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CHAPTER X CLIMATE AND PEATLANDS

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X.1 Introduction

Following the pioneering work of Blytt (1876), Sernander (1908) and Von Post and Sernander (1910), peatlands are currently regarded as important potential archives of climatic changes (Blackford, 2000; Chambers and Charman, 2004). Peatlands cover around 4.3 million km² of the world's surface, and although most extensive peatlands are found particularly in the cooler regions of the Northern Hemisphere, they are also located in the tropics and in the Southern Hemisphere (Chambers and Charman, 2004). Palaeoclimatic research based on peat provides important information on past climates for many regions in the world. Climatic changes throughout the Holocene have been reconstructed from peat, using a wide array of biological, geochemical and mineral proxies. Many different proxy-indicators can be derived from peat cores, allowing for a multi-proxy approach for climatic reconstructions (Chambers and Charman, 2004). Peat-based climatic and environmental reconstructions are currently available from many sites in Europe (see e.g. Hughes et al., 2000; Barber et al., 2003; Chambers and Charman, 2004), North America (e.g. Nichols et al., 2006; Jones et al., 2009), South America (e.g. Chambers, 2007; Markgraf et al., 2007), New Zealand (e.g. McGlone , 2002; Hajdas et al., 2006), South Atlantic Islands (e.g. Van Der Putten et al., 2004; McGlone et al., 2007) and Australia (e.g. Fletcher and Thomas, 2007; Muller et al., 2007). Such studies complement other terrestrial reconstructions (based on e.g. tree-rings or lake sediments) and thereby provide a more complete reconstruction of past climatic and environmental changes (e.g. Kokfelt et al., in press).

Ombrotrophic peatlands, in particular, are frequently used for climatic reconstructions since their waterbalance and nutrient status depends on the input of atmospheric water and evapotranspiration from the bog surface (see Charman (2002) for a description of different peat bog types). In peatland systems that function close to their climatic thresholds, small changes in external factors may cause large alterations in ecosystem functioning, making these areas sensitive indicators of past as well as current climatic changes. For example, monitoring studies on peatlands in the Alpine region (e.g. Bragazza, 2008) and in the discontinuous permafrost regions of northern Fennoscandia (e.g. Christensen et al., 2004) have indicated the high sensitivity of these systems to climatic change.

Currently, much research is focused on the role of peatland areas as potentially large sources and sinks of carbon dioxide and methane (e.g. Christensen et al., 2004; Johansson et al., 2006). High-latitude wetland ecosystems play an important role in the global carbon budget as they store up to one-third of global soil carbon (Beilman et al., 2008). In general, these ecosystems are net sinks for atmospheric CO₂ owing to the prevailing waterlogged, anoxic and cool conditions that effectively reduce decomposition rates, thereby favouring the formation of peat. However, these conditions also favour anaerobic decomposition, making wetlands significant sources of atmospheric methane (Ström and Christensen, 2007). In a warming climate, the release of methane due to permafrost decay may have strong and unexpected feedbacks on the

global climate (e.g. Zona et al., 2009), and improved estimates of the amount of greenhouse gases and their rate of release are required. Although peatlands in permafrost areas receive most attention in the greenhouse gas debate, the large number of mined peatlands in northwest Europe, when restored, could potentially also act as a considerable carbon store (Moore, 2002; Samaritani et al., *in press*).

Here we review recent developments in a selection of climate proxy-indicators, as well as advances in dating methods. Reconstructions of atmospheric CO₂ from subfossil leaves as well as the potential impact of CO₂ changes on plant physiology are also discussed. We then briefly review recent findings on climatic changes reconstructed from peatlands. In the third section we focus on the role of peatlands as sources and stores for carbon dioxide and as sources for methane. Sub-arctic paludal mires are used as an example of extremely climate-sensitive ecosystems. Next, the possible regeneration of mined peatbogs in Western Europe is considered in detail.

X.2 Peatlands as archives of past climate variability

With an increasing number of proxy reconstructions from peat bogs becoming available from many regions in the world, a direct comparison between records from different sites and different archives can be made. In theory, a compilation of multi-proxy reconstructions from different terrestrial archives in one region covers more climatic factors and seasons than reconstructions based on only one type of archive. However, for a reliable comparison two factors are of crucial importance: chronological errors must be minimal, and the 'climatic' meaning of each different proxy must be clear. Below we discuss a selection of frequently used proxies and recent developments in each field, as well as advances in dating techniques and examples of modern studies applying these techniques. An overview of additional proxy methods can be found in Blackford (2000), Charman (2002) and Chambers and Charman (2004).

X.2.1 Chronologies of wetlands

Author: Maarten Blaauw

Peat stratigraphy was applied early to estimate the ages of layers in peat (von Post, 1946). Layers of different peat composition were thought to reflect past climate changes, and the superposition of these layers, when linked to independent dating evidence (e.g., the Swedish varve chronology, links of pollen zones in peat with archaeological zones), allowed for chronologies at millennial precision.

These chronologies were relative, at best, because they depended on inferred temporal links (simultaneous reactions) with other archives that did possess independent chronologies. With the application of radiocarbon dating from the 1950s, absolute instead of relative ages could now be obtained, resulting in precisely and independently dated wetland archives (as long as the carbon in the organic matter is younger than the limit of ^{14}C dating at 50,000 ^{14}C years). Indeed, ^{14}C dating of pollen zones across the British Isles led Smith and Pilcher (1973) to reject the previous paradigm that these zones were simultaneous over large areas.

For ^{14}C dating of a peat core, generally organic material is sampled at regular intervals or at depths with major proxy changes across the core. As only milligrams of carbon are needed for an AMS (accelerator mass spectrometer) ^{14}C date, a cubic centimetre of bulk peat (or several milligrams of selected fossil plant remains such as leaves, seeds or pollen) often contains sufficient carbon. However, small amounts of contamination with modern carbon can result in unreliable dates, so care should be taken to remove unwanted material.

Radiocarbon dating of tree rings with dendrochronologically obtained calendar ages calibration of the ^{14}C time scale (Reimer et al., 2004). Resulting calibrated age confidence intervals are often considerably larger than the original lab-provided measurement uncertainties, especially during periods where the calibration curve shows wiggles or plateaux. For peat deposits spanning the last few decades to centuries, other types of dating can additionally be applied, e.g., bomb-pulse ^{14}C dating (van der Linden et al., 2008) or lead-210 (^{210}Pb) dating (Turetsky et al., 2004). Moreover, well-dated volcanic ash layers can provide additional precise dating points, and can also be used to link together proxy archives across a region (Pilcher et al., 1995).

Constraints with dateable material, and often funding prohibit dating at dense sediment interval, and additionally ^{14}C dates themselves can show considerable scatter (Scott, 2007). Therefore some form of interpolation is needed to provide age models for each level of a core. The most basic method for such age-depth model is linear interpolation between the depths and ages of the dated levels (Bennett, 1994). More ecologically realistic age-depth models include linear accumulation (at least over limited time intervals; Belyea and Clymo, 2001; Blaauw and Christen, 2005), convex models (as deposits reach a height limit; Belyea and Baird, 2006), concave models (owing to decomposition of fossil matter; Yu et al. 2001), and flexible Bayesian 'Poisson' models (Bronk Ramsey, 2007). Each type of model has its merits and limitations, and the choice of age-depth model will impact the on the age estimates assigned to depths in a peat core (Bennett and Fuller, 2002; Telford et al., 2004; Yeloff et al., 2006; Blockley et al., 2007).

A special case of age-model which has been studied intensively in peat deposits is ^{14}C wiggle-match dating, where wiggles in high-density ^{14}C dated sections of a core are matched to those of the ^{14}C calibration curve by assuming linear accumulation rates (van Geel and Mook, 1989; Christen et al., 1995; Kilian et al., 1995; 2000; Mauquoy et al., 2002b; Blaauw et al., 2003; Blaauw and Christen, 2005). This works best during periods where the calibration curve shows major wiggles, e.g., during the Little Ice Age (Mauquoy et al. 2002b) or around c. 3000-2000 years ago (Kilian et al., 1995, 2000). Although ^{14}C wiggle-match dating is a time-consuming and expensive method as dozens of ^{14}C dates are needed, it can provide age-models at (multi-) decadal precision. Moreover, using Bayesian methods, additional information such as prior knowledge of accumulation rates or hiatus sizes can be included to obtain more realistic age-models (e.g. Blaauw and Christen, 2005).

Whereas it is important to obtain reliable age-models for single peat cores, it is just one step towards their environmental interpretation. Indeed, any fossil proxy archive should be put in context with other contemporary archives in the region and beyond, in order to be of use for constructing past environmental conditions. For such analyses, reliable age-models are needed, as well as quantitative comparisons of leads, lags or simultaneous events between cores, sites and regions. Although most comparisons to date have been through subjective visual comparisons, quantitative alternatives are

emerging (Blaauw et al., 2007; Blaauw et al., *in press*; Parnell et al., 2008; Charman et al., 2009). Through applying recent numerical methods to peat proxy archives, we are now able to obtain realistic estimates for the ages, uncertainties and spatiotemporal nature of past environmental events.

X.2.2 Determination of peat humification

Author: Frank M. Chambers

Peat humification is a measure of the degree of peat breakdown or decomposition, most of which is assumed to take place while the plant (and other) material is in the upper part of the peat- the aerated acrotelm, the assumption being that far less breakdown occurs below in the permanently saturated catotelm (Clymo, 1984; Belyea and Clymo, 2001). The degree of peat humification is therefore taken to indicate the prevailing environmental conditions at (or shortly after) the time of peat accumulation (Aaby and Tauber, 1975), with dark-coloured highly humified peat indicating dry or warm conditions (and so either a longer time in the acrotelm, or faster decomposition), and light-coloured unhumified peat accumulating under wet or cool conditions (with a short transfer time to the catotelm, or a slow rate of decomposition). It can be assessed visually in the field using von Post's 10-point scale (von Post and Granlund, 1926), or Troels-Smith's (1955) 5-point scale, or by using a range of measures (colour; fibrosity, etc.). The most widely used laboratory technique is colorimetry, based on light-absorbance or light transmission measured by colorimeter or spectrophotometer at a fixed wavelength through an alkali extract of 0.2 g dried and ground peat (see Blackford and Chambers, 1993, for review; <http://www2.glos.ac.uk/acrotelm/humproto.html> for laboratory protocol).

The colorimetric technique was first applied on *Sphagnum*-rich raised mire peats in Denmark (Bahnsen, 1968; Aaby and Tauber, 1975; Aaby, 1976). Its potential for providing a proxy-climate signal from highly humified blanket peat was then explored by Chambers (1984). It has since been applied in a range of peat types, especially in Northwest Europe (e.g. Blackford and Chambers, 1991; Nilssen and Vorren, 1991; Roos-Barracough *et al.*, 2004; Borgmark, 2005) but also in North America (e.g. Booth and Jackson, 2003) and more recently, in South America (Chambers *et al.*, 2007a). It has been regarded as one of three standard principal proxy-climate indicators from peats (cf. Hughes *et al.*, 2006), the other two being macrofossil analysis (see Mauquoy, this chapter), and analysis of testate amoebae (see Lamentowicz, below).

The strengths of the technique are that it is easy to use; can be applied on slim (0.5 or 1 cm) contiguous slices of peat, providing a continuous record; is largely operator-independent (provided the batches of samples adhere to a strict time schedule); and the data are easily graphed for visual inspection and interpretation. It can also provide proxy-climate information in those parts of a *Sphagnum* peat core in which the peat macrofossil composition is largely uniform, being 'locked in' to a species dominant, such as *Sphagnum austinii* (*S. imbricatum*), or *S. magellanicum*, and so not able to provide any indication of climate change.

Practitioners have focussed on identifying 'wet shifts', when relatively unhumified peat succeeds well-humified peat, as these are thought to be less susceptible to secondary

decomposition, and were believed easier to date using conventional bulk-sample radiocarbon dating, as the peat may be accumulating faster. In moisture-receiving (as opposed to moisture-shedding) peat macrotopes, such as valley or basin mires, the degree of peat humification may instead indicate the balance between the amount of woodland (with moisture interception and high evapotranspiration in the catchment) and the degree of woodland clearance and agricultural land-use (and so higher run-off) from surrounding land (Chambers, 1988).

The weaknesses of the technique include the question as to what compounds are being measured and what the data really indicate; that there is likely to be a plant-species signal in the data (Chambers et al., 1997; Yeloff and Mauquoy, 2006); that (theoretically) there may be secondary decomposition if a very dry spell of climate succeeds a wet period; and that the technique can in some peat horizons give contrary indications from other peat proxy-climate techniques, especially testate amoebae data, with no clear explanation. It is problematic when used in sedge-rich peat, as very different readings can arise from adjacent samples if one sample mainly comprises decay-resistant sedge macrofossils (e.g. *Eriophorum*, with the appearance and texture of frayed string), and the next comprises more humified material. The assumption that the use of alkali will extract mainly humic (and fulvic) acids has been questioned by Caseldine et al. (2000), and explored using size-exclusion chromatography by Morgan et al. (2005).

In recent years, multi-proxy approaches, particularly using the three principal proxy-climate measures referred to above, have become more common, but how to combine the data to derive a single 'bog-wetness climate proxy' (e.g. Hughes et al., 2006) remains problematic, especially when the temporal resolution of macrofossils and testate amoebae often does not match that of peat humification: of the three, it was the technique that is likely to be conducted on the thinnest samples, and always contiguously, so providing a higher-resolution proxy-record of climate change. Even in cores in which all three are conducted contiguously on the same thickness of samples, the contra-indications may be important, albeit difficult to interpret or explain, and so it may be more appropriate to present all three supposed climate-proxies separately. Despite reservations expressed by Yeloff and Mauquoy (2006), which were based on a comparison of peat humification and macrofossil data from a single profile, the peat humification colorimetric technique has much to recommend it, and may be the only one of the three that is feasible in highly humified peats containing few testate amoebae. Nevertheless, chronological control is important, and it is recommended that radiocarbon dating be conducted on small samples of above-ground plant components (preferably *Sphagnum* leaves) using AMS, and that samples be grouped for potential ¹⁴C wiggle-match dating (see Blaauw, above). In view of the potential role of solar forcing on both climate and cosmogenic isotope production (Beer and van Geel, 2008), it may be no coincidence that 'wet-shifts', identified in peat cores by marked changes in peat humification, provide the best periods for potential wiggle-matches (cf. Mauquoy et al., 2004), although a brief dry shift featured in a successful wiggle-match in Tierra del Fuego (Chambers et al., 2007a), in which both the peat humification and plant

macrofossil data suggested a dry interlude at precisely the same time (2650 ¹⁴C yrs BP; 2800 cal. BP) as a pronounced wet shift in continental Europe (e.g. Speranza et al., 2000, 2002).

X.2.3 Peat Macrofossils

Author: Dmitri Mauquoy

Sub-fossil plant macrofossils of mosses, dwarf shrubs and graminoids preserved in peat samples have been used to reconstruct the temporal variability of local peat bog vegetation in hummock/hollow complexes at the microform scale (McMullen et al., 2004; Blundell et al., 2007). The preservation of the macrofossils in these samples can be excellent and species level identification of taxa is frequently possible. Multiple profiles have also been recovered from single raised peat bogs to reconstruct the spatial and temporal variability of peat bog vegetation at the mesoform scale (Barber et al., 1998; Hughes et al., 2000; Mauquoy et al., 2002a). Deposits collected from ombrotrophic (rain-fed) peat bogs have largely been used to make palaeoclimate reconstructions, since a range of *Sphagnum* mosses, Cyperaceae and dwarf shrubs are sensitive to changes in mire surface wetness which is in turn dependent upon changes in precipitation and temperature (Barber and Charman, 2003, Barber et al., 2004; Mauquoy et al., 2008). The macrofossil data produced from this research have also been used to reconstruct peatland carbon accumulation rate changes (Oldfield et al., 1997; Mauquoy et al., 2002a; Heijmans et al., 2008) and the identification of successional processes in peatlands, for example the nature and timing of the fen-bog transition (Hughes and Barber, 2004). Macrofossil data generated using plant macrofossil data are also valuable in applied palaeoecological research, since long-term base line data for the origin, nature and potential causes of local vegetation changes can be generated. This information can then be used to guide and aid conservation of threatened blanket peat and raised peat bog ecosystems (Chambers et al., 1999; 2007b). The nature and timing of recent human disturbance to ombrotrophic bogs, for example burning and drainage, has also been assessed (Pellerin and Lavoie, 2003). Macrofossil analyses can help to ensure the generation of precise and accurate ^{14}C chronologies since above-ground parts of identified plants can be selected for ^{14}C AMS dating (preferably *Sphagnum* stems and leaves free of fungal contamination), and cyperaceous roots and the stem bases and attached lower parts of *Eriophorum vaginatum* leaves can be avoided (Mauquoy et al., 2004). These have been shown to be younger (because of downward growth) than bryophyte fragments in the same ^{14}C dated stratigraphic levels (Kilian et al., 2000). Accurate and precise chronologies generated using ^{14}C Bayesian chronologies on peat sequences have served to pinpoint rapid environmental changes, and possible climate forcing factors, for example changes in solar activity (Mauquoy et al., 2004). Peat sequences are also capable of providing high-resolution studies as a ~1310 year old peat profile from Denmark recorded rapid accumulation rates up to 2–3 yr cm⁻¹ (Mauquoy et al., 2008).

Selective preservation is a potential limitation with the analyses of mire and peat macrofossils, particularly for the above-ground parts of dwarf shrubs and Cyperaceae. Regarding the identification of mire and peat macrofossils, an excellent overview is presented by Birks (2007), whilst identification plates are available in Mauquoy and van

Geel (2007, see Figure 4.33). Decay-resistant *Sphagnum* mosses have different decomposition rates (Johnson and Damman, 1991). It is not always possible to identify *Sphagnum* species to the lowest taxonomic level, particularly where their stem leaves are absent. Cyperaceous remains are also difficult to identify consistently, since in many instances seeds and diagnostic epidermal tissues are simply not present. Owing to these problems, successional and/or palaeoclimate reconstructions produced from mire and peat macrofossils need to be interpreted cautiously and ideally should be combined with other techniques, such as pollen, non-pollen and testate amoebae analyses (Swindles et al., 2007; Yeloff et al., 2007).

Quantitative reconstructions of mire surface wetness which use the relationship between the modern peat-forming vegetation and water-table depth are now possible (Väliranta et al., 2007). Transfer functions have been generated using plant macrofossils in the same way as those applied to testate amoebae data (Charman et al., 2007), and offer the prospect of more refined water-table depth reconstructions using plant macrofossil data. A key question regarding raised peat bogs is what ultimately drives local water table depths: summer precipitation or temperature? It is highly important to identify this in order to provide accurate palaeoclimate data for the climate modelling community. Correlations between instrumental measurements of water table depths and climate variables presented in Charman et al. (2009) suggest that water-tables in Northwest European peat bogs are controlled by warm season moisture deficits, and these deficits are more strongly correlated with precipitation than with temperature. More analyses of the relationships between climate variables and water table depths in other regions will serve to confirm the importance of warm season moisture deficit.

Since northern peatlands store a large proportion of global soil carbon (Beilman et al., 2008), there is an important need to understand how carbon sequestration rates in peatlands in the boreal and subarctic regions have responded to previous periods of climate change. This may give clues to their likely future response to projected climate warming scenarios. Given that the rate of carbon accumulation has been shown to be dependent upon the botanical composition of peat deposits (Oldfield et al., 1997; Mauquoy et al., 2002a), more of these studies are needed to identify the spatial and temporal response of northern peatlands to former episodes of climate change. In the Mauquoy et al. (2002a) study, peat accumulation rates decreased during Little Ice Age climatic deteriorations following the Medieval Warm Period, owing to the presence of aquatic *Sphagnum cuspidatum* leaves. These have lower decay resistance than *Sphagnum* section *Acutifolia* and *Sphagnum imbricatum* leaves. Future research will serve to confirm the importance of species composition upon reconstructed carbon accumulation rate changes.

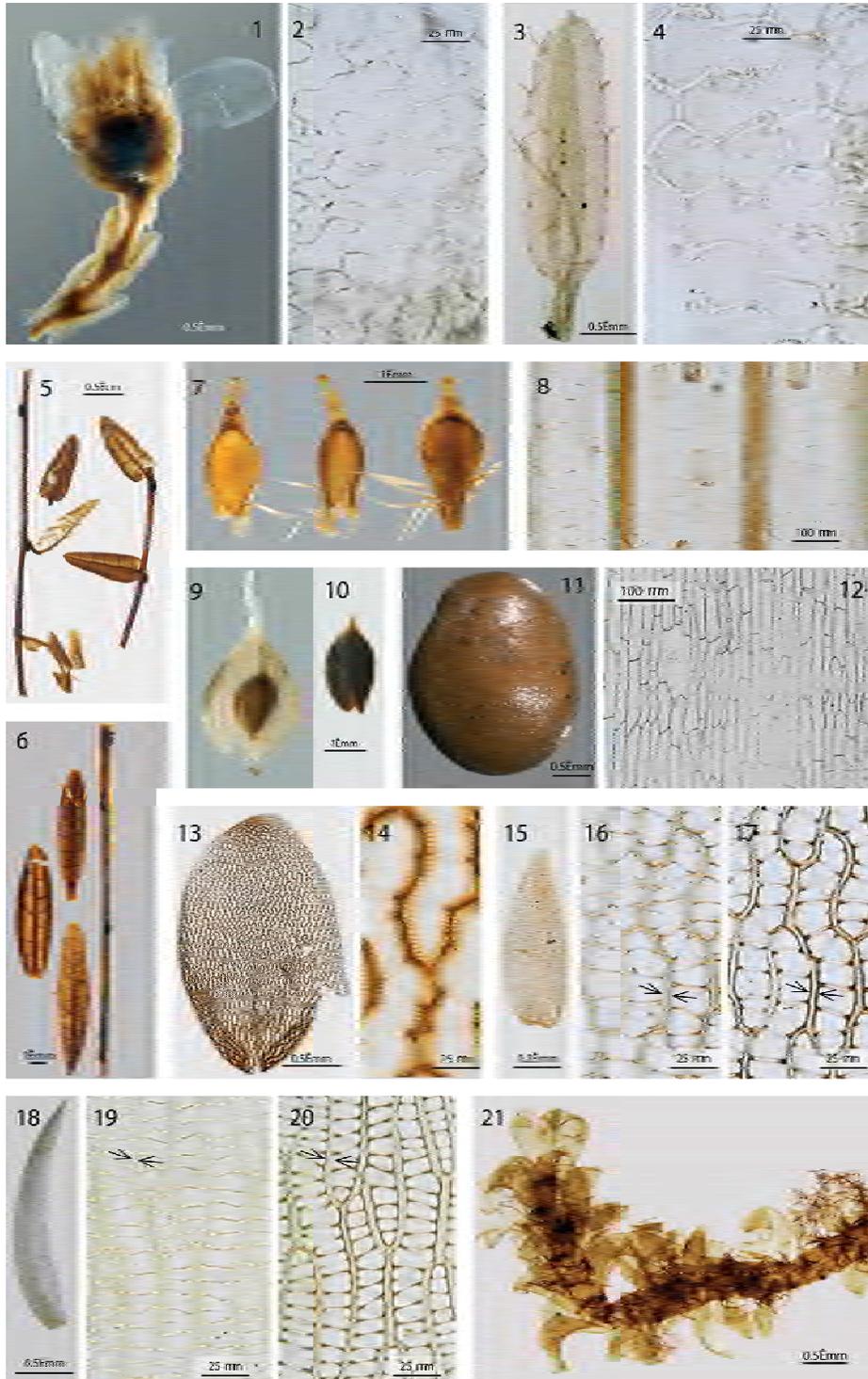


Figure X.1. 1 and 2: *Calluna vulgaris*, stem with flower and leaf epidermis. 3 and 4: *Erica tetralix*, leaf and leaf epidermis. 5: *Vaccinium oxycoccus*, twigs with leaves. 6: *Andromeda polifolia*, leaves and twig. 7: *Rhynchospora alba*, seeds. 8: *Eriophorum vaginatum*, epidermis. 9 and 10: *Carex rostrata*, perigynium and achenes. 11 and 12: *Menyanthes trifoliata*, seed and leaf epidermis. 13 and 14: *Sphagnum austinii*, leaf. 15-17: *Sphagnum* sect. *Acutifolia*, leaf and ventral high and low focus. 18-20: *Sphagnum* sect. *Cuspidata*, leaf and ventral high and low focus. 21: *Paludella squarrosa*. This figure was kindly provided by B. van Geel.

X.2.4 Testate amoebae

Authors: Mariusz Lamentowicz and Edward A. D. Mitchell

Testate amoebae are unicellular organisms that live mainly in fresh water, soils, mosses, sand and lake sediments and are especially abundant and diverse in peatlands. They are divided into two taxonomic groups, having either lobopodia (Arcellinida) or filopodia (Euglyphida and related Cercozoan testate amoebae) (Meisterfeld, 2001a, 2001b). They form shells (tests) of different types (agglutinating, idiosomic, and proteinaceous) that are used for identification of living as well as fossil testate amoebae (Figure 4.34). Testate amoebae play an important functional role in the cycling of elements in terrestrial ecosystems (Schröter et al., 2003; Aoki et al., 2007; Wilkinson, 2008).

The structure of testate amoeba communities in peatland varies in relation to ecological gradients such as moisture and water chemistry (Lamentowicz et al., 2008a; Mitchell et al., 2008a). Their shells are well preserved in peat deposits, thus allowing palaeoenvironmental reconstructions (Charman, 2001). The analysis of subfossil testate amoebae is also a useful tool for the management of peatlands (Buttler et al., 1996; Davis and Wilkinson, 2004; Mitchell et al., 2008a). The link between climate and testate amoeba assemblages is strong as they depend directly on micro-macroenvironmental conditions that are strongly affected by climate. They provide information on the coring location as they live, die and remain *in situ* in the peat. This tight link between local conditions and testate amoeba assemblages allows for detailed ecological reconstructions. However, this ecology is in part also controlled by non-climatic autogenic processes in the peatland as well as by direct and indirect human impact (e.g. on local hydrology).

The taxonomy of testate amoebae is complex and confusing. Taxonomy was, until recently, based only on morphological criteria, but molecular methods have been introduced in combination with detailed morphological analyses (e.g. by scanning electron microscope). This combination reveals a higher than expected diversity (Lara et al., 2008; Lara et al., 2007) and the existence of pseudo-cryptic species (i.e. genetically different but with morphological differences that are easily overlooked when observed under light microscope or that can be seen only with a scanning electron microscope).

(Wylezich et al., 2002; Todorov et al., 2009; Heger et al. *submitted*). This has been reported for other groups of protists as well (Pawlowski and Holzmann, 2002; Saez et al., 2003).

As a prerequisite to their use in paleoecology, the ecology of testate amoebae in peatlands has been studied extensively, e.g. in Canada (Warner, 1987; Charman and Warner, 1997), New Zealand (Charman, 1997), the United States (Payne et al., 2006; Booth, 2008), the Jura Mountains of Switzerland and France (Mitchell et al., 1999), the Swiss Alps (Lamentowicz et al., 2009c), Russia (Mazei and Embulaeva, 2009; Mazei et al., 2009; Muller et al., 2009), the United Kingdom (Woodland et al., 1998), Finland (Tolonen et al., 1994a; Tolonen et al., 1994b), Poland (Lamentowicz and Mitchell, 2005; Lamentowicz et al., 2008c), Greece (Payne and Mitchell, 2007), Turkey (Payne et al., 2008) and for Europe in general (Charman et al., 2007). Most ecological studies showed a strong correlation between testate amoeba community structure and bog surface wetness (usually expressed as water-table depth) in controlling the assemblages of testate amoebae in ombrotrophic peatlands (e.g. Blundell et al., 2008; Charman, 2007; Charman et al., 2006; Hendon et al., 2001). The rationale behind these different studies is that, depending on the biogeographical and climatic location, testate amoeba faunas and the responses of cosmopolitan taxa to ecological gradients may differ. For that reason, high-quality training sets from the same biogeographical and climatic settings are preferred for reliable palaeoclimatic reconstructions.

Although a relatively large number of ecological and palaeoecological studies of peatland testate amoebae have been published, the geographical distribution of the research effort is uneven. For Western Europe a large number of studies and training sets are available, in particular from the UK, where a regional curve of water table change was constructed on the basis of subfossil testate amoebae (Charman et al., 2006; Blundell et al., 2008; Swindles et al., 2009). However, in Eastern Europe testate amoebae are not yet extensively used as a tool in palaeoecological research; to this date only four peatlands in Poland have been studied (Lamentowicz et al., 2007, 2008b, 2008c, 2009b). A new training set for testate amoebae in Poland was recently developed (Lamentowicz et al., 2008c). These studies have provided data on climatic change (wet and dry phases) and human impact on the landscape (deforestation and peatland exploitations) during the last centuries and millennia (Lamentowicz et al., 2008b, 2009b; De Vleeschouwer et al., 2009). In the Alpine region so far only a few studies have used testate amoebae as a tool for palaeohydrological reconstructions. Modern feedbacks between temperature, hydrology and precipitation in Alpine peatlands are not well known. The first testate amoeba training set from the Alpine region was constructed on the basis of samples collected in the Engadin Valley (south-east Switzerland) from a variety of peatland types (Lamentowicz et al., 2009c). This transfer function was applied to a finely sub-sampled core (near-annual resolution) from the Mauntschas peatland to reconstruct variations in the water table during the past 135 years (Lamentowicz et al., 2009a). Comparison with measured temperature data showed a correlation to air temperatures since AD 1864..

Studies describing more environmental variables than water table depth and/or including other groups of organisms such as plants are very rare (Tolonen et al., 1994a). Minerotrophic peatlands (fens) have more plant and testate amoebae species and are characterized by a complex hydrochemistry (Heal, 1961; Hájek et al., 2006; Opravilova and Hájek, 2006). More work is needed over broader ecological gradients than just *Sphagnum*-dominated peatlands of the temperate to boreal zones, and including several key ecological variables, as well as comparative studies of different groups of organisms. Such studies would allow for an improved assessment of the bioindicative potential of each species in neoecology (restoration ecology) and palaeoecology.

Outlook

Testate amoeba analysis is now a well-established method in Quaternary science and, despite several shortcomings, its progress during the recent decade is very promising (Mitchell et al., 2008a). However, effort should be put into improving this tool to make it even more useful. The three priorities we see are:

1. Taxonomy. Good taxonomy combining morphological and molecular methods is urgently needed. Paleontologists and biologists sometimes use different taxonomic approaches and this causes confusion. Ecologists often pool testate amoebae taxa in species complexes because it is difficult or impossible to identify species with any certainty (Charman et al., 2000). It is therefore unclear if these closely related taxa have different ecological requirements. Future work should aim to determine if these closely related taxa have different ecologies. If this were the case, then using a higher taxonomic resolution would improve the precision of ecological inferences based on testate amoebae.

2. Ecology. Interpretation of testate amoeba communities data requires a sound understanding not only of species-environment correlations but also of the mechanisms responsible for these patterns. Beyond correlative studies such as those currently used to build transfer function models, a good ecological understanding based on a combination of descriptive and experimental studies is essential to support palaeoclimatic reconstructions (Mitchell et al., 2008a). Such studies are, however very rare (Mitchell, 2004; Mitchell and Gilbert, 2004). The integration of descriptive ecological and experimental studies on testate amoebae in field and laboratory conditions will be advantageous. Studies on the fine scale spatial variations in testate amoebae communities and their seasonal patterns are also scarce (Heal, 1964; Mitchell et al., 2000; Warner et al., 2007). Further studies are needed to understand the timing and patterns of testate amoebae response to factors such as temperature and hydrology. For the reconstruction of palaeohydrology of peatlands in general, a challenge is the application of testate amoeba analysis in minerotrophic fens, which also includes the basal part of most peatland palaeoecological records. In fens the complexity of testate amoeba communities and identification increases (Heal, 1961; Lamentowicz et al., 2009a) and most transfer functions do not cover the minerotrophic

end of the gradient well (Mitchell et al., 2008b; Payne and Mitchell, 2009; Wall et al., 2009).

3. Theoretical aspects. Recently several studies have addressed questions such as how the number of counted individuals and the mesh-size of filters used for sample preparation affect the reliability of community estimates and the quality of palaeoecological inferences (Mitchell et al., 2008b; Payne and Mitchell, 2009; Wall et al., 2009). More work is needed to optimize the protocols for sample preparation and analysis.

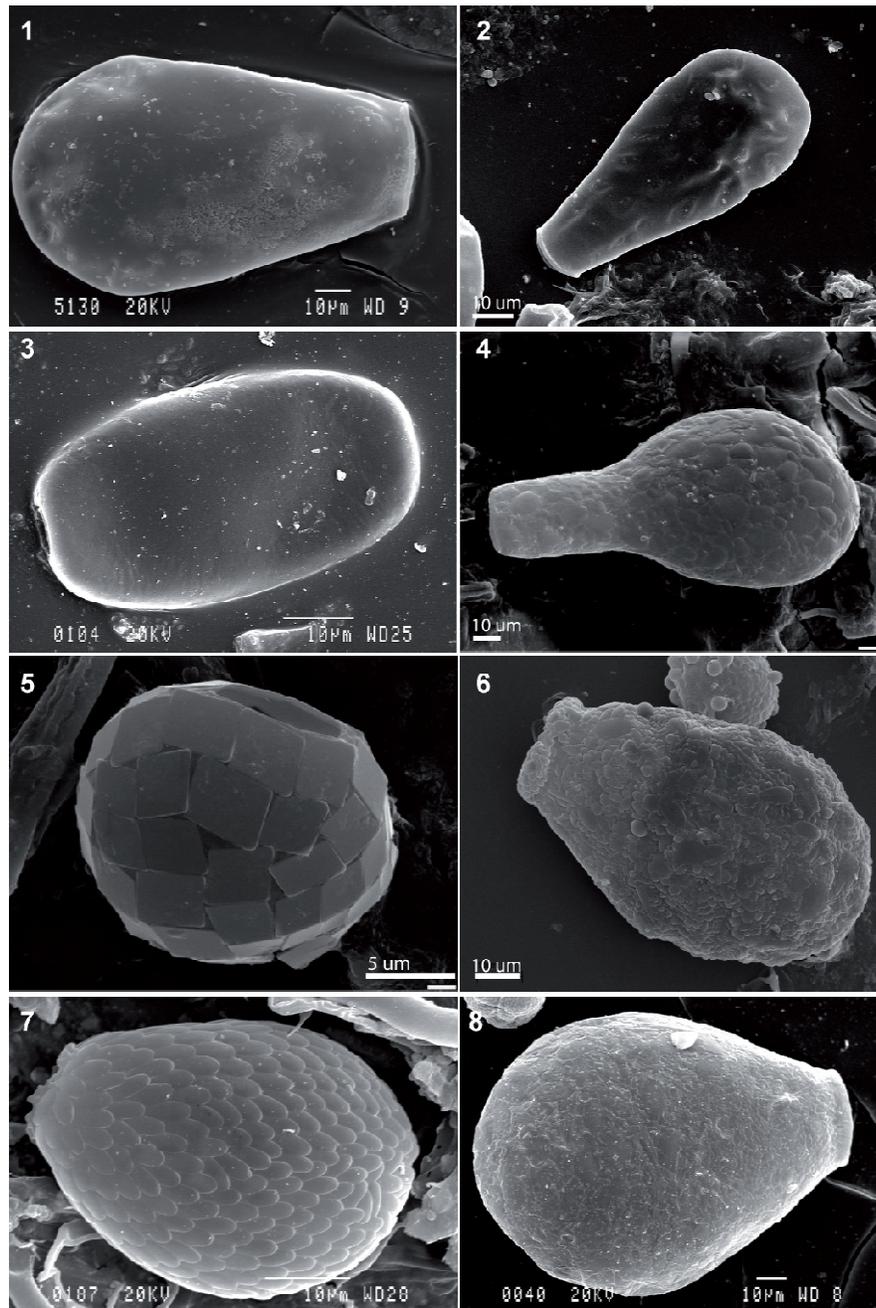


Figure X.2. Scanning electron microscope pictures of selected testate amoebae species from various peatland habitats: 1) *Hyalosphenia papilio* Leidy, 1879 (Phot. M. Lamentowicz); 2) *Hyalosphenia elegans* Leidy, 1879 (Phot. M. Lamentowicz); 3) *Amphitrema flavum* Archer, 1877 (Phot. M. Lamentowicz); 4) *Nebela langeniformis* Penard (Phot. L. Lamentowicz), 1890; 5) *Paraquadrula irregularis* (Archer, 1877) Deflandre, 1932 (Phot. L. Lamentowicz); 6) *Physochilla griseola* Penard, 1911 (Phot. L. Lamentowicz); 7) *Assulina muscorum* Greeff (Phot. M. Lamentowicz), 1888; 8) *Nebela tincta* (Leidy, 1879), Awerintzew, 1906 (Photo M. Lamentowicz).

X.2.5 Biomarker Compounds and Stable Isotope Ratios as Indicators of Environmental Change in Peatlands

Author: Jonathan E. Nichols

X.2.5.1 Biomarkers

Organic biomarkers, or molecular fossils, are recalcitrant compounds whose origin can be traced to a particular taxon of organism. These compounds can be used to create reconstructions similar to traditional plant macrofossils. In peatlands, these compounds are typically produced by plant epicuticular waxes and are especially useful when decay leaves macrofossils unidentifiable. Molecules used in reconstructions can be general indicators of broad groups of plants. Saturated hydrocarbons and their homologues (*n*-alkanes, *n*-fatty acids, and *n*-fatty alcohols) are a typical example. The shorter chain varieties of these molecules (20 to 26 carbons) are produced mainly by *Sphagnum*, while the longer chain varieties (26 to 34 carbons) are produced mainly by vascular plants (Baas et al., 2000; Nott et al., 2000; Pancost et al., 2002). The relative abundance of short and long chain molecules can be used as indicators of the past vegetation assemblages (Nichols et al., 2006). Specific biomarkers, molecules that are produced by plants belonging to only one genus, have also been identified. These include 5-*n*-alkylresorcinols, a biomarker for the family Cyperaceae (Avsejs et al., 2002) and *n*-alkan-2-ones, a biomarker for the genus *Sphagnum* (Nichols and Huang, 2007).

Biomarker methods of paleoenvironmental reconstruction benefit from automation and user-independent results. Traditional methods of counting macrofossils and palynomorphs are time consuming and are dependent on the skill of the person performing the analysis. However, the library of species-specific biomarkers is incomplete; the most useful biomarker reconstructions from peatlands use general biomarkers that distinguish broadly between *Sphagnum* and vascular species.

X.2.5.2 Environmental Stable Isotopes

The natural abundance ratios of stable isotopes of several common elements (H, O, C) can be used as environmental indicators. Hydrogen and oxygen isotopes are used as

indicators of hydrologic change, and carbon isotopes are indicators of carbon cycle and hydrologic cycle changes. Guidelines for interpreting these types of data follow.

Oxygen isotope ratios are typically measured from cellulose extracted from peat. Cellulose is often converted first to nitrocellulose to eliminate exchangeable oxygen atoms from the molecule. The cellulose itself can be extracted from bulk peat, or from picked *Sphagnum* macrofossils. Extracting cellulose from picked macrofossils can be time-consuming, and can result in low cellulose yields, as compared with bulk peat. However, isotope measurements from a single taxon are much easier to interpret. Hydrogen isotopes are typically measured from leaf-wax biomarkers (*n*-alkanes and *n*-fatty acids) using an isotope ratio mass spectrometer coupled to a gas chromatograph through a continuous flow device. Carbon isotopes can be measured both from cellulose and from leaf-wax compounds (Xie et al., 2004).

X.2.5.3 Hydrogen and Oxygen Isotopes

Since the ultimate source of the hydrogen and oxygen isotope ratios (δD and $\delta^{18}O$) of *Sphagnum* molecules is environmental water, these measurements are an excellent way of tracking past changes in the hydrologic cycle. The sediments of ombrotrophic peatlands are particularly well suited to this task as the only input of water to these systems is by direct precipitation. The hydrogen and oxygen isotopic composition of *Sphagnum* molecules is therefore dictated by two factors: the isotopic composition of the precipitation and any enrichment by evaporation of water inside and between the *Sphagnum* individuals. The δD and $\delta^{18}O$ of precipitation are extremely useful parameters for paleoclimate reconstructions and provides information about temperature, rainfall amount and moisture source (Clark and Fritz, 1997). The amount of evaporation from peatland surfaces is also an important palaeoclimate parameter which can be gleaned from the δD and $\delta^{18}O$ of *Sphagnum* molecules. Both precipitation isotopes and in-situ evaporation must be taken into account when interpreting hydrogen and oxygen isotope data from peatlands.

X.2.5.4 Carbon Isotopes

Interpretation of carbon isotope measurements of *Sphagnum* molecules can be a complicated matter (Xie et al., 2004). Two competing factors influence the carbon isotope ratio of fossil *Sphagnum* molecules (e.g. cellulose, leaf waxes, etc.). The first is the carbon isotope ratio of the CO_2 used for photosynthesis. Though the preindustrial $\delta^{13}C$ value for atmospheric CO_2 is often assumed constant for the Holocene, not all the CO_2 used by *Sphagnum* comes from the atmosphere. Up to 15% of the CO_2 used by *Sphagnum* can come from recycled methane from lower in the peatland (Raghoebarsing et al., 2005). Because the $\delta^{13}C$ value of methane is so low, (-40‰ to -60‰) it can dramatically affect the ultimate $\delta^{13}C$ of the *Sphagnum* molecules. The amount of recycled CO_2 available to *Sphagnum* is influenced mainly by the wetness of the surface of the peatland. When the peatland is wetter, more methane-derived CO_2 is available at

the surface for use by *Sphagnum* ($\delta^{13}\text{C}$ decreases). A record of $\delta^{13}\text{C}$ of *Sphagnum* lipids from a Norwegian peatland has been interpreted this way to represent surface moisture (Nichols et al., 2009). Wetness of the *Sphagnum* itself also directly influences the $\delta^{13}\text{C}$ of its molecules. When the *Sphagnum* plant is more saturated, the water film over the photosynthetic cells impedes the incorporation of CO_2 and thus the plant becomes less selective against ^{13}C ($\delta^{13}\text{C}$ increases) (Williams and Flannagan, 1996). Because of these competing factors, $\delta^{13}\text{C}$ records derived from peat sequences are, at this time, rare, and must be evaluated carefully.

X.2.6 Sand grain and dust influx in peat bogs as proxies of past circulation strength

Authors: R. de Jong, F. De Vleeschouwer, G. Le Roux

The interest in past atmospheric circulation changes, as well as changes in dust flux, has increased during the recent decades (Goudie and Middleton, 2006). Although past changes in atmospheric circulation vigour and the position of Westerlies have been reconstructed using, for example, sea-salt spray indicators in ice cores from Greenland (e.g. Majewski et al, 1997; Meeker and Majewski, 2002), many reconstructions from north-west Europe are indirect; changes in effective precipitation, reconstructed from glaciers (e.g. Bakke et al., 2008), lake sediments (e.g. Seppä et al., 2005) or peat bogs (e.g. Swindles et al., 2009), are often interpreted in terms of atmospheric circulation changes. However, few records exist that can also be directly interpreted in terms of increased or decreased cyclone frequency and/or intensity. As a result, little is known about this climatic parameter prior to documentary evidence (e.g. Lamb, 1977). In addition, the sources and flux variability of dust storms are poorly understood; however, dust flux is of particular importance as it has strong feedbacks with global (Goudie and Middleton, 2006) and local (Painter et al, 2007) environmental and climatic changes. During the last century, an increase in the frequency of dust storms has been observed for some areas (for example, in North America; Neff et al, 2008). The origin (natural or anthropogenic) of this increase is still poorly understood. Therefore, it is necessary to study the fluctuation of atmospheric dust flux during pre-anthropogenic times in detail.

X.2.6.1 Sand grains in peat deposits

Recently, detailed analysis of mineral sand grains ($> 60 \mu\text{m}$) in peat bogs has been carried out in different studies in North-West Europe (e.g. Björck and Clemmensen, 2004, De Jong et al, 2006; 2009, Sjögren, 2009). These studies discuss the use of the sand particle content in peat bogs as a proxy for past atmospheric circulation characteristics. In raised bogs, in the absence of inflowing streams, non-biogenic mineral particles found in peat cores are assumed to have been transported through the air. However, this is only true if the peat bog is very large, or situated in a flat or gently sloping topography, so that surface runoff onto the peat surface can be excluded as a source for (large) mineral particles (see e.g. Caseldine et al., 2005). In addition, changes in the availability of erodible materials as well as bog microtopography have to be taken into account.

Sand grains are transported either by strong winds alone, or in combination with a snow cover on the peat surface which would facilitate sand grain transport over the bog surface (Björck and Clemmensen, 2004). Therefore, the quantity and size ranges of these sand grains can be used to reconstruct past atmospheric circulation strength (cyclone frequency and/or intensity) in a region. The total aeolian sediment influx (ASI, quartz grains $> 125 \mu\text{m}$) has been used to derive the occurrence and frequency of strong cyclonic activity in south-west Sweden during the past 6500 years (Björck and

Clemmensen, 2004; De Jong et al., 2006, 2007, 2009). Similarly, Sjögren (2009) used sand mass accumulation rates (SMAR, quartz grains > 60 µm) in peat profiles in northern Norway as a proxy for past atmospheric circulation types. In the aforementioned studies, peat bogs are situated near the local shorelines and in close proximity to sandy deposits, such as coastal dunes. Therefore, sand availability was not a limiting factor for sand transport. A direct comparison between pollen records and ASI values from two sites showed that changes in landuse were not a driving force behind the ASI peaks either (De Jong et al., 2009).

X.2.6.2 Dust particles in peat bogs

Reconstructed soil dust flux and peat geochemistry are also used as proxies for past circulation strength (De Vleeschouwer et al., 2009). Because peat bogs are typical for humid climates where the soil would naturally be stabilized by vegetation, wind erosion of the soil is reduced to a minimum (Mattson and Koutler-Andersson, 1954). Therefore a large contribution of fine dust in peat bogs may be long-distance transported. Sahara dust, for example, is a main source of mineral dust to European peat bogs (Shotyk et al., 1996; Kylander et al., 2005) and is mainly composed of quartz, clays, carbonates and feldspars (Bücher et al, 1984).). Ti (Titanium), like other conservative elements (Al, Sc, La etc.), can be used as a proxy for soil dust influx. By taking into account the mean Ti concentration in soils (in the upper continental crust, Ti = 4100 µg/g, McLennan, 2001), the mean accumulation rate of peat and the density of the peat, the amount of atmospheric soil dust flux (ASD) into the peat bog can be calculated (Shotyk et al., 1998). ASD can be used as a proxy for the combined effects of the degree of soil erosion and atmospheric circulation strength over a region. In ombrotrophic bogs, variations in Ti concentrations have been linked to variations in soil dust inputs (Holynska et al., 1998; Shotyk et al., 1998, Görres, 1993) originating from either agricultural activities (Hölzer and Hölzer, 1998) or variation in natural atmospheric soil dust input (Shotyk et al., 1998). Recently, de Vleeschouwer et al (2009) reconstructed ASD fluxes using Ti concentrations, bulk densities and accumulation rates from a peat bog in North-West Poland, which showed strong fluctuations during the Little Ice Age (Figure 4.35).

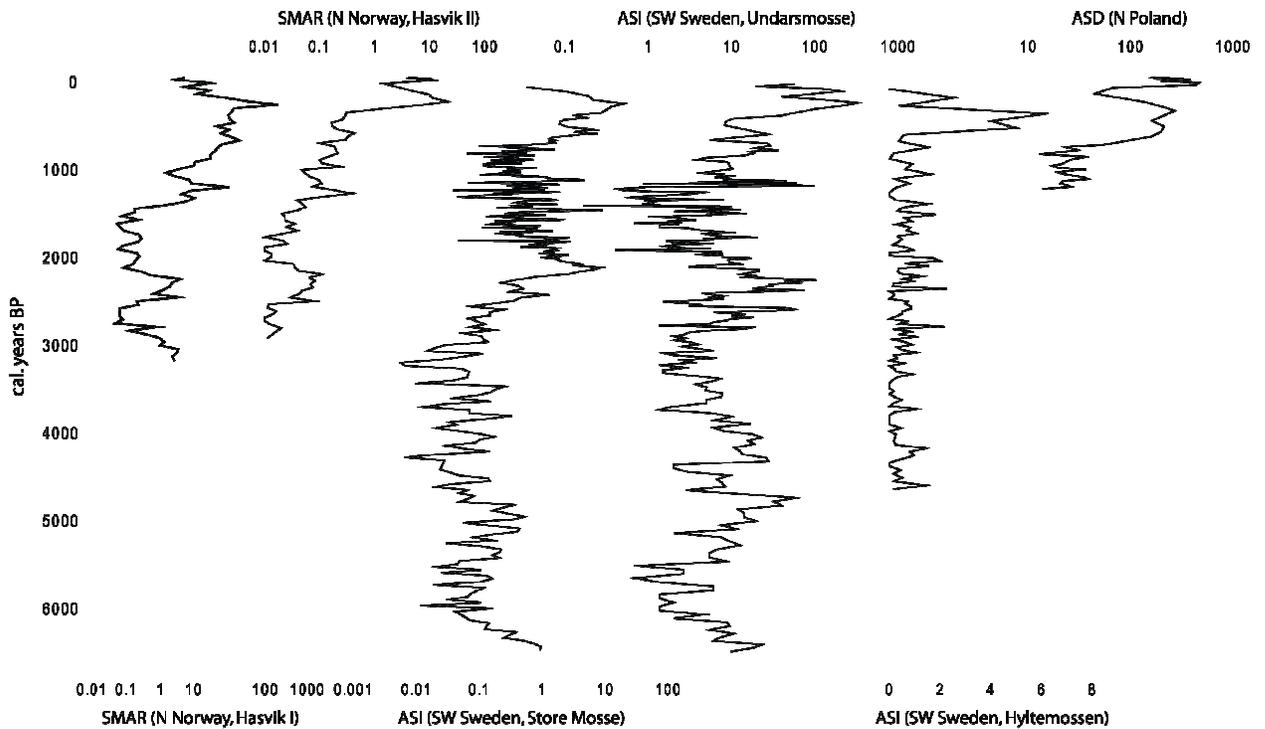


Figure X.3. Reconstructions of mineral influx into peat bogs in Northwest Europe, showing SMAR (sand mass accumulation rates, Sjögren 2009) for two cores from Hasvik, northern Norway (notice the logarithmic scale on the x-axis); ASI (aeolian sediment influx) from the Store Mosse bog (De Jong et al., 2009), Undarsmosse Bog (De Jong et al., 2006)(notice the logarithmic scale on the x-axis) and Hyltemossen bog (Björck and Clemmensen, 2004); ASD (aeolian soil dust flux) from Slowínskie Blota bog, northern Poland (De Vleeschouwer et al., 2009). The majority of the records reflect increased mineral particle influx values around 2700-2000 cal yrs BP and around 600-100 cal. yrs BP, which was interpreted as an increase in atmospheric circulation vigour. During the most recent phase, increased sediment availability most likely enhanced peak amplitudes.

X.2.6.3 Tracing the sources of dust input

To discriminate between remote and local dust sources, geochemical analyses can be used. Conservative lithogenic elements in the peat column can be used as fingerprints of the dust input. The preferred elements are Titanium, Scandium and Yttrium (Ti, Sc, Y) and Rare Earth Elements (REE). For example, several studies have shown that most of the Ti comes from natural sources (e.g. soil erosion). Most of the particles coming from soil and rock erosion are silicates and aluminosilicates. These particles have low sensitivity to dissolution, even in the acidic environment of a peat bog (Le Roux et al., 2006 and Le Roux and Shotyk, 2006 and references therein). Despite their anoxic and reductive conditions, Aubert et al (2006) have recently demonstrated that the REE signal is preserved in the peat column. This has been used to reconstruct dust origin in the

Southern Hemisphere: Australia (Kylander et al. 2007; Muller et al 2008), New Zealand (Marx et al. 2009) and Indonesia (Weiss et al, 2002).

As in ice cores, the dust origin can be traced with radiogenic isotopes of strontium, lead and neodymium. However, lead only represents natural dust input earlier than ca. 6000 BP, before lead metallurgy. Strontium is problematic since it can be mobile in the peat column. However, the strontium isotope signature can be measured in acid insoluble particles, where strontium is assumed to be unaffected by post-mobilization processes (Sapkota, 2006). Neodymium (a REE) isotope analysis has so far not been used on peat bog sediments. Kamenov et al. (2009) used this method to trace dust input in a core from Florida Bay marsh, which may indicate that this method can be applied successfully to peat cores as well.

X.2.6.4 Reconstructions of past atmospheric circulation characteristics

ASI reconstructions from two peat bogs in south-west Sweden, situated ca. 60 km apart, show a nearly identical sand influx pattern throughout the past 3000 years (De Jong et al., 2009). ASI values reconstructed from two additional bogs in south-west Sweden (Björck and Clemmensen, 2004; De Jong et al., 2007) also show generally similar trends. Furthermore, comparison with reconstructed dune-reactivation phases along the west coast of Denmark (Clemmensen et al., 2009) shows broadly similar patterns, indicating the reliability of the ASI method as a proxy for regional-scale circulation strength. In south-west Sweden, increased circulation strength was recorded in particular after ca. 2800 cal. yrs BP (De Jong et al., 2006; 2009)

Similarly, SMAR measured in three peat profiles from an ombrotrophic bog situated on the west coast of northern Norway (Sjögren 2009) gave consistent signals, although the magnitude of total sand accumulation fluctuated strongly between the three profiles and over time (figure 4.35). Strong increases in SMAR values around 3150–2800, 2500–2100, 1450–1100, 950–550 and 250 to +50 cal yrs BP were interpreted mainly as periods of major shifts in the wind regime. However, overgrazing and intense agricultural activities have certainly played an important role during some of these phases (Sjögren, 2009).

The ASD profile reconstructed from the Slowínskie Blota Bog in northern Poland (De Vleeschouwer et al., 2009) also showed increased values during LIA cold shifts (Fig. 4.35). Focusing on the period between AD 1000 and AD 1900, the ASD displays two main peaks around ca. AD 1370 and ca. AD 1650. These ASD peaks are also reflected in the density and the Ti profiles (De Vleeschouwer et al., 2009), indicating increased soil erosion around these times.

X.2.6.5 Strengths and weaknesses

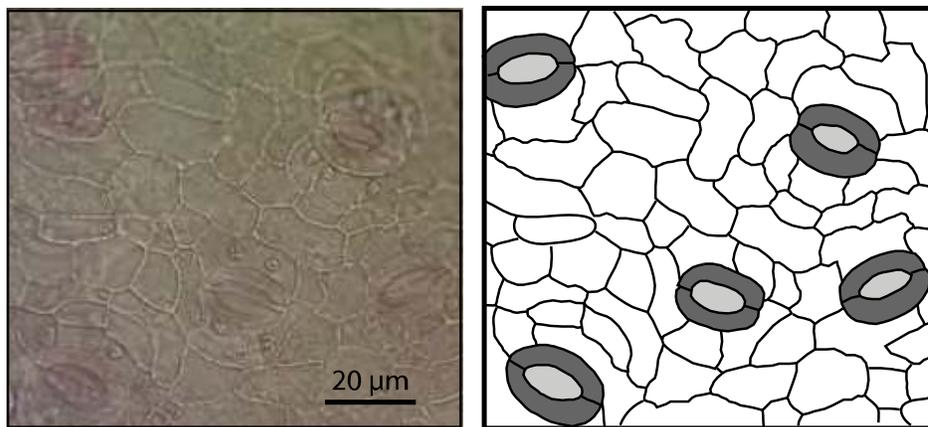
For the interpretation of minerogenic influx into peat bogs, it has to be kept in mind that the three mentioned proxies (ASI, SMAR and ASD) reflect the accumulation of different sizes of mineral particles, the last reflecting the smallest fraction. Therefore, ASI is likely to reflect extreme events only, whereas ASD is likely to record overall changes in the mean wind strength. Flux reconstructions should be used only in records with robust, high-resolution age-depth models since changes in accumulation rates strongly affect flux values. Moreover, as it involves the density of the peat, this latter parameter should be measured with great care, by taking multiple bulk peat samples of a specific volume to minimize the error. It is not possible to reconstruct whether high particle concentrations are related to single extreme events or to a series of moderately strong wind events. Moreover, the quantity and size range of particles is not just dependent on wind characteristics but also on sediment availability. Throughout the course of the Holocene, sediment availability in most regions in North-West Europe has fluctuated. This is partly due to natural causes (e.g. vegetation succession, climate change) and to an increasing extent due to human impact on the landscape. Large-scale deforestation, grazing and the development of agriculture has caused a high degree of openness of the landscape (e.g. Berglund et al., 1991). Intense agriculture has led to the nearly complete exposure of soils to wind erosion, in particular in autumn and winter, which is the season in which westerly storms are most frequent and strong in North-West Europe (Alexandersson et al., 1998; Nilsson et al. 2004). For a correct interpretation of the different mineral fractions in the peat, a reconstruction of land use and deforestation is necessary. For the fine fractions, an estimation of particle emissions from, for example, mines and cement factories would be helpful to assess the particle input into the atmosphere over time. If human impact has been accounted for, these proxies have the potential to provide detailed information on large-scale variability of past atmospheric circulation strength.

X.2.7 Stomatal records from subfossil leaves as proxies of plants' responses to past atmospheric CO₂ variations

Author: Walter Finsinger

Carbon dioxide (CO₂) is the most important anthropogenic greenhouse gas and a large percentage of its recent change is attributed to anthropogenic carbon emissions (IPCC 2007). Over the past 800,000 years atmospheric CO₂ concentrations have varied from minima of 170-200 parts per million by volume (ppmv) in glacials to maxima of 280-300 ppmv in the recent interglacials (Petit et al., 1999; Lüthi et al., 2008). Present CO₂ concentrations already exceed the natural variability of this greenhouse gas and predictions for atmospheric CO₂ concentrations over the next two centuries suggest that CO₂ concentrations will increase at a rate that will depend on the reductions of anthropogenic emissions (Meehl et al., 2007).

Photosynthesis by C₃ plants is highly sensitive to variations of CO₂ concentrations in the air. Stomata are small pores on the protective leaf cuticle around the outside of the aerial parts of land plants (Figure X.4). They are the main link between the plants' interior and the atmosphere, and are necessary because land plants have internalised their gas exchange surfaces and developed waterproof coatings to avoid water loss. Stomata allow CO₂ in for photosynthesis and let water molecules out, thus carbon gain and water loss are intimately connected (McCarroll and Loader, 2004).



*Figure X.4. Left panel: Image of a *Betula nana* leaf cuticle. Right panel: Schematic figure with guard cells of stomata (dark grey), stomatal pores (light grey), and epidermal cells (white).*

Plants are able to regulate water loss and carbon gain with mechanisms that respond to short-term as well as to long-term changes in CO₂. After the completion of leaf expansion, stomatal densities remain constant while the stomatal aperture changes on

short timescales (in the order of minutes) in response to environmental signals, including CO₂ concentrations. These signals can trigger alterations to guard cell turgor, cytoskeleton organization, membrane transport and gene expression (Hetherington and Woodward, 2003 and references therein; Young et al., 2006). It has been shown that leaf stomata can close in response to high CO₂ levels and open at low CO₂. For example, experiments carried out under high (double than present) atmospheric CO₂ concentrations show that stomatal apertures are reduced by 20–40% in several plant species (e.g. Bunce, 2004). Such changes in stomatal apertures can also occur in response to changes in photosynthesis and respiration, which are influenced by the light/dark transitions (in the dark CO₂ increases in leaves by cellular respiration). Hence, stomatal apertures change also along with the diurnal cycle.

In addition to stomatal aperture, stomatal density (SD, i.e. the number of stomata per unit area) or the stomatal index (SI, i.e. the ratio of stomata versus epidermal cells per unit area) can vary. Woodward (1987) first reported changes in SD in response to changes in atmospheric CO₂ concentrations for seven species of temperate forest trees and a shrub species. Responses of SD and/or SI to an increased atmospheric CO₂ concentration have since then been reported for several C₃ species (Royer, 2001). According to Hetherington and Woodward (2003), the mean response is an 11% reduction with a doubling of the CO₂ concentration. However, several plants show an increase or no change at all of stomatal densities in response to CO₂ increases.

Although the regulating pathway is not yet completely defined, the discovery of the *HIC* gene in *Arabidopsis thaliana* indicates a genetic control for the CO₂ response of stomatal development (Gray et al., 2000). Additional support for developmental control emerges from experiments showing that the CO₂ concentration around mature leaves determines the SD of new leaves (Lake et al., 2001). However, any mechanism should be valid for the entire range of species-specific responses to CO₂ increases including increases, decreases, or no response of SD (Hetherington and Woodward, 2003). Lake and Woodward (2008) proposed a putative mechanism that involves stomatal-development control by transpiration rate and leaf abscisic acid (ABA) concentrations.

X.2.7.1 Experimental settings to study stomatal frequency responses

Stomatal frequency (SF, i.e. SD and SI) responses to changes in atmospheric CO₂ concentrations can be studied using several techniques, including CO₂ enrichment experiments, herbarium studies, and palaeorecords. CO₂ enrichment experiments (whether glasshouse, open top chambers (OTCs), and free-air CO₂ enrichment (FACE) experiments) have the advantage of allowing short-term (interannual to subdecadal scales) investigation of plants' responses to CO₂ changes while keeping other environmental variables (e.g. light intensity, temperature, soil conditions, and humidity) constant or continuously monitored (Tricker et al., 2005; Körner, 2006; Ainsworth and Rogers, 2007). By contrast, to assess longer-term adaptation of plants to CO₂ changes

(e.g. at decadal or centennial scales), leaves collected from herbaria as well as subfossil leaves from peat bogs or lake sediments are useful (e.g. Woodward, 1987; Wagner et al., 1996). The method involves the analysis of cuticles, which mirror the morphological structure of the leaf epidermis, including stomata. However, herbarium studies do not cover timescales longer than the past ca. 200 years and leaves analysed in such studies often have diverse provenances and indeterminable environmental conditions. Subfossil leaves, in contrast, have the advantage of providing long-term records of plant species' responses over centennial and millennial timescales. Since cuticles are made of waxes resistant to degradation under anoxic conditions (e.g. in peat or lake sediments), subfossil leaf cuticles accumulated in wetlands retain a record of long-term stomatal responses and adaptation to CO₂ changes. This approach allows the assessment of responses to external factors over a longer time scale than that available to modern ecologists, and it provides a temporal perspective on responses under different climatic conditions and in times of rapid climatic change. It thus helps to assess the results of "experiments conducted by nature" (Deevey, 1969).

X.2.7.2 Methods of assessing stomatal frequency

Stomata on modern and fossil leaves can be observed and counted either using epifluorescence or transmitted light microscope. By using an image analysis system connected to the microscope, additional morphometric measurements can be obtained, such as stomatal pore length, stomatal pore width, and cell wall undulation (e.g. Kürschner, 1997). The stomatal frequency of angiosperm leaves is conventionally expressed in terms of SD and/or SI. Counting fields should be limited to interveinal areas because stomata are mostly absent on leaf veins. To obtain accurate estimates of the mean SF per leaf, it is necessary to analyse several counting fields per leaf and to limit the analysis to the central leaf lamina because, as shown on specimen of *Alnus glutinosa*, up to 2.5 fold variations of stomatal frequencies were observed (Poole et al., 1996; Poole et al., 2000). In addition, the separation of sun and shade leaves may be important as the position of leaves within the canopy influences the leaf growth, which in turn can affect SD (Poole et al., 1996; Kürschner, 1997). In conifers, the arrangement of stomata into rows occurring either in single file or grouped in bands parallel to the long needle axis prevents assessment of stomatal frequency based on small counting fields. Thus a series of techniques have been developed to estimate stomatal responses to CO₂ changes of conifer species, such as the stomatal number per length, the SD per length, and the true SD per length, which is a measure of the number of stomata per unit needle length (see for example McElwain et al., 2002; Kouwenberg et al., 2003, Eide and Birks, 2006).

Models used to infer CO₂ based on SF have been developed using different approaches: i) "calibration in time" based on historical series as described above, and ii) "calibration in space" using leaves collected along altitudinal transects. For calibration in space, responses are modelled using records along altitudinal transects, because CO₂ partial

pressure decreases with altitude. In several cases the two approaches have been combined to increase the gradient length of the modern datasets. Some training sets were developed including closely related species assuming that the species-specific responses to CO₂ changes are similar (e.g. Wagner et al., 1999; Jessen et al., 2005). Interestingly, the stomatal responses are not always equivalent between studies, as indicated by different results on stomatal responses of *Betula pubescens* (Wagner et al., 1999; Eide and Birks, 2006).

X.2.7.3 Ice core and stomatal based reconstructions of atmospheric CO₂ concentrations

Air bubbles in Antarctic ice cores offer the most direct measurements of past atmospheric CO₂ concentration (e.g. Siegenthaler et al., 2005), providing a continuous record of CO₂ changes for the past 800,000 years (Lüthi et al., 2008). Older CO₂ concentrations have been estimated by various techniques, including stomatal frequencies (e.g. Beerling and Chaloner, 1992; Van der Burgh et al., 1993; McElwain and Chaloner, 1995; Pagani et al., 1999; Boom et al., 2002; Kürschner et al., 2008). Stomatal-based inference models have, however, also been used to reconstruct CO₂ changes for time periods for which ice-core derived CO₂ records are available. The interest lies in the smoothed nature of ice-core gas measurements in comparison to the indirect and potentially less smoothed stomatal-based reconstructions from deciduous plants. In ice cores, air bubbles are not closed off from the atmosphere until they reach the base of the firn layer. The rate of this process varies in time and space. Nevertheless, analysis of air extracted from multiple suitable ice cores with different snow-accumulation rates are all consistent with pre-industrial variations of CO₂ during the past millennium. These variations are limited to changes of 12 ppmv at most (Siegenthaler et al., 2005). This shows that ice-core derived CO₂ concentration measurements are highly comparable. Moreover, they are in good agreement with records of a large network of direct atmospheric measurement stations starting in AD 1958 on Mauna Loa and the South Pole (Keeling et al., 2005; 2008).

Further back in time, however, snow-accumulation rates were lower (e.g. during the late glacial-early Holocene transition). According to Neftel et al. (1988), CO₂ fluctuations with a duration of less than twice the bubble enclosure time (for example, up to 550 calendar years in Dome Concordia (Monnin et al. 2001)) cannot be detected. By contrast, leaves of deciduous plants are formed each year and potentially provide an indirect record of CO₂ changes at annual resolution. While some stomatal-based reconstructions support the main trends in CO₂ changes as recorded by ice cores (e.g. Rundgren and Beerling, 1999), others suggest high-amplitude variations of past atmospheric CO₂ concentrations at centennial or even decadal timescales during the last deglaciation and the Holocene (Beerling et al., 1995; Wagner et al., 1999; McElwain et al., 2002; Wagner et al., 2004; Kouwenberg et al., 2005; Van Hoof et al., 2005; Jessen et al., 2007). For example, stomatal-inferred reconstructions and ice-core derived CO₂ measurements diverge during the Younger Dryas. Based on leaves of various species

from records in the Northern Hemisphere (Norway, Beerling et al 1995; Canada, McElwain et al., 2002) a CO₂ concentration drop of ca. 65 ppmv at the onset of the Younger Dryas and an increase of ca. 50 ppmv CO₂ at the transition to the Holocene (11,650 cal yrs BP) was reconstructed. Another reconstruction obtained with a composite record of three different plant species from Sweden suggested a drop of CO₂ concentrations of ca. 50 ppmv during 12,700 – 12,400 cal yr BP followed by a gradual increase during the Younger Dryas stadial and stable CO₂ values during the transition to the Holocene (Rundgren and Björck, 2003). By contrast, there is no sign of a CO₂ reduction in Antarctic ice cores (Monnin et al., 2001; Lüthi et al., 2008). The causes for these discrepancies are strongly debated (see e.g. Monnin et al., 2001 ; McElwain et al., 2002).

The difference between the stomatal-based CO₂ reconstructions and the ice-core derived CO₂ measurements is important for understanding the carbon cycle, and for modelling climate responses to changes in the atmospheric CO₂ concentration. For example, as noted by Joos and Spahni (2008), the 20th century increase in CO₂ and its radiative forcing occurred more than an order of magnitude faster than any sustained change during the past 22,000 years as recorded in ice cores. Because stomatal-based reconstructions may indicate that the past CO₂ concentration changed at rates similar to CO₂ concentration changes during the past 200 years, it is essential to evaluate uncertainties, potentials, and pitfalls of stomatal-based CO₂ reconstructions (Poole et al., 1996; Finsinger and Wagner-Cremer, 2009).

X.2.7.4 Signal or noise: Validation of stomatal-based CO₂ reconstructions?

The most powerful means to validate palaeo-proxy reconstructions is to compare proxy-based reconstructions to measured CO₂ records. A methodical assessment of the CO₂-prediction quality of SF data with herbarium-training sets and measured-SF records for three subtropical species showed significant differences in prediction accuracy (Wagner et al., 2005). Although these results were promising, they emphasised the need to validate SF-inferred CO₂ reconstructions. More recently, using a well-dated stomatal record of subfossil *Betula nana* leaves collected from a peat bog in Kiruna, northern Sweden, Finsinger and Wagner-Cremer (2009) were able to compare reconstructed vs. measured CO₂ concentration records for the past 140 years. They used two inference models developed with the same herbarium-training set of *Betula nana* and *Betula pubescens* (Figures Xa and Xb) and reconstructed CO₂ changes based on the subfossil Kiruna leaf record. They could show that reconstruction uncertainties can be as large as ~70 ppmv, a span that corresponds to CO₂ changes that occurred during glacial/interglacial transitions (Petit et al., 1999). The large uncertainties were obtained by combining two different sources of uncertainties: i) those of the inference models used for the reconstruction (method error) (Figure X.5 a,b) and ii) those derived from the difference between reconstructed and expected values (validation error) (Figure X.5c). These uncertainties are thought to result from the inherent variability of SF within and between leaves of individual plants. In addition, although it is recommended to limit

the analysis to the central leaf lamina (Poole et al., 1996, 2000; Poole and Kürschner, 1999), it is often difficult to determine the location of the central leaf lamina if only leaf fragments are available for analysis.

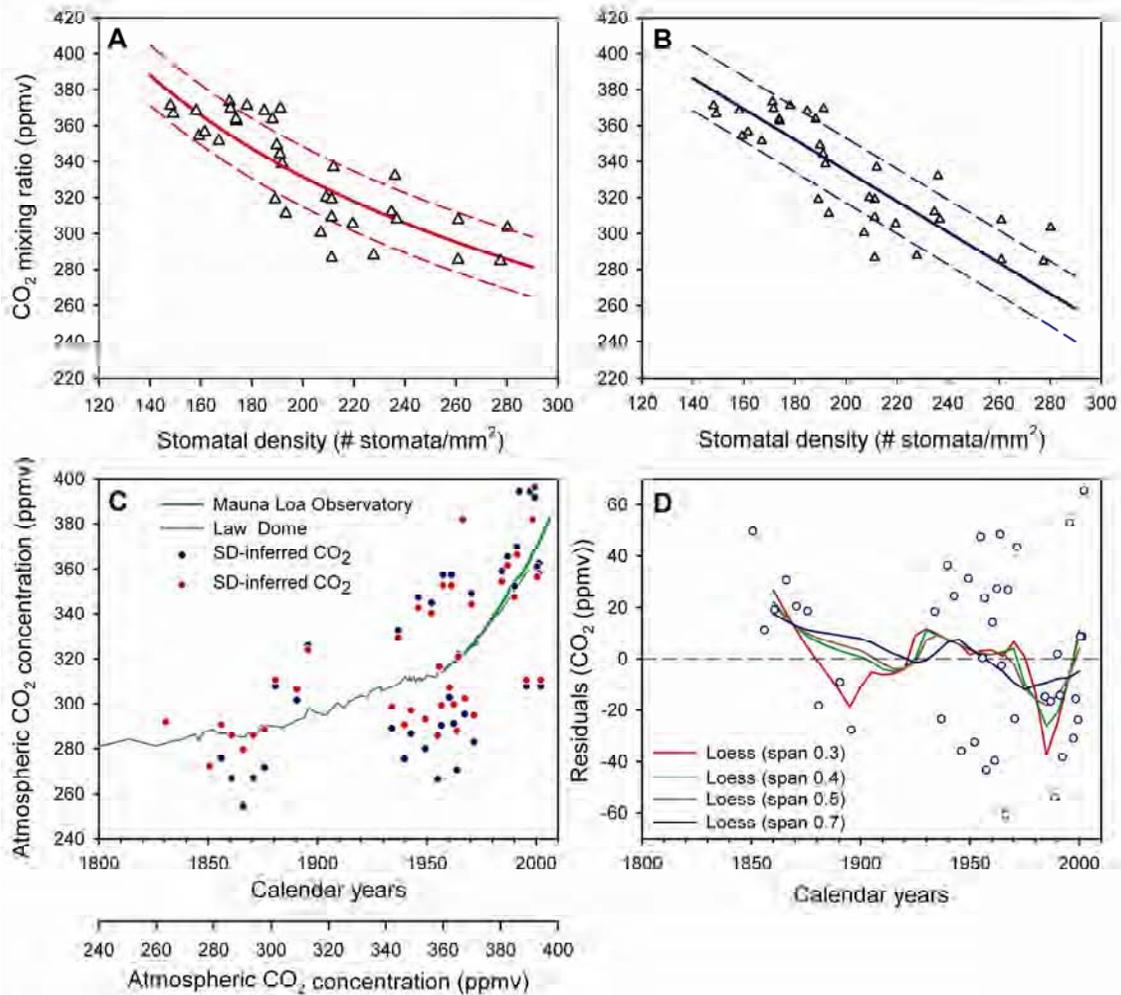


Figure X.5 a and b. Stomatal density-based inference models (thick lines) for atmospheric CO₂ reconstruction based on herbarium leaves (empty triangles) (from Finsinger and Wagner-Cremer 2009). Thin lines: ± 1 RMSE. c: Stomatal density-inferred atmospheric CO₂ concentration reconstruction obtained with the inference models (a and b) and a stomatal density record from the Kiruna mire (Sweden) (not shown). Atmospheric CO₂ concentrations are from Mauna Loa (Keeling et al. 2008) and from Law Dome ice core (Antarctica, MacFarling Meure et al., 2006) (modified from Finsinger and Wagner-Cremer, 2009). d: Residuals (expected – predicted) of stomatal density-inferred reconstructed values. Empty blue circles: unsmoothed reconstruction; lines: smoothed

stomatal density-inferred CO₂ reconstruction. Smoothing was performed using locally weighted regression (Loess, Cleveland and Devlin 1988) with different smoothing windows (spans).

On the other hand, as shown in Figure X.5d, decreasing residuals (reconstructed – measured) attests to the higher prediction ability of smoothed reconstructions. This is consistent with Van Hoof et al (2005), who used stomatal-based CO₂ reconstructions between the 10th and 16th centuries and showed that the discrepancies between the amplitudes estimated by the stomatal record and ice-core records diminished when the raw stomatal record was smoothed. However, these authors attributed the discrepancies to the smoothed nature of CO₂ records from ice cores. Finsinger and Wagner-Cremer (2009) could show that strong discrepancies occur between the stomata-inferred CO₂ concentration and the annual instrumental CO₂ record (Figure X.5d). This clearly indicates that the apparent disagreement between ice core and stomatal-based CO₂ reconstructions cannot be solely explained by the inherently smoothed nature of ice core records, as suggested by Blunier et al. (2005). It also indicates that it is essential to validate stomatal-based inference models to estimate uncertainties of reconstructed CO₂ concentrations. Clearly, a reconstruction cannot have a smaller uncertainty than the model uncertainty. Hence, stomatal-based CO₂ reconstructions should be limited to low-frequency changes after smoothing the records. It is therefore suggested that the degree of smoothing for subfossil records should be consistent with the smoothing required for the validation, instead of the degree of smoothing given by the firn densification model of ice cores (Finsinger and Wagner-Cremer, 2009). This may be feasible when subfossil leaves are abundant and continuously present in high-sedimentation rate natural archives.

X.2.8 Impacts of CO₂ changes on plants and ecosystems

Stomatal geometry and stomatal density are the dominant variables controlling the complex parameter of stomatal conductance (g_s). This in turn influences plants' water-use efficiency (WUE), a measure for the amount of water loss at the leaf level per unit of carbon gain. Globally, annual precipitation over the land is about 110,000 km³ and evapotranspiration accounts for a total of about 70,000 km³ (Jackson et al. 2001), though annual total transpiration from terrestrial vegetation is clearly highest in the tropics and decreases toward the poles (Hetherington and Woodward, 2003). Based on evidence for lower stomatal frequencies in several plant species under lower-than present CO₂ concentrations, Woodward (1987) first inferred decreased g_s (i.e. increased WUE) under modern CO₂ concentrations due to changes in stomatal densities. If one assumes that stomatal geometry does not change after leaves are shed, then maximal stomatal conductance (g_{max}) can be inferred using SD, maximum pore length, and width (Franks and Beerling, 2009). Clearly, g_{max} measurements from subfossil leaves will have large uncertainties likely due to within-leaf, within-plant, and between-plant variability of stomatal densities and geometry. However, the long-term trend of g_{max} changes can be filtered out by smoothing such records. For example, using the stomatal density and

geometry record of *Betula nana* from the Kiruna peat bog (Finsinger and Wagner-Cremer, 2009), an average g_{max} decrease of ca. 20% from AD 1800 to present is observed (Figure 4.29). Interestingly, the variability of the dataset increases towards the present and the absence of low g_{max} values before AD ~1870 may be due to the low number of subfossil leaf fragments. Therefore it is essential to study more leaf-rich natural archives to better estimate g_{max} changes in response to atmospheric CO₂ changes.

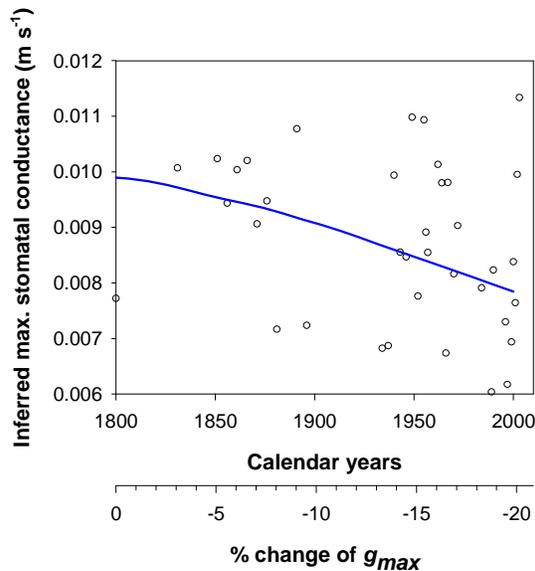


Figure X.6. Stomatal-density and stomatal-geometry-inferred maximum stomatal conductance changes of *Betula nana* leaves from Kiruna (Sweden) over the past ~200 years as a function of time. Empty circles: average values for leaf fragments of individual samples; Thick line: smoothed maximal g_s (Loess span = 0.7).

Present CO₂ concentrations already exceed the upper limit of its natural variability over the past ca. 800,000 years and predictions for atmospheric CO₂ concentrations over the next two centuries suggest that CO₂ concentrations will very likely increase further (Meehl et al., 2007). The continued rise in CO₂ concentrations will potentially further decrease g_s and increase WUEs, so plants will become more efficient at water use (Bunce, 2004; Saurer et al., 2004). However, species differ significantly in their CO₂ responses, which thus influences vegetation dynamics (e.g. Woodward 2002; Zweifel et al. 2009). These aspects are gradually being integrated into models used to reconstruct past vegetation dynamics (e.g. Wu et al., 2007; Prentice and Harrison, 2009) and to predict vegetation changes at the biome scale.

In addition to exerting (i) a radiative forcing on the climate system and (ii) having an influence on vegetation dynamics, increasing concentrations of atmospheric CO₂ may also (iii) alter the climate system through direct effects on plant physiology (Forster et al., 2007). As suggested by recent studies, the resulting 'CO₂ physiological forcing'

(Sellers et al., 1996; Betts et al., 1997) may have a significant impact on a model's climate sensitivity (e.g. Boucher et al., 2009; Doutriaux-Boucher et al., 2009). The effect of the CO₂ physiological forcing, caused by plant stomatal responses to CO₂ changes that may alter the evapotranspiration of terrestrial ecosystems is, however, still poorly understood and it has an unknown impact on radiative forcing and on feedbacks dependent on global-mean temperature (Doutriaux-Boucher et al., 2009).

One uncertainty for the prediction of future climates lies therefore in the response rate of plants to increasing atmospheric CO₂ concentrations. Clearly, stomatal density can never be zero and WUE cannot rise indefinitely. Using subfossil leaves and herbarium specimens, Kürschner et al. (1997) suggested a non-linear (sigmoid) response of stomatal frequency changes for two birch and one oak species and predicted species specific response limits to CO₂ at ~350 and 400 ppmv, respectively. Accordingly, some species that did not alter their stomatal frequency in the past decades may be beyond their response limits (Woodward et al 1991). The change in g_{max} of individual plants may be scaled up through to the community level assuming that plants do not tend to develop leafier canopies (Woodward et al., 1991). Consistent evidence for response limits comes from evidence of stable carbon isotope changes ($\delta^{13}C$) from tree rings, indicating that WUE in some trees across northern Europe is no longer rising (Waterhouse et al., 2004). Long-term records derived from subfossil leaves preserved in wetlands may thus be a valuable source to constrain the response limits of plants (e.g. in terms of g_{max}) to past atmospheric CO₂ changes. In combination with whole-plant WUE records (e.g. from $\delta^{13}C$ records) they may be used to better constrain the response limits of individual plant species to changing atmospheric CO₂ concentrations.

X.3 Climate variability reconstructed from peat bogs

Author: Rixt de Jong

Since the early part of the last century, peat bog stratigraphy has been used to reconstruct past climatic changes. Because the typical peat accumulation rate for the past ca 2000 years in Europe is 10 to 20 years per cm, finely sampled peat cores can provide data on a decadal time scale for this period (Blackford, 2000). Recent advances in dating methodologies allow for high-precision reconstructions of specific climatic events and their possible causes. However, a remaining difficulty is the interpretation of proxy data, since the exact climatic meaning of, for example, bog surface wetness (BSW) changes remains illusive. Increases in BSW are often described as being the results of 'wetter and/or cooler' conditions, which is not always helpful for climatic inferences (Charman, 2007). However, as described in the previous sections, the use of transfer functions and a multi-proxy approach could be the way forward to improve climatic reconstructions from peatlands (Blackford, 2000). Furthermore, studies with a high chronological precision can be compared from different localities, which allows for regional-scale climatic reconstructions with minimal chronological offsets (see e.g. Swindles et al., 2007 and Mauquoy et al., 2008).

Environmental reconstructions from peatlands often register considerable changes that appear to be simultaneous over large regions (for an overview, see e.g. Hughes et al., 2000; Barber et al., 2003). Many studies find particularly large variability around 2750 ¹⁴C yrs BP (see e.g. van Geel et al., 1996) and between 500–100 cal. yrs BP (encompassing the so-called Little Ice Age, see e.g. Mauquoy et al. 2002b; Lamentowicz et al., 2008a). These periods are characterized by rapid changes in bog surface wetness (BSW), as well as fluctuations in minerogenic influx (see fig. X.3). The causes for these BSW variations are debated (Plunkett and Swindles, 2008). Both mentioned time periods are characterized by large variations in solar activity, as reconstructed from ¹⁴C variations. Therefore, a 'solar link' for these BSW variations is often implied (e.g. van Geel et al., 1996; Mauquoy et al., 2002a; 2008). Detailed ¹⁴C wiggle-match dating of finely sampled peat records, mainly from the North Atlantic region, has provided strong arguments for a 'solar link' to these variations in BSW. For the time period ~2750 ¹⁴C yrs BP, findings from the Northern Hemisphere are supported by studies from Chile (van Geel et al., 2000) and southern Patagonia (Chambers et al., 2007), which also show a rapid change in BSW at this time, pointing to a globally synchronous climatic response.

However, the response time of the recorded environmental changes to decreased solar irradiance appears to vary between sites (e.g. Swindles et al., 2007). This may in part be due to a natural 'smoothing' that occurs in peat bogs with low accumulation rates (e.g. Mauquoy et al., 2008). However, it may also point to a different process, such as oceanic circulation changes in response to solar forcing (Swindles et al., 2007; Plunkett and Swindles, 2008), which would in turn have a delayed impact on precipitation and evaporation rates in the oceanic climates of North-West Europe. More high-resolution,

multi-proxy studies with very tight chronological precision from different regions are required to resolve the issue. In addition, comparison with other high-resolution records (e.g. lakes, speleothems) with independent dating would improve our understanding of the processes that caused rapid changes in BSW.

X.4 Impact of climate change on peatlands and potential feedback mechanisms on climate

Authors: Ulla Kokfelt, Margareta Johansson, Stefan Fronzek, Torben R. Christensen

X.4.1 Palsa mires in a changing climate

Permafrost that exists at its margins is very sensitive to environmental and climatic changes (Sollid and Sörbel, 1998; Fronzek et al., 2006; Parviainen and Luoto, 2007). As a result of projected climate change, the geographic position of the climatic envelope for discontinuous permafrost is likely to shift in the future. "Palsa mires" are wetland complexes with permanently frozen peat hummocks. Palsas and peat plateaus are characteristic permafrost features that are located in wetlands in the zone of discontinuous permafrost (Figure 4.36). The peat forms with permanently frozen cores elevated above the surrounding wetland. Palsas are isolated permafrost features generally less than 100 metres in diameter with a height of 1-7 m. Peat plateaus are flat-topped, generally lower and more extensive landforms which may, in some cases, cover areas over 1 km² (Thie, 1974). In Canada palsas occur most frequently in the southern part of the discontinuous permafrost zone whereas peat plateaus occur predominantly in the northern part (Beilman et al., 2001). In Fennoscandia palsa mires are treeless bogs with dry surface vegetation communities dominated by bryophytes, dwarf shrubs and lichens. In contrast to this, in North America dense stands of black spruce are common on subarctic bogs containing permafrost (Zoltai and Tarnocai, 1971; Thie, 1974; Vitt et al., 1994). Palsas and peat plateaus have been most intensively studied in Fennoscandia and Canada whereas data from Russia are relatively scarce (Oksanen, 2005).

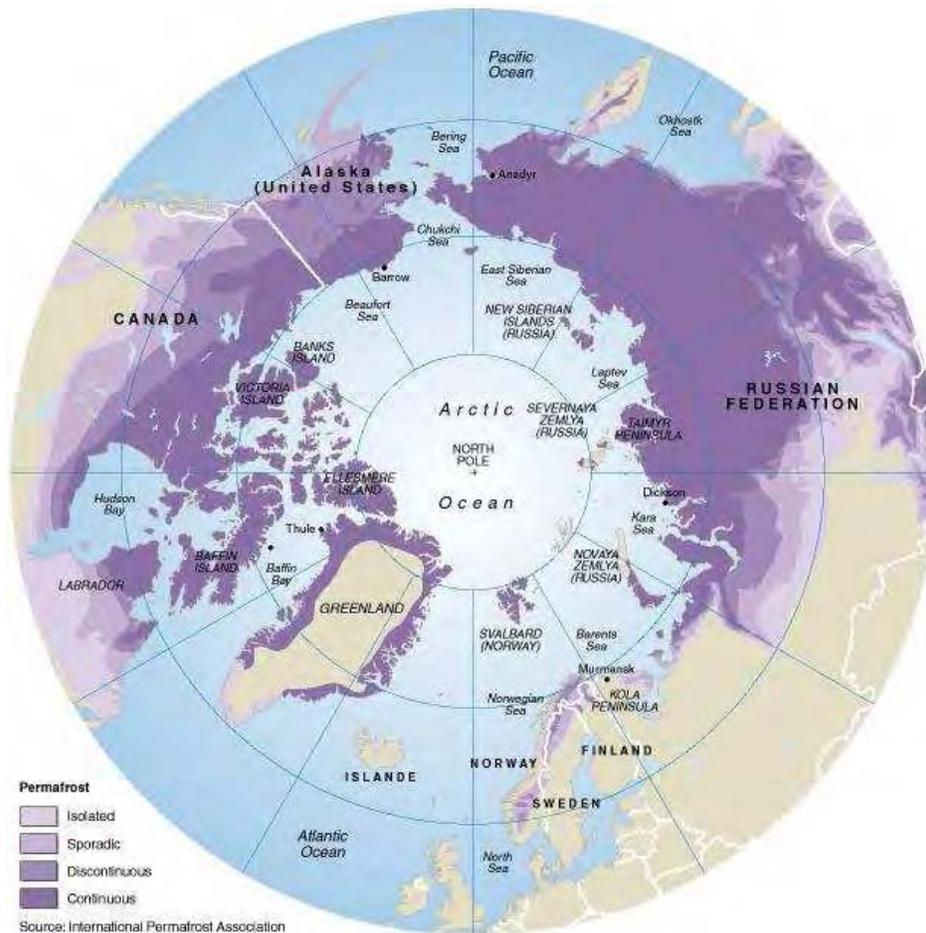


Figure X.7. The distribution of permafrost in the Northern Hemisphere (Brown et al., 1998). Palsa mires and peat plateaus occur in the margins of the discontinuous zone and in the zone of sporadic permafrost.

Both local and climatic factors are important for the presence or absence of permafrost in wetlands. Permafrost aggradation most often occurs in *Sphagnum* deposits where pore waters are significantly colder than in other types of wetland deposits (Vitt et al., 1995), but permafrost landforms also develop directly from sedge peat accumulated in fens (Brown, 1980; Couillard and Payette, 1985). Optimal climatic conditions for the existence of palsas are long, cold winters with little precipitation or strong winds (Seppälä, 1986), and mean annual temperatures of -5 to -3°C (Luoto et al. 2004a). However, palsas are found at higher mean annual temperatures; for example in northern Fennoscandia, where the distribution of lowland permafrost is closely related to the precipitation shadow east of the Scandes Mountains (Luoto et al. 2004a). Vegetation cover may also be decisive for the presence of permafrost. Whereas low vegetation or barren ground on palsas in Fennoscandia promote snowdrift and thereby exposure to low winter temperatures (Seppälä, 1986), the presence of a dense tree cover on palsas in subarctic North America reduces the amount of incoming solar

radiation and snow to the ground surface (Zoltai and Tarnocai, 1971). Further, lichen covers are frequent on both tree covered and treeless palsas and cause an increase in the albedo. In this way, both a sparse and dense vegetation cover on the palsa surface may in different ways contribute to a negative energy balance and thereby efficiently promote maintenance of permafrost belowground. Soil moisture is also an important factor for the formation and maintenance of permafrost. At the onset of freezing, a saturated peat layer increases the thermal conductivity and allows heat transfer from the ground to the atmosphere, whereas during summer, a dry peat layer insulates permafrost from high air temperatures (Seppälä, 1986).

Palsas are cyclic features in occurrence. They grow and when they have reached a mature stage they start to collapse at the edges by block erosion along surface cracks. The frozen core starts to thaw as soon as the peat layer covering it is lost. Such a development may result in internal lawns, collapse scars or thermokarst ponds; often the only remains of a palsa (e.g. Vitt et al., 1994; Payette et al., 2004). Permafrost degradation on treed palsas causes trees to tilt, and complete permafrost thaw may cause the trees to fall over, be submerged and eventually overgrown by fen communities to create internal lawns. In the boreal Haut Fagnes Plateau in Belgium, so called “viviers” have been interpreted to represent remnants of past mineral-cored palsas (lithalsas) that aggraded permafrost during the Younger Dryas cold spell 11,500 years ago (Pissart, 2003).

X.4.2 Dating of permafrost phases in palsa mires

Various methods can be used to determine when permafrost formed in a peatland. Frost heave resulting from aggradation of permafrost promotes the development of a dry surface layer, suitable for the growth of certain shrubs and trees. The oldest trees on palsas may by their age potentially indicate a minimum age of a permafrost phase. The frequent occurrence of wildfires in these ecosystems, however, affects the age distribution of trees on a palsa. The age distribution of black spruce on treed palsas may therefore reflect the occurrence of past wildfires (Zoltai, 1993), in turn causing damage to local permafrost lenses in wetlands (Turetsky et al., 2002; Myers-Smith et al., 2008). Mortality dates of black spruce stems submerged in thermokarst ponds as determined by tree-ring analysis, can be used to assess the timing of permafrost decay (Vallée and Payette, 2004). Radiocarbon dating of the lowermost layers of older palsa deposit offers another possibility to date the timing of a permafrost phase (Oksanen, 2005; Seppälä, 2005). Peat stratigraphies and reported radiocarbon dates from palsa mires in northern continental Europe (including NW Russia) indicate the initiation of permafrost aggradation during the second half of the Holocene (reviewed by Oksanen 2002; 2005). In Canada, early signs of permafrost aggradation have also been dated to the later part of the Holocene in response to regional cooling (e.g. Zoltai, 1993; Kuhry and Turunen, 2006). Multiple permafrost aggradation and degradation phases within wetlands are frequently reported; the latest during the Little Ice Age after ca. 700 cal BP (e.g. Zuidhoff and Kolstrup, 2000 Oksanen, 2006; Kuhry, 2008; Kokfelt et al., in press). Cautious

sampling and knowledge of peat stratigraphy is necessary to interpret radiocarbon dates originating from dynamic permafrost environments, where highly humified peat layers as well as erosion surfaces may occur between strata. By combining detailed information on peatland stratigraphy, biogeochemical changes and a detailed chronology based on a combination of ^{210}Pb and ^{14}C dating, Kokfelt et al. (in press) demonstrated the existence of a low accumulation layer in a peat core from the Stordalen Mire in northern most Sweden. This layer spans ca. 1500 years and has been interpreted to mirror an early period of permafrost dynamics in the wetland. In the same study, sediment sequences of adjacent lakes were used to support conclusions regarding permafrost dynamics of the peatland based on peat stratigraphy. Permafrost phases dated from peat deposits were found to correlate with periods of relatively acidic lake water conditions, resulting from the formation of poor fen and bog communities in the peatland in response to frost heave.

X.4.3 Ecosystem protected permafrost in palsa mires

Although the geographic position of the climatic envelope for discontinuous permafrost is likely to shift if global warming continues, the occurrence of palsas and peat plateaus does not necessarily follow this shift in the same pace. Peat thickness, vegetation cover and snow depth are also important factors for palsa development and preservation (Luoto et al., 2004a, Seppälä, 2005; Fronzek et al., 2006). Permafrost is present in peatlands under climatic conditions that do not support permafrost in other types of soils, because of the insulating properties of accumulated *Sphagnum* peat (Halsey et al., 1995; Yi et al., 2007). Such permafrost, so called “ecosystem protected permafrost” (Shur and Jorgensen, 2007), has formed under colder climates but can persist as patches in a warmer climate. “Ecosystem protected permafrost” is typically found in climates where the current mean annual air temperature is approximately 2°C to -2°C (Shur and Jorgensen, 2007). Hence, small changes in precipitation and air temperature may cause erosion and degradation of permafrost in palsas and peat plateaus and thereby alter hydrology, ecology and biogeochemical cycling of these wetlands.

In a climate warming scenario, peat plateaus and palsas will be affected and are expected to decrease dramatically during the next 100 years (Fronzek et al., 2006).

X.4.4 Carbon cycling in relation to degradation of permafrost in palsas mires

Describing carbon cycling of a landscape includes a complex array of mechanisms and interactions between major carbon compartments: atmosphere, living vegetation, aquatic environments and sediment stores such as peat and lake sediments. Palsa mires in particular have distinct features and dynamics in relation to emissions of the greenhouse gas methane (Fig. 4.37); a very strong greenhouse gas with a radiative potential 25 times that of CO₂ over a time period of 100 yrs (IPCC, 2007). Intact palsas emit insignificant amounts of methane (Bubier *et al.*, 1995). Permafrost degradation can, however, cause waterlogged conditions and changes in vegetation composition whereby the proportion of anaerobic to aerobic degradation of organic matter together with the transport of methane via sedges cause an increased production and flux of methane to the atmosphere (Christensen *et al.* 2004; T. Johansson *et al.* 2006; Ström and Christensen, 2007). At the Stordalen mire complex (northernmost Sweden) microtopography and hydrological changes as indicated by vegetation change alone were calculated to have caused an increase in the landscape-scale methane (CH₄) emissions ranging between 22 and 66% from AD 1970 to 2000 (Christensen *et al.*, 2004). Ström and Christensen (2007) concluded that the hydrological changes promoted the expansion of plant species that stimulate the production and transport of methane to the atmosphere. Johansson *et al.* (2006) made a combined analysis including both CO₂ and CH₄ exchanges at the same mire, and showed an increased radiative forcing functioning of this ecosystem owing to the relative importance of increased CH₄ emissions. Similarly, Turetsky *et al.* (2002) showed that permafrost degradation features (such as internal lawns) emit 1.6 to 30 times more CO₂ and CH₄ relative to palsas.

Changes in the delivery of organic carbon to aquatic environments as a result of permafrost decay serve another important source of increased emissions of CO₂ and CH₄ to the atmosphere. In the aquatic environment organic carbon is efficiently respired by lake bacteria that cause lake water to become supersaturated with respect to CO₂, which is subsequently emitted to the atmosphere (Kling *et al.*, 1991). Along this path, approximately 50% of the terrestrial derived carbon is emitted back to the atmosphere (Cole *et al.*, 2007). Landforms formed from degrading palsas such as thermokarst ponds, internal lawns and collapse scars all emit significantly higher amounts of methane than intact palsas and peat plateaus (Bubier *et al.*, 1995; Christensen *et al.*, 2004; Turetsky *et al.*; 2007). A recent study of a lake adjacent to a palsa mire in northern Sweden indicates that the carbon emissions from lake surfaces may be as large as emissions from adjacent palsa mires with degrading permafrost (Karlsson *et al.*, *submitted*).

The sink or source function of a terrestrial ecosystem is typically measured by eddy covariance or chamber measurement techniques, as the balance between fluxes (photosynthesis versus respiration) to and from the atmosphere (e.g. Johansson *et al.* 2006). Measurements of this net ecosystem exchange (termed NEE) quantifies the carbon flux in and out of a system, where a positive value denotes a net source to the atmosphere and a negative value denotes a net sink from the atmosphere to the

terrestrial system. However, NEE measurements typically overestimate the sink function of terrestrial ecosystems (Roulet et al., 2007), as carbon losses to aquatic environments are not accounted for. Such losses are important to incorporate in carbon budgets of catchments containing permafrost in peatlands, as the export of dissolved organic carbon (DOC) to rivers, streams and lakes may increase dramatically in response to thawing of permafrost (Frey and Smith, 2005).

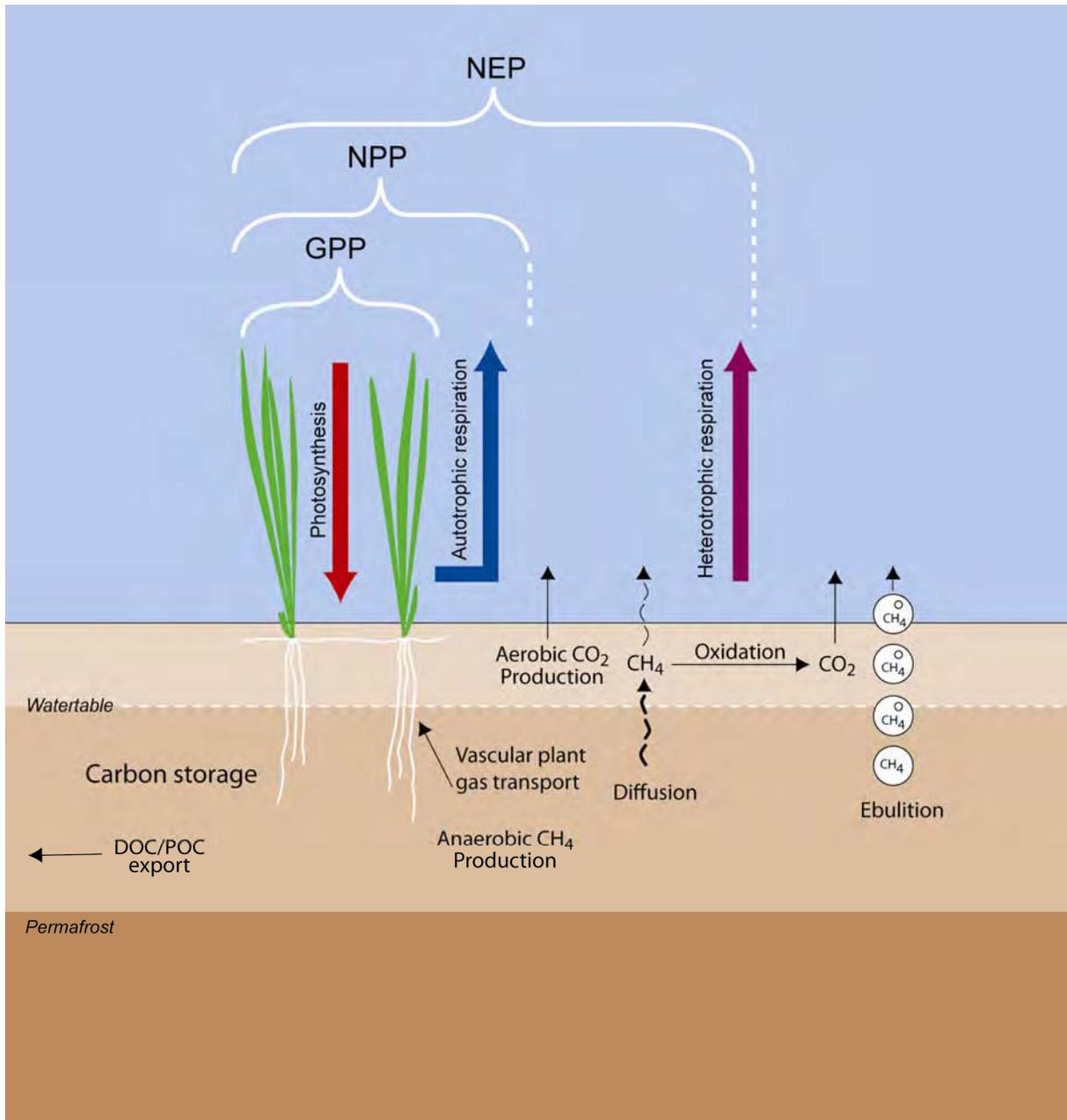


Figure X.8. Schematic diagram of the processes governing the net ecosystem carbon balance, including pathways of CO₂ and CH₄ exchange with the atmosphere, in a permafrost environment (Christensen et al., 2009).

X.4.5 Current and future development of palsa mires

Palsa mires are currently degrading at many sites throughout their distributional range, probably due to regional climatic warming (Johansson et al. 2009). In Norway, Hofgaard (2006) reported on a decreasing peat plateau at Hagutjørnin, Dovre, which has been documented over a 31-year period (1974 to 2005). From the same area, Sollid and Sørbel (1998) reported that palsa plateaus that were almost intact in the 1960s had almost completely disappeared by the end of the 1990s. In sub-arctic Sweden, permafrost thawing has been reported from palsa mires and peat plateaus (Christensen et al., 2004; Johansson et al., 2006; Åkerman and Johansson, 2008; Sannel and Kuhry, 2009). In the Abisko area (68°20'E, 19°02'E) this has been associated with wetting of peat plateaus (Christensen et al., 2004; Johansson et al., 2006, Kokfelt et al., 2009) whereas in Tavvavuoma, northeast of Abisko, the opposite scenario was observed and thermokarst drainage has occurred during the last four decades (Sannel and Kuhry, 2009).

Degrading permafrost in palsa mires has also been reported from Finland (Luoto and Seppälä, 2003), North America (Payette et al., 2004; Camill, 2005) and Western-Siberia (Kirpotin et al., 2007)

X.4.5.1 Active layer and permafrost temperatures

The trend in active layer thickness is not uniform throughout the distribution range of palsas and peat plateaus. Wright *et al.* (2009) reported that the active layer thickness in a peat plateau in Canada at the end of the season had increased from 1999 to 2006, even though there was great inter-annual variability. In northern most Sweden, active layer thickness had increased, ranging from 0.69 to 1.26 cm per year during the last three decades in nine peat mires in the Torneträsk catchment. In addition, the permafrost had disappeared completely at one site and at another 81% of the sampling points during the same time period (Figure 4.38). The increased active layer thicknesses are correlated with increases in mean summer air temperature, Degree-Days of Thawing (DDT) and in five of the nine sites also with increases in snow depth (Åkerman and Johansson, 2008). In contrast to these trends in increasing active layer thickness, Seppälä (2003) reported that in Finland, no unusual development in the active layer on palsas had been detected and that new permafrost had formed in small peat hummocks.

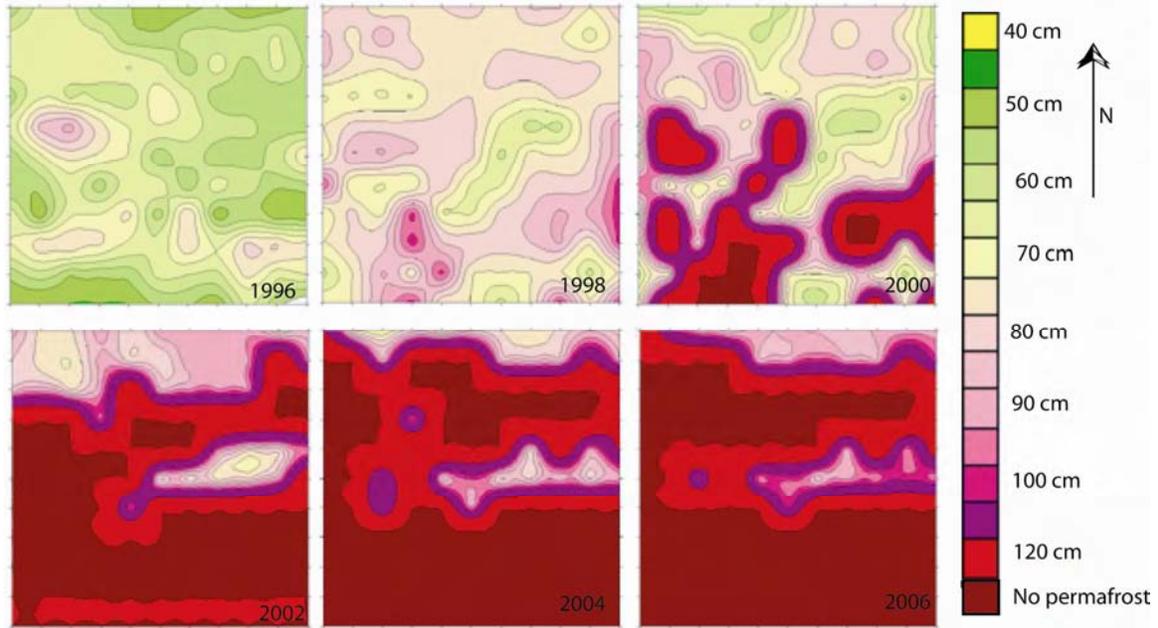


Figure X.9. The permafrost disappeared in 81% of a palsamire in less than a decade (Åkerman and Johansson, 2008).

Associated with the increases in air temperatures recorded in the Arctic during recent decades, ground temperatures in areas underlain by permafrost have increased (Walsh et al., 2005) by 0.5 to 2°C at the depth of zero annual amplitude (the distance from the ground surface downward to the level beneath which there is practically no annual fluctuation in ground temperature) (Brown and Romanovsky, 2008). Permafrost thawing occurs at the southern limits of the permafrost zone (Brown and Romanovsky, 2008) and this has contributed to a northward shift of the southern boundary of discontinuous permafrost (Lemke et al., 2007). Monitoring of permafrost temperatures in palsamires in northernmost Sweden shows that lowland permafrost is currently degrading. Borehole recording showed increasing ground temperatures of 0.04 to 0.05 °C per year in the upper 1 m and 0.03 to 0.04 °C per year in the lower 12-15 m between 1980 and 2002 (Figure 4.39). However, no trend was detected in the middle of the profile. The changes in ground temperatures were correlated with increasing air temperature and increasing summer precipitation. At lower depths, the increases may be due to possible increased heating from a slightly warmer or more freely flowing ground water (Johansson et al., 2008).

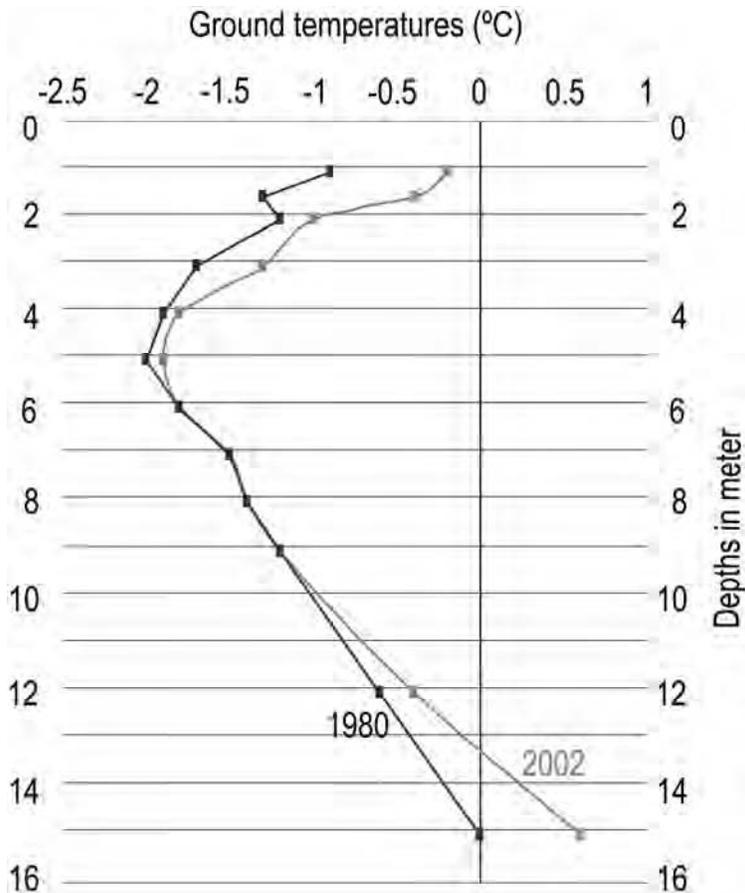


Figure X.10. Ground temperatures are rising in palsa mires in the Abisko area and permafrost is thawing (Johansson *et al.*, 2008)

X.4.5.2 Experimental snow depth manipulation

A thin snow cover is required in the winter to preserve the permafrost in palsa mires. In the Abisko area, northernmost Sweden, a century-long trend of increasing snow depth has been recorded during the last Century (Kohler *et al.*, 2006) and this is projected to continue until the end of the 21st Century (Saelthun and Barkved, 2003). The observed change in snow cover has affected peat mires in the area as thawing of permafrost, increases in active layer thickness, and associated vegetation changes have been reported during the last decade (see text above). To be able to predict future changes due to climate change, it is necessary to look at both vegetation and permafrost changes. An experimental manipulation was set up in autumn 2005 to simulate future snow cover on a peat mire, as was projected for the end of the century (Johansson *et al.*, *submitted*). After three years of treatment (plots with snow fences and control plots), statistically significant differences in ground temperatures were detected for mean winter (October – May) temperatures (0.5 to 1°C higher at the treated plots) as well as for minimum winter temperatures (3 to 5°C higher at the treated plots). No significant difference was detected in the mean summer soil temperature and the

maximum soil temperatures. A difference could also be detected between active layer thickness in the control plots. The abundance of species did not differ between treated and control plots, although vegetation stayed greener for a longer time in treated plots. This was related to a higher soil moisture content in the treated plots at the end of summer. However, the expected increase in soil moisture in the beginning of the season in treated plots, due to additional snow, could not be detected for any of the three years of treatment (Johansson et al., *submitted*).

X.4.5.3 Modelling future palsa distribution

Climate envelopes of palsa mires are narrow and hence they can be expected to be extremely sensitive to changes in future climatic conditions (Parviainen and Luoto, 2007). Luoto et al. (2004a) mapped the spatial distribution of palsas in northern Fennoscandia, north of the Arctic Circle on a regular 10' x 10' grid (Figure 4.40). The distribution was then modelled using climate envelope techniques that determine a statistical relationship between climate variables and the spatial distribution of palsa mires. The models were studied with respect to their sensitivity to altered climate, and climate change scenarios were applied to assess possible impacts on the palsa distribution during the 21st Century (Fronzek et al. 2006; 2009). These models achieved a good to very good agreement with the observed palsa distribution, which suggests a strong dependency on climate. Even small increases of temperature (1°C) and precipitation (10%) resulted in considerable losses of areas suitable for palsa development. The models predicted the total disappearance of suitable regions for palsa development with an increased mean annual temperature of 4°C. Under climate change scenarios based on seven Atmosphere-Ocean General Circulation Models (AOGCMs) the models indicated that the degradation of palsas might proceed very quickly (Figure 4.40). All but one climate scenario resulted in the total disappearance of suitable regions for palsa development by the end of the 21st Century (Fronzek et al. 2006).

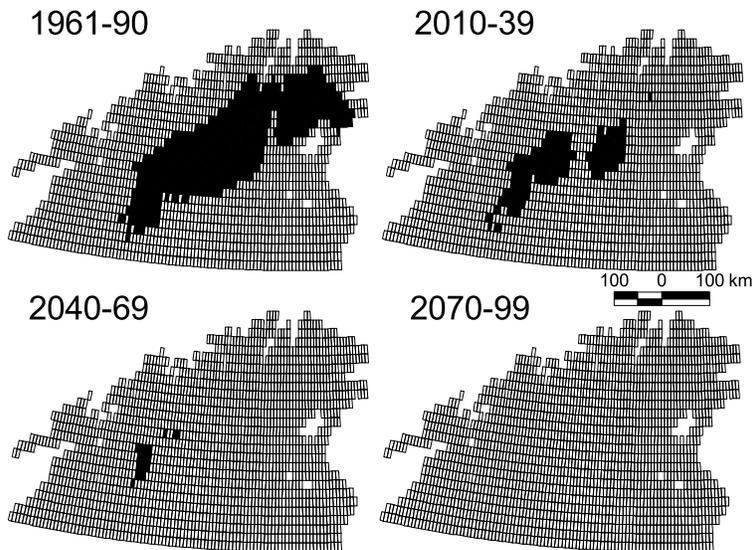


Figure X.11: Palsa mire distribution (solid black grid cells) according to simulations with present-day climate and for future time periods, 2010-2039, 2040-2069 and 2070-2099, using a scenario based on the HadCM3 General Circulation Model with the A2 emission scenario. Modified from Fronzek et al., 2006.

Recent progress in estimating probabilities of future climate change from ensembles of model projections offers an opportunity to go beyond "what if" types of scenario analysis to a quantified assessment of risks to natural or human systems. However, the application of a potentially high number of ensemble climate projections as inputs to impact models may prove impractical. An alternative method makes use of the probabilistic representation of future climate in combination with impact response surfaces (Fronzek et al. 2009). The palsa model was applied to construct impact response surfaces that show the change in palsa areas as a function of mean annual temperature and annual precipitation. These were combined with probabilistic climate change projections derived from an ensemble of 15 AOGCMs using a resampling method (Räisänen and Ruokolainen, 2006). These authors estimated it as very likely (>90% probability) that a loss of area suitable for palsa mires to less than half of the baseline distribution would occur by the 2030s and likely (>66%) that all suitable areas would disappear by the end of the 21st Century under the A1B and A2 emissions scenarios. For the B1 scenario, it was more likely than not (>50%) that a small proportion of the current palsa mire distribution would remain until the end of the 21st century (Figure 4.41).

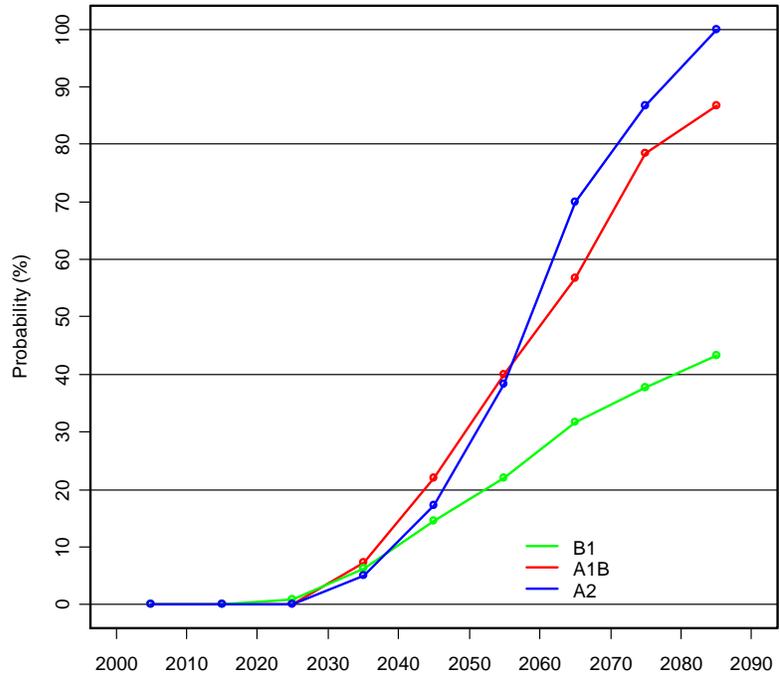


Figure X.12. Probability of the total loss permafrost in palsa mires during the 21st century based on probabilistic projections of climate change from a resampled ensemble of 15 GCM for three emission scenarios. Modified from Fronzek et al., 2009.

X.5. Impact of climate change on regenerating cutover bogs: the future does not look bright

Authors: Emanuela Samaritani and Edward A. D. Mitchell

Northern peatlands have been heavily impacted by mining, drainage and forestry, causing the release of CO₂ to the atmosphere and the loss of their CO₂ sink function (Chapman *et al.*, 2003; Joosten & Clarke, 2002). The restoration of mined peatlands, which in Western Europe cover more surface than natural peatlands, could reverse this trend (Moore, 2002) and there is hope that such regenerating peatlands could act as strong carbon sinks. It is, however, unclear if these peatlands could recover their C-sink function over the long-term (Waddington & Warner, 2001) and what effects climate change may have on the regeneration process and the carbon balance of secondary bogs.

In order to assess how changes in temperature and water table fluctuations might affect the CO₂ balance and hence the long-term fate of the regeneration process of cutover bogs, we used models of photosynthesis (P_G) and respiration (R_{tot}) fluxes derived from gas flux measurements on three regeneration stages of a cutover peatland in the Swiss Jura Mountains, respectively 29, 42 and 51 years after abandonment of exploitation (Samaritani *et al.*, *submitted*). Three temperature increases (+0.5°C, +1.0°C and +1.5°C - corresponding to observed increases in average annual temperature in the 20th century in Switzerland (Rebetez & Reinhard, 2007)), and two increases in water table variability were used in the fitted models from the study site. We increased the hydrological variability by 10 and 20% in comparison to the median value of the water table depth. Temperature changes were applied to both air and soil temperatures. Net Ecosystem Exchange (NEE) for all different scenarios were also calculated on model parameters inferred from re-sampled datasets. To estimate the stability of each model, 500 new datasets of model parameters were generated by bootstrapping. R_{tot} and P_G were re-calculated for each of these pseudo-replicate datasets. The 1st and 3rd quartiles of NEE calculated on these pseudo-replicates are illustrated on the figures as error bars.

X.5.1. Modelling Net Ecosystem Exchange (NEE)

In spring and autumn all sites accumulated carbon, but in summer the youngest site was a net carbon source, the intermediate site alternated between sink and source, and the most advanced site acted as a sink. Further details are given elsewhere (Samaritani *et al.*, *submitted*). Over the entire growing season, the youngest site was a carbon source, whereas the intermediate and advanced sites accumulated carbon (Fig. 1). This agrees with vegetation differences among the sites and especially the percentage cover of *Sphagnum* (a keystone genus for carbon accumulation) and changes from fen to bog vegetation (indicating differences in soil fertility and litter quality which affect net primary production and decomposition rates): 1) *Sphagnum* cover was higher in the intermediate and the most advanced sites than in youngest site, and 2) the intermediate

site, which had a poor fen vegetation with the highest *Eriophorum* cover, was more active (higher P_G and R_{tot}) than the most advanced site, which had a bog-like vegetation (Kummerow *et al.*, 1988; Tuittila *et al.*, 1999).

The responses to simulated climate change contrasted along the regeneration sequence (Fig. 4.42). In the youngest site, all scenarios resulted in strong increases in carbon release. In the intermediate site, NEE decreased both with increasing water table depth variations and temperature, becoming a source of C when warming exceeded 1.0°C. In the most advanced site the NEE was little affected by the different simulated climate changes.

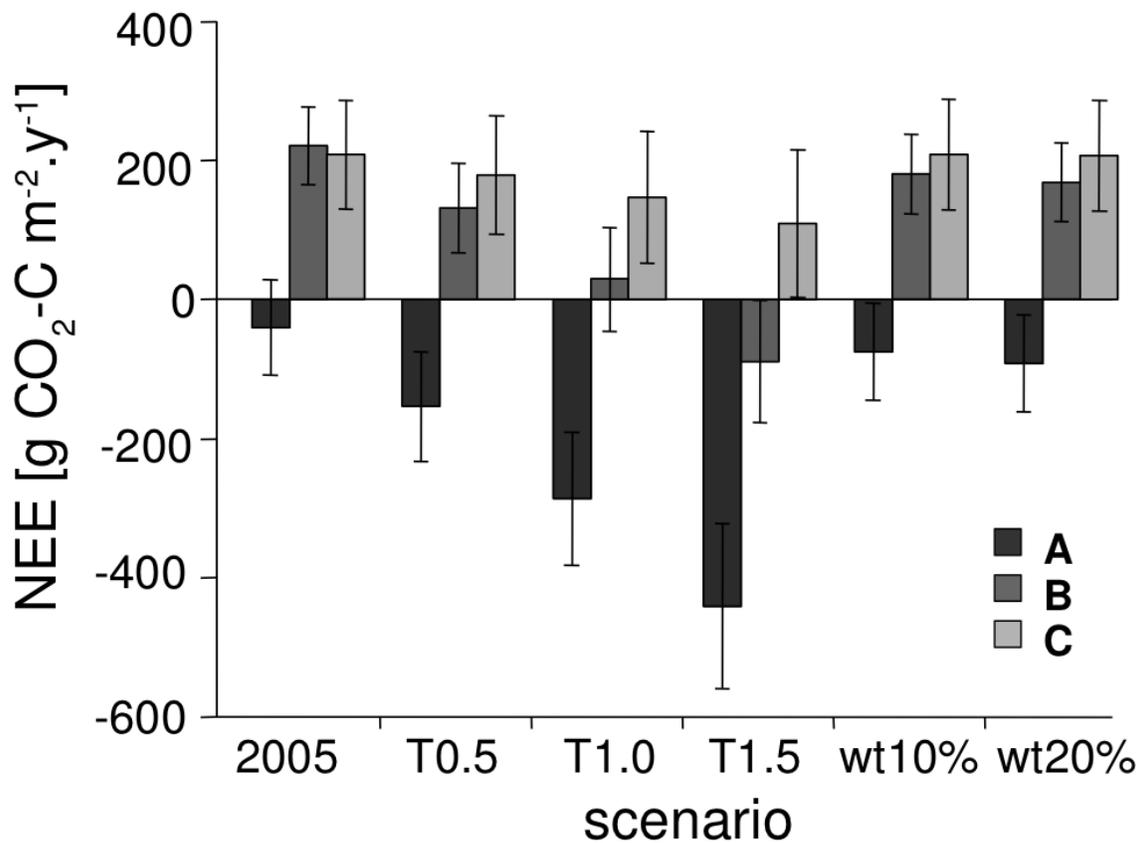


Figure X.13. Simulated effect of climate change on Net Ecosystem Exchange (NEE) of early to advanced bog regeneration stages. NEE estimated for the growing season 2005 in the three sites A (29 years after abandonment of peat extraction; dark grey), B (42 yrs; intermediate grey) and C (51 yrs; light grey), for three air and peat temperature increase scenarios and for two water table depth (wt) variation scenarios. Air temperature and peat temperature at 30 cm depth were increased by 0.5, 1.0 and 1.5°C. The water table variation around the median value was increased by 10% and 20%. Error bars indicate the 1st and 3rd quartiles values obtained by bootstrapping.

The decreasing temperature effect on the carbon balance along the regeneration gradient suggests a higher resistance to climate change in the more advanced site. After 30 years of regeneration, not only does the younger site still release CO₂, but our models suggest that such early regeneration stages are also highly sensitive to climate change. Both a warmer climate and more variable precipitation would cause a strong loss of carbon, making it less likely for these abandoned mined peatlands to return to the structure and carbon-sequestering function that is characteristic of natural bogs. In the present climatic conditions, about 40 years of regeneration are needed for minerotrophic plant species to be replaced by typical bog species. However, the NEE models suggest that the carbon-sequestering function is still fragile then, and increases in temperature can easily convert these regenerating peatlands into a source of atmospheric CO₂. After five decades, secondary bogs are more similar to natural pristine peatlands both in terms of vegetation and carbon dynamics.

This study has important implications for conservation and management of mined bogs and the associated potential carbon sequestration. There might be a tipping point in the secondary succession beyond which regenerating peatlands become more resistant to climate fluctuations. However, the risk is that rather than evolving towards bogs and having a cooling effect on global climate, regenerating peatlands may turn back to fens and thereby contribute to warming. Any action that speeds-up the regeneration of mined peatlands, such as the blocking of drainage ditches which decreases water table fluctuations and thus increases the thermal inertia of soils, will therefore increase the likelihood of mined peatlands to recover fully and durably and contribute to mitigating the ongoing increase in atmospheric CO₂ concentrations.

Concluding remarks

The scope of topics covered in this chapter clearly illustrates the breadth of research that is concerned with peatlands. Peatland research includes the reconstruction of past climatic and environmental conditions, which can range thousands of years back in time. Peatland areas therefore form an important archive for terrestrial palaeo-environmental and climatic reconstructions. For these reconstructions a good chronological control is crucial. Recent advances in dating methods and age-depth modelling have strongly contributed to the development of highly resolved reconstructions with minimal chronological errors. The research field has also gained strongly from the introduction of novel proxies and the development of large training sets, which allow for a quantitative approach to reconstructions. Well-dated, multi-proxy studies have provided comprehensive reconstructions that can be used for the interpretation of climatic changes and their causes.

Peatland research also focusses on the functioning of plants and ecosystems, ecosystem sensitivity and responses to environmental changes. Peatland areas that are situated near environmental thresholds, such as palsas and high-alpine peatlands, were shown to be particularly sensitive to change. Changes in past and modern palsa characteristics can be used for environmental reconstructions as well as for future projections of palsa distributions. Furthermore, peatland experiments and monitoring studies provide important clues to processes controlling greenhouse gas storage and release, potential climatic feedbacks and peatland responses to environmental changes. Research activity in this field is increasing.

Peatland research thus has the potential to provide detailed information on past conditions, as well as recent and ongoing responses to climatic and environmental changes. Thus far, research activity was focussed predominantly on (ombrotrophic) bogs in the northern Hemisphere. With new techniques becoming available, the scope and resolution of such studies can be increased to include detailed reconstructions of different climatic factors, that can be compared more easily to other records. In addition, since peatland areas are found worldwide, the potential in this field of research is vast.

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