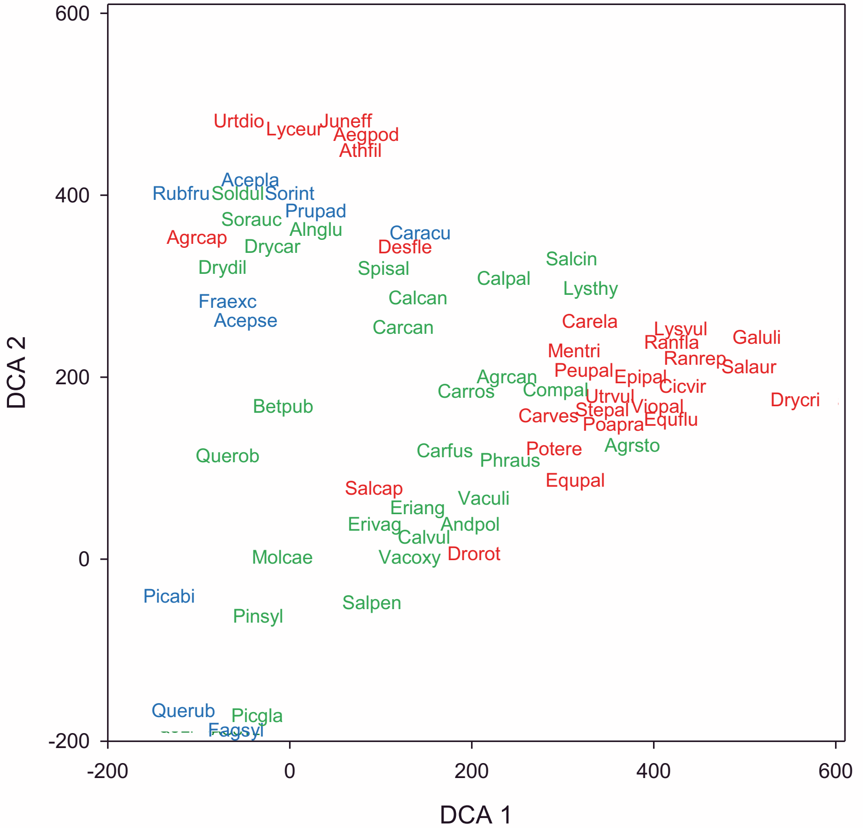

Fig. 7: DCA ordination plot showing plant species composition in the regenerating bog 'Gammelmose'. Red species were extinct 1963, 1981 and/or 2005, blue species were new in 2005, all other species green. Species are abbreviated with the first three letters from genus name and species epithet; see Table 2 for full species names.

Abb. 7: DCA-Ordinationsplot der Artenzusammensetzung des regenerierenden Moores ‚Gammelmose' 1861–2005. Arten, die 1963, 1981 und/oder 2005 ausgestorben waren, in Rot, ‚blaue' Arten erstmals 2005 gefunden, alle anderen Arten grün. Als Abkürzung wurden die drei Anfangsbuchstaben der wissenschaftlichen Artnamen verwendet (alle Arten sind in Tabelle 2 aufgeführt).

Table 2: List of vascular plants from six surveys in the regenerating bog 'Gammelmose' (* woody species without dwarf shrubs). Presence is given as percentage frequency in 18 permanent plots of 113 m^2, respectively. In 1844 only presence-absence within the plots was recorded (0, +); in 1861 and 1885 also species presence outside the plots was investigated (+). These data were not included in the ordination analysis.

Tabelle 2: Liste aller Gefäßpflanzen von sechs Aufnahmen des regenerierenden Moores ‚Gammelmose' (* Gehölze ohne Zwergsträucher). Angegeben ist die prozentuale Frequenz in 18 Dauerflächen von jeweils 113 m^2. Für 1844 liegen nur Präsenz/Absenzdaten vor (0, +); 1861 und 1885 wurde auch das Vorkommen der Arten außerhalb der Dauerflächen notiert (+). Diese Daten sind nicht in die Ordinationsanalyse eingegangen.

Species	**1844**	**1861**	**1885**	**1963**	**1981**	**2005**
Total no. spp. in plots	40	50	75	38	18	38
*Acer platanoides**	.	.	.	.	.	6
*Acer pseudoplatanus**	.	.	.	.	.	28
Achillea ptarmica	.	.	+	.	.	.
Aegopodium podagraria	.	.	.	6	.	.
Agrostis canina	.	+	31	18	.	6
Agrostis capillaris	.	7	.	.	.	.
Agrostis stolonifera	.	33	13	.	.	.
Alisma plantago-aquatica	.	.	+	.	.	.
*Alnus glutinosa**	.	.	.	18	.	22
Alopecurus geniculatus	.	.	+	.	.	.
Andromeda polifolia	.	7	6	.	13	6
Athyrium filix-femina	.	.	.	6	.	.
*Betula pubescens**,#	.	+	6	100	100	100
Calamagrostis canescens	+	20	25	65	.	28
Calla palustris	+	33	31	12	.	28
Calluna vulgaris	+	27	38	53	100	39
Cardamine pratensis	.	.	+	.	.	.
Carex acutiformis	.	.	.	.	.	11
Carex canescens	+	13	25	29	.	33
Carex disticha	.	.	+	.	.	.
Carex elata	.	.	6	6	.	.
Carex fusca	+	33	31	29	38	50
Carex rostrata	+	27	38	29	13	22
Carex vesicaria	+	13	+	.	.	.
Cicuta virosa	+	+	19	.	.	.
Cirsium palustre	.	.	+	.	.	.
Comarum palustre	+	60	50	29	.	6
Dactylorhiza incarnata	.	.	+	.	.	.
Dactylorhiza majalis	.	.	+	.	.	.
Deschampsia cespitosa	.	.	+	.	.	.
Deschampsia flexuosa	+	+	+	12	.	.
Drosera rotundifolia	+	7	25	29	25	.
Dryopteris carthusiana	+	+	+	6	.	28
Dryopteris cristata	+	.	6	.	.	.

Species	**1844**	**1861**	**1885**	**1963**	**1981**	**2005**
Total no. spp. in plots	40	50	75	38	18	38
Dryopteris dilatata	.	.	.	6	.	33
Elymus repens	.	.	+	.	.	.
Empetrum nigrum	.	.	+	.	.	.
Epilobium palustre	.	+	44	.	.	.
Equisetum fluviatile	+	40	44	.	.	.
Eriophorum angustifolium	+	40	56	59	100	61
Eriophorum gracile	.	+	+	.	.	.
Eriophorum vaginatum	+	13	75	65	100	78
*Fagus sylvatica**	.	.	.	.	13	22
*Fraxinus excelsior**	.	.	.	.	.	33
Galium palustre	.	.	+	.	.	.
Galium uliginosum	+	7	6	.	.	.
Galium verum	.	.	+	.	.	.
Glyceria fluitans	.	.	+	.	.	.
Glyceria maxima	.	.	+	.	.	.
Gnaphalium uliginosum	.	.	+	.	.	.
Hammarbya paludosa	.	.	+	.	.	.
Hottonia palustris	.	.	+	.	.	.
Hydrocharis morsus-ranae	+	+	+	.	.	.
Hydrocotyle vulgaris	.	+	+	.	.	.
Iris pseudacorus	.	.	+	.	.	.
Juncus articulatus	.	.	+	.	.	.
Juncus bufonius	.	.	+	.	.	.
Juncus effusus	+	20	+	12	13	.
Lemna minor	.	.	+	.	.	.
Lemna trisulca	.	.	+	.	.	.
Luzula multiflora	+	+	+	.	.	.
Lychnis flos-cuculi	.	.	+	.	.	.
Lycopus europaeus	+	+	+	12	.	.
Lysimachia thyrsiflora	+	13	25	24	.	11
Lysimachia vulgaris	.	+	6	.	.	.
Lythrum salicaria	.	+	+	.	.	.
Mentha aquatica	+	.	+	.	.	.
Menyanthes trifoliata	+	13	19	12	.	.
Molinia caerulea	+	13	6	53	88	67
Myosotis laxa	.	.	+	.	.	.
Myosotis palustris	.	.	+	.	.	.
Peucedanum palustre	+	40	88	12	.	.
Phragmites australis	+	13	19	18	25	28
Phalaris arundinacea	.	.	+	.	.	.
*Picea abies**	.	.	.	.	.	6
*Picea glauca**	.	.	.	6	13	6

Species	1844	1861	1885	1963	1981	2005
Total no. spp. in plots	40	50	75	38	18	38
*Pinus sylvestris**	.	.	.	24	88	67
Poa pratensis	.	.	19	.	.	.
Potamogeton natans	+	+	.	.	.	.
Potentilla erecta	+	+	6	.	.	.
*Prunus padus**	.	.	.	.	.	6
*Quercus robur**	.	.	.	29	88	100
*Quercus rubra**	.	.	.	.	.	6
Ranunculus flammula	.	.	6	.	.	.
Ranunculus lingua	+	.	.	.	.	.
Ranunculus reptans	.	.	.	6	.	.
Rubus fruticosus agg.*	.	.	.	.	.	6
*Rubus idaeus**	+	.	.	.	.	.
Rumex acetosella	.	+	.	.	.	.
*Salix aurita**	+	7	13	.	.	.
*Salix caprea**	.	.	.	6	.	.
*Salix cinerea**	+	7	6	.	.	11
*Salix pentandra**	.	.	.	6	13	6
Scheuchzeria palustris	.	+	.	.	.	.
Solanum dulcamara	.	.	.	18	.	17
*Sorbus aucuparia**	.	.	.	6	.	22
*Sorbus intermedia**	.	.	.	.	.	11
*Spiraea salicifolia**	.	+	.	24	.	.
Spiraea alba var. *latifolia**	.	.	.	.	.	17
Stellaria palustris	+	+	6	.	.	.
Typha latifolia	+	+	.	.	.	.
Urtica dioica	.	.	.	6	.	.
Utricularia minor	+	+	.	.	.	.
Utricularia vulgaris agg.	.	+	6	.	.	.
Vaccinium oxycoccos	+	13	75	65	100	56
Vaccinium uliginosum	+	7	6	6	25	11
Veronica scutellata	+	+	.	.	.	.
Viola palustris	+	+	44	.	.	.

#At least partly hybrids with *Betula pendula.*

Table 3: Complete moss survey of the regenerating bog 'Gammelmose' in 2005. Average frequency is given for species occurring in 108 random frames; six frequency frames of 0.25 m^2 (25 grid cells per frame) in each of 18 permanent plots. Also species presence outside the plots was investigated (+).

Tabelle 3: Erhebung der Moosflora des regenerierenden Moores ‚Gammelmose' im Jahr 2005. Angegeben ist die mittlere Frequenz in 108 zufälligen Probeflächen; sechs 0.25 m^2-Probeflächen mit jeweils 25 Teilflächen in jeder der 18 Dauerflächen.

Species	**Frequency in plots**
Atrichum undulatum	+
Aulacomnium androgynum	+
Aulacomnium palustre	2.9
Brachythecium rutabulum	0.6
Brachythecium velutinum	<0.1
Calliergon cordifolium	+
Calliergon stramineum	0.6
Calliergonella cuspidata	+
Campylopus introflexus	<0.1
Dicranella heteromalla	0.1
Dicranoweisia cirrata	+
Dicranum bonjeanii	0.3
Dicranum majus	+
Dicranum polysetum	+
Dicranum scoparium	0.1
Eurhynchium praelongum	0.1
Homalothecium sericeum	+
Hylocomium splendens	0.1
Hypnum cupressiforme	+
Orthodontium lineare	+
Plagiomnium ellipticum	+
Plagiomnium undulatum	+
Plagiothecium denticulatum	+
Plagiothecium laetum	+
Pleurozium schreberi	+
Pohlia nutans	+
Polytrichum commune	2.1
Polytrichum juniperinum	+
Polytrichum strictum	0.3
Rhizomnium punctatum	0.3
Sphagnum angustifolium	+
Sphagnum fallax	13.9
Sphagnum fimbriatum	0.9
Sphagnum palustre	0.3
Sphagnum russowii	+
Sphagnum squarrosum	1.8
Tetraphis pellucida	+
Ulota crispa	+

4. Discussion

4.1. Regeneration of the peat layer

During preparation of an eventual protection of Gammelmosen in 1844, there was a discussion among Danish scientists about the potential of exploited bogs to regenerate and to produce economically valuable fuel (VAUPELL 1862). The most optimistic guess was that 30 years should be enough for regeneration of a substantial peat layer, while others proposed some 100 years. Certainly, peat regeneration is proceeding far more slowly. DIERßEN (1996) described about 1.5 mm annual peat increment for intact bogs in Scandinavia, while the results for Gammelmose were more variable. For the deepest part of the bog it looks like about 1 m of peat accumulated within 145 years, corresponding to ca. 7 mm yr^{-1}. In other parts, little change was observed, but these inconsistent results could be partly due to methodological constraints. However, the surface of the regenerating bog has become slightly convex in 1971 and 2005. Although today the question of peat regeneration is no longer relevant for energy supply, it is even more interesting to understand the long-term dynamics of bog regeneration.

The water level of the bog in 1970 and 2005 was with about 17 cm belowground close to the limit of suggested as appropriate for a raised bog, and within the variation measured in intact bogs (BRIDGHAM & RICHARDSON 1993). However, the tree invasion, observed 30–80 years ago, suggests at least episodically reduced water levels in the mid-20th century, when also urbanisation around the bog took place.

4.2. Vegetation change

The succession of Gammelmose follows roughly the main stages described for degraded bogs after peat extraction (SMART et al. 1989, PFADENHAUER & KLÖTZLI 1996). After excavation of the bog for fuel at least some parts were left with bare peat and heavily disturbed lower peat layers (‘catotelm’). Fen species such as *Agrostis canina*, *Calamagrostis canescens* and *Comarum palustre* had their peak after 50–100 years, but more recently decreased in abundance as the canopy of the birch-pine forest reached considerable cover. Other shade-intolerant fen species, as *Cicuta virosa* and *Peucedanum palustre*, disappeared from the permanent plots. The same was observed for *Drosera rotundifolia* in 2005, while for the other species acidification of the increasingly rain-fed bog could be an additional factor. Interesting changes were also observed for the moss vegetation with dominating *Sphagnum fallax* and *S. fimbriatum* in 2005, which are tolerant of some shade as well as of higher nutrient concentrations (SMART et al. 1989).

This is also observed in other Danish bogs (AABY 1994), and most likely due to atmospheric nitrogen deposition (ASMAN & RUNGE 1991). These fast growing *Sphagnum* species are considered as significant first step in the regeneration of raised bogs (PFADENHAUER & KLÖTZLI 1996), although the process is slow, and typical raised bog *Sphagnum* species are still lacking or rare, probably because they have no diaspore bank and no close-by populations from where they can spread, but also because they cannot compete with *S. fallax* and *S. fimbriatum*.

Tree invasion by *Betula pubescens* and *Pinus sylvestris* has often been observed in drained bogs (e.g. HANSEN & MADSEN 1984), and the resulting changes in light climate and soil moisture clearly affect the ground vegetation. Thus, during the near-natural regeneration of Gammelmose relatively wet and species-rich fen communities developed into slightly drier bog vegetation. Unfortunately, we have little information on parallel changes in nutrient conditions and soil pH.

Pinus sylvestris is not a typical bog tree in Denmark, but in Sweden it is the most common tree species invading raised bogs, and here it reaches ages of more than 100 years (LINDERHOLM & LEINE 2004). One important difference between the two regions is that the bogs in Sweden were rarely cut for peat but drained for agriculture or forestry. Therefore, the peat layer in the cutover bogs in Denmark is less compact and has a lower carrying capacity for heavy trees. This was evident in Gammelmose where old trees show reduced growth and began to sink into the instable peat layer, some of them leaning or thrown over by winter storms (ROELSGAARD 2006).

There are still numerous questions for continued monitoring, and further studies should investigate whether or not the open birch-pine forest is a stable bog community or either more terrestrial forest types or *Sphagnum*-dominated bog vegetation will take over. Most likely, this balance depends on the water level which will be affected by climate change (WELTZIN et al. 2003); in case of warmer (and drier) summers the hydrological regime of Gammelmose should be reconsidered to prevent unacceptable low water levels as recorded during measurements in 2009 (J. Kollmann, unpubl. data). However, current observations suggest that the peat layer in the forest bog is still growing and at least partly has lost its contact to minerogen ground water. This is a sign of on-going regeneration of this (potentially) raised bog.

5. Conclusions

The long-term observations in Gammelmose indicate that autogenic recovery can be a successful method of 'passive restoration' for small bogs that were heavily impacted but still have appropriate hydrological conditions, as also suggested by GROOTJANS et al. (2006). Spontaneous re-vegetation of mined peat lands was reviewed by LAVOIE et al. (2003), concluding that this might be a risky strategy for large, industrially exploited systems, where *Sphagnum* re-immigration can be slow (GIRARD et al. 2002).

Degraded bogs in Denmark and in other parts of Europe are often managed by conservation authorities to reduce eutrophication and drainage, and to prevent or to reduce tree invasion. This is a labour-intense and expensive approach; it can disturb sensitive bog remnants, and does rarely produce self-supporting near-natural conditions. Cutting birch in such bogs without applying herbicides would just rejuvenate this problematic species leading to an even denser cover, and thus reduced abundance of bog species.

A new development is the observed invasion of naturalised garden plants in the study bog which might also occur in other suburban wetlands. However, in a non-intervention site like Gammelmose, this development is part of the succession to be observed, since it very unlikely that this 'biological pollution' will be regulated by law in near future. A caveat from historical data, as in the case of Gammelmose, is that the starting conditions for bog regeneration today are different from the mid-19th century when eutrophication, invasive alien plants and climate change were less significant environmental factors.

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