National Environmental Research Institute
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Hydrology, nutrient processes and vegetation in floodplain wetlands

PhD thesis

Hans Estrup Andersen

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THE ROYAL VETERINARY AND AGRICULTURAL UNIVERSITY

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Paper 4

Andersen, H. E. and Svendsen, L. M. (1997)

Suspended sediment and total phosphorus transport in a major Danish river: methods and estimation of the effects of a coming major restoration 35

Aquatic Conservation, Vol. 7, 265-276.

National Environmental Research Institute

Dansk Sammenfatning

Denne afhandling afslutter mit PhD-studium udført ved dels Den Kongelige Veterinær- og Landbohøjskole (KVL), Afdeling for Jordbrugsvidenskab, Laboratoriet for Agrohydrologi og Klimatologi, dels ved Danmarks Miljøundersøgelser, Afdeling for Ferskvandsøkologi. Mine vejledere var professor Henry E. Jensen og lektor Søren Hansen, begge fra KVL. Sektionsleder Lars M. Svendsen var min interne DMU-vejleder.

Formålet med studiet var at beskrive og kvantificere hydrologiske processer og disses betydning for næringsstoffer og vegetation i hyppigt oversvømmede ådale.

Afhandlingen omfatter fire videnskabelige artikler og en sammenfatning. En artikel er publiceret i Aquatic Conservation, en artikel er accepteret for publicering i Hydrological Processes og en artikel er indsendt til Nordic Hydrology. Den fjerde artikel foreligger som et manuskript, der er forberedt til indsendelse til Journal of Vegetation Science.

Tre af artiklerne omhandler arbejde udført i et vandløbsnært, hyppigt oversvømmet vådområde på den nedre del af Gjern Å. Den første artikel karakteriserer vådområdet og indeholder en analyse af de styrende forhold for vand- og kvælstofbalancen. Der er lagt vægt på umættede og mættede hydrauliske karakteristika af vådområdesedimenterne. Der er en ringe tilstrømning af grundvand til vådområdet og vandudveksling med atmosfæren er dominerende. Store vandmængder oversvømmer vådområdet, men pga. sedimenternes karakteristika er infiltrationen ringe. Denitrifikationen udgør 71 kg kvælstof pr. år og er begrænset af tilførslen af nitrat. 75% af denitrifikationen udgøres af reduktion af nitrat, der diffunderer ned i sedimentet under oversvømmelse af vådområdet med åvand.

Den anden artikel fokuserer på evapotranspirationen fra vådområdet. Evapotranspirationen er estimeret udfra kontinuerte målinger med en Bowen ratio-opsætning gennem hele vækstsæsonen i 1999. Evapotranspirationen er højere end de fleste publicerede værdier for vådområder med en gennemsnitlig rate for vækstsæsonen på 3.6 mm dag^{-1}. Gennemsnitligt over vækstsæsonen udgør evapotranspirationen 128% af reference-evapotranspirationen beregnet med Penman-Monteith-formlen som anbefalet af FAO. De høje rater forklares dels ved at de kapillære egenskaber af sedimenterne opretholder nær-mættede forhold i rodzonen gennem hele vækstsæsonen, dels ved lokal advektion.

Den tredje artikel indeholder en analyse af plantefordelende faktorer i vådområdet. Quantile regression, en ny metode til analyse af økologiske data, testes og viser sig velegnet til at reducere effekten af umålte faktorer, hvorved effekten af de målte faktorer tydeliggøres. Artiklen indeholder ligninger, der kvantificerer responsen af 18 plantearter til 6 miljøfaktorer. Det vises, at basemætningsgrad, fosfatindhold, oversvømmelseshyppighed, samt grundvandsspejls-amplituden er dominerende faktorer i den rumlige fordeling og dækningsgrad af plantearter i vådområdet.

Den fjerde artikel omhandler arbejde udført på en større skala, nemlig et moniteringsstudie udført på den nedre del af Skjern Å forud for restaureringen af de nederste 18 km. Der udvikles empiriske modeller for åens transport af suspenderet sediment og total-fosfor. Det vurderes, at effekten af restaureringen vil være en reduktion i tilledningen til Ringkøbing Fjord af suspenderet stof og total-fosfor på hhv. 37% og 20% pga. sedimentation i søer og på oversvømmede enge.

I sammenfatningen beskrives faktorer af betydning for hydrologien, næringsstofprocesserne og vegetationen i hyppigt oversvømmede ådale, som ikke er blevet tilstrækkeligt belyst i artiklerne. De særlige forhold, der adskiller tørv fra mineraljorde omtales grundigt. Resultaterne præsenteret i artiklerne sættes i forhold til den internationale litteratur. Samtidig perspektiveres resultaterne ved sammenligning med resultater fra et studie udført i et vådområde, som også ligger i Gjern Å-systemet, men som adskiller sig væsentligt fra det i artikel 1 - 3 undersøgte.

English Summary

This thesis represents the conclusion on my PhD study carried out jointly at The Royal Veterinary and Agricultural University (KVL), Department of Agricultural Sciences, Laboratory for Agrohydrology and Bioclimatology, Copenhagen, and at The National Environmental Research Institute (DMU), Department of Freshwater Ecology, Silkeborg. My supervisors were Professor Henry E. Jensen and associate Professor Søren Hansen, both from the KVL. Senior scientist Lars Moeslund Svendsen was my internal DMU-supervisor.

The purpose of the study was to describe and quantify hydrological processes, and the implication of these for nutrient processes and vegetation in floodplain wetlands.

The thesis comprises four scientific papers and a review. One of the papers is published in Aquatic Conservation, one paper is accepted for publication in Hydrological Processes, and one paper is submitted to Nordic Hydrology. The fourth paper is a manuscript prepared for Journal of Vegetation Science.

Three of the papers are on work done in a floodplain wetland in the lower part of the river Gjern. The first paper characterises the wetland and comprises an analysis of the controls on the water and nitrogen balances. Emphasis is put on unsaturated and saturated hydraulic characteristics of the wetland sediments. There is a minimal inflow of groundwater to the wetland and water exchange with the atmosphere is dominant. Large amounts of water flood the wetland, however, due to the characteristics of the sediments, infiltration is low. Denitrification amounts to 71kg nitrate per year and is limited by the supply of nitrate. Reduction of nitrate diffusing into the sediments during flooding of the wetland constitutes 75% of total denitrification.

The second paper focuses on evapotranspiration from the wetland. Evapotranspiration was estimated from continuos measurements with a Bowen ratio-set up throughout the growing season of 1999. With an average rate for the growing season of 3.6 mm day^{-1} evapotranspiration was higher than most published values for wetlands. The wetland evapotranspiration comprised 128% of reference-evapotranspiration calculated by the Penman-Monteith formula as prescribed by FAO. The high rates are explained partly by the capillary characteristics of the wetland sediments, which sustain near-saturated conditions in the rootzone throughout the growing season, and partly by local advection.

The third paper contains an analysis of plant species distributing factors in the wetland. Quantile regression, a new method for analysing ecological data, was tested. The method was evaluated as adequate for reducing the influence of multiple combined factors and thus to clarify the relation to single factors. A set of equations quantifying the response of 18 floodplain wetland species to six environmental factors is given in the paper. It is shown that that degree of base-saturation, exchangeable phosphate, groundwater amplitude and flooding duration are major factors in determining plant species distribution and cover in the wetland.

In the fourth paper the scale is enlarged to the subcatchment-level. The results of a monitoring study on the lower 18 km of the river Skjern, prior to the river restoration project, is described. Empirical models for riverine transport of suspended sediment and total phosphorus is developed. Assessment of the effects of the restoration, based on measured transport and estimated retention rates for suspended sediment and total phosphorus for different area types of the river system, revealed that suspended sediment and total phosphorus will be reduced by 37 and 20%, respectively.

Factors of importance for the hydrology, nutrient processes and vegetation in floodplain wetlands, and which have not been considered sufficiently in the papers, are described in the review. Emphasis is put on the differences between peat and mineral soils regarding hydraulic properties. The results presented in the papers are discussed relative to the international literature and compared to results from a wetland study also in the river Gjern system, but with a hydrology and nutrient turnover deviating from that of the floodplain wetland analysed in papers 1 – 3.

Review of hydrology, nutrient processes and vegetation in floodplain wetlands

1. Introduction

1.1 Interactions between a river and its surroundings

Riparian ecosystems encompass the stream channel between the low- and high-water marks. They also encompass the terrestrial landscape above the high-water mark where vegetation may be influenced by elevated water tables or flooding and by the ability of the soils to hold water (Naiman and Décamps, 1997). River systems and their riparian zones can be viewed as open ecosystems dynamically linked longitudinally, laterally and vertically (Ward, 1989). From a hydrological point of view streams and rivers as surface-water bodies are integral parts of groundwater flow systems. It is generally assumed that topographically high areas are groundwater recharge areas and topographically low areas are groundwater discharge areas. However, this is primarily true for regional flow systems (Winter, 1999). Local flow systems associated with surface-water bodies are superpositioned on the regional framework resulting in complex interactions between groundwater and surface-water regardless of regional topographic position. Despite of this an overview of groundwater surface-water interactions within a catchment is provided by the following conceptual model, Fig. 1 (Nilsson *et al.*, 2002). The model assumes a homogenous geology and equal precipitation within the entire catchment and divides a watercourse into sub-reaches of characteristic hydrogeology and geomorphology. Fig. 1 shows a longitudinal transect of a river together with an assumed linear course of the regional water divide. The difference in elevation between the water divide and the river along a groundwater streamline illustrates the hydraulic potential, which drives the regional groundwater flow towards the surface water. It is apparent from the Fig. that the largest hydraulic potential is found along the middle reach of the river. Thus it is expected that the largest and most stable regional groundwater discharge will take place on this section. Upstream and downstream the hydraulic potential diminishes and the discharge of deep groundwater will be less. In the headwater area local groundwater flow systems will dominate and contribute young groundwater. The flow system will depend on precipitation and be unstable. The upper reach will be dominated by local and intermediary flow systems. Along the lower reach the deep groundwater discharge has diminished, local and intermediary systems can contribute, and flooding occur due to the lower slope of the river.

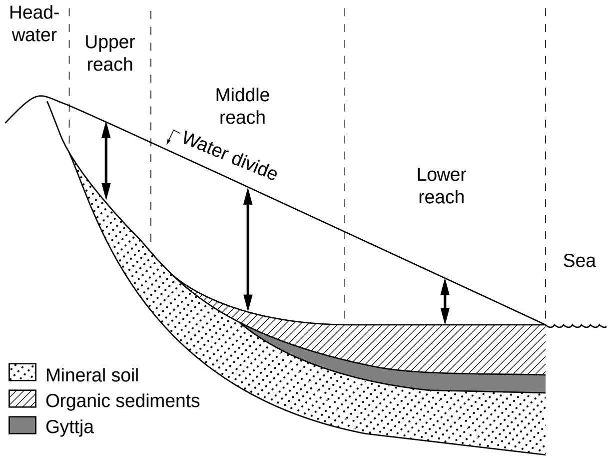

Fig. 1. Division of a water course into sub-reaches with characteristic hydrogeology and geomorphology (after Nilsson *et al.*, 2002).

There has been considerable focus on riparian wetlands in Denmark during the past decade due to their ability to modify diffuse pollution of surface waters. In fact, the Danish Parliament in 1998 decided on the restoration of 16,000 hectares of wetlands with the chief purpose of reducing agricultural nitrate loading to the aquatic environment. A number of Danish studies on the hydrology and nutrient processes of riparian wetlands located on the upper and middle reaches of water courses have been carried out (Brüsch and Nilsson, 1990; Hoffmann *et al.*, 1993; Dahl, 1995; Paludan, 1995; Hoffmann, 1998a; Blicher-Mathiesen, 1998, Hoffmann *et al.*, 2000). Less work has been done on the lower reaches subject to frequent flooding – the floodplains (Hoffmann *et al.*, 1998); Hoffmann, 1998b; Kronvang *et al.*, 2001, Andersen, 2002; Andersen *et al.*, 2002). However, knowledge about the characteristics and functioning is important in order to restore and maintain floodplain wetlands.

1.2 The floodplain wetland

Internationally as well has there been considerable interest in the function and value of wetlands (e.g. Carter, 1986). Floodplain wetlands, in their natural state, have been cited to be of particular value since they have a high biodiversity, provide critical habitats for many plants and animals, and are an important, natural element in the maintenance of water quality (Mitsch and Gosselink, 1986; Whiting and Pomeranets, 1997; Takatert *et al.*, 1999; Hupp, 2000).

The characteristics and function of a floodplain is intimately linked to the river that flows upon it. When unregulated, floodplains are highly dynamic like most fluvial landforms, and frequently inundated by overbank floods. Compared to the upper parts of the catchments groundwater level is shallow – near or above soil surface – facilitating the build up of peat (Grootjans, 1985). Typically, the river is bordered by levees consisting of relatively coarse material. The levees are often the highest points on the floodplain, which may otherwise be extremely flat. This has the effect that elevation differences of just few centimeters create differences in hydroperiod (length of inundation), and hence a profound zonation in vegetation pattern (Mitsch and Gosselink, 1986).

Sediment trapping on a floodplain is strongly influenced by the length of the hydroperiod, and hence by the height of the levees. The floodplain may act as a very important sink for nutrients carried by the river. Permanent deposition of Phosphorus (P) during flooding of a Danish lowland river floodplain was found to be 100 kg P ha^{-1}year^{-1}, equalling the loss of P from 200 ha agricultural land (Kronvang *et al.*, 2001). In a study prior to the restoration of the lower 18 km of the river Skjern, Denmark, mean annual riverine transport of suspended sediment (SS) and P was determined to 12,200 t SS and 100 t P, respectively (Andersen and Svendsen, 1997). The effect of the restoration, mainly by allowing frequent flooding of riparian areas, was estimated to be a reduction in the transport of SS and P of 37% and 20%, respectively.

Analysis of time series for all major Danish streams has shown an increasing trend over the past 80 years in annual mean runoff (statistically significant in 6 out of 32 stations). This increase is most likely caused by the increase in precipitation of 0.76 mm yr^{-1} observed over the period 1874-1998 (p=0.02%) (Ovesen *et al.*, 2000). If these are continuing trends the importance of floodplains as buffers for water and sediment will increase.

2. Hydrology of wetlands

Hydrologically, a wetland is distinguished from adjacent upland areas by the presence of water, which creates alternatingly or permanently saturated conditions. The consequential effect is substantial water storage within wetlands, and the development of a readily identifiable wetland vegetation, which is adapted to periodic anoxic conditions (Bradley and Gilvear, 2000). Thus, the water-budget provides the framework from which to investigate environmental conditions in a wetland (Lent *et al.*, 1997) and linkages between upland, wetland, and river (Drexler *et al.*, 1999), Fig. 2. In spite of this only relatively few comprehensive water balance studies of wetlands exist (e.g. Gilvear *et al.*, 1993; Hyashi *et al.*, 1998; Raisin *et al.*, 1999). Since the surface and subsurface hydrologic processes within a wetland are inseparable (Roulet, 1990) a water balance needs to quantify both surface and subsurface water fluxes. The main inputs of water include precipitation (P), influent river seepage (q_i), overbank floods (q_{ov}), and groundwater inflow (q_{gr_i}). Outflows of water are evapotranspiration (ET), effluent river seepage (q_o), surface runoff (q_{su}), and groundwater outflow (q_{gr_o}). Problems in quantifying the water fluxes by direct measurements have often been articulated in the literature, especially concerning the groundwater flux (e.g. Gilvear *et al.*, 1993; McKillop *et al.*, 1999). The physical determination of this water flux is commonly based on observations of hydraulic head in piezometers and point-measurements of hydraulic conductivity, neither of which necessarily can be extrapolated. A direct means of determining the groundwater flux is by tracer study (e.g. Blicher-Mathiesen, 1998). In other cases groundwater flow models have been applied instead of measurements (e.g. Bradley, 1996; Zeeb and Hemond, 1998; Stewart *et al.*,1998; Restrepo *et al.*, 1998). Direct measurement of evapotranspiration is also often omitted and substituted by empirical formulas or determined as the residual in the water-budget equation (Carter, 1986). Some wetlands are permanently water saturated, however many wetlands exhibit partly unsaturated conditions, typically during the growing season. The unsaturated zone is potentially very important for wetland ecology for a number of reasons: (i) water content in the root zone is a strong determinant of species composition of vegetation communities due to different adaptions (e.g. Bridgham and Richardson, 1993; Grevilliot *et al.*1998; Silvertown *et al.*, 1999, Schröder *et al.*, 2002); (ii) the degree of saturation and thus aeration substantially influences decomposition of organic matter and mineralisation of nutrients (Ponnamperuma, 1984); (iii) the water-budget is affected since evapotranspiration is dependent on soil water content (Brandyk *et al.*, 1995), and with the existence of a substantial unsaturated zone some or all precipitation infiltrating the surface will be retained here rather than percolate (Winter and Rosenberry, 1995). However, in water balance studies of wetlands the unsaturated zone is generally neglected. Exceptions are e.g. Bradley and Gilvear (2000), who described conditions in the unsaturated zone via modelling, and Andersen (2002) who undertook measurements of saturated as well as unsaturated water balance components. The literature, however, contains examples on studies directed more specifically towards the unsaturated characteristics of wetland soils; e.g. Bloemen (1982); Brandyk et al.(1985); da Silva *et al.*(1993); Weiss *et al.*(1998).

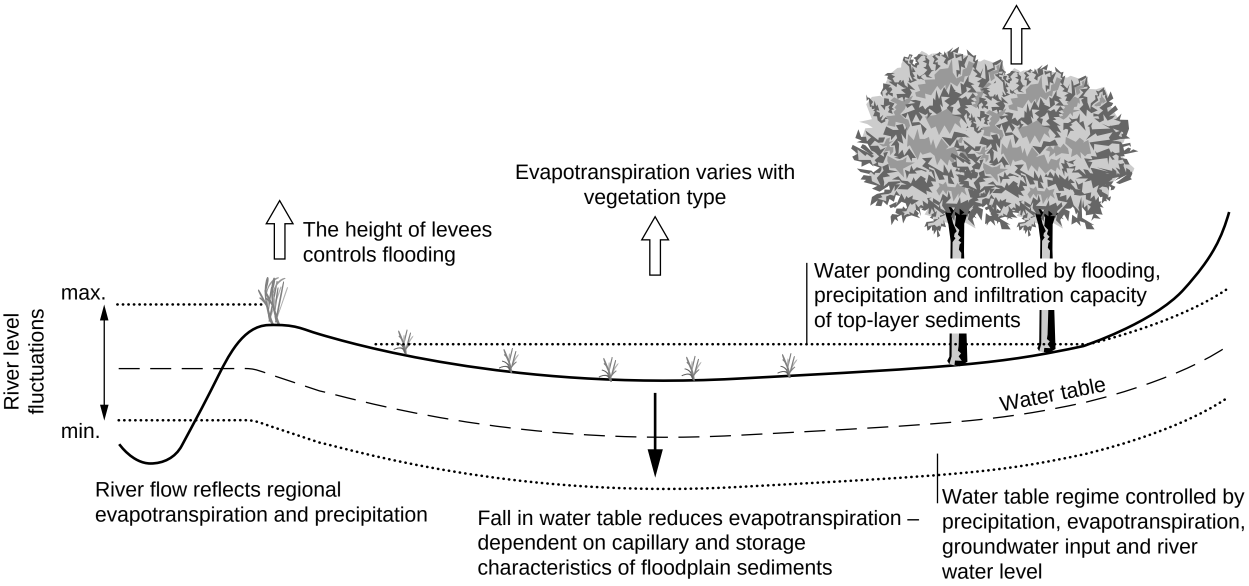

Fig. 2. Key controls upon the wetland water balance along a floodplain transect.

2.1 Hydraulic properties of peat

The hydraulic characteristics of wetland sediments can vary significantly over short horizontal and vertical distances (e.g. Zeeb and Hemond, 1998). This reflects the coincidence, in floodplain wetlands, of alluvial coarse sediments and fine silt and clay from overbank deposition with heterogenous organic deposits of peat (Bradley, 1996). The presence of peat is a characteristic feature of many floodplains (Mitsch and Gosselink, 1986). Peat accumulates where the decomposition of plant remains is retarded due to prevalent anaerobic conditions as in a permanently or intermittently water saturated soil (Ingram, 1983). The hydraulic properties of peat vary in relation to species composition, humification and inorganic content. Further, the extreme compressibility of peat relative to mineral sediments have significant hydrological consequences which so far are scarcely recognized (Price and Schlotzhauer, 1999). Peat is thus of special interest and will be treated here in some detail.

Peat is by definition (Vedby, 1984) a biogenic material containing at least 12 - 18% organic carbon in the form of completely or partly decomposed plants deposited in a more or less anaerobic environment. Soil Taxonomy (Creutzberg, 1975) groups organic soils into three categories based on their fiber content (a fiber is a fragment of plant tissue larger than 0.15 mm): *fibric soils* have a fiber content of at least 3/4 of the soil volume, *hemic soils* are intermediate between fibric and *sapric soils,* where the latter has a fiber content less than 1/6 of the soil volume. A fibric peat is an undecomposed peat whereas a sapric peat is strongly humified. Since bulk density increases with humification this parameter has also been used to characterize peat.

Structure of peat

Studies of the structure of peat (e.g. Loxham and Burghardt, 1986) reveal that peat is a highly structured material with both connected and dead end pores. Very large pores can be present. Two extreme types of peat can be described between which all other peat gradations exist. These two types are the highly humified ‘amorphous granular’ peat, in which the soil particles are mainly of colloidal size and most of the pore water is absorbed around the grain structure, and the undecomposed ‘fibrous peat’, which has essentially an open structure with interstices filled with a secondary structural arrangement of non-woody fine fibrous material. Porosity is thus at least to some extent a function of degree of humification. Boelter (1965) measured the variation in porosity of a moss peat profile. Values ranged from 0.966 of the undecomposed peat to 0.833 of the decomposed peat. Vedby (1984) measured porosity of different peats. Values ranged from 0.757 to 0.972, highest for very fibrous peat and lowest for less fibrous peat and peat with a high amount of minerals.

The decrease in porosity with increasing humification is reflected in increasing bulk density (Boelter, 1969; Paivanen, 1973). In the study of Vedby (1984) dry bulk density ranged from extremely low values in undecomposed *Sphagnum* peat; 0.034 - 0.041 g cm^{-3}, to 0.2 - 0.3 g cm^{-3} for very decomposed peat. However, given the higher specific density of minerals (approx. 2.6 g cm^{-3}) compared to peat (1.31 - 1.38 g cm^{-3} (Galvin, 1976); 1.5 g cm^{-3} (Vedby, 1984)) the bulk density of peat is highly dependent on the size of a possible inorganic fraction. Presence of minerals can thus obscure the correlation between bulk density and degree of humification.

Water retention in peat

It is not only the total pore volume that changes upon humification, but also the pore size distribution and hence the water retaining capabilities. In an undecomposed peat the large pores will dominate whereas with increasing degree of humification the amount of fine pores will increase along with a decrease in total pore volume (Eggelsmann, 1971). This means that total water content at saturation will be the highest for low humified peats. For high tension values (pF 3 - 4) on the other hand the water content is higher in the more humified peat (Fig. 3). This implies that decomposition of peat apart from an increase in fine pores also results in the formation of smaller particle sizes having larger specific surfaces facilitating water adsorption since at high tension water molecules are adsorped rather than being held by capillarity (e.g. Jury et al., 1991). For comparison with mineral soils Fig. 3 also contains retention data from a sandy and a loamy soil (Jacobsen, 1989).

For a non-swelling soil the relationship between pore water pressure and water content is represented by the water retention curve (Fig. 3). Pore water pressure can be measured in the field by a tensiometer. Ignoring hysteresis there thus exists a unique relation between a tensiometer reading and actual water content. For a swelling soil such as peat (see below) the relationship between pore water pressure and the water content is more complicated because the water content also depends on the load applied to the soil matrix (Towner, 1981). For a given water content the pore water pressure increases (becomes less negative) the higher the applied load. Thus there is a series of curves, one for each specified load applied to the point of observation in the soil matrix, as suggested in Fig. 4. In order that the appropriate curve in Fig. 4 can be selected the applied load must also be known.

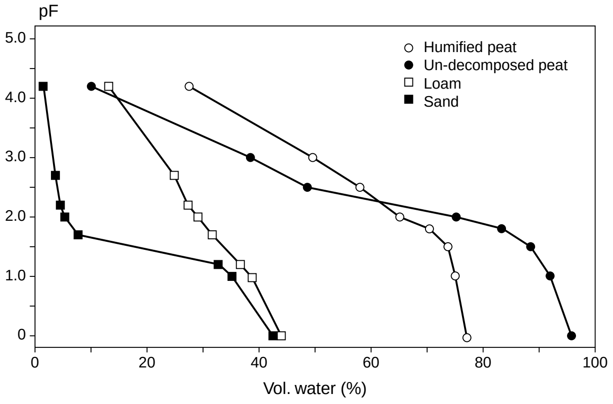

Fig. 3 Retention curves drawn from data published in Loxham and Burghardt (1986) and Jacobsen (1989). The un-decomposed peat has a bulk density of 0.09 g cm^{-3}, while the humified peat has a bulk density of 0.36 g cm^{-3}. The sandy soil is “Jyndevad, 90 cm” having 2.5% clay and 0.5% silt. The loam is “Askov, 50 cm” having 24.4% clay and 11.5% silt.

For the determination of total soil water potential, ψ_T, in a swelling soil, e.g. for flow calculations, however, one need not to know the applied load. This is due to the fact that the pressure potential, ψ_p, measured with the tensiometer encompasses all effects on soil water other than gravity (specified in the gravitational potential, ψ_g) including the applied load at the point of observation (e.g. Jury et al., 1991).

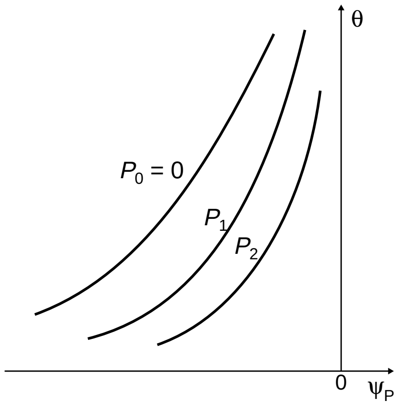

Fig. 4 Relationship for a swelling soil between the water content, θ, and pore water pressure, ψ_p, under different load pressures, $P_0 < P_1 < P_2$ on the soil matrix. After Towner (1981).

Compressibility

The analysis of transient flow in a saturated porous medium requires introduction of the concept of compressibility. Equally important is the concept of compressibility in the understanding of the consolidation (natural or man induced) of peat which is accompanied by drastic changes in permeability. Following Hillel (1980) the term compression comprises two different processes or phases, viz. compaction - the compression of an unsaturated soil body resulting in reduction of the fractional air volume - and consolidation - the compression of a saturated soil by squeezing out water.

Compression is defined (e.g. Freeze and Cherry, 1979) as strain/stress - $d\varepsilon/d\sigma$ - the change in volume, or strain, induced in a material under an applied stress. The term is utilized for both elastic and nonelastic materials. When a stress (N m^{-2}) is applied to a saturated porous material there are three mechanisms by which a reduction in volume can be achieved: (i) by compression of water in the pores, (ii) by compression of the individual building blocks of the soil skeleton (sand grains in the case of a sandy deposit, organic molecules in the case of a peat), and (iii) by a rearrangement of the soil skeleton into a more closely packed configuration. The first of the mechanisms is controlled by the fluid compressibility β, which can be considered as a constant having a value for water of 4.4 x 10^{-10} m^2 N^{-1}. The second mechanism is normally assumed negligible for mineral constituents; we will apply the same assumption regarding the compressibility of the constituents of a peat soil. In order to treat the third mechanism of volume reduction we will have to introduce the Terzaghi-principle of effective stress (e.g. Skempton, 1961): Considering the stress on a normal plane in a saturated porous medium (Fig. 5) σ_T is the total stress acting downward on the plane. It is due to the weight of overlying solids and water. This stress is borne in part by the solid skeleton of the porous medium and in part by the fluid pressure ψ_p of the water in the pores. This is in contrast to shear stress which when applied to a porous medium must be carried exclusively by interparticle forces in the solid skeleton, since as first proposed by Terzaghi (1936) the water (and air) phase cannot carry shear stress but only normal stress. The portion of the total stress that is not borne by the fluid is called the effective stress σ_e. This is the stress, that is actually applied to the constituents of the porous medium. Rearrangement of the solids and the resulting compression of the solid skeleton is caused by changes in the effective stress, not by changes in the total stress. The two are related by the equation

(1) $$\sigma_T = \sigma_e + \psi_p$$

As an example we will calculate the effective stress in depth z in a saturated soil without external loading: The normal stress is the weight of the overlying solids and water divided by the surface area of a normal plane

(2) $$\sigma_T = \rho_b \, g \, z$$

where

ρ_b = (wet) bulk density

g = acceleration due to gravity

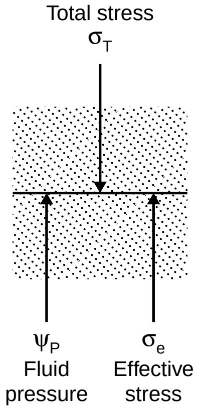

Fig. 5 Total stress, effective stress, and fluid pressure on a normal plane through a saturated porous medium. After Freeze and Cherry (1979).

If there is no flow the water pressure is hydrostatic

(3) $$\psi_p = \rho \, g \, z$$

where

ρ = density of water.

Thus effective stress is growing downwards in the soil proportionally to the density difference

(4) $$\sigma_e = \sigma_T - \psi_p = (\rho_b - \rho) \, g \, z$$

For cases where the total stress does not change with time - which holds true for many transient subsurface flow problems according to Freeze and Cherry (1979) - the effective stress at any point in the system, and the resulting volumetric deformations there, are controlled by the fluid pressures at that point, as can be seen from (1).

Equation (1) has been shown (Skempton, 1961) to be an excellent approximation to the truth for saturated soils. Experimental support for the validity of (1) also for negative pore water pressures has been given (Bishop and Eldin, 1950), provided the system remains apparently saturated (that is, saturated by all practical measurable means). Thus, a negative pore water pressure contributes positively to the effective stress in the solid framework of the soil system. For significantly unsaturated soils anomalies arise, because both air and water are present in the voids, and in general these are under different pressures owing to the curvature of air-water interfaces. This means that a hydrostatic pressure distribution does not exist in an unsaturated soil. However, an expression similar to (1) has been proposed for unsaturated soils:

(5) $$\sigma_T = \sigma_e + \chi \psi_p$$

where χ denotes the degree of saturation. The implication of (5) is that also for negative pore water pressures will a decrease in pore water pressure (more negative) increase the effective stress acting on the solid skeleton given a constant external load. Experimental evidence for (5) has been given (Bishop, 1961; Jennings, 1961; Aitchison, 1961), however its validity has also been questioned (e.g. Bradford and Gupta, 1986). Van der Molen (1975) reports, based on experience with shrinkage due to dessication of peats in the Netherlands, that equating mechanical stresses to soil moisture stresses gives good results. The connection between shrinkage and negative pore water pressure has also been observed by Vedby (1984) while determining water retention characteristics on peat samples.

The compressibility of a porous medium is defined as

$$(6) \qquad \alpha = \frac{-dV_T/V_T}{d\sigma_e}$$

where

V_T = total volume = $V_s + V_v$
V_s = volume of solids
V_v = volume of water-saturated voids
σ_e = effective stress

Typical values of compressibility ($m^2\ N^{-1}$) are for clay 10^{-6} - 10^{-8} and for sand 10^{-7} - 10^{-9} (Freeze and Cherry, 1979). Galvin (1976) made measurements on a number of different irish peat deposits. He reported values of compressibility ranging from 8 x 10^{-6} to 2 x 10^{-5}; the younger the peat the larger the value of compressibility.

The high compressibility of peat and the increase in effective stress downwards in a peat profile (4) combined with the continuous increase in total stress due to the increase in load in the form of accumulating plant residues on the peat surface, result – together with decomposition of the peat - in the often observed increase in bulk density and corresponding decrease in porosity and permeability with depth (e.g. Boelter, 1965; Vedby, 1984, Gafni and Brooks, 1990). The application of a load increases on the first hand the pore water pressure. During the process of consolidation the pore water pressure in excess of hydrostatic pressure slowly equalizes by a release of water possibly in the form of upward flow as observed by Dasberg and Neuman (1977).

Partly de-watering of a peat deposit consolidates the remaining saturated part by two mechanisms: (i) according to equation (1) a decrease in pore water pressure increase the effective stress acting on the deeper layers. A lowering of the water table of 1 m decreases the hydrostatic pressure by 9807 N m^{-2} (1 m H_2O) and hence increases effective stress with the same amount. (ii) De-watering the upper layer of the peat increases effective stress acting on the deeper layers by increasing the effective weight of the unsaturated peat. Since there is no continuous hydrostatic contact between the water in the unsaturated zone and the water in the saturated layer, the weight of the water in the unsaturated zone cannot be transferred to the water in the saturated layer. Instead the water stored in the unsaturated zone adds to the weight of the peat here. The water content at field capacity is considerable (Fig. 3) meaning that de-watering increases the effective weight significantly. The effective weight of the unsaturated peat is calculated as the sum of the dry bulk density and the water content at the actual pore water pressure. This effective weight is unreduced transferred to the solid skeleton of the saturated peat as effective stress.

Storage

Another property of a porous medium to be considered when dealing with transient flow processes is the storage capacity of the medium. For a saturated aquifer the specific storage S_s (m^{-1}) is defined as the volume of water that a unit volume of aquifer releases from storage under a unit decline in hydraulic head, h_T. Since $h_T = p + z$ $(p = \psi_p/\rho g)$, and z being constant at the point in question, a decrease in hydraulic head infers a decrease in fluid pressure and an increase in effective stress σ_e. The water that is released from storage under conditions of decreasing h_T is produced by two mechanisms: (i) the compaction of the aquifer caused by increasing σ_e, and (ii) the expansion of the water caused by decreasing ψ_p. The first of these mechanisms is controlled by the aquifer compressibility α and the second by the fluid compressibility β. The specific storage S_s is given by (7)

$$(7) \qquad S_s = \rho g(\alpha + n\beta)$$

where

n = porosity.

Since water is not significantly compressible under the range of pressures encountered in shallow systems (7) reduces to $S_s = \rho g \alpha$.

For a confined aquifer (i.e. the pore water pressure at the top of the aquifer is higher than atmospheric pressure) the storativity (or storage coefficient) S is defined as $S_s b$, where b is the thickness of the aquifer. The storativity is normally determined by indirect methods such as pumping test analysis. According to Neuman and Witherspoon (1972) the specific storage S_s can also be inferred from consolidation curves. Specific storages range from 10^{-4} m^{-1} (clay) to 10^{-6} m^{-1} (sand) (Rosbjerg, 1987). Dasberg and Neuman (1977) report specific storage for peat in the Hula Basin in Israel ranging from 0.086 m^{-1} to 0.118 m^{-1}, with the lowest values for deeper more compacted peat. The implication is that a unit volume of saturated peat can release about 10^5 times more water due to compression than a unit volume of sand, when the hydraulic head drops by one unit.

For an unconfined aquifer (i.e. under water table conditions where the pore water pressure in the top of the aquifer is at atmospheric pressure) the storage term is traditionally known as the specific yield, S_y. S_y is defined as the volume of water that an unconfined aquifer releases from storage per unit surface area of aquifer per unit decline in the water table. The usual range of S_y for mineral soils is 0.01 - 0.3 (Rosbjerg, 1987) and can be inferred from the water retention curve as the difference in water content between saturation and field capacity. Accepting field capacity as represented by a negative pore water pressure of 1 m H_2O S_y values for peat ranging from 0.1 - 0.3 can be read out of published water retention data by Dasberg and Neuman (1977) and Loxham and Burghardt (1986). Price (1996), from a Canadian cutover bog, reported a range from 0.048 to 0.55. Lower values are for decomposed peat, and higher values are for undecomposed or living mosses. Andersen (unpublished results) found for floodplain peat deposits of sedges and herbaceous plants and with a considerable fraction of inorganic material a more narrow range from 0.09 to 0.26 for hemic to fibric peat. The relatively high values for unconfined aquifers reflect the fact that releases from storage in unconfined aquifers represent an actual dewatering of the soil pores, whereas releases from storage in confined aquifers represent only secondary effects of water expansion and aquifer compaction. Since for mineral soils S_y is normally so much higher than S_s in unconfined units, S_s is often ignored in the overall aquifer storativity, where $S_{tot} = S_y + bS_s$. However, also in studies involving peat hydrology the significance of storage changes caused by peat compaction has typically been ignored (Price and Schlotzhauer, 1999). Price and Schlotzhauer (1999) measured S_y and S_s in an unconfined cutover peat deposit with a fluctuating water table and found S_s was in fact 67 to 170% larger than S_y. Considerable hysteresis was observed with S_s averaging 0.094 m^{-1} during drying periods, but only 0.026 m^{-1} on rewetting. Thus, as also recommended by Dasberg and Neuman (1977), compressibility must not be neglected in dealing with fluid flow through peat layers, irrespective of whether these layers are confined or unconfined.

In the unsaturated zone storage is given by the moisture content θ. Changes in storage are accompanied by changes in the pressure head p, through the θ (p) relationship displayed on the water retention curve (Fig. 3). The slope of this curve represents the unsaturated storage property of a soil, where the specific moisture capacity C is defined as

$$C = d\theta / dp \tag{8}$$

Saturated hydraulic conductivity

Permeability or hydraulic conductivity, K_s, was early recognized as a crucial hydraulic variable in the study of the hydrology of peatlands. As a result, K_s became the most studied parameter of organic soils according to Gafni and Brooks (1990). However, different methods applied coupled with the variation among organic soils mentioned above have yielded a wide range of values. In a review by Rycroft et al. (1975a) some seven orders of magnitude of K_s- values are reported for peat. Several researchers who have studied the variation in hydraulic conductivity have noted a negative effect of depth and degree of decomposition on K_s (Boelter, 1965; Paivanen, 1973; Gafni and Brooks, 1990). Boelter (1969) found on basis of 119 samples from 12 Minnesota bogs a linear relationship between K_s and the degree of decomposition expressed as fibric, hemic and sapric peat, respectively. Table 1 lists the range in K_s-values together with bulk density and porosity. Table 2 lists similar characteristics, but for floodplain deposits where peat is mixed with inorganic sediments derived from floodings with surface water.

Table 1. Range in physical characteristics of fibric, hemic and sapric peat materials from northern Minnesota bogs. After Boelter (1969).

Organic material	Bulk density	Total porosity	Hydraulic conductivity
	$g\ cm^{-3}$	%	10^{-7} $m\ s^{-1}$
Fibric	< 0.075	> 90	> 180
Hemic	0.075 – 0.195	85 - 90	2.1 - 180
Sapric	> 0.195	< 85	< 2.1

Table 2. Physical characteristics of fibric and hemic peat from a Danish floodplain wetland. Organic content was 67% and 40% for fibric and hemic peat, respectively (after Andersen, 2002).

Organic material	Bulk density	Total porosity	Hydraulic conductivity
	g cm^{-3}	%	10^{-7} m s^{-1}
Fibric	0.16	90.8	1100
Hemic	0.36	82.5	0.6

Table 1 and Table 2 demonstrate the range in physical characteristic encountered for peat materials in various degrees of decomposition. Also illustrated is the effect on bulk density of inclusion of inorganic material originating from flooding of the floodplain wetland. From the tables it is clear that the hydraulic conductivity can be indeed very low for well decomposed peat even though total porosity remains high. Various explanations have been offered for this apparently anomalous behaviour: clogging of the pores by fine peat particles and colloidal humus (Rycroft et al., 1975a), compression of the peat matrix due to overburden pressure stress (Hemond and Goldman, 1985), occlusion of the pores by bubbles of methane gas generated by in situ anaerobic decomposition of plant biomass (Mathur and Levesque, 1985). All explanations appear plausible. Chow *et al.*, (1992) measured K_s in a compaction experiment on a moderately decomposed fibrous *Sphagnum* peat. K_s decreased 3 orders of magnitude when dry bulk density was increased from 0.1 g cm^{-3} to 0.2 g cm^{-3}. This was primarily due to a reduction of the amount of macropores: the proportion of pores 148 µm – 594 µm decreased from 17.5% to less than 2%, while the proportion of pores smaller than 59 µm remained relatively constant. It has been shown (Loxham and Burghardt, 1986) using chemical tracer tests on undisturbed peat samples, that at saturation water flows through a few interconnected channels bypassing the rest of the pores. Also, experimental evidence for the probability of the theory of occlusion by methane gas bubbles has recently been obtained in laboratory experiments by Reynolds et al. (1992). They compared the course of water content, θ, and K_s over time between sterilized and non-sterilized peat columns flowed continuously under positive pressure. Over time periods ranging from 44 to 78 days, K_s decreased on average by 1.6 orders of magnitude, θ (measured in situ with TDR) decreased by 20 percentage points, and gaseous methane increased 12-fold in the non-sterillized columns. In the sterilized column on the other hand, hydraulic conductivity and water content increased to stable, relatively high values (explained by the gradual removal of artifact carbon dioxide gas produced by the sterilization process), while only trace levels of methane was detected. By flushing the non-sterilized columns with low pressure helium gas and resaturating them it was possible to regenerate the initial high values of water content and hydraulic conductivity, indicating that the observed decline was not due to changes in the physical peat matrix.

Measurement of saturated hydraulic conductivity

Even though the literature displays examples on laboratory measurements of hydraulic conductivity in peat, the bulk of the published data are derived from field measurements. When field and laboratory measurements have been compared those obtained in the laboratory have usually been higher (Boelter, 1965; Paivanen, 1973; Dasberg and Neuman, 1977; Schlotzhauer and Price, 1999). This is explained by possible damage to the peat upon sampling, increased decomposition in the laboratory, leakage along the interface between the inside wall of the sampling cylinder, and a possible effect of removing vertical stress.

In the field hydraulic conductivity has traditionally been measured conducting a head recovery test where water is added to (slug test) or removed from (slug withdrawal or bail test) a standpipe piezometer and the recovery to the original water level is recorded. The theory describing the response time of open hydraulic piezometers in rigid soil was developed independently by Kirkham (1945) and Hvorslev (1951). Hvorslev (1951) developed a solution for equalisation during a head recovery test for any shaped piezometer and gave shape factors describing the geometry of the flow field around the piezometer. His theory was developed assuming an incompressible and isotropic soil or an anisotropic soil with the principal directions of anisotropy coinciding with the horizontal and vertical plane. In the case of anisotropy the ratio of horizontal to vertical hydraulic conductivity need to be known. The method of Hvorslev (1951) has predominantly been used in aquifer studies. The piezometer method of Kirkham (1945) has mainly been employed in agronomic research and peatland studies. In this method (as described in Luthin and Kirkham, 1949) a standpipe piezometer with a fairly small diameter is installed in the soil and a cavity is augered below the pipe (Fig. 6). The value of K_s is calculated by the equation (Kirkham,1945) :

$$K = \frac{\pi r^2}{At} \ln \frac{y_o}{y_t} \qquad (9)$$

where

y_0 = initial change in water level
y = water level at time t

r = radius of cavity
A = shape factor depending on the geometry of the system.

For the Kirkham piezometer method shape factors have been developed using electrical analogues (Frevert and Kirkham, 1948; Luthin and Kirkham, 1949; Youngs, 1968) and more recently by finite element modelling (Brown and Hodgson, 1988).

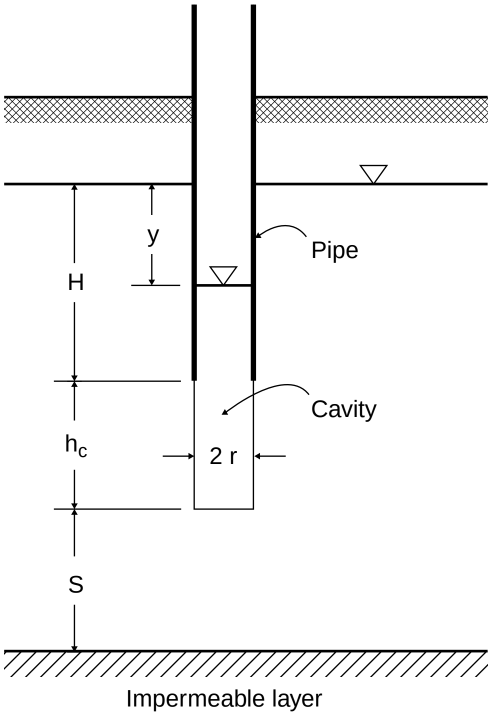

Fig. 6 Geometry and symbols for the piezometer method. Typical values for r and h_c are 0.75 - 1.5 cm and 5 - 10 cm, respectively. After Bouwer and Jackson (1974).

Anisotropy of the soil, usually considered in vertical and horizontal direction only, can be estimated by comparing K_s obtained with methods that differ in the direction in which K_s is measured - preferably on the same soil region to minimise the effect of soil heterogeneity (Bouwer and Jackson, 1974). Topp and Sattlecker (1983) claimed to measure vertical and horizontal conductivity directly by using pipes either open only at their basal end or open only at a perforated section, but closed at the bottom. According to Boelter (1965) certain peat materials have a very pronounced horizontal laminar structure, particularly the herbaceous peats formed from remains of reed- and sedge-type plants. Thus anisotropy might be expected. Boelter (1965), however, in his work on peat in various degrees of decomposition found no significant anisotropy. Schlotzhauer and Price (1999) measured K_s in the laboratory on core samples of a *Sphagnum* peat and found that vertical conductivity was 4 times less than horisontal conductivity.

Non-Darcian flow in peat?

A number of workers have reported apparently anomalous head recovery test results which seem that hydraulic conductivity is time dependent and increases with the applied head. This was interpreted as non-Darcian flow behaviour in peat (Dai and Sparling, 1973; Ingram *et al.*, 1974; Rycroft *et al.*, 1975b; Waine *et al.*, 1985). Hemond and Goldman (1985) proposed that much of the apparent non-Darcian behaviour in peat was an artifact of the inappropriate application of steady-state piezometer formulae to transient experiments in a material having significant non-zero elastic storativity, S_s (see above): during a piezometer test with falling or rising head pore water pressures near the porous/slotted tip are altered. One result is a change in effective stress, σ_e, since total vertical stress, σ_T, is constant (equation 1) leading to compression or expansion of the peat matrix and transient changes in water content of the peat. Hence a fraction of the water measured initially in the piezometer test represents pore water coming into or out of storage near the well - not a steady-state flow field. This leads to higher rate of water level change in the early stages of a rising or falling head test and to higher calculated values of K_s over short periods. The observed dependency in K_s on applied head was explained by expansion of horizontal flow paths in the peat under decreased effective stress when pore water pressure is increased, i.e. as long as the elevated head is maintained in the piezometer

Unsaturated hydraulic conductivity

The literature exhibits only few examples on the subject of unsaturated hydraulic conductivity of peat. The interest in the subject has primarily been in investigating the ability of a drained unsaturated peat layer to supply plants with water from an underlying water table by capillarity.

It is experimentally demonstrable (Loxham and Burghardt, 1986) that shrinkage, which accompanies the early stages in drainage, is attributable to collapse of the large channels without significant change in the fine (micro-pore) capillaries. Hence, at least in less decomposed peat with a relatively large proportion of macro-pores an initial sharp decrease in hydraulic conductivity must be anticipated upon de-saturation.

Only laboratory measurements have been encountered in the literature collected for this study: Bartels and Kunze (1973) using a double-membrane apparatus; da Silva et al. (1993) and

Olszta (1977) using steady state flux control methods. Bartels and Kunze (1973) examined the effect f decomposition, flux direction, mineral content and bulk density. The correlation to unsaturated conductivity decreased in the sequence: decomposition, flux direction, mineral content, bulk density. The authors found conductivity to be dependent on flux direction, i.e. anisotropy, with horizontal unsaturated conductivity being 3 - 4 times larger than vertical, the ratio increasing up to pF = 2.5. However for pF = 3 they found no difference between horizontal and vertical conductivity. As expected, it was shown that unsaturated hydraulic conductivity generally is larger in the less humified peat. Even at high tension there are considerable amounts of water in the peat (e.g. Fig. 3: 40 % at pF = 3) meaning that there are many water filled pores. From the retention curve it is seen, that water in the less humified peat is stored in relatively larger pores (i.e. lower tension at the same volumetric water content) than in the more humified peat. According to Poiseuilles Law the flux through a capillary tube is proportional to the squared radius indicating a higher unsaturated conductivity in the less humified peat.

Saturated hydraulic conductivity of mineral soils is generally larger than of peat – except for the undecomposed peat. However, the picture is reversed for negative pore water pressures. The reason for the higher unsaturated conductivities in peat is the larger amount of water filled pores relative to mineral soils at the same tension. In water filled pores water will flow due to a given gradient at a higher velocity than water creeping along the hydration films over the particle surfaces in desaturated pores (Hillel, 1980).

Measurement of unsaturated hydraulic conductivity is time consuming , involving many technical difficulties and is subject to measurement errors due to the swelling/shrinking properties of peat. In recent years efforts have been made to apply various mathematical functions to describe and predict unsaturated hydraulic conductivity. These functions have in general been developed for mineral soils but also by some researchers sought transferred to organic soils: Bloemen (1983) - based on 227 measurements of air entry value, saturated hydraulic conductivity, K_s, and bulk density - developed a modified Brooks and Corey-expression requiring only bulk density to be known. Brandyk (1985), da Silva et al. (1992), Brandyk (1995) used the van Genuchten formula for unsaturated hydraulic conductivity which requires two parameters that can be derived from the retention curve, besides K_s as a matching factor. da Silva et al. (1993) compared estimated unsaturated hydraulic conductivities to measured values and found very good agreement.

2.2 Evapotranspiration from wetlands

Evapotranspiration (the combined processes of evaporation and transpiration) is a fundamental and often a major component of the hydrological cycle of wetlands (e.g. Lafleur, 1990; Doss, 1993; Campbell, 1997). Furthermore, evapotranspiration influences on nutrient cycling by affecting subsurface water flow-pattern. Water lost by evapotranspiration may be replenished by capillary rise resulting in a more upward flow, whereby nutrients are transported into soil layers with e.g. a higher nutrient turnover or binding capacity (Hoffmann *et al.*, 1993; Andersen, 2002).

The most important factors influencing evapotranspiration are: (i) input of energy as global radiation and advection; (ii) vapour pressure deficit between surface and air; (iii) air movement; (iv) vegetation specific factors: stomates, root depth, crop species and crop structure; (v) soil specific factors: porosity, pore size distribution, permeability (determining the movement of water in the soil).

Canopy radiation balance

The radiant energy available at the surface of the earth to drive physical and biological processes originates from the sun. At the canopy level, the properties of the canopy influence the energy exchange and thereby determine the energy available for canopy processes.

At the top of the atmosphere the incoming solar radiation (wave lengths 0.3 - 3 μm) is approximately constant 1373 W m^{-2} (the solar constant). On average 25% of this radiation is attenuated due to molecular and particle scattering and absorption particularly by water vapour on its way through the atmosphere. Part of the remaining radiation reaches the ground in a direct solar beam (S_b) and part of it (typically 15 - 25% in clear-sky conditions and up to 100% in overcast conditions) in a diffuse form after being scattered (S_d).

Part of the short-wave radiation is reflected. The reflection coefficient, ρ, of a particular surface is strongly dependent on the solar elevation. The reflection coefficient is the average reflectivity over all wave lengths in the solar spectrum (0.3 - 3 μm). For natural surfaces it is often called the albedo. In general, ρ for forests is 0.11 - 0.16, and for agricultural crops the values are higher, ρ = 0.15 - 0.26. In a review Burba *et al.* (1999) found the following albedo values for wetlands: 0.12 – 0.16 for *Sphagnum*-sedge bogs; 0.12 for swamp forest; and 0.11 – 0.17 for open *Sphagnum* fen.

The net short-wave radiation (S_n) is the part of the total incident short-wave radiation (termed global radiation, S_t) that is captured at the ground surface. S_n is given by (10)

(10) $S_n = (1 - \rho)\, S_t = (1 - \rho)\, (S_b + S_d)$

where S_b and S_d are direct and diffuse radiation, respectively.

At longer wave lengths (3 - 100 µm) radiation is exchanged between the ground and the atmosphere by blackbody (or full radiator) emission. As the ground, on average, is warmer than the atmosphere, and as the atmosphere is not a full radiator (only clouds are full radiators) the net result is a loss of energy as thermal radiation from the ground.

The net long-wave radiation (L_n) is given by (11)

(11) $L_n = L_i - L_o = \varepsilon_a \sigma T_a^4 - \varepsilon_s \sigma T_s^4$

L_i is the incoming long-wave radiation to the surface with temperature T_s, and L_o is the outgoing long-wave radiation to the atmosphere with the temperature T_a. σ is the Stefan-Boltzman constant, and ε_a (< 1) and ε_s (≈ 1) are the apparent emissivities of the atmosphere and the surface of the earth, respectively. For most surfaces 100 W m^{-2} may be a good average Fig. for the net loss to a clear sky, whereas in overcast weather the net loss approaches 0 W m^{-2}.

The net flux of all radiation across unit area of a plane is called the net radiation, R_n. R_n is given by (12)

(12) $R_n = (1 - \rho)\, S_t + L_i - L_o$

Due to the throughflow of cold groundwater and the higher water content and the consequently higher soil heat capacity, the soil temperature of wetlands will be lower than that of mineral upland soils. This leads to relatively lower outgoing long-wave radiation resulting in higher net radiation over the wetland. Andersen et al., (2002) found that the lower soil temperature and lower albedo of a fen wetland increased net radiation by 20% relative to a cultivated grass field.

The radiant energy intercepted by a plant is partly absorbed, partly reflected, and partly transmitted as seen from the identity (13)

(13) $\alpha + \rho + \tau = 1$

where α is the absorption coefficient, and τ is the transmission coefficient. The radiative transfer within canopies depends on the architecture of the plants and is very complex to describe. A simplified way of describing the distribution of radiant energy within a canopy is to use Beer's law and an empirical extinction coefficient, *K*. The average irradiance at any level *z* in the canopy is related to the irradiance above the canopy, *S(0)*, and to the accumulated leaf area *L(z)* from the top of the canopy down to level *z*:

(14) $S(z) = S(0) \cdot \exp(-K \cdot L(z))$

Energy balance of an evaporating surface

The energy budget of a vegetated surface can be expressed in terms of available energy being partitioned into latent and sensible heat. Considering a volume of a plant stand of unit cross section, extending from a plane below the soil surface, where temperature changes are negligible, to a plane at reference level above the canopy, where the net radiation balance, R_n, is determined, the energy balance is given by (15)

(15) $R_n - G - J - M - A_d = \lambda E + H$

G is the heat conducted into the soil (soil heat flux), *J* is the sensible and latent heat temporarily stored within the volume, *M* is the net energy absorbed by metabolism (photosynthesis minus respiration), and A_d is the net loss of energy due to horizontal advection by air movement. E is the rate of evaporation from the soil surface and the vegetation, λ is the latent heat of vaporisation of water, and *H* is the upward flux of sensible heat by thermal convection.

M and *J* are often ignored since they only constitute a small fraction of the overall energy balance. In 'oasis' conditions the horizontal transport (advection) may be large, but generally A_d is neglected in order to obtain a simplified one-dimensional energy balance:

(16) $R_n - G = \lambda E + H$

However, Devitt et al.(1998) found the energy balance for a riparian corridor in Southern Nevada to be dominated by advection in one out of two years of study. Andersen et al. (2002) found evapotranspiration of a floodplain fen wetland to be enhanced by local advection in periods with high evaporative demand and low precipitation. During these periods warm, dry air was formed over drier upland areas. This is a condition opposite to that reported in a number of other wetland studies (e.g. Lafleur, 1990; Souch et al., 1998) in which proximity to large water bodies result in humid sea/lake breezes flowing across the wetland during the daytime thus preventing advective enhancement of evapotranspiration rates.

The soil heat flux, *G*, is an energy storage term, being the change in sensible heat in the soil depending on the soil temperature gradient and on the thermal properties (specific heat, c_s, and thermal conductivity, *k*) of the soil. These properties depend on soil type and soil water content. During the day, *G* is largest around midday when the air temperature and net radiation to the ground are at maximum. In wetlands with open water *G* can be a considerable sink of energy during daytime (G/R_n = 0.2 – 0.4) (Souch et al., 1998; Burba et al., 1999). On a daily (24 hr) basis Burba et al., (1999) found *G* to be small, whereas Souch et al. (1998) even on a daily basis found *G* to consume 30% of R_n. Andersen et al.(2002) found *G* of a floodplain wetland to constitute only 5% and 1.5% of R_n, respectively during daytime and on a daily (24 hr) basis. They attributed the low values to the presence a mat of dead vegetation and a dense canopy, which effectively isolated the soil surface from incident radiation.

The rate of transfer of sensible heat (*H*) from a surface into the atmosphere is proportional to the temperature gradient between the surface and the environment and is governed by the magnitude of an exchange coefficient that depends on the turbulent conditions above the surface.

Similarly, the rate of evaporation (λE) is proportional to the vapour pressure gradient between the evaporating surface and the environment, and is governed by the turbulent exchange conditions for latent heat.

Wetland evapotranspiration rates

Two reviews of wetland hydrology (Linacre, 1976, and Ingram, 1983) conclude that studies of evapotranspiration over a wide range of wetland types have produced a number of conflicting and inconclusive findings. Of particular controversy has been the influence of vascular vegetation cover on wetland evapotranspiration. Some authors suggest that the presence of vegetation increases evapotranspiration above lake (i.e. open water) evaporation, E_0, while others maintain that evapotranspiration from vegetated wetlands is always less than lake-evaporation. Ingram (1983) who extensively reviewed the literature on evapotranspiration from fens and bogs, concluded that vegetation covers with differing characteristics (e.g. species composition, stand density and height) have varying degrees of influence on evapotranspiration. On the other hand, Linacre (1976) stated in his review of evapotranspiration from swamps, that the presence and nature of vegetation have relatively minor influence on evapotranspiration rates, compared with regional climate and local advection of sensible heat. One important difference between *Sphagnum*-dominated wetlands and wetlands with vascular vegetation is, that the roots of the vascular vegetation are capable of extracting soil water so as to maintain a high transpiration rate even though the water table drops. This is in contrast to the situation in *Sphagnum*-dominated wetlands. Several studies report that the level of the water table affects the evaporative capacity of the *Sphagnum* surface (Ingram, 1983, Phersson and Petterson, 1997). This is due to the lack of vascular tissue and low matric potentials, which means that much larger surface resistances are imposed as water table declines below the ground surface.

There are significant correlations between stomatal conductance and habitat (Roberts, 2000), with wetland plants having a relatively high stomatal conductance. However, very little is known about the water requirements and consumption of wetland species (Tabacchi et al., 2001), except for man-influenced, homogeneous woody communities (poplar plantations, coppiced willows). Table 3 is a review of evapotranspiration rates measured in wetland studies. In order to compare studies across wetland types and different climates Penman's potential open water evaporation, E_0, has traditionally been used as a reference. E_0, however, cannot be considered a true reference since net radiation has been actually measured at the experimental sites over vegetated surfaces with albedos differing from a free water surface. Table 4 lists results from three Danish wetland studies in which measured evapotranspiration rates have been compared to an independent reference. In the studies of Vedby (1984) and Hoffmann *et al.* (1993) evapotranspiration was measured using vegetated lysimeters, which could be weighed, 1 m deep and with a surface area of 1000 cm^2.

Table 3 Mean daily evapotranspiration rates including range, E/E_0 and $\lambda E/R_n$ reported in wetland studies.

Wetland type	E (mm day^{-1})	E/E_0	$\lambda E/R_n$	Author
Floodplain wetland, Denmark	3.6[a] (0.8 – 5.6)	1.10	0.82	Andersen et al. (2002)
Sub-Arctic coastal wetland				Lafleur (1990)
Dry site	2.6[b] (1.0 – 4.5)	0.74	0.50	
Wet site	3.1[b] (1.4 – 6.0)	0.90	0.57	
Quaking fens, Netherlands	2.5[c] (1.0 – 4.1)	0.77		Koerselman and Beltman (1988)
Transition peatland, Japan	2.5[d] (- 4.6)		0.37 – 0.68[e]	Tagaki et al.(1999)
Open water marsh/sedge meadow, Indiana Dunes National Lakeshore	3.58[f]	1.03	0.44	Souch et al. (1998)
Prairie wetland, Nebraska	3.75[g] (0.5 – 6.5)		0.8 – 1.0[h] 0.6 – 0.8[i] 0.3[j]	Burba et al., (1999)
Lakeshore Typha marsh, Ontario	4.9[k] (3.5 – 6.3)	1.0	0.78	Price (1994)
Czechoslovakia				Priban and Ondok (1986)
Willow carr	3.5[l] (2.4 – 4.9)		0.86	
sedge-grass marsh	3.0[l] (2.3 – 3.7)		0.72	
Raised peat bog, New Zealand, dry canopy	1.54[m] (- 2.13)	0.34	0.23	Campbell and Williamson (1997)

[a] Daylight values, April – September
[b] Daylight values, May – August
[c] Daily values, April – October. Average for three vegetation types
[d] Daily values, June – October
[e] Read from Fig. 6 in Tagaki et al.(1999)
[f] Daylight values, June
[g] Daily values, June – October
[h] Early and peak growth
[i] During senescence
[j] After senescence
[k] Hours 600 - 1800, June – August
[l] Daily values, July – September. Range of monthly means
[m] Daylight values, November – March.

Table 4. Ratio of actual to reference evapotranspiration reported in Danish wetland studies.

Wetland type	E/E_{ref}	Author
Floodplain wetland, frequently flooded. Sedge-herbs-grass community.	1.28[a]	Andersen et al. (2002)
Undrained riparian meadow vegetated with herbs and grasses.	1.04[b]	Hoffmann *et al.* (1993)
Sphagnum mire		Vedby (1984)
hummock	0.93[c]	
hollow	1.21[c]	
Riparian fen wetland, frequently flooded. Vegetated with grasses and willow shrubs.	1.29[c]	Vedby (1984)
Cutover *Sphagnum* mire vegetated with shrubs and trees.	0.86[c]	Vedby (1984)

[a] Daylight values, April – September
[b] Daily values, full year
[c] Daily values, April – October.

Reference evapotranspiration, E_{ref} , was calculated using the formula of Penman (1956) with parameters measured at a nearby climate station over a vegetation cover of short, well-watered grass. Andersen *et al.* (2002) estimated evapotranspiration using the Bowen ratio energy balance approach. Following the recommendation by FAO (Allen *et al.*, 1998) they calculated a reference evapotranspiration using the Penman-Monteith method for a hypotethical crop with an assumed height of 0.12 m, with surface resistance of 70 s m^{-1} and an albedo of 0.23. Net radiation was calculated using measured values of incident shortwave radiation, air temperature and relative humidity as prescribed by Allen *et al.* (1998). It should be noted, however, that the method of Allen *et al.*, (1998) has been shown (Detlefsen and Plauborg, 2001) to yield results which in Denmark are 7 – 13% below evapotranspiration calculated by the Penman formula (Penman, 1956), when the Penman formula was applied as in Vedby (1984) and Hoffmann *et al.* (1993).

2.3 Wetland waterbalances

In order to illustrate the range in hydrologic controls on riparian wetlands follows a presentation of two water balance studies. The studies were carried out in the same river system. One study was carried out on a tributary stream to the river Gjern, Denmark (Dahl, 1995) (Fig. 7), while the other was done further downstream on the floodplain of the lower Gjern (Andersen, 2002) (Fig. 8).

The stratigraphy of the wetland on the tributary stream is 50 cm of fibric, highly conductive peat on top of 2 m mixed layers of peaty sand underlain by gyttja. The wetland is situated below a steep slope. Due to the topography and sedimentology inflowing groundwater is forced upwards and forms overland flow at the foot of the hillslope. Because the wetland is fed by a constant and large groundwater influx of both local and regional origin the surface water level is very stable (10 cm above the ground surface).

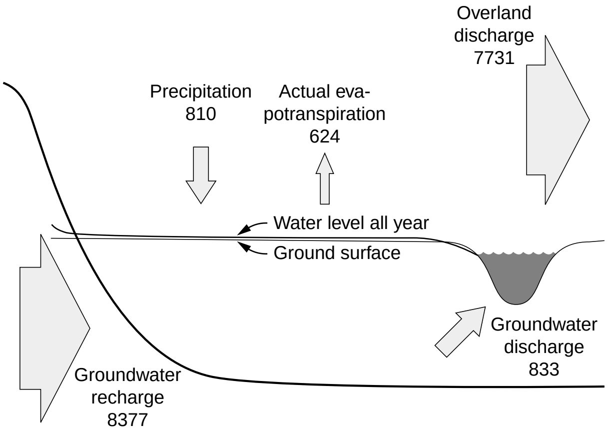

Fig. 7. Water balance of a riparian wetland located on a tributary stream to river Gjern, Denmark. Numbers are mean values for a dry year, 1992, and a wet year, 1993 (mm yr^{-1}). (After Dahl, 1995).

The floodplain wetland is also underlain by gyttja. On top of the gyttja is 4 –5 m peaty-sandy deposits. The peaty sand is overlain by 1.5 m mainly hemic peat, and a 40 cm silty-clayey layer of sediments deposited by flooding river water constitutes the surface layer. The gyttja prevents hydraulic contact between the floodplain and deeper groundwater aquifers.

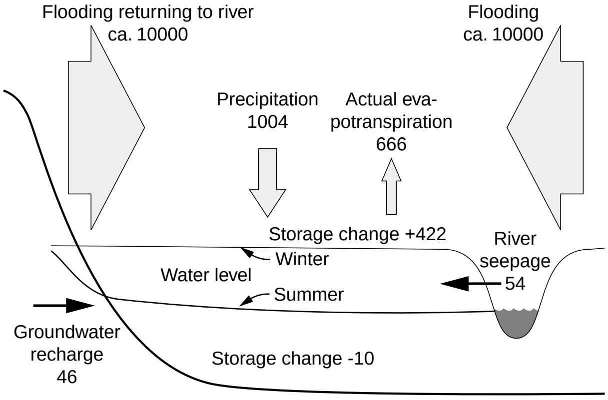

Fig. 8. Water balance for a floodplain wetland on the lower river Gjern, Denmark for the calendar year 1999 (mm yr^{-1}). (After Andersen, 2002).

Hydraulic conductivity of the sediments below the river bottom is also low meaning that exchange of water between the river and the floodplain takes place only through and above the riverbank. There is a small influx of groundwater of local origin from the hillslope to the floodplain. During the growing season an unsaturated zone develops with a maximum depth of 60 cm. Evapotranspiration is maintained at a high rate because precipitation is supplemented by capillary rise of water from storage within the underlying peat layer. During autumn, winter and spring the floodplain is frequently flooded by the river. Large amounts of water flow across the riverbank during flooding events, and even though the vast majority returns to the river the levees, which rise 40 cm above the floodplain, trap some of the water. Due to the low conductivity of the silty-clayey layer infiltration is low and water ponds on the floodplain most of the time outside the growing season.

The wetland on the tributary stream had a water turnover rate of 8 times per year corresponding to a hydraulic residence time of 44 days. This wetland is characterised by having a stable flow pattern controlled by groundwater recharge and being hydrologic open. The floodplain wetland has three storages, namely the surface water storage, the soil water storage and the groundwater storage. During a flooding event the hydraulic residence time of the surface water storage is in the order of hours. Water ponds on the surface in between flooding with an average depth of 17 cm. Since the average number of floods is 4 per year distributed over 7 months hydraulic residence time is ca. 50 days. The soil water storage has a residence time in the same order of magnitude, 46 days, whereas flow through the groundwater storage is very slow with a residence time of 11.7 years. Thus the floodplain wetland is hydrologically closed concerning groundwater flow and governed by vertical water exchange with the atmosphere and with ponding water. Large amounts of surface water flow across this wetland during flooding situations and concerning surface water exchange this floodplain wetland is a very open system.

3. Nutrient processes in wetlands

3.1 Chemical conditions of a waterlogged soil

Redox conditions and pH

The determining characteristic of a waterlogged soil is the absence of oxygen (Reddy et al., 1980). Since oxygen has a low solubility in water (11.28 mg O_2 l^{-1}) and the diffusivity of oxygen in water is 10,000 times lower than in air (Armstrong, 1978) the input of oxygen via groundwater, flooding surface water and diffusion from the atmosphere cannot fulfil the respiratoritive demands from plant roots and microbial metabolism. Within a few hours of flooding an air-dry soil, the bulk of the soil is rendered practically devoid of molecular oxygen (Ponnamperuma, 1984). Consequently, aerobes are replaced by facultative anaerobes, which in turn are superseded by strict anaerobes. Soil microorganisms oxidize organic matter in order to get energy and building materials for maintaining cell metabolism and building up new biomass. Under anaerobiosis microbial metabolism uses other substances and compounds as terminal electron acceptors as alternatives to oxygen in thermodynamic sequence (Table 5): NO_3^-, manganic compounds, ferric hydroxides, SO_4^{2-}, and CO_2. Compared to aerobic respiration the energy output from anaerobic respiration is lower. Decomposition of organic matter in an intermittently saturated soil is thus slow and organic matter accumulates. The redox potential of a soil is a qualitative measure for whether compounds will be reduced or oxidized. Depending on temperature and pH reduction and oxidation of compounds will take place in a specific redox interval. Elements which are not reduced or oxidized themselves can be influenced by changed redox conditions if they are constituents of a compound containing elements which are affected. An example is the release of phosphate from sparsely soluble Fe(III)-compounds when Fe(III) is reduced to the more soluble Fe(II). Some of the reductants resulting from the anaerobic respiration have a proven phytotoxic effect: the reduced form of manganese, ferrous iron, sulphides and organic products of various types (Armstrong, 1978).

pH in anaerobic soils generally lies between 6 and 7. However, humic acids produced by microbial metabolism may lower pH (Ponnamperuma, 1972).

Table 5. Summary of different types of respiration and corresponding redox potential (after Hoffmann, 1998): 1. Oxygen respiration, 2. Nitrate respiration (heterotrophic denitrification), 3. Manganese respiration, 4. Iron respiration, 5. Sulphate respiration, 6. Nitrate respiration with pyrite (autotrophic denitrification), 7. Methanogenesis.

		Redox potential (mV)
1	$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$	700 – 300
2	$5C_6H_{12}O_6 + 24NO_3^- + 24H^+ \rightarrow 30CO_2 + 12N_2 + 42H_2O$	300 – 100
3	$C_6H_{12}O_6 + 12MnO_2 + 24H^+ \rightarrow 6CO_2 + 12Mn^{2+} + 18H_2O$	200 – 100
4	$C_6H_{12}O_6 + 24Fe(OH)_3 + 48H^+ \rightarrow 6CO_2 + 24Fe^{2+} + 66H_2O$	100 - -100
5	$C_6H_{12}O_6 + 3SO_4^{2-} \rightarrow 6CO_2 + 3S^{2-} + 6H_2O$	-100 - -200
6	$2FeS_2 + 6NO_3^- + 2H_2O \rightarrow 2N_2 + 2FeOOH + 4SO_4^{2-} + 2H^+$	
7	$4H_2 + CO_2 - CH_4 + 2H_2O$	-200 - -300

Likewise will acid soils low in organic matter or in active iron attain lower pH-values (less than 6.5). pH is a complex parameter since it interacts with chemical processes due to the involvment of hydrogen ions in chemical equilibria (e.g. Table 5) and determines the solubility of many substances. The effect of pH on hydroxide equilibria can be described by (Ponnamperuma, 1984)

$$pH + \tfrac{1}{2} \log M^{2+} = K \qquad (17)$$

where M is Fe, AlOH, Zn, or Cu; and K = 5.4 for Fe, 2.2 for AlOH, 3.0 for Zn, and 1.6 for Cu. From (17) it follows that a decrease in pH from 7.0 to 6.5 in ferruginous soil may increase the concentration of water-soluble iron from 35 to 350 mg l^{-1} and cause iron toxicity.

Nitrogen

Nitrogen occurs in soils and sediments chiefly as complex organic substances, ammmonia, molecular nitrogen, nitrite, and nitrate. The transformations that they undergo are largely microbiological interconversions regulated by the physical and chemical environment.

The mineralization of organic nitrogen in submerged soils stops at the ammonia stage because of the lack of oxygen to carry the process via nitrite to nitrate leading to an accumulation of ammonia in anaerobic soils (Ponnamperuma, 1972). Although aerobic decomposition of organic matter may be more rapid than the anaerobic process, inorganic nitrogen is released in larger quantities and faster in anaerobic soils due to less immobilization in anaerobic soils (Broadbent and Reyes, 1971). Nitrogen immobilization in anaerobic soils is less because the microbiological activity is less intense and thus the requirement for nitrogen lower than in aerobic soils. Soils vary widely in their capacity to produce ammonium depending on the content of organic matter.

Nitrate can be formed by nitrification of ammonium in the oxidized layer or imported convectively by ground water or by diffusion from flooding surface water. Nitrate moves by convection or diffusion to the reduced zone, where it is denitrified (converted to nitrous oxide, N_2O, or gaseous nitrogen, N_2 (Knowles, 1982)). The process is microbial respiration and takes only place under anoxic conditions (Table 5). Denitrification is normally a fast process; within a few days the bulk of native or added nitrate disappears from a submerged soil (Ponnamperuma, 1972). Denitrifying organisms need a source of H^+ ions and electrons to reduce nitrate and a carbon source and ammonia for cell synthesis. In soils, organic matter is the source of all these ingredients. Thus denitrification is absent or slow in soils low in organic matter (Ponnamperuma, 1972). Other substances can also be used, however, including pyrite (Table 5) (e.g. Hoffmann, 1998). The process is termed heterotrophic denitrification when a carbon source delivers energy to the process and autotrophic denitrification when the energy is derived from e.g. pyrite. For a Danish freshwater fen wetland Paludan (1995) attribute 65% of nitrate reduction in the wetland to be autotrophic using pyrite, while heterotrophic denitrifiers are responsible for the remaining reduction. Apart from the abscence of oxygen and the presence of organic matter or e.g. pyrite, the process of denitrification depends on the presence of nitrate. Denitrification rate is often limited by the nitrate concentration (Reddy and Patrick, 1984). Studies of denitrification in wet meadows and fens in Danish river valleys show rates ranging from 57 to 2179 kg NO_3^- ha^{-1} yr^{-1} corresponding to 56 – 99% of NO_3^- input to the area (review by Hoffmann (1998)).

Uptake by plants can also be an important sink for nitrogen, and subsequent grazing or hay harvest can lead to a net export of nitrogen from the area in question. Andersen (unpublished results) measured 89 and 156 kg N ha^{-1} in above ground biomass in two vegetation zones on a non-fertilised floodplain wetland dominated by *Deschampsia caespitosa* and *Glyceria maxima*, respectively. Hoffmann *et al.* (1993) measured 70 – 100 kg N ha^{-1} in above ground biomass harvested on a wet meadow dominated by species characteristic of a nutrient rich soil.

The N cycle is driven by processes that occur on or at the interface of particulate material (e.g. Piany *et al.*, 2002). Critical for the ability of a particular wetland to retain nitrogen is thus the degree of contact between nitrate-containing groundwater or surface water and the wetland sediments. Consequently, understanding the hydrologic controls on a wetland is crucial in understanding its behaviour regarding nitrogen retention. The importance of hydrology can be illustrated by two Danish wetland studies. The wetland in the study of Dahl (1995) is illustrated in Fig. 7. The wetland is a discharge area for groundwater of both local and regional origin (see also Fig. 7). Due to a large through-flow of nitrate-rich groundwater the denitrification rate is very high, 2179 kg NO_3-N ha^{-1} yr^{-1}. Andersen (2002) studied a floodplain wetland on the lower reach of the river Gjern (Fig. 8). This wetland received only a small input of local groundwater, whereas the main water exchanges was through precipitation, evapotranspiration and flooding by the river. The floodplain sediments have a very high potential for nitrate reduction, however denitrification was limited by supply of nitrate. Andersen (2002) reported a rate of 71kg NO_3-N ha^{-1} yr^{-1} of which reduction of nitrate diffusing into the sediments during ponding accounted for 75%.

Phosphorus

Phosphorus exists in soils as (i) dissolved in porewater, (ii) precipitated with Fe, Al or Ca to poorly soluble compounds, (iii) adsorped to clay, $CaCO_3$, and Al- and Fe-oxides, and (iv) incorporated in plant and microbial tissue and in peat. Only dissolved phosphate is bio-available.

Richardson (1985) showed that the concentration of Al-oxides was a more important factor regarding P-sorption than content of organic matter, pH and concentration of Fe-oxides. Sediments with a large mineral content thus have a higher P-adsorption capacity than organogenic sediments. Since the bulk density of organic matter-rich soils is much smaller than of soils with a high mineral content, the per hectare P-sorption capacity is much lower in the former soils. The presence of reducible Fe(III)-compounds is considered to be important in controlling the concentration of porewater dissolved phosphate (Paludan, 1995). When Fe(III) is reduced to Fe(II) in anoxic sediments, phosphate bound to reducible Fe(III)-compounds is mobilised and enters the porewater.

Due to the low content of mineral material in an organogenic soil, storage of P in plants, microbial tissue and peat is relatively more important than in a mineral soil. Thus Richardson and Marshall (1986) found vegetation and microorganisms in an organic fen to efficiently retain P from porewater and store a substantial portion of the available P pool throughout the growing season. Immobilisation in plants and microorganisms is temporary while immobilisation in peat is the only permanent biotic storage. Richardson and Marshall (1986) reported that 35% of P stored in plants in a fen peatland was returned to the surface water the first year and almost all of P stored in microbial tissue. Accumulation of P via peat formation amounts to 0.05 – 2.4 kg P ha^{-1} yr^{-1} (Richardson, 1985), while plant uptake is reported to 10 – 25 kg P ha^{-1} yr^{-1} in above ground biomass (Richardson and Marshall (1986), Hoffmann *et al.* (1993)). Some wetlands are depending on P release and recirculation from dead organic matter since the external loading is small relative to plant requirement (e.g. Paludan, 1995). However, external supply of nitrate can enhance mineralisation of organic matter by heterotrophic denitrification and thus mobilise P. Paludan and Bilcher-Mathiesen (1996) found that the organic matter decomposition rate more than doubled in an organic sediment when the availability of nitrate was high. Autotrophic denitrification, on the other hand, may improve the phosphate adsorption capacity since autotrophic denitrifiers can utilize reduced Fe and S compounds as energy sources, which eventually results in the formation of Fe(III) (Table 5, reaction 6) (Paludan, 1995).

In contrast to the N-cycle gas-flux is insignificant in the P-cycle. Consequently, influx and efflux of P mainly take place in the liquid phase (Paludan, 1995). Mass balance studies of P transport in Danish freshwater wetlands (mainly irrigated with drainage or stream water) generally show that P is retained, albeit with a variation ranging from 0% to 100% of the P loading (review by Hoffmann (1998)). One study of a natural fen wetland, however, showed a large P export of 16.55 kg P ha^{-1} yr^{-1}. Denitrification rate in this wetland was very high. Mobilisation of P as a result of enhanced decomposition of organic matter driven by heterotrophic denitrification was thought to be the explanation for the high P loss rate (Paludan and Hoffmann, 1996).

Eutrophication of many shallow surface waters is controlled by diffuse loss of P from arable land (e.g. Grant *et al.*,1996). Deposition of P-rich sediments on riparian areas by flooding stream water can be a significant mechanism of P retention. Andersen and Svendsen (1997) estimated the P retention rate resulting from a planned major restoration of the lower river Skjern, where the river would be allowed to frequently flood riparian areas, to be 2 – 20 kg P ha^{-1} yr^{-1} corresponding to a 20% reduction in riverine P transport. Kronvang *et al.*, (2001) measured a permanent deposition of P during flooding of a Danish lowland river floodplain to be 100 kg P $ha^{-1}year^{-1}$.

4. Riparian wetland vegetation

4.1 Factors controlling plant species distribution in riparian wetlands

Plants growing in riparian wetlands are subjected to the influence of both floods and the water table level. These two hydric factors strongly influence the floristic richness and diversity (e.g. Bridgham and Richardson, 1993, van der Valk *et al.*, 1994, David, 1996, Oomes *et al.*, 1996, Grevilliot *et al.*, 1998, Silvertown *et al.*, 1999), and often a distinct zonation across very short (metres) lateral distances in species distribution following the hydric gradient is seen (Mitsch and Gosselink, 1986, Ward, 1998, Hupp, 2000).

The strong control of soil water content owes to the often total lack of molecular oxygen in the soils of these areas and the production of phytotoxines associated with anaerobic respiration. This means that plants have to be able to tolerate phytotoxines and at the same time fulfil their own energy requirement in a soil devoid of free oxygen. Despite these potentially harmful properties of the waterlogged soil, many plants are endemic to wetland sites. Many others can withstand some degree of soil anoxia yet are unable to compete successfully with wetland species. Presumably the degree to which individual species have adapted to anoxia-related stresses controls the distinct changes in vegetation composition.

As anoxic conditions are absolutely detrimental to plant roots even for a short time, internal ventilation has emerged as a vital property of the wetland root system, as has the phenomenon of rhizosphere amelioration by radial oxygen loss through the root wall. Indeed, tolerance to flooding is determined primarily by the capacities of plants to aerate their root systems (Armstrong, 1978). Phytotoxines are immobilised by direct oxidation by the molecular oxygen within, or leaking from, the root system. Anoxia tolerance is not a constant characteristic of a plant species but can vary during the life span of the plant and over the year (Crawford and Braendle, 1996) which means that the response of plants to water level changes is dependent on the conditions under which these changes occur. Of determining influence is the length of time the rooting zone is waterlogged (Wierda *et al.*, 1997), the time when the rooting zone is drained in spring (Crawford and Braendle, 1996) and maximum depth to the water table in the vegetative period (Wierda *et al.*, 1997, Kotowski *et al.*, 1998).

Grevilliot *et al.* (1998) found that vegetation in frequently flooded and thus often waterlogged areas could be characterised by high aerial biomass and low species density. Dominating species (e.g. *Glyceria maxima* and *Phalaris arundinacea*) showed characteristics of a competitive strategy: erect and tall stature, large leaf areas and a high growth rate. Density and height of the canopy is responsible for the disappearance of regeneration niches which are necessary for the maintenance of species richness (Grubb, 1977). This illustrates the concept of realised niche vs. fundamental niche (Kotowski *et al.*, 1998, Blanch *et al.*, 1999): the presence of a plant species will depend on its tolerance to prevailing ecological factors, but also on the presence of other, competing species. However, even though species diversity locally may be low due to stress and competition, on the scale of the floodplain species diversity is greater than in upslope habitats (Gregory *et al.*, 1991). This is caused by the high diversity of microsites and complex, high-frequency disturbance regimes found along the floodplain.

The need for nutrients of plants is basic, however the craving for various compounds varies among species depending on among other things growth rate and plant size. Availability and concentration of nutrients therefore influences species distribution. In wetlands focus is often on nitrogen and phosphorus both because these as macro nutrients are necessary in large quanta and because they might be supplied from bordering agricultural areas or by flooding stream water. Changes in the availability of N have been found to alter species distribution (Grootjans *et al.*, 1985). Similar results have been found regarding P availability (Boyer and Wheeler, 1989, Walbridge, 1991). Bridgham and Richardson (1993) found that a gradient in nutrient concentration effectively differentiated the plant community composition of two wetlands. Fertilisation is known to increase biomass production and decrease species diversity (e.g. Vermeer and Berendse, 1983). The disappearance or regression of species following fertilisation is the result of two linked phenomena (Grevilliot *et al.*, 1998): (i) the increase in soil fertility which encourages competitive species with high growth rates and which are able to respond quickly to an increase in nutrient supplies like *Alopecurus pratensis* and *Poa pratensis,* and (ii) the earlier and more frequent mowing enabled by nitrogen application. This disfavors tall forbs and sedge species like *Filipendula ulmaria*, *Phalaris arundinacea* and *Carex acuta,* which cannot survive in heavily-cut meadows.

Grime (1979) devised a model for the relationship between species richness and biomass production. According to this theory an optimum curve exists with maximum species number occuring at intermediate biomass production. In vegetation of low biomass there will be severe stresses or disturbances operating leading to conditions in which only a few species can survive. Up to a certain limit there will be a positive correlation between the availability of nutrients and species number. When the availability of nutrients exceed this limit, dominance of only a few species will occur as a result of competition for light and space. Vermeer and Berendse (1983) studied nine different plant communities ranging from dry grassland to wetlands and were able to demonstrate an optimum curve. They found that species richness increased with increasing biomass at low production levels (< 400-500 g m^{-2}) and decreased with increasing productivity at higher production levels (>400-500 g $^{-2}$). Similar results were found by Berendse et al. (1992) who analysed results of long term meadow fertilisation experiments. Grevilliot *et al.*, (1998) found the principle to be valid also regarding the effect of soil moisture. Thus they observed the maximum species number at intermediate soil moisture levels, i.e. soils regularly flooded but where water does not stand for a long time.

One aim of vegetation science is to develop models for predicting vegetation changes due to a changing environment. For computer aided ecological modelling, quantitative descriptions of the plant species response to environmental factors are needed (Schröder et al., 2002). Consider a field study on the effect of one or more environmental factors on plant species distribution. Vegetation could be recorded as e.g. the percentage cover of the present plant species in a number of samples. At the sample sites would also be measured environmental factors, e.g. exchangeable phosphate. Plotting the percentage cover for individual species vs. the environmental factor would often form a diffuse cloud with data points widely scattered beneath an upper limit. In the classical approach a regression function would be modelled through the centre of the distribution to describe species response to the environmental factor (Huisman et al. 1993). However, as argued by Thomson et al. (1996), most ecological information in such a graph resides in the upper limit, because the most extreme response of the species to the measured factor could be considered least affected by unmeasured or unknown factors. In ecological situations, numerous factors can intervene, and it will often be impossible to account for them all. Thus the upper limit describes the action of the measured variable as a limiting factor, and the interior of the distribution is where other factors intervene. Cade et al. (1999) introduced the quantile regression approach to ecological science. This approach, which to some extent allows unknown factors influencing the response variable without hampering the result of the regression analysis, have been used in econometrics for more than two decades (Koenker, 1978). Schröder et al. (2002), in an attempt to quantitatively describe the response of floodplain wetland plant species to environmental factors, tested the quantile regression approach. They used the 95 % regression quantile and found the approach adequate to reduce the influence of multiple combined factors and thus to clarify the relation to single factors. They gave a set of equatations quantifying the response of 18 floodplain wetland species to six environmental factors.

During the last century floodplains have often been subjected to intensive agricultural use including drainage, fertilisation and frequent mowing. The resulting impoverishment and changes in floristic composition are well documented, e.g. Berendse *et al.*, (1992). However, experiments have shown that species replacement after cessation of fertilisation and re-wetting is a very slow process and pointed out the difficulty to restore species diversity (review by Grevilliot *et al.*, 1998). Berendse *et al.*, (1992) concluded that low productivity levels are essential but cannot guarantee succesful restoration of species-rich meadows. Absence of a seed bank is a possible explanation for the slow recovery (Hald and Vinther, 2000). Likewise is a certain level of disturbance to create sites suitable for germination and seedling establishments necessary (Berendse *et al.*, 1992).

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Paper 1, accepted by Hydrological Processes

Hydrology and nitrogen balance of a seasonally inundated Danish floodplain wetland

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Abstract

The present paper characterises a seasonally inundated Danish floodplain wetland in a state close to naturalness and includes an analysis of the major controls on the wetland water and nitrogen balances. Emphasis is put on unsaturated and saturated hydraulic characteristics of floodplain sediments.

The main inputs of water are precipitation and percolation during ponding and unsaturated conditions. Lateral saturated subsurface flow is low. The studied floodplain owes its wetland status to the hydraulic properties of its sediments: the low hydraulic conductivity of a silt-clay deposition layer on top of the floodplain maintains ponding water during winter, and parts of autumn and spring. A capillary fringe extends to the soil surface, and capillary rise from groundwater during summer maintains near-saturated conditions in the root zone, and allows a permanently very high evapotranspiration rate; average for the growing season of 3.6 mm day^{-1} and a peak rate of 5.6 mm day^{-1}. In summer, the evapotranspiration is to a large degree supplied by subsurface storage in a confined peat layer underlying the silt-clay.

The floodplain sediments are in a very reduced state indicated by low sulphate concentrations. All nitrate transported into the wetland is thus denitrified. However, due to modest water exchange with surrounding groundwater and surface water, denitrification is low; 71 kg NO_3-N ha^{-1} during the study period of 1999. Reduction of nitrate diffusing into the sediments during water ponding accounts for 75% of nitrate removal. Biomass production and nitrogen uptake in above-ground vegetation is high – 8.56 t dry matter ha^{-1} yr^{-1} and 103 kg N ha^{-1} yr^{-1}. Subsurface ammonium concentrations are high, and convective upward transport into the root zone driven by evapotranspiration amounted to 12.8 kg N $ha^{-1}yr^{-1}$. The flodplain wetland sediments have a high nitrogen content, and conditions are very favourable for mineralisation. Mineralisation thus constitutes 72% of above ground plant uptake.

Paper 2, submitted to Nordic Hydrology

Evapotranspiration from a riparian fen wetland

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Abstract

Evapotranspiration rates were measured in a riparian fen wetland dominated by vascular vegetation and surrounded by open agricultural areas and forests. The wetland is situated on a floodplain in central Denmark. Measurements were taken throughout the growing season (April – September) of 1999.

Evapotranspiration rates were higher than those published for most other wetlands, with an average of 3.6 mm day^{-1} during the growing season and a peak rate of 5.6 mm day^{-1}. Daily average evapotranspiration was 110% of Penman's potential open water evaporation, and considerably higher than results published for other wetland types.

Evapotranspiration was the dominant sink in the energy balance of the wetland studied. During the day, evapotranspiration accounted for 82% of the available radiant energy, R_n. Due to the presence of deposited fine-grained sediments, soil-water availability was kept high at all times which resulted in moderate canopy resistances, r_c (overall mean = 32 s m^{-1}). Evapotranspiration was controlled by a combination of driving forces: R_n , saturation vapour pressure deficit, D, and r_c .

The results presented in this study are conditioned by the proximity of the wetland to drier upland areas. During periods with high evaporative demand and low precipitation, warm, dry air is formed over these areas, and wetland evapotranspiration rates are enhanced by local advection. Although the absolute magnitude of the results reported is only directly relevant to similar sites in Denmark, the processes and controls described are believed as being representative of riparian wetlands subjected to frequent flooding and/or with a high groundwater table, with vascular vegetation, and being narrow corridors in open agricultural landscapes.

Paper 3, submitted to Journal of Vegetation Science

Rejecting the mean - estimating the response of wetland plant species to environmental factors by non-linear quantile regression

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Abstract

Data-sets in vegetation field studies are characterised by a large number of zeros and they are incomplete in respect to the factors which possibly influence plant species distribution. Thus it is problematic to relate plant species abundance to single environmental factors by the ordinary least square regression technique of the conditional mean. The non-parametric quantile regression is a promising approach for this kind of regression problem. In this article we employ non-linear regression quantiles in the analysis of plant species cover in relation to environmental factors. 18 wetland species and six factors were selected (flooding duration, groundwater amplitude, soil organic matter, S-value, soil content of exchangeable phosphate and potassium). 95 % quantiles were used in order to reduce the impact of multiple unmeasured factors in the regression analysis. Our results show that the standard regression of the conditional mean underestimates the rates of change of species abundance due to the factor in focus in comparison to upper regression quantiles. The parameters of the response functions are given for each species and factor. The fitted response curves indicated a general broad tolerance of the studied species to different flooding durations but a narrower range concerning the groundwater amplitude. Soil exchangeable potassium had only a minor influence on plant species cover whereas there was a distinct relation between species cover and the soil content of exchangeable phosphate and the base-richness (S-value).

Paper 4

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Suspended sediment and total phosphorus transport in a major Danish river: methods and estimation of the effects of a coming major restoration

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ABSTRACT

1. Planned restoration of the lowermost 18 kilometres of the Skjern river system (catchment area 2,490 km^2) through remeandering the river to its former course with consequent frequent flooding of riparian areas and the creation of a shallow lake and ponds is the hitherto largest river restoration project in Europe. An important aspect of the project planning and design has been to measure suspended sediment (SS) and total phosphorus (TP) transport in the project area, and to assess the inter-annual variation.

2. SS and TP concentrations were measured continuously (every fourth hour) from 1993 to 1995 in the river Skjern and its main tributary, the river Omme, using automatic sampling equipment (ISCO). In addition, discrete samples were collected monthly in the remaining five smaller tributaries. Estimated SS transport in the Skjern river system in 1994 and 1995 determined on the basis of continuous sampling was approx. 60% greater than that determined on the basis of discrete sampling. Empirical models for SS and TP transport were developed based on the data collected in this study and applied to a 31-year time series of daily discharge values. Mean annual transport amounted to 12,220 tonnes SS and 100 tonnes TP corresponding to 5 tonnes SS km^{-2} yr^{-1} and 41 kg TP km^{-2} yr^{-1}, respectively.

3. Assessment of the effects of the coming restoration project based on measured transport and estimated SS and TP retention rates for different areas of the lower river system revealed that SS and TP transport in the river will be reduced by 37% and 20%, respectively. Restoration will therefore considerably enhance the natural self-purification capacity of the river system. In addition, restoration will reduce nitrogen and ochre loading of Ringkjøbing Fjord, thereby improving environmental conditions, and remeandering will improve habitat quality and diversity in the river system. The study stresses the importance of considering streams and riparian areas as an entity when evaluating the effects of restoration activities.

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Hydrology, nutrient processes and vegetation in floodplain wetlands

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