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Research paper

Palaeoecological reconstructions of vegetation successions in two contrasting former turbaries in the Netherlands and implications for conservation

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ABSTRACT

Terrestrialization stages of mire vegetation are important to Dutch nature conservancy because of high biodiversity, particularly of base-rich fens. In recent turbaries, terrestrialization has however not shown development of such a stage, while existing rich fens show accelerated development towards species-poor *Sphagnum*-dominated vegetation, due to acidification and lack of base-rich water input. We apply the analysis of microfossils and macroremains in two peat cores in order to get a better understanding of terrestrialization in the past, and thus provide information on actual vegetation successions, which is directly relevant to nature conservation.

The sampling site Stobbenribben showed a vegetation succession under relatively nutrient-poor conditions. The site at Westbroek underwent two peat digging events with one vegetation sequence starting in the 16th/17th century under nutrient-poor conditions, and another during the last century under relatively nutrient-rich conditions. Results from Westbroek showed that if the pond is shallow, rich-fen bryophytes develop relatively close to the bottom of newly formed peat, due to structural support by species such as *Equisetum fluviatile* and *Schoenoplectus lacustris*. For Stobbenribben, where the pond is much deeper, rich-fen bryophytes only established after development of a floating root mat with *Stratiotes aloides*. For both Stobbenribben and 20th century Westbroek, the base-rich fen stage took 60 years to establish and remained for only 30 years without additional input of base-rich water.

Our palaeoecological records can be used to provide a longer temporal perspective to address conservation issues of base-rich fens. We conclude that digging up new turf ponds may not be enough to meet the obligations of the Natura 2000 Habitat Directive, if extra measures to prolong the lifespan of rich fens through e.g. temporary inundations with base-rich and nutrient-poor water are not taken into account.

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1. Introduction

Vegetation succession in turf ponds (Dutch: petgaten) created by peat dredging in the Netherlands is important, because the different stages, with their specific environmental conditions, allow for a range of rather rare species to develop over time (Verhoeven, 1992). Due to their high ecological value, all succession stages, from open water with *Chara* species (Habitat type H3140) or

Stratiotes aloides (H3150) to base-rich and base-poor transitional fens (H4170A and B) and wet heaths with *Erica tetralix* (H4010), are protected by the Natura 2000 Habitat Directive, which states that these habitats within the European Union must be kept in a 'Favourable Conservation Status' (Ostermann, 1998). The base-rich fen stage is particularly important because of its species-richness and rareness (Wassen et al., 2005; van Diggelen et al., 2006), and an increase in base-rich fen habitats must be promoted. Many Dutch Red List species, such as *Menyanthes trifoliata* and *Potentilla palustris* play a role in the base-rich fen vegetation (Bootsma et al., 2002). The term base-rich, in this paper, refers to minerals, such as calcium, and nutrient-rich refers to nitrogen and phosphorus content (van Tooren and Sparrius, 2007).

Abbreviations: NPP, non-pollen palynomorph; WB, Westbroek; ST, Stobbenribben.

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In the Netherlands, very few base-rich fen areas are left. Rich fens are threatened by acidification and eutrophication (Kooijman, 1992; Lamers et al., 2015). The transition from the alkaline and species-rich vegetation, generally with *Scorpidium scorpioides* and other brown mosses, to acidic and species-poor *Sphagnum*-dominated vegetation is accelerated in the Netherlands due to insufficient input of base-rich water to the fens (compare Sjörs, 1950; Wheeler and Proctor, 2000; Soudzilovskaia et al., 2010), in combination with high atmospheric deposition of acidifying components related to human activity (Gorham et al., 1987; Kooijman, 2012). Once *Sphagnum* sp. have established, brown mosses do not get a real chance of surviving because the *Sphagnum* actively acidify their environment (Clymo, 1963; Kooijman and Bakker, 1994). Many attempts have been made to reverse the *Sphagnum* stage, but this has shown to be ineffective on a larger scale (Beltman et al., 1996; Klimkowska et al., 2007), although local success has been obtained by inundation with base-rich, nutrient-poor surface water (Cusell et al., 2015; Kooijman et al., 2016). The rich-fen habitats are also threatened by a lack of renewal by terrestrialization in new turf ponds. In an effort to recreate the base-rich fen stage, new ponds were dug in the last decades (Cusell et al., 2013; Weijs and van Tooren, 2013). Terrestrialization in these areas did not yet take place, or slowed down because water during the 1960's and 1970's was highly polluted with nutrients and pesticides from agriculture, and heavy metals from communal wastewater (Kuks, 2002). Even after water quality improved after the 1980's, only initial terrestrialization was observed, but not yet development towards the base-rich fen stages (Cusell et al., 2013).

Palaeoecological reconstructions of vegetation successions, based on the analysis of microfossils and macroremains, may help to understand the problems of present-day terrestrialization. Palynology is the most widely used tool for reconstructing past landscape developments (Gaillard et al., 2008). Peat deposits are very valuable archives to study vegetation history, more specifically pollen and spores, non-pollen palynomorphs (NPP) and macroremains (Chambers et al., 2011). NPP represent a variety of organic microfossils besides pollen and spores, such as fungal spores, cyanobacteria, algae and zoological remains and are used as palaeo-environmental indicators for, e.g., local hydrological changes and changing trophic conditions (van Geel, 2001). Moreover, botanical macroremains (fruits, seeds, mosses) in the peat deposits give important information for the reconstruction of vegetation successions (Mauquoy and van Geel, 2007). Macrofossils can be easier identified to species-level than pollen and NPP, and due to their size and weight they are not transported very far from where they were formed, thus allowing for a more accurate reconstruction of the local vegetation history (Mauquoy et al., 2010). In the present study, two terrestrialized turbaries were compared, a deep one with relatively nutrient-poor conditions, Stobbenribben (ST), and a shallower one with relatively nutrient-rich conditions, Westbroekse Zodden (WB). At the end of the 1980's, both ST and WB fens formed the best example of base-rich fen vegetation in their particular areas, respectively Weerribben and Vechtplassen (Kooijman, 1993a). Palaeoecological reconstructions of peat cores from ST and WB, may help to understand how terrestrialization developed in the past, and consequently may deliver information about the question why the terrestrialization process has become problematic nowadays. Palaeoecological information can then be used to help and improve management decisions (Willis and Birks, 2006; Willis et al., 2007). The research questions are: (1) How did vegetation succession of past terrestrialization in WB and ST develop and can differences between the two areas be explained by nutrient status and/or pond depth? (2) Which plant species are important for terrestrialization, and when do bryophytes such as *S. scorpioides* play a role? (3) How long did it take for the base-rich fen stage to

Fig. 1. Sampling sites Stobbenribben (ST) and Westbroekse Zodden (WB) in the Netherlands.

establish, and how long for the *Sphagnum*-dominated phase to take over?

2. Methods

2.1. Sample locations

For the present study, two sampling sites were selected: Stobbenribben (ST; 52° 47'04.5"N, 5° 58'59.4"E) and Westbroek (WB; 52° 9' 51.1"N, 5° 7' 12.4"E). The location of these study areas is shown on a map in Fig. 1.

ST forms part of the Weerribben–Wieden National Park, which is one of the largest fen marshland in Western Europe. This nature reserve is one of the rare areas where different stages of terrestrialization still can be observed, including base-rich fens with well-developed bryophyte layers (Cusell et al., 2013). Also it is home to many red-list species and includes important Natura 2000 habitats. In the national park, peat digging for fuel already started in the 12th century, but became more important after the 15th century, with peaks in the 17th and 18th century (Gonggrijp et al., 1981). The pond of the Stobbenribben fen was probably dug out around 1900 (van Wirdum, 1991). In the national park, the abundance of aquatic vegetation increased substantially between 1998 and 2010, but further development of floating vegetation has only occurred to a limited extent, even in turf ponds of more than 70 years old (Cusell et al., 2013). New quaking fens with brown mosses of base-rich conditions (like *S. scorpioides* and *Campylium stellatum*) are not yet present, although floating reedland with marsh fern (*Thelypteris palustris*) has started to develop. In the National Park, 126 ha of new rectangular turf ponds were dug in this area since 2006, in order to initialise the terrestrialization process again, and consequently to stimulate the development of vegetation types of base-rich conditions (Cusell et al., 2013).

WB forms part of the Vechtplassen area. According to [Weijs and van Tooren \(2013\)](#), turf ponds were dug to use peat for fuel in the 19th century. The studied pond was probably dug out around 1900. Following terrestrialization, the ponds became very species-rich until far into the last century, but as succession continued with *Sphagnum* lawns they became less and less diverse. From 1989 onwards, 60 new ponds were dug to create new opportunities for terrestrialization, but they have not shown significant signs of terrestrialization yet ([Weijs and van Tooren, 2013](#)).

As indicated above, both ST and WB turbaries were supposedly dug out at the beginning of the 1900's (SEM Fig. 1; [van Wirdum, 1991](#)). Also, both ST and WB fens formed the best example of base-rich fen vegetation in their particular areas ([Kooijman, 1993a](#)). There are however differences between the two sites in hydrology, nutrient status and depth of the pond. The ST pond is 285 cm deep (distance between sandy subsoil and present water table) and supplied with calcium-rich surfacewater, which flows in from an adjacent ditch ([van Wirdum, 1991](#)). Agricultural activities are scarce inside the Wieden–Weerribben National Park but the area is surrounded by low-lying agricultural polders, which supply surface water to the nature reserve in wet periods. The WB pond is 140 cm deep to the sandy bottom, and supplied with calcium- and iron-rich groundwater, although it is also connected with the surfacewater system in the polder ([Koerselman, 1989](#)). WB is more threatened by eutrophication than ST, due to agricultural land-use inside the nature reserve ([Creutzberg et al., 1969](#)). In 1988, ammonium and phosphate concentrations in the fen water were much higher in WB than in ST ([Kooijman, 1993a](#)). In 1988, both fens were in the rich-fen stage, but the moss layer in ST was dominated by *S. scorpioides*, and in WB by *Calliergonella cuspidata*, which is a more eutrophic species ([Kooijman, 1993b](#); [Kooijman and Bakker, 1995](#)). In both sites, however, *Sphagnum* species had already established.

2.2. Methodology

For both sampling sites, the entire succession sequences were sampled, from the aquatic phase to the base-rich phase, followed by a sphagnaceous phase. Both sample locations were selected in areas where the rich-fen mosses *S. scorpioides* (ST) or *C. cuspidata* and *Calliergon megalophyllum* (WB) were still present in 1988, but where the first *Sphagnum* spp. (*Sphagnum subnitens* and/or *Sphagnum squarrosum*) had already established ([Kooijman, 1993a](#); [Kooijman et al., 2016](#)).

2.3. Peat column extraction and sample preparation

In each fen, the peat column was sampled with a rectangular, 50 cm high metal box with sharp edges, which was pushed into a newly made profile. The deepest, oldest samples from the metal box were checked for aquatic taxa, to make sure that a representative sample containing all the succession stages was taken, and no further, deeper sampling was needed. After removing the possibly contaminated outer layer of the material with scissors and a knife, a continuous series of 1 cm thick peat samples was taken. Two samples were taken for every layer: one of ca. 1 cm³ for microfossil analysis and one for the analysis of macroremains. The size of the microfossil sub-samples was ca. 30 cm³. The microfossil samples were prepared according to [Faegri and Iversen \(1989\)](#) and the macrofossil samples were prepared according to [Mauquoy et al. \(2010\)](#).

2.4. Palaeoecological analysis

Microfossil analysis of the WB core was done for every 4th centimetre and for the additional 1, 11, 15, 19, 23, 27, and 31 cm levels.

Macroremains were analysed for every cm level. In ST, microfossil and macrofossil analyses were carried out for every 5th cm, with the additional depths 1, 3, 4, 17, 27, 32, 33, 34, 36, 37 and 38 cm from the surface. Microfossil analysis was worked out at 400× magnification. Occasionally, 1000× magnification was used. Guides of [Moore et al. \(1991\)](#) and [Beug \(2004\)](#) were used for the identification of pollen grains and spores. Macrofossil analysis ([Mauquoy and van Geel, 2007](#)) was done using a stereomicroscope. Identifiable remains were put aside in glycerin for further identification. *Juncus* seeds, *Sphagnum* leaves and other macroremains, such as epidermis fragments were identified using identification keys ([Körber-Grohne, 1964](#); [Hölzer, 2010](#); [Bouman et al., 2002](#); [Laine, 2009](#); [Grosse-Brauckmann and Streitz, 1992](#)). After analysis, the samples were sealed in plastic bags and stored in a fridge for prospective future analysis. Microfossils were quantified in numbers for percentage calculations and macroremains were quantified in estimated volumetric percentages (e.g., mosses) or given as numbers (e.g., seeds). Diagrams of the vegetation succession were constructed by using TILIA ([Grimm, 1991–1993](#)). Macrofossils are shown as bars, while microfossils are shown as percentage curves expressed on total pollen. The taxa were divided in local and regional taxa. Some taxa, such as *Pinus sylvestris*, occur in all subsamples while the species did not play a role in the local vegetation succession, but come from the surrounding areas as part of the regional pollen rain. When constructing the diagram for the local vegetation succession, the non-local taxa, such as trees, shrubs and human impact indicators were left out, and plotted in separate diagrams (SEM Figs. 2, 3, 4 and 5). For the different plant taxa, ecological information is based on the Dutch standard list ([Tamis et al., 2004](#)) and on [Weeda et al. \(1985, 1994\)](#). Additional information regarding bryophytes was taken from [Kooijman \(1993a,b\)](#) and [van Tooren and Sparrius \(2007\)](#). The ecological information of NPP is based on [Kuhry \(1997\)](#); [van Geel \(1978\)](#) and [van Geel et al. \(1983, 1989\)](#). The local taxa were put in an order that best represents the succession from the aquatic phase to the *Sphagnum* phase. Due to different ecological amplitudes of species, some of the decisions about where to put zone boundaries for local assemblage zones were somewhat arbitrary, and were done by eye. Some newly recorded NPP were illustrated and described in [Appendix A](#). Special attention was given to the bryophytes, as they are much better indicators of the hydrological surface conditions than vascular plants ([Sjörs, 1950](#); [Gorham et al., 1987](#); [Kooijman and Paulissen, 2006](#)). Bryophytes are not only important in terms of biomass dominance, but are also good indicators of environmental conditions, because they have no roots and mineral nutrients are absorbed immediately through the one-cell thick leaves ([Proctor, 1982](#)).

2.5. Radiocarbon dating

For ST, two samples were radiocarbon dated, at 20 and 35 cm depth, more or less representing the start and end of the base-rich fen phase with *S. scorpioides*. For WB, five samples at depths 10, 18, 23, 27 and 33 cm were dated, following transitions in the species composition. The choice of depths depended partly on the availability of material, because only aboveground material such as seeds was suitable for dating. The two ST samples and the three most recent WB samples were matched with the ¹⁴C bomb peak using OxCal ([Appendix B](#); [Bronk Ramsey, 1995](#)).

3. Results

3.1. Stobbenribben — local vegetation succession

For the reconstruction and description of successive local stands of vegetation in ST five zones were distinguished, varying from aquatic to rich-fen and *Sphagnum*-dominated stages. The radiocarbon sample

Fig. 2. Local vegetation succession in Stobbenribben – Part 1 (focus on zones 1 and 2).

at 20 cm depth, near the end of the rich-fen stage, was dated to 1993–1996 AD (Appendix B). The sample at 35 cm, at the start of the rich-fen stage, most probably dates to 1962–1963 AD. In theory, this radiocarbon date could also correspond to the time interval 1972–1974 AD, but given the existing information on vegetation development at Stobbenribben during the latter period, this is unlikely because during 1972–1974, the rich-fen had already established (Bergmans, 1975).

Zone 1 (Fig. 2; 50–47 cm depth) is represented by *Potamogeton*, *Lemna*, *S. aloides* and other botanical and zoological taxa indicating relatively nutrient-rich aquatic conditions.

Zone 2 (Fig. 2; 47–36 cm depth) is also still aquatic, with taxa like *S. aloides*, *Gloeotrichia* colonies, gemmulae of freshwater sponges, Cladocera and Bryozoa. Nymphaeaceae were also

found (*Nuphar lutea* pollen and trichosclereids, HdV-129, and basal hair cells, HdV-127). These taxa generally occur in relatively nutrient-rich waters. *Gloeotrichia* points to alkaline conditions. In zone 2, the first semi-terrestrial taxa arrived: *Typha latifolia*, *Mentha aquatica/arvensis*, *M. trifoliata*, *Hydrocotyle vulgaris*, *Juncus articulatus*-type (including *Juncus acutiflorus* and *Juncus bulbosus*), and *Iris pseudacorus*. The monolete psilate fern spores may point to the presence of *T. palustris*. The only bryophyte found in this zone was *Oxyrrhynchium speciosum*, a species from mesotrophic to slightly eutrophic base-rich water. The transition to zone 3 is characterized by Characeae, indicating a decline of available nutrients.

In zone 3 (Fig. 3; 36–21 cm depth), aquatic taxa mostly disappeared except for *Utricularia*. However, *Sparganium* and *Caltha*-type,

Fig. 3. Local vegetation succession in Stobbenribben – Part 2 (focus on zone 3).

Fig. 4. Local vegetation succession in Stobbenribben — Part 3 (focus on zones 3 and 4).

which could not be further identified, indicate rather wet conditions. *Lysimachia vulgaris*, *Agrostis* sp., Type HdV-128A and *Spirogyra* indicate semi-terrestrial, although still relatively eutrophic conditions. *Epilobium*, *Potentilla*-type, *Apiaceae* and *Valeriana* were also found, but could not be identified to species level. *Valeriana officinalis* indicates eutrophic conditions and *Valeriana dioica* indicates mesotrophic conditions (Weeda et al., 1988); the latter is most probable to occur in the fen habitats and is also present at the site today. Type HdV-823 and remains of the plant hopper *Conomelus anceps* (HdV-195) and Oribatidae mites were also recorded in zone 3. *Typha angustifolia*, *Alisma*, *Thalictrum*, *Juncus*

subnodulosus, *Phragmites australis*, *Diporotheca* (ascospores; HdV-143) and Type HdV-124 fungal spores also indicate rather base-rich and mesotrophic conditions. At the beginning of zone 3, *Characeae* were found. The bryophytes occurring in this zone are *S. scorpioides*, *Bryum pseudotriquetrum* and *C. stellatum*. These species also grow under base-rich and nutrient-poor conditions, indicating that those were the local surface conditions during this phase. Zone 3 is thus considered to be the real rich fen stage. Given the radiocarbon dates of the samples collected at the lower and upper part of zone 3, the rich-fen stage started around 1962 and ended around 1993, approximately 30 years later.

Fig. 5. Local vegetation succession in Stobbenribben — Part 4 (focus on zone 5).

Fig. 6. Local vegetation succession in Westbroekse Zoden – Part 1 (focus on zones 1 and 2).

Zone 4 (Fig. 4; 21–12 cm depth) is a transition zone dominated by *Sphagnum* remains of the section *Cuspidata* and by Type HdV-567, which co-occurs with *Sphagnum* and indicates acidifying conditions. The presence of *Viola palustris* supports the transition towards more acidic conditions. The presence of *Aulacomnium palustre* indicates relatively dry conditions within the *Sphagnum* vegetation. However, the presence of *Pedicularis palustris* together with the bryophyte *Rhizomnium pseudopunctatum* indicates that at this stage the local superficial hydrological conditions continue to be relatively base-rich and rather nutrient-poor. Type HdV-128B, which generally occurs in mesotrophic conditions, was also found. *Carex acuta*-type, Type HdV-827 (algal spore), *Dictyosporium*-type (HdV-824) and zoological remains of ants and mayflies were also recorded in zone 4. *C. acuta*-type can be one of the following species: *Carex acuta*, *Carex nigra*, *Carex trinervis* or *Carex elata*. The latter taxon is a mire species occurring elsewhere in the fen nowadays and it is probably the species recorded here.

Zone 5 (Fig. 5; 12–0 cm depth), representing the vegetation succession up to the present day, is characterized by *E. tetralix*, *Myrica gale*, the testate amoeba *Assulina* sp., the fungus *Entophlyctis lobata* (HdV-13) and by the bryophytes *Sphagnum palustre* and *Rhytidiadelphus squarrosus*, which all point to acidic and ombrotrophic conditions. *Eriophorum angustifolium*, *Filipendula ulmaria* and *Lotus*, in addition to Type HdV-91, and the conidia of *Helicoon pluriseptatum* (HdV-30) also play a role in this phase. The terrestrialization at the sampling site of ST is at an acidic stage and includes some taxa (*Assulina*, *E. lobata*, Type 91 and *H. pluriseptatum*) that also occur in ombrotrophic raised bogs (van Geel, 1978).

3.2. Westbroek – local vegetation succession

In WB, seven zones were distinguished (Fig. 6). The three upper radiocarbon samples (23, 18, and 10 cm depth) have roughly been dated to respectively 1958, 1988 and 2006 (Appendix B). The vegetation recorded at 18 cm depth also corresponds to field

Fig. 7. Local vegetation succession in Westbroekse Zoden – Part 2 (focus on zones 2 and 3).

Fig. 8. Local vegetation succession in Westbroekse Zodden – Part 3 (focus on zones 3 and 4).

observations of that time (Kooijman, 1993a). The lowest two samples, at 33 and 27 cm depths, however, have been roughly dated to the 16th/17th century. This means that the local vegetation succession has been interrupted, and that two different terrestrialization phases were recorded here. The initial turf pond was excavated in the 16th/17th century. However, only the lower 25 cm of its peat infill has been preserved. We do not know how the first local vegetation developed on top of this, because the area was dug out again, probably at the beginning of the 20th century, when a new, second terrestrialization phase developed. The hiatus level around 25 cm depth is indicated with a striped black line.

The first few taxa shown at the left side of Fig. 6 (*Ericales*, *Juncus effusus*, and *Sphagnum imbricatum*, *Sphagnum magellanicum*, *Sphagnum papillosum*, fern sporangia and *Tilletia sphagni*) do not play a role in the local succession of the 16th/17th century turbary pond. Most probably, the remains of these taxa are 'reworked' and come from the 16th/17th century mire surface developed before peat was cut. *S. imbricatum* is extinct in the Netherlands at present, but it has been an important peat-forming species of raised bogs in the past (van Geel, 1978). We found *S. imbricatum* in a core taken

in the original peat as present in the baulk ('legakker' in Dutch) along the Westbroek fen.

In zone 1 (Fig. 6; 50–48 cm depth), an aquatic phase is represented by gemmulae of freshwater sponges, *Plumatella*-type and *Cristatella mucedo* (Bryozoa), the fish parasite *Piscicola geometra*, Cladocera, algae (*Botryococcus*, *Pediastrum*, Types HdV-128A and 128B) and cyanobacteria (*Gloeotrichia*), which are all aquatic taxa. Larval headcapsules of chironomidae and mouthparts of alderfly larvae were also recorded. *Equisetum* (probably *Equisetum fluviatile*) was also dominant. It can grow in an array of environments but is generally indicative of wet, phosphate-poor and iron-rich conditions.

Zone 2 (Fig. 6; 48–34 cm depth) was still aquatic, and dominated by *Potamogeton*, Nymphaeaceae, *Alisma*, *Sparganium* and *Schoenoplectus lacustris* that grow in base-rich waters. Nymphaeaceae are represented by *Nymphaea alba* and *N. lutea*. *E. fluviatile* was still dominant. Characeae and the bryophyte *S. scorpioides* were found at this rather early stage in the succession, indicating base-rich and nutrient-poor conditions. *S. scorpioides* also indicates the establishment of the rich-fen stage. *Botryococcus*, *Pediastrum* and Types HdV-128A and 128B occur in meso- to eutrophic water.

Fig. 9. Local vegetation succession in Westbroekse Zodden – Part 4 (focus on zones 5, 6 and 7).

Gaeumannomyces sp. (HdV-126) is a parasitic fungus on *Carex* species.

S. scorpioides and Characeae disappear at the transition from zone 2 to zone 3 (Fig. 7), when the vegetation of zone 3 (Figs. 7

and 8; 34–25 cm depth) becomes dominated by *Carex pseudocyperus* and *Carex rostrata*, indicating semi-terrestrial conditions. *Mentha*-type, *Stellaria palustris* and *M. trifoliata* were found in this zone, which still points to base-rich and mesotrophic conditions. *Baldellia*

Stobbenribben

Fig. 10. Cartoon (cross section) showing effect of peat digging and successive stages of vegetation in Stobbenribben. A: before peat digging. B: after peat digging and dredging at the beginning of the 20th century. C: stage with dominance of *Stratiotes*. D: further terrestrialization during vegetation succession. E: present state with dominance of *Sphagnum*; Stages A–E all take place within the 20th century.

ranunculoides and *Myriophyllum spicatum* are aquatic species that were recorded at a relatively late stage. It is possible that they were transported from the surrounding areas and that they were not part of the local succession at the WB sampling site. Spores of the *Zygnema*-type occurred in this zone and point to temporary, shallow, mesotrophic open water.

Zone 4 (Fig. 8) represents the start of the second terrestrialization phase in the 20th century, under relatively wet conditions in a newly created rectangular pond (Fig. 8; 25–19 cm depth). A sample at 23 cm

depth, in the middle of this zone, was dated back to around 1958. *J. subnodulosus*, *T. latifolia*, *T. angustifolia*, *F. ulmaria*, *Peucedanum palustre*, *Drepanocladus polygamus*, fungal spores of *Cercophora* (coprophilous fungi), zoological remains of *Prionocera* and *C. anceps* occurred. *T. latifolia*, and *F. ulmaria* are species of relatively wet, base-rich and nutrient-rich conditions. This is confirmed by the presence of *D. polygamus*, so the second terrestrialization in WB at the beginning 1900's started off with base-rich and relatively nutrient-rich conditions.

Fig. 11. Cartoon (cross section) showing effect of peat digging and vegetation succession in Westbroekse Zodden. A: before peat digging. B: after peat digging and dredging around the 16th century. C: helophytes dominate local vegetation. D: helophytes and a variety of species further contribute to the formation of peat. E: peat deposit before second phase of peat digging. F: situation after second phase of peat digging at the beginning of the 20th century. G: present state with dominance of *Sphagnum*; Stages A–D all take place in the 16th century, Stage E lasts from the 16th until the 20th century, Stages F–G take place in the 20th century.

Zone 5 (Fig. 9; 19–13 cm depth) represents the 20th century rich-fen stage. The radiocarbon sample taken at 18 cm depth at the start of this zone was dated around 1988. Zone 5 is characterized by *Carex paniculata*-type (includes *C. paniculata*, *Carex appropinquata* and *Carex diandra*). *C. diandra* is a mire species that was present in the fen area in 1988, and is probably the species recorded here. *Lotus*, *Poa palustris*, *H. vulgaris*, Apiaceae, Gentianaceae, *Potentilla*-type, *J. articulatus*-type and ferns producing monolet psilate spores were also found in this zone. Oribatid mites are most dominant in this zone, even though they occur approximately throughout the whole core. The presence of the bryophytes *C. cuspidata*, *Calliergon giganteum* and *Straminergon stramineum*, which started partly already in zone 4, indicates relatively nutrient-rich conditions (Kooijman, 1993b). The first two moss species also suggest that conditions were still relatively base-rich. The *Sphagna* appearing in zone 5 belong to the section *Acutifolia*, which given the high prominence of this species in the field (Kooijman et al., 2016) is most probably *S. subnitens*, a species of slightly base-rich conditions.

In Zone 6 (Fig. 9; 13–8 cm depth), *Sphagnum* spp. have become the dominant mosses. Zone 6 shows a decline of *C. cuspidata*, while *Sphagna* of the sections *Acutifolia* and *Cuspidata*, the latter most probably *Sphagnum fallax*, *S. palustre*, *C. acuta*-type, and Type HdV-90, are indicators of ombrotrophic conditions. Local conditions have become more acidic. The radiocarbon sample at 10 cm depth was dated around 2006.

In zone 7 (Fig. 9; 8–0 cm depth), *S. palustre*, *Sphagnum* of the section *Acutifolia*, *Drosera rotundifolia* or *Drosera anglica*, *Polytrichum commune* and *Assulina* sp. have become important local taxa, all indicating acidic conditions. The local vegetation of the sampling site in WB is currently at an oligotrophic and acidic stage.

4. Discussion and conclusion

Most records used to assess ecosystem changes are based on short-term ecological data, spanning only a few decades, but with paleoecological methods we can reconstruct successions in a longer-term perspective. Willis and Birks (2006) and Willis et al. (2007) highlight the potential of palaeoecological records in conservation biology, including application to biodiversity maintenance.

4.1. Differences in nutrient availability

The double terrestrialization in WB, which started in the 16th century and restarted after peat extraction in the 20th century, was rather unexpected. This makes it difficult to compare the two recorded vegetation successions, but a few patterns can be pointed out below (Figs. 10 and 11). The two sites clearly differed in nutrient availability in 1988, during the base-rich fen stages of ST and WB. At that time, phosphate concentrations were three times higher in WB than in ST (Kooijman, 1993a). This is confirmed by the bryophyte species, which generally are good indicators for local conditions (e.g., Sjörs, 1950; Proctor, 1982; Gorham et al., 1987). The occurrence of *S. scorpioides*, *C. stellatum* and *R. pseudopunctatum* in ST indicate rather base-rich and nutrient-poor conditions in the rich-fen stage. In WB, the occurrence of *S. scorpioides* during the 16th/17th century terrestrialization also indicates rather nutrient-poor conditions. This was supported by the occurrence of Characeae, which were only recorded in ST and 16th/17th century WB. During the 20th century terrestrialization in WB, the occurrence of *C. giganteum* and especially *C. cuspidata* indicate more nutrient-rich conditions, compared to the other two terrestrializations (Kooijman, 1993b). In

the 20th century, WB was probably too eutrophic for dominance of *S. scorpioides* although there was one spot where the species was present in 1988.

Differences in nutrient availability were less obvious within the vascular plant composition. *S. aloides*, an aquatic species of mesotrophic conditions (Smolders et al., 2003), was recorded in ST but not in WB, not even in the 16th/17th century, even though the species is present in the WB area nowadays (Geurts, 2010). The 16th/17th century WB succession was perhaps too nutrient-poor for *Stratiotes* (Smolders et al., 2003). On the other hand, this floating macrophyte was also absent during the 20th century, when the pond was connected to more eutrophic waters from drainage ditches and canals. The absence of *Stratiotes* might be due to the much lower pond depth in WB than in ST, rather than differences in nutrient availability. Especially in the 20th century succession, the low abundance of algae suggested that an open water stage was lacking, although taxa such as *M. trifoliata* and *Typha* spp., as well as *Cladocera* indicate that some open water was present. Also, in dense vegetation of *E. fluviatile* and/or *T. angustifolia*, the growth of *S. aloides* may be restricted due to lack of space (Creutzberg et al., 1969). Other taxa differing between ST and WB were Poaceae, the fruits of which indicate local occurrence. *P. australis* was only present in ST, which started as a reedland (van Wirdum, 1991). In the 16th/17th century succession in WB, Poaceae fruits were not found, and in the 20th century succession, only *P. palustris* fruit was present. *E. fluviatile* was not recorded in ST, but was clearly present in both WB successions, with dominance in the 16th/17th century succession. *E. fluviatile* thrives in wet places and in phosphate-poor and iron-rich conditions (Husby 2013; Weeda et al., 1985). The ST site is however fed by calcium-rich surface water instead of iron-rich groundwater (van Wirdum, 1991; Koerselman, 1989), which may explain absence of the species.

Differences in nutrient availability between the two sampling sites may to some extent be reflected in the end stages of succession. In both sites, *S. palustre* is a dominant species. In ST, *S. palustre* is accompanied by *M. gale* and *E. tetralix*, while in WB by *P. commune*, which is a more eutrophic species. However, thickness of the *Sphagnum* peat layer is similar for both sites, with 20 cm in ST and 18 cm in WB. The *Sphagnum* vegetation probably grew beyond the fen water level, and was mainly fed by rainwater, of similar quality (pH and nutrients) in both locations.

4.2. Influence of pond depth on initial structure development

There were clear differences between ST and WB in the development of a support structure during the first stages of terrestrialization, probably related to pond depth. In the 285 cm deep ST, a floating root mat developed before the base-rich fen stage (*S. scorpioides*) established, starting with *S. aloides*. In the floating layer, in addition to *S. aloides*, *J. subnodulosus*, *T. latifolia*, *T. angustifolia*, *P. australis*, *M. trifoliata* and ferns with monolet psilate spores (probably *T. palustris*) played an important role in the mat formation. Characeae and rich-fen bryophytes such as *S. scorpioides* established once this mat was formed. This mechanism is in accord with Verhoeven (1992), who indicates that floating root mats develop before the establishment of the brown moss phase and these mosses effectively fill in the space between the surface of the mat and the water table. In 16th/17th and 20th century WB, where the sandy bottom nowadays is found at 140 cm depth, *S. aloides* was not found. Instead, in this floating fen, structural support for Characeae and *S. scorpioides* was provided in the early stages of succession by *E. fluviatile* and *S. lacustris* in the 16th/17th century WB, and by species such as *T. angustifolia*,

T. latifolia and *J. subnodulosus* in the 20th century WB. Those species probably started from the bottom of the pond to the fen surface, where the rich-fen species established. In both series, the base-rich fen stage established early during succession, with the presence of *S. scorpioides* (16th/17th century WB), *C. giganteum* and *C. cuspidata* (20th century WB) already in semi-aquatic stages. In ST, the pond was, with 285 cm, probably too deep for the support species to grow and first a floating mat had to be formed, providing support for rich-fen bryophytes like *S. scorpioides*. The floating support system observed in ST fits with traditional concepts about terrestrialization (Verhoeven, 1992). The support systems in WB with *E. fluviatile* and *T. angustifolia* are to some extent described in Creutzberg et al. (1969).

4.3. Duration of development

Both ST and WB locations were dug out at the beginning of the 20th century, although for WB this occurred for the second time. The base-rich fen stage established in ST around 1962–1963 and in WB probably a few years after 1958. In 1988, the rich-fen stage had existed for some time already (Kooijman, 1993a). For both recent terrestrializations, it took approximately 60 years for the base-rich fen stage to establish. For the 16th/17th century WB, the base-rich fen stage with *S. scorpioides* was already present at the beginning of the terrestrialization process in zone 2, and the dates are insufficient to discuss the start or duration of the base-rich fen stage. In 16th/17th century WB, *S. scorpioides* was not replaced by *Sphagnum*, but disappeared after local establishment of Cyperaceae. Since the fens were probably not mown at that time, overgrowing vascular plants and lack of light may explain why they were overtaken by Cyperaceae instead of *Sphagnum*. In the 20th century, however, the base-rich fen stage in ST and WB was replaced by *Sphagnum*, and lasted for roughly 30 years. The bomb peak enables inference of the calendar years with good precision, especially close to the peak in 1963. The ^{14}C activities measured around the start of the base-rich fen stage are close to this peak, with measurement uncertainties of about 1–2 calendar years (Reimer et al., 2013; Hua et al., 2013). For the 1990's, representing the end of the base-rich fen stage, this is about 3–4 calendar years. Taking into account other uncertainties such as from sampling and analysis, the durations of establishment (60 years) and development (30 years) of the base-rich fen stage have uncertainties of less than a decade.

The residence time of the base-rich fen stage strongly depends on the hydrological conditions. In hydrologically isolated fens, where rain is the only water input, succession to *Sphagnum*-dominated stages takes place in much less than 30 years (Koerselman et al., 1990; van Diggelen et al., 1996). If there is input of base-rich water into the system, like in ST closer to the local ditch, the rich-fen vegetation may however persist for more than 50 years (Kooijman et al., 2016). In ST, the fen surface is probably supplied with base-rich water closer to the ditch by flooding. However, in the central part of ST, where the core was taken, base-rich water is only present underneath the floating root mat (van Wirdum, 1991). This root mat has grown 35 cm in thickness since 1962–1963, and has probably become too thick to stay in contact with base-rich water (Soudzilovskaia et al., 2010), especially since there is no groundwater pressure, but downward seepage of water to the low-lying agricultural polders. In WB, input of calcium- and iron-rich groundwater is still substantial (Koerselman, 1989). However, the peat layer has also grown, and became 23 cm thicker since 1958. Also, succession towards species-poor *Sphagnum* vegetation happens faster

under nutrient-rich conditions than when the local environment is nutrient-poor (Kooijman, 1993a). Eutrophic *Sphagnum* species, such as *S. squarrosum*, are much larger in size, have higher growth rates and acidification potential than mesotrophic species (Kooijman and Bakker, 1994, 1995; Harpenslager et al., 2015). In eutrophic rich-fens, such as WB, rich-fen mosses are replaced fairly quickly by *Sphagnum*, even without major changes in hydrology.

4.4. Conclusion and implications for management

Palaeoecological records can add valuable information for management plans, and provide a longer temporal perspective to address conservation issues (Willis and Birks, 2006). The present study shows that a palaeoecological approach is a valuable way to reconstruct sub-recent vegetation successions, which helps to understand how rich-fens develop, and how long this process in former turbaries may take.

Nutrient availability clearly differed between ST and WB in the 1980s, with phosphate concentrations of 0.01 mg l^{-1} in ST and $0.28\text{--}0.48 \text{ mg l}^{-1}$ in WB (Kooijman, 1993a), which led to different species composition in the rich fen phase. Differences were however less obvious before and especially after this phase. Early successional aquatic stages may be more dependent on depth of the turf pond than on nutrient availability. Later successional *Sphagnum* stages have become hydrologically isolated from the base-rich water in the pond and mainly receive rainwater, and are probably not dependent on nutrients in the fen any longer.

The ST and 20th century WB radiocarbon results showed that it took about 60 years for both base-rich fen stages to establish and both lasted for roughly 30 years. The brown moss stage took such a long time to establish, and the transition towards *Sphagnum*-fen was so fast, that digging up new turf ponds – in order to keep the rich fen stage – does not seem to be very efficient without further measures. To prolong the life-span of base-rich fens, once it has established, nutrient-poor conditions and sustained input of base-rich water are also needed (Kooijman et al., 2016). When rich fens are e.g., regularly inundated with nutrient-poor, but calcium- and bicarbonate-rich water, the brown moss stage can be sustained much longer.

A next step would be to study more vegetation successions from samples of the same wetland areas to improve our knowledge of the species that played a role in the local succession, and from samples of other areas with different ecological conditions to get a better understanding of how local conditions impact the vegetation succession. This should also lead to more data on the time it takes for the base-rich fen stage to establish and the sphagnaceous phase to take over. Further studies would give a better insight into management necessary to comply with the ecological goals defined by the Natura 2000 Habitat Directive.

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Appendix A. Description and illustrations of some non-pollen palynomorphs

Fig. A. Some NPPs found in the Stobbenribben and Westbroekse Zodden cores. 1 and 2: *Cercophora*-type ascospores; 3 and 4: Type HdV-173; 5–7: Type HdV-822; 8 and 9: Type HdV-823; 10 and 11: *Dictyosporium toruloides*-type (HdV-824); 12–16: Type HdV-825; 17: Type HdV-826; 18: Type HdV-827.

Type HdV-112C: *Cercophora*-type (Plate I, Figs. 1 and 2; compare [van Geel et al., 1983](#))

Ascospores ca. $22 \times 10 \mu\text{m}$. Truncate at the basal side and a ca. $1 \mu\text{m}$ wide pore at the top. One septum without constriction. Fragments of the hyaline appendage at the basal side still preserved in some spores. According to [van Geel et al. \(1983, 1989\)](#), *Cercophora* species occur on faeces or decaying wood, and on herbaceous stems and leaves. In the present study the *Cercophora*-type ascospores were recorded in a peat layer dominated by *Juncus*

subnodulosus at the Westbroek site (zone WB-4, on top of the hiatus) under moist, mesotrophic conditions, together with the fungi HdV-173, HdV-823 and HdV-824.

Type HdV-173A (Plate 1, Figs. 3 and 4; compare van Geel et al., 1989)

Conidia or chlamydospores ca. $18\text{--}25 \times 8\text{--}10\text{ }\mu\text{m}$ (length depending on number of septa), transversally one-septate or two-septate, brown, slightly constricted at the septa. Basal cell provided with a protruding ca. $1\text{ }\mu\text{m}$ wide pore (possibly a former point of attachment with a mycelium). Van Geel et al. (1989) recorded Type HdV-17A in *Carex*-peat of Allerød age. In the present study, it was recorded in a peat layer dominated by *Juncus subnodulosus* at the Westbroek site (zone WB-4, on top of the hiatus) under relatively moist and mesotrophic conditions, together with the fungi HdV-112, HdV-823 and HdV-824.

Type HdV-822 (Plate 1, Figs. 5–7; morphologically closely related to HdV-208, compare van Geel et al., 1989)

X-shaped or H-shaped thin-walled, hyaline microfossils, ca. $70\text{--}75 \times 50\text{--}55\text{ }\mu\text{m}$ (H-shaped) or $70\text{--}75 \times 70\text{--}75\text{ }\mu\text{m}$ (X-shaped) containing a round or quadrangular (square-shaped with blunt corners), light-brown spore of ca. $45\text{ }\mu\text{m}$ in diameter. According to van Geel et al. (1989), these microfossils are probably fossilized conjugating filament cells of a zygomataceous taxon, showing the zygospore inside. In the present study Type HdV-822 occurs in peat material in Westbroek under relatively moist, meso- to eutrophic conditions (Zones WB-4 and WB-5).

Type HdV-823 (Plate 1, Figs. 8 and 9)

Conidia multiseptate, composed of two juxtaposed brown rows of three cells, each one $7\text{--}10\text{ }\mu\text{m}$ in size, and a more hyaline row of 4 to 5 cells, connected with one of the main two rows and becoming smaller (from 7 to $2\text{ }\mu\text{m}$) towards the former attachment to mycelium.

The HdV-823 conidia were recorded in peat material in Stobbenribben under base-rich and mesotrophic conditions and in Westbroek under relatively moist and mesotrophic conditions. At both sites, Type HdV-823 occurs together with *Typha angustifolia* and *Juncus subnodulosus*.

Type HdV-824: *Dictyosporium toruloides*-type (Plate 1, Figs. 10 and 11; cf. Ellis, 1971, Fig. 26)

Conidia flattened in one plane, multiseptate and composed of 6 rows of cells of unequal length, the middle rows being the longest. The rows of cells develop as a branched system and a conidium looks like a hand with fingers held close together. The cells of the conidia are brown with hyaline terminal cells. Width of the conidia is ca. $25\text{ }\mu\text{m}$ and the longest branch of cells is ca. $40\text{ }\mu\text{m}$. Each cell ca. $5\text{ }\mu\text{m}$ in size with a total number of ca. 38 cells. In the present study the conidia were recorded at the Stobbenribben and at the Westbroek site. They occur under various environmental conditions: relatively wet and mesotrophic (Westbroek), drier, base-rich and mesotrophic conditions (Stobbenribben) and acidic and oligotrophic conditions (Stobbenribben).

Type HdV-825 (Plate 1, Figs. 14–16)

Rounded to oval-shaped or pear-shaped light to dark brown microfossils, $35\text{--}40 \times 35\text{--}55\text{ }\mu\text{m}$, cell walls with characteristic, irregularly placed thickenings. During the macrofossil analysis the HdV-825 microfossils appeared to be embedded in a hyaline to light brown, probably parenchymatic plant tissue (Figs. 12 and 13). Type HdV-825 mainly occurs in the aquatic phase of the Westbroek succession under nutrient-poor and base-rich conditions. Among the possible local species with parenchymatic tissue were *Juncus subnodulosus* and *Carex pseudocyperus*, but a specific link could not yet be established.

Type HdV-826 (Plate 1, Fig. 17)

Microfossils composed of two (fungal?) cells. One dark, rounded cell, $13 \times 15\text{ }\mu\text{m}$, with one distal and one proximal ca. $5\text{ }\mu\text{m}$ wide pore and a septum next to the proximal pore, separating it from a second, tube-like, less dark cell, $20 \times 8\text{ }\mu\text{m}$, with a wide opening at the end.

It occurs in the Stobbenribben site but does not seem to have a limited preference concerning environmental conditions as it occurs in the aquatic phase under base-rich and nutrient-poor conditions, during the transition from brown moss to *Sphagnum* under base-rich and mesotrophic conditions, and in the *Sphagnum*-dominated phase under acidic and oligotrophic conditions.

Type HdV-827 (Plate 1, Figs 18a–18e)

Square-shaped algal (zygomataceous?) spores, $18\text{--}20 \times 18\text{--}20\text{ }\mu\text{m}$ in size, with concave sides and a characteristic sponge-like structured brown wall, thickened at the corners.

In the present study, this spore occurs at the Stobbenribben site during the transition to the *Sphagnum* phase, in mesotrophic and still rather alkaline conditions.

Appendix B. Stobbenribben and Westbroek radiocarbon dating

B.1. Radiocarbon dates

Sample	Depth (cm)	Number	^{14}a (%)	^{14}C age (BP)
Stobbenribben 1	20	GrA-61962	112.45 ± 0.37	–
Stobbenribben 2	35	GrA-61965	143.97 ± 0.42	–
Westbroek 1	10	GrA-60711	106.09 ± 0.42	–
Westbroek 2	18	GrA-60712	117.13 ± 0.46	–
Westbroek 3	23	GrA-60713	115.59 ± 0.45	–
Westbroek 4	27	GrA-60715	95.57 ± 0.39	364 ± 33
Westbroek 5	33	GrA-60718	96.69 ± 0.40	270 ± 33

Here the ages have not been rounded (normally the rounding is done based on significant numbers, which is 5 in this case).

The ^{14}C concentrations are reported according to the convention (i.e. measured relative to the oxalic acid standard; isotopic fractionation is corrected for using ^{13}C ; ages are calculated using the half-life of 5568 years) (Mook and Streurman, 1983).

Nuclear bomb tests between 1950 and 64 increased the atmospheric ^{14}C content. The maximum is a factor of roughly 2 in 1963. For that year ^{14}a is about 2 or 200%. It is meaningless to express the ages of samples in BP because those would be expressed as large negative numbers. For that reason the laboratory reports such measures in ^{14}a (or F^{14}C , which is equivalent).

B.2. Calibration

Calibration is the conversion of ^{14}C BP dates into calendar years AD/BC.

For the calibration of ^{14}C measurements, the curve IntCal13 (Reimer et al., 2013) is used for dates younger than 1950 (or $^{14}\text{a} < 1$). For the bomb peak ($^{14}\text{a} > 1$), the record of atmospheric ^{14}C concentrations for the Northern Hemisphere zone 1 (Hua et al., 2013) is used as an extension of IntCal13.

The plots below (Figs. B1–B5) show the results for Stobbenribben samples 1 and 2, for Westbrook samples 1, 2, 3 (based on Northern Hemisphere zone 1), and for Westbrook samples 4 and 5 (based on IntCal13). Fig. B1 Calibration curve for ST1.

B.3. Summary of the results

Stobbenribben 1 (20 cm)
 Stobbenribben 2 (35 cm)
 Westbrook 1 (10 cm)
 Westbrook 2 (18 cm)
 Westbrook 3 (23 cm)

1957–1958 or 1993–1996
 1962–1963 or 1972–1974
 (1957*) or 2005–2008
 1958 or 1988–1989
 (1958*) or 1989–1991

(continued)

Westbroek 4 (27 cm)	1458–1522, 1576–1585 or 1590–1624
Westbroek 5 (33 cm)	1524–1559, 1564–1569, 1631–1665 or 17,866–1793

The dates have been calibrated straightforward, the 1-sigma results shown in the table. For Westbroek 1 and 3. 1957/1958 is not given by the programme because the probability is not within the 1-sigma range. However, it becomes significant at the 2-sigma level. We have included these solutions by (*) in the table.

B.4. Discussion

The numbering Stobbenribben 1–2 follows the sample sequence from top to bottom, ST1 (20 cm) being more recent than ST2 (35 cm). This allows us to exclude the date interval 1957–1958 for ST1, meaning ST1 corresponds to the date interval 1993–1996. According to Bergmans (1975) vegetation survey of Stobbenribben, in 1973 *Typha angustifolia* was well established at the sample location. This does not exclude the 1972–1974 interval for ST2 but because the species was already well established, it makes it most probable that ST2 corresponds to 1962–1963.

The numbering Westbroek 1–5 follows the sample sequence from top to bottom. When we combine the knowledge about the vegetation development of the site (based on field observations in the past) and the recorded sequence based on microfossils and macroremains we can exclude some of the dating intervals as given above.

Westbroek radiocarbon samples 1, 2, 3, 4 and 5 respectively correspond to depths 10 cm, 18 cm, 23 cm, 27 cm and 33 cm. The Westbroek core sample was taken on a plot where *Calliergonella cuspidata* was dominating in 1988. According to the paleoecological diagram of the local vegetation succession in Westbroekse Zodden, *C. cuspidata* roughly comes in at depth 15 cm and disappears again roughly at depth 9 cm. 1988 must then roughly be situated between depths 9 cm and 15 cm. Westbroek sample 2 (18 cm depth) and Westbroek sample 3 (23 cm depth) have the option of being situated around 1988 but sample 2 is closest to the 9–15 cm interval for the occurrence of *C. cuspidata*. Moreover, keeping in mind that chronologically Westbroek 2 must come after Westbroek 3, 1989–1991 can be excluded for Westbroek 3 and 1958 can be excluded for Westbroek 2. For Westbroek 1, the only possible option with the sequence is 2005–2008. Based on stratigraphical positions, Westbroek 4 being younger than Westbroek 5, we can exclude some of the time intervals of the probability distribution in calendar ages. Thus Westbroek 4 is situated around 1576–1585 or 1590–1624 and Westbroek 5 around 1524–1559 or 1564–1569.

B.5. Summary of the final dating results

Name	Location	Depth (cm)	Material	Lab number	¹⁴ a (%)	¹⁴ C age (BP)	Calibrated (final) ages
ST1	Stobbenribben	20	– Betula seeds – Carex seeds – Vegetative remains	GrA-61962	112.45 ± 0.37	–	1993–1996
ST2	Stobbenribben	35	– Betula seeds – Carex seeds	GrA-61965	143.97 ± 0.42	–	1962–1963
WB1	Westbroek	10	– Betula seeds – Carex seeds – Vegetative remains	GrA-60711	106.09 ± 0.42	–	2005–2008
WB2	Westbroek	18	– Carex seeds – Juncus seeds	GrA-60712	117.13 ± 0.46	–	1988–1989
WB3	Westbroek	23	– Carex seeds – Juncus seeds	GrA-60713	115.59 ± 0.45	–	1958
WB4	Westbroek	27	– Juncus seeds – Vegetative remains	GrA-60715	95.57 ± 0.39	364 ± 33	1576–1585 or 1590–1624
WB5	Westbroek	33	– Carex seeds	GrA-60718	96.69 ± 0.40	270 ± 33	1524–1559 or 1564–1569

Appendix C. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.revpalbo.2016.07.007>.

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