

13 Eco-Hydrological Functioning of the Biebrza Wetlands: Lessons for the Conservation and Restoration of Deteriorated Wetlands

MARTIN J. WASSEN, TOMASZ OKRUSZKO, IGNACY KARDEL,
JAREK CHORMANSKI, DOROTA SWIATEK, WALDEMAR MIODUSZEWSKI,
WŁADIMIR BLEUTEN, ERIK P. QUERNER, MOHSSINE EL KAHLOUN,
OKKE BATELAAN, and PATRICK MEIRE

13.1 Introduction

Human activities have led to the loss of a large proportion of biodiversity in riverine wetlands in western Europe (Van Urk 1984; Cirujano et al. 1996). In the second half of the twentieth century, many floodplains, fens, and riparian woodlands were cultivated for agricultural purposes. In addition, the remaining riverine wetlands lost species due to the impact of human activities (Rich and Woodruff 1996; McCollin et al. 2000). Recently, policy has become more focused on conservation of the remaining wetlands and on rehabilitation of disturbed rivers and floodplains (Jongman 1998). The management and rehabilitation of wetlands is difficult without adequate knowledge of the hydrological and ecological processes responsible for the functioning and biodiversity of undisturbed wetlands.

The last decade has seen an increasing interest in using eco-hydrological knowledge in environmental management. Eco-hydrology studies the two-way linkage between hydrological processes and plant growth (Baird and Wilby 1999) and more specifically is a landscape ecological specialization aiming at a better understanding of hydrological factors determining the development of wet ecosystems. It includes the study of the origin, flow, and quality of groundwater and surface water and their ecological implications for wetlands (Wassen and Grootjans 1996) and takes into account the functional interrelations between hydrology and biota at the catchment scale (Zalewski 2000). Eco-hydrological knowledge is essential for successfully restoring wetlands. Research focusing on general relationships between hydrology and

wetland ecosystems, however, is hampered by the fact that many of the ecosystems studied are influenced strongly by a combination of man-induced disturbances, e.g. hydrological changes, increased levels of atmospheric nitrogen deposition, and presence of contaminants. For instance, studies of quite undisturbed floodplains reveals that flood duration, water tables, and soil wetting are primary factors regulating riparian vegetation abundance (Cellot et al. 1984; Stromberg 1993a; Large et al. 1994), while in catchments heavily influenced by man these relationships are less clear, since pollution of the river water and physical changes such as regulation, normalization, and constructing embankments have a dominant effect on vegetation (Girel 1994; Trémolières et al. 1994).

Hence, there is a strong need for relatively undisturbed reference ecosystems. Such reference wetlands may help to determine target communities (cf. Bakker and Berendse 1999) and to define the environmental conditions necessary for establishment of these target communities in restoration projects. Relationships between ecological variables including productivity, species richness and abundance of threatened species and for instance depth of the groundwater table in a relatively undisturbed area can be used in a space-for-time substitution to predict effects of raising the groundwater table in a drained area (Stromberg et al. 1996; Toner and Keddy 1997; Stromberg 2001). The lowland Biebrza valley in northeastern Poland contains fairly undisturbed floodplain marshes and fens. The river has not been regulated nor embanked, the valley is characterized by a relatively low level of contamination, and hydrology is not dominated by man. Atmospheric deposition is less than $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$, which is low for European standards compared to the $30\text{--}80 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in western Europe (Holland et al. 1999). Thus, the Biebrza valley may offer a reference site for comparable floodplain and fen ecosystems elsewhere in Europe (Wassen et al. 2002).

In this chapter, we summarize eco-hydrological research results from the Biebrza wetlands. After introducing some general features of the Biebrza wetlands, we present studies on hydrology and plant ecology giving an overview of groundwater and surface water patterns, processes, and relations with plant communities. From these studies, we will be able to learn about the importance of water flow and water quality for species composition. The spatial patterns are different for different parts of the valley. Further coupling between productivity, nutrient limitation, and species composition of marsh and fen vegetation is reported. We discuss the observed patterns and processes in the context of other European river marginal fens and floodplains and we discuss how information from Biebrza can be used for the conservation and restoration of deteriorated wetlands.

With respect to the used methods, we refer to previously published papers as much as possible. Methods new to this paper are briefly described when appropriate.

13.2 General Characteristics of the Biebrza Valley

13.2.1 Introduction

Biebrza is an almost natural lowland river of intermediate size (156 km long, average annual discharge in the lower course ca. $30 \text{ m}^3 \text{ s}^{-1}$), running through a valley of about 1000 km^2 in northeastern Poland ($22^\circ 30' - 23^\circ 60' \text{ E}$, $53^\circ 30' - 53^\circ 75' \text{ N}$). The valley contains non-drained floodplains, marshes, and fens and is surrounded by a post-glacial landscape with ice-pushed hills, moraines, and outwash plains (Succow and Jeschke 1986; Okruszko 1990). The altitude of the valley ranges from ca. 95 m to 130 m above mean sea level; and the catchment area of ca. 7000 km^2 has a maximum altitude of ca. 220 m (Byczkowski and Kicinski 1984). The average precipitation is 583 mm, of which 244 mm falls in summer. The average annual temperature is $6.8 \text{ }^\circ\text{C}$; and the growing season is ca. 200 days (Kossowska-Cezak 1984). The almost natural character of the Biebrza peatlands is reflected in a regular pattern of plant communities (Palczynski 1984). Parts of the valley are mown or are grazed by cattle and the rest is grazed and browsed by wildlife such as elk (*Alces alces*) and roe deer (*Capreolus capreolus*). The river is not regulated and it has many oxbow lakes, which are overgrowing. Extensive areas are flooded by the river in spring. Further away from the river, groundwater-fed rich fens cover large areas. On the moraines, agriculture is practised at a low intensity. The dunes in and around the valley are mainly covered by woods. Population pressure is low. Occasionally, ditches and canals are present, especially in the Middle Basin (Fig. 13.1).

13.2.2 Geomorphology, Lithology, and Geo-Hydrology

The Biebrza valley is surrounded on the east, south, and west by morainic plateaux of the last but one glaciation (Saalien). In the north, it contacts the Elk Lake District in the northwest and the Augustow Outwash Plain in the northeast (Fig. 13.1). Both were formed during the last glaciation (Weichselien). During the whole Pleistocene, the successive ice-sheet advances and retreats were associated with repeated erosive and accumulative processes. As a result, highly diversified surfaces of individual beds and great lithologic variability are present in the Pleistocene formations (Pajnowska et al. 1984). There are boulder clay strata of varying thickness and deep gravel-sand-silt series. The quaternary deposits range from ca. 130 m to 210 m in thickness.

Within the valley, the following lower-order morphological units can be distinguished: the Upper, the Middle, and the Lower Basin (Fig. 13.1).

The Upper Basin is ca. 34 km long and 6–7 km wide. The Upper Basin consists of a 5–10 m trough cut in the morainic upland. The valley is com-

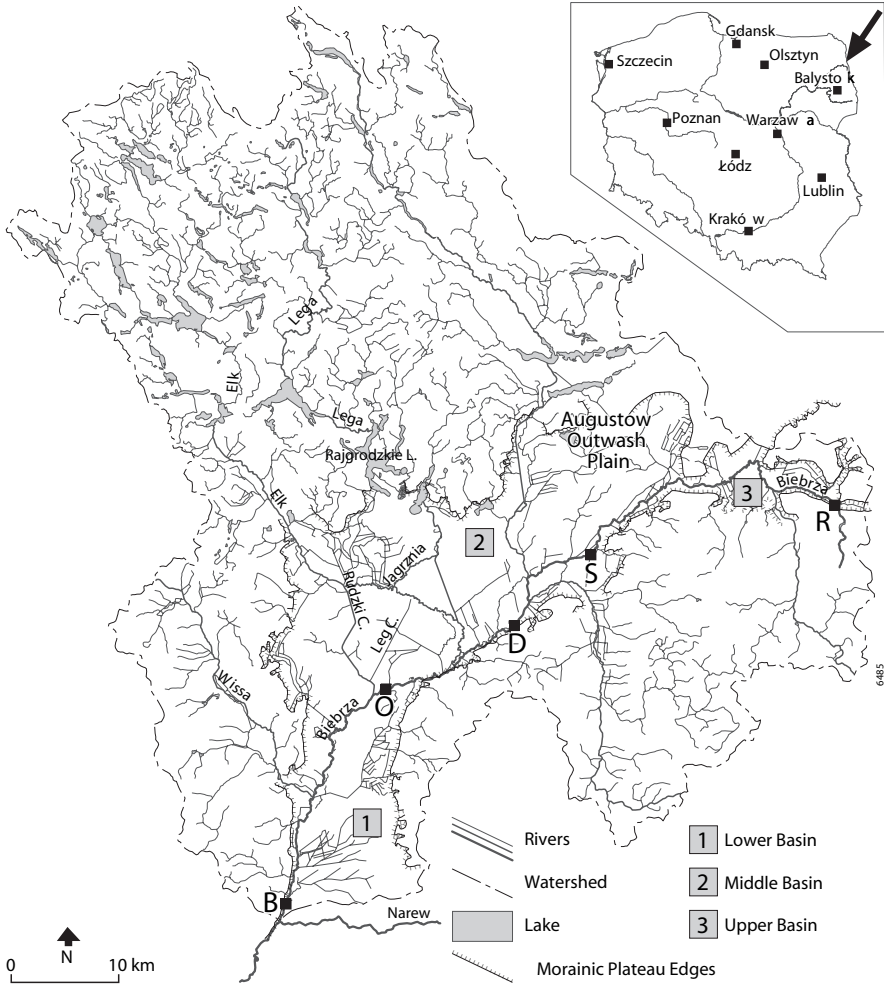


Fig. 13.1 The Biebrza catchment, location in Poland, and general topographic features. Characters refer to the gauge stations in Table 13.1 (R Rogozyn, S Sztabin, D Dolistowo, O Oswiec, B Burzyn)

pletely peat-covered, with peat deposits of 3–7 m thickness partly underlain by calcareous gyttja. Together, they overlie a sandy-gravel bed, to a depth of 10 m. In the north, the valley joins without any distinct elevation difference with the rather flat sandy plain of the Augustów outwash extending 40 × 12 km. In the south, the valley is delimited by erosive edges of the morainic plateau that rises gradually from 125–135 m to 160 m or even 200 m a.s.l. (Zurek 1984).

The Middle Basin is ca. 33 km long and up to 23 km wide. Peats are less thick than in the Upper Basin and form only 1–3 m beds. They are underlain

by sands, with gravel series at the bottom of the northern part and silts and clays in the southern part. To the north and west, the valley passes into slightly higher (1–4 m) outwash levels that are in turn delimited by plateau edges. The valley contacts directly with the 10–14 m slope of the morainic plateau in the east and southeast only. The plateau rises to 140–150 m a.s.l. The Middle Basin is distinguished by extensive sandy tracts, transformed in many places by aeolian processes to dunes partly covered by peat (Zurek 1984).

The Lower Basin is 25 km long and up to 15 km wide. The river runs at the right-hand side of the valley. The valley floor slopes down to 104 m a.s.l. at the confluence with the Narew. The peat is usually not more than 2 m thick and is underlain by thick sandy gravel beds locally covered by loam and silt deposits. Small dunes form islands several metres high, submerged in the peat of the surrounding flat floodplain. Numerous oxbows are situated in a 1–2 km muddy zone along the river. The Lower Basin is separated from the downstream Wizna Basin by a fluvial cone stretching out along and deposited by the Narew River. This cone makes the passage from the Biebrza Lower Basin to the Wizna Basin very narrow (<1 km). To the west and east, the valley is bordered by morainic plateaux. Steep high slopes accompany the valley in the southwest, whereas the edges are long and gentle in the remaining parts (Zurek 1984).

Recurring glaciations produced a great lithologic variability, resulting in a diverse pattern of aquitards, semi-permeable layers and aquifers. The Biebrza valley is fed: (a) from below, by water under pressure coming from confined aquifers by diffuse upward groundwater flow or through hydrogeologic windows, and (b) from the sides, by subsurface phreatic groundwater flows or by groundwater flow coming from semi-confined aquifers, both directed from the watershed towards the valley (Pajnowska et al. 1984).

13.2.3 Vegetation

The valley harbors a well preserved, almost natural peatland, with a variety of fen and river marginal floodplain types. These differ in species richness and productivity and are arranged in regular zones, which run both from upstream in the downstream direction as well as parallel to the river (Palczynski 1984). The floodplain contains highly productive tall sedge, reed, and grass communities, whereas outside the reach of the river floods, low-productive rich fen and moderately rich fen communities occur. In the Middle Basin, drainage has led to extensive areas of fen meadows. Plant species include boreal and continental species such as *Betula humilis*, *Trichophorum alpinum*, *Dianthus superbus*, *Pedicularis sceptrum-carolinum*, and *Saxifraga hirculis*, but more than 90 % of plant species present at Biebrza also belong to the Western European flora (Bootsma 2000).

13.2.4 Birds and Mammals

Birdlife includes 157 breeding species, of which 21 species are considered as threatened in Europe (Dyrzcz et al. 1985). The Biebrza wetlands are famous for their breeding populations of great snipe (*Gallinago media*, 300–400 displaying males) and aquatic warbler (*Acrocephalus paludicola*, ca. 3000 pairs; Dyrzcz and Zdunek 1993). In spring and autumn, large numbers of rough geese and ducks rest and feed in the wetlands. Furthermore, mammals like wolf (*Canis lupus*, ca. ten individuals), elk (*Alces alces*, 500–700 individuals), otter (*Lutra lutra*, ca. 50 individuals), and European beaver (*Castor fiber*, ca. 300 individuals) are present.

13.3 Hydrology of the Biebrza Valley

13.3.1 Surface Water: Hydrography and Hydrology

The headwaters are located at an altitude of 162 m a.s.l.; the confluence with the Narew River is at 102.5 m. The width of the riverbed ranges from 10 m to ca. 80 m. The major part of the drainage system (75 %) is to the north of the river, in the Elk and Augustow lakeland. The free surface slopes are variable. The averages over several years range from 0.07 % in the Middle Basin to almost 3.0 % near to the Biebrzas origin. The average slope from the origin to the mouth is 0.36 %. The fluctuation in the free water surface is large. Over several years, these fluctuations range from up to 1.5 m close to the origin to about 3.0 m at the lower course. Because of such large variations, vast areas along the river are flooded, particularly in spring.

The Biebrza and its tributaries are primarily draining rivers. Numerous lakes are also part of the Biebrza Basin drainage system. They lie outside the valley, on the upland, especially in the northern part of the watershed (Fig. 13.1). Other significant waterways in the area are six canals built over the past 150 years in or northward of the Middle Basin. Hydrologic conditions of the Biebrza river are described by characteristic discharges (mean discharge, mean low discharge, mean high discharge) calculated for six gauges (Table 13.1). Mean discharge in the Lower Basin is ca. seven times the discharge of the Upper Basin (respectively, 30.6 m³ s⁻¹ and 4.61 m³ s⁻¹). This ratio resembles the ratio of the discharge areas (ca. 1:8), which implies that the specific discharges of the Upper and Lower Basins are comparable and amount to 5.45 dm³ s⁻¹ km⁻² and 4.43 dm³ s⁻¹ km⁻².

The acidity of the river water is neutral to slightly alkaline and the water is quite rich in nutrients. No large differences in water quality were observed going downstream: both nutrient concentrations and specific nutrient loads

are in the same order of magnitude as the Upper and Lower Basins (Table 13.2).

Three numerical models have been developed that describe the river flow in the Upper, Middles and Lower Basins. These models either work independently or can be merged in a single unit. They include river network models

Table 13.1 Discharge characteristic of the Biebrza River. *SNQ* Mean low discharge, *SNq* mean low specific runoff, *SQ* mean discharge, *Sq* mean specific runoff, *SWQ* mean high discharge, *SWq* mean high specific runoff. For locations of gauge stations, see Fig. 13.1

Biebrza basin	Gauge station	Area (km ²)	SNQ (m ³ s ⁻¹)	SNq ($\frac{\text{dm}^3}{\text{s}\cdot\text{km}^2}$)	SQ (m ³ s ⁻¹)	Sq ($\frac{\text{dm}^3}{\text{s}\cdot\text{km}^2}$)	SWQ (m ³ s ⁻¹)	SWq ($\frac{\text{dm}^3}{\text{s}\cdot\text{km}^2}$)
Upper	Rogozyn	102.8	0.17	1.69	0.62	6.02	3.23	31.4
	Sztabin	846.0	1.23	1.45	4.61	5.45	31.6	37.4
Middle	Dolistowo	3065.1	3.83	1.25	15.2	4.96	53.8	17.6
	Oswiec	4365.1	6.48	1.48	20.1	4.60	81.9	18.8
Lower	Burzyn	6900.4	10.6	1.53	30.6	4.43	138.0	21.1

Table 13.2 Water quality and nutrient loads of the Biebrza River. Winter sampling was carried out in April 1992 and 1993 during spring floods ($n=2$), summer sampling in July 1987, 1990, 1991, 1992, and 1993 ($n=5$). For average discharge data for winter (including spring floods) and summer, see Table 13.1 and Byczkowski and Kicinski (1984). See Fig. 13.1 for location of the sampling and discharge measurement stations (Sztabin, Burzyn). See Wassen et al. (1990) for sampling and analyzing methods. *EC* Electro-conductivity

	Upper Basin (Sztabin)		Lower Basin (Burzyn)	
	Winter	Summer	Winter	Summer
pH	7.7	8.0	8.2	7.8
EC ($\mu\text{S cm}^{-1}$)	410	388	410	398
Ca (mg l ⁻¹)	87	73	79	75
N (mg l ⁻¹)	1.15	0.46	1.12	0.59
P (mg l ⁻¹)	0.23	0.13	0.19	0.17
K (mg l ⁻¹)	2.0	1.5	3.2	3.0
Nutrient loading rates				
N loading rate (t [0.5 year] ⁻¹)	110.4	22.7	652.8	225.2
(t year ⁻¹)	133	878		
P loading rate (t [0.5 year] ⁻¹)	22.0	6.4	111.0	63.4
(t year ⁻¹)	28	174		
K loading rate (t [0.5 year] ⁻¹)	192.4	72.6	1867.2	1145.0
(t year ⁻¹)	265	3012		
Specific nutrient load				
N load/catchment area (kg km ⁻² [0.5 year] ⁻¹)	130.4	26.8	94.6	32.6
P load/catchment area (kg km ⁻² [0.5 year] ⁻¹)	26.0	7.4	16.0	9.2
K load/catchment area (kg km ⁻² [0.5 year] ⁻¹)	227.4	85.5	270.6	166.0

of instream flow in Biebrza and its main tributaries. For the Lower and Middle Basins, the floodplain is also included in the models. The geometry of the floodplain has been reproduced using cross-sections obtained from a digital elevation model (DEM). DEM was also used in order to compare the model flood extension with the flooding range obtained by analysis of satellite images for specific records. For details, see Kubrak and Okruszko (2000), Swiatek et al. (2002), and Verhoeven et al. (2004). The models were used for the analysis of floods (see Section 13.3.3) and assessment of the effect of water management strategies on the discharge and flooding regime of Biebrza. There is a good match between modelled flood zones and the natural vegetation patterns. The existing hydraulic structures in the Middle Basin appear to have a large impact on the hydrology of the northern part of the Middle Basin but seem to have an almost negligible effect for flooding features in the Lower Basin.

13.3.2 Groundwater

In the Upper Biebrza Basin, groundwater plays a key role in the contribution of water to the valley; it seeps out in the wetlands all over the valley bottom. The fens of the Biebrza Upper Basin are typical soligenous fens, i.e. fens with relatively little restriction of water outflow but kept wet by constancy of water supply, mostly groundwater discharging into the fen. A MODFLOW groundwater model has been set up to predict the area and magnitude of the upward flux of groundwater discharge (Batelaan and Kuntohadi 2002). Strong upward fluxes occur in the river bed, in the northern part of the basin in the lower part of the Augustow outwash, and also along the morainic edges (Fig. 13.2). In general, these locations correspond well with the occurrence of peat as derived from peat thickness mappings.

Hydrological modelling of the Middle and Lower Biebrza shows a set of superimposed flow systems of various orders. The size and the distribution of the local systems depend on the hydraulic conductivity of the peat soils and the underlying sandy soil, but also on the changing precipitation and evapotranspiration patterns within a year (Mioduszewski and Wassen 2000; Mioduszewski and Querner 2002).

13.3.3 Flooding

In the Upper Basin, flooding is restricted to a narrow belt of approximately 10–20 m along the river. This is because the river discharges are relatively small (Table 13.1) and the peat body is loosely structured, since there is no sediment deposited. The peat, 3–7 m thick, rises and shrinks with water level fluctuations, preventing it from being flooded by the river. In the Middle and

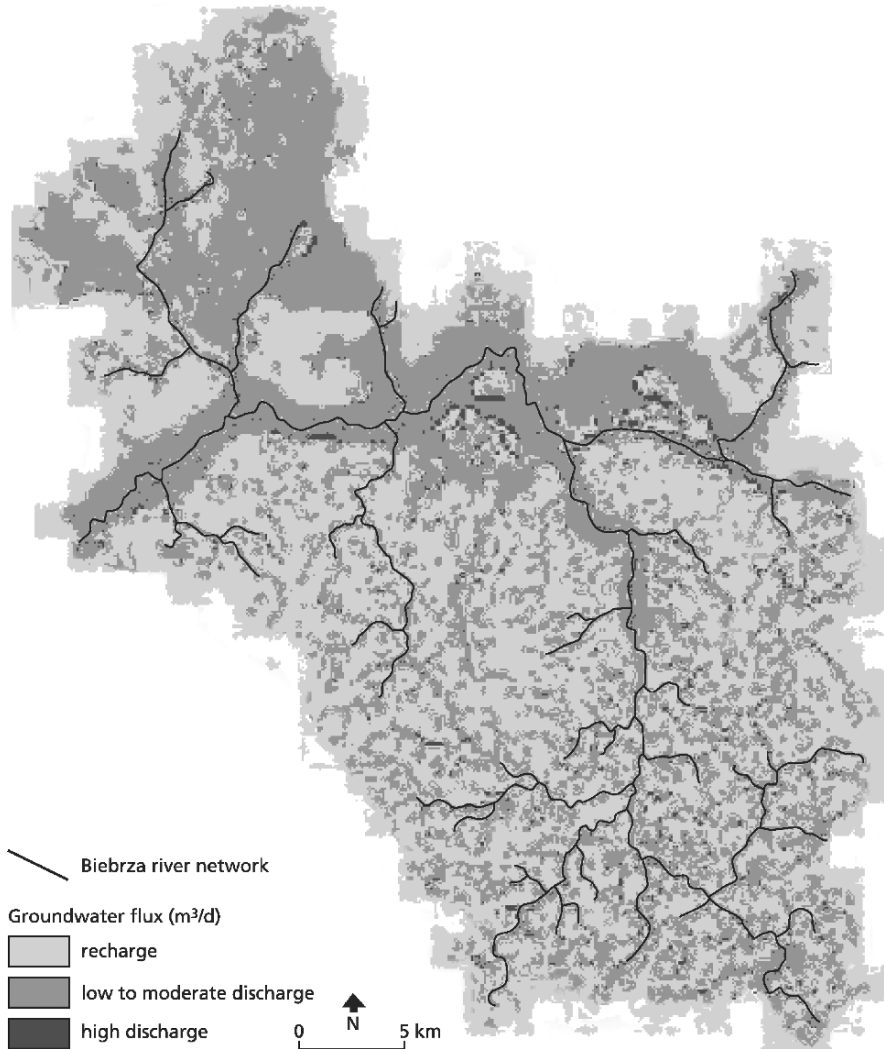


Fig. 13.2 Upward fluxes of groundwater simulated for the Upper Biebrza Basin using MODFLOW (after Batelaan and Kuntohadi 2002)

Lower Basin, river water levels exceed bankful conditions during a significant number of days in most years (Fig. 13.3), leading to almost annual spring floods. Especially in the Lower Basin, the inundated zone is very wide in the flat valley in which the river floodplain and the topogenous fen (i.e. flat fens kept wet by retention of water) merge. This inundation water may derive from three different sources: the atmosphere (rain water/melting snow), river water, and groundwater. Chormanski (2003) was able to distinguish these water sources during spring inundations, using a combination of hydrological

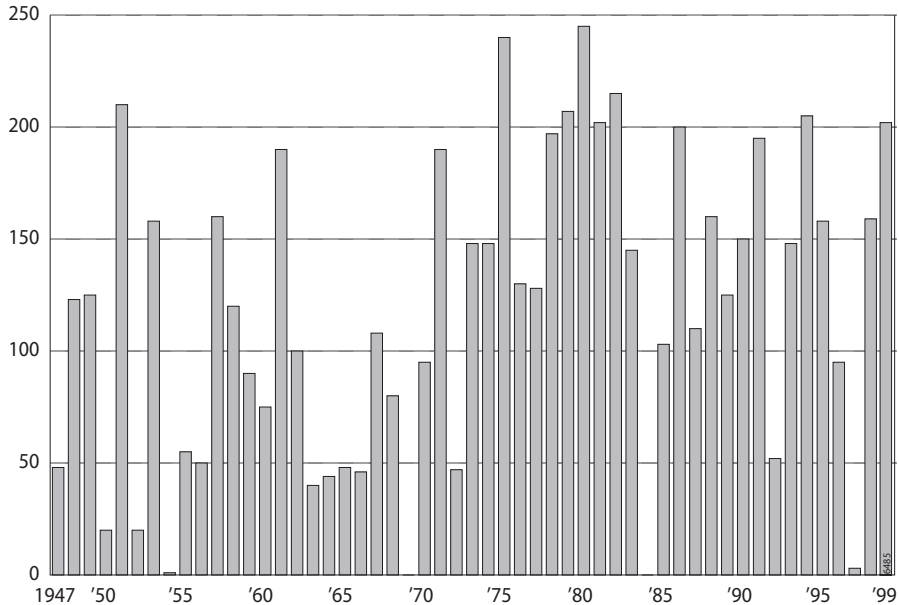


Fig. 13.3 Flood duration in the Lower Biebrza Basin: number of days when river water levels exceed bankful for the period 1947–1999 (calculated for Burzyn gauge station; Okruszko et al. 2003)

modelling, remote sensing, GIS, and statistical analysis of a large water chemistry data base. The area flooded by the river in spring 2002 determined in this way covered 89 km² (Fig. 13.4). The total inundated area was 214 km², of which 125 km² was inundated with rainwater/meltwater and groundwater discharging to the surface (Chormanski 2003).

13.3.4 Drainage

Drainage for grassland farming undertaken in the past has resulted in moist conditions, especially in the Middle Basin. The result is an accelerated mineralization of peat in fen meadows (Okruszko 1990) and, when hay cutting is abandoned, a succession towards vegetation types dominated by scrubs and trees, leading to a loss of biodiversity. To counterbalance these negative effects, the Biebrza National Park (which was founded in 1993) aims to restore the original hydrological regime. For this purpose, we developed dynamical models for assessing the effects of drainage by large canals in the Middle Basin (Mioduszewski and Wassen 2000) and shallow ditches in the Lower Basin (Mioduszewski and Querner 2002). Recently, several re-wetting measures have been realized in the Middle Basin (raising the local drainage basis

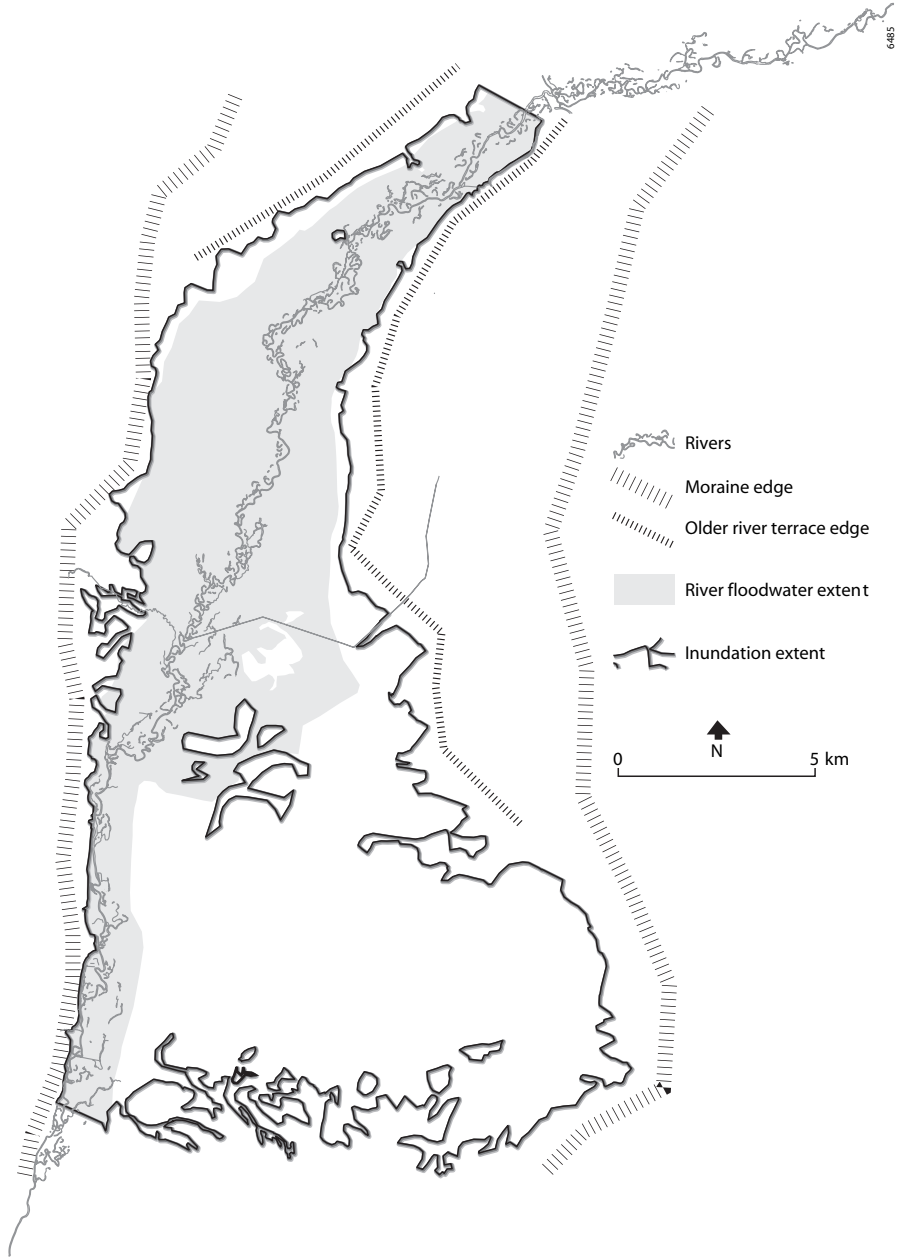


Fig. 13.4 Inundation extent in 2002 and extent of river flood zone in 2002 for the Biebrza Lower Basin (after Chormanski 2003)

by the construction of submerged weirs in canals, re-opening of former river sections, closing small ditches and canals, and filling-in canals). For the Lower Basin, we showed that re-wetting by complete closing of the shallow drainage systems (canals and ditches) results in a water level rise of 0.2–0.5 m and a significant increase in the width of the area fed by groundwater discharge. In large areas of groundwater discharge, the vertical fluxes increased by more than 0.5 mm day⁻¹ during late spring and early summer (Fig. 13.5). Based on these results, the Biebrza National Park will realize re-wetting measures in the Lower Basin in the near future.

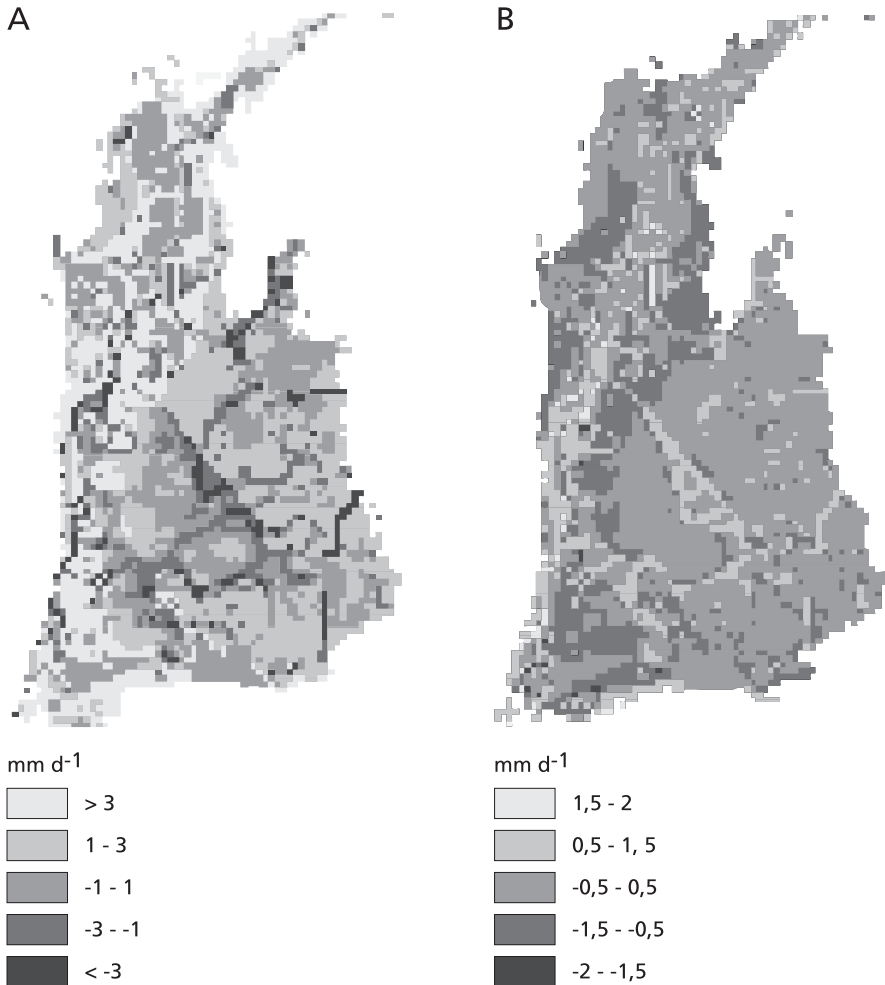


Fig. 13.5 A Calculated average vertical groundwater flux of June 2002 for the Biebrza Lower Basin using MODFLOW and PC-raster. Negative values in A are upward flow; *d* days. B Changes in vertical groundwater flux after closing the drainage system (canals and ditches; negative values depict an increase in upward groundwater fluxes)

13.4 Relation Between Hydrology and Vegetation Zoning

The original zoning of plant communities has disappeared in the Middle Basin, due to drainage works. The characteristic zoning in the Upper and Lower Basin is still present and can be summarized as follows: (a) floodplain marshes along the river (absent in the Upper Basin), (b) rich fens in the occasionally flooded belt further away from the river, (3) moderately rich fen outside the reach of river floods, and finally again (d) rich fen along the valley edges. These vegetation gradients are smooth.

The floodplain contains highly productive marshes which belong syntaxonically to *Glycerietum maximae*, *Caricetum gracilis* and *C. elatae* (Palczynski 1984). These are tall sedge, grass, and herb vegetations, relatively poor in species (Table 13.3). Typical associations of the occasionally flooded belt are *C. caespitosae* and *Peucedano-Caricetum appropinquatae*.

Moderately rich fen is found in an intermediate belt, outside the reach of the seasonal river floods on places where the calcareous groundwater from the moraines does not reach the fen surface. It is fed mainly by rainwater (Wassen et al. 1990) and belongs syntaxonically to *Betuletum humilis*, with affinity to *C. rostrato-diandrae*. It is a thin dwarf-shrub vegetation with low sedges and occasionally some *Sphagnum* hummocks (*S. recurvum*, *S. squarrosum*, *S. palustre*). The moss layer has a fairly high standing crop (Table 13.3).

In a belt along the moraines, but also further away from the moraines, provided that the calcareous groundwater still reaches the fen surface (Wassen et al. 1992), low sedge-rich fen types are abundant. In the Biebrza valley, several species-rich associations of this fen type (the *Caricion diandrae*) are present (Palczynski 1984). These are low-productivity sedge and herb vegetation with a well developed moss layer of Hypnaceae.

Water levels show a large seasonal dynamics in the floodplain (Table 13.3). In dry summers, as for instance the summer of 1992, the water levels in the floodplain even dropped >0.5 m below the peat surface (see also Palczynski and Stepa 1991). The floodplain is relatively nutrient-rich; potassium concentrations are especially higher than in the fens. The rich-fen type has the lowest phosphorus concentration in both peat water (in summer) and in peat. The peat of the moderate rich fen has a large phosphorus content. Phosphorus availability is larger than in the rich fens, which is probably due to the dissolution of precipitated calcium phosphates by infiltrating rainwater (Wassen et al. 1990).

Floodplain and rich fen are calcareous and have a near-neutral pH; the moderate rich fen is slightly acidic. Both inorganic the nitrogen concentration in the peat water in summer and the total nitrogen content in the peat do not differ much between the distinguished wetland ecosystems (Table 13.3).

Table 13.3 Average values of groundwater, peat, and vegetation variables of three characteristic wetland ecosystems in the Biebrza river valley. Values were measured at the peat surface. Spring sampling was carried out in April 1992 during spring floods (wet spring conditions), summer sampling in July 1987 (average summer conditions). Superscript letters (*a, b, c*) refer to significant differences between average values (different letters indicate significant differences; Tukey test, $P < 0.05$). See Wassen et al. (1990) for sampling and analyzing methods. Limitation refers to nutrient limitation as determined by fertilization experiments (Wassen et al. 1998; and unpublished data). *EC* Electro-conductivity, *n* number of samples, *s* summer, *w* winter. *none* In a second fertilization experiment in the floodplain, we measured no significant growth response upon nutrient addition, indicating that plant growth was not limited by nutrients (Wassen et al. 1998)

Wetland ecosystem		Floodplain marsh	Rich fen	Moderately "rich fen"
Groundwater	(<i>n, w/s</i>)	(5/6)	(16/26)	(7/11)
Level (cm surface)	Winter	-54.8±6.8 ^b	-3.5±6.2 ^a	0.6±1.3 ^a
	Summer	4.0±6.5 ^{ab}	2.2±3.8 ^a	6.1±4.2 ^b
pH	Winter	8.12±0.14 ^a	7.10±0.21 ^b	6.58±0.19 ^c
	Summer	6.59±0.36 ^a	6.51±0.40 ^a	6.01±0.16 ^b
EC (μS cm ⁻¹)	Winter	377±1 ^a	233±43 ^b	180±71 ^b
	Summer	413±110 ^a	392±106 ^a	248±14 ^b
Ca (mg l ⁻¹)	Winter	74±1 ^a	44±10 ^b	29±11 ^c
	Summer	102±14 ^a	56±14 ^b	24±15 ^c
N (mg l ⁻¹)	Winter	0.39±0.08 ^a	0.15±0.06 ^b	0.17±0.04 ^b
	Summer	1.72±1.11 ^{ab}	1.43±0.65 ^a	1.04±0.39 ^b
H ₂ PO ₄ (mg l ⁻¹)	Winter	0.21±0.10 ^a	0.13±0.13 ^a	0.17±0.08 ^a
	Summer	0.19±0.16 ^a	0.01±0.04 ^b	0.27±0.36 ^a
K (mg l ⁻¹)	Winter	2.95±0.09 ^a	0.42±0.28 ^b	0.55±0.34 ^b
	Summer	0.88±0.32 ^a	0.55±0.50 ^b	0.29±0.23 ^c
Peat (summer, <i>n</i>)		(3)	(11)	(5)
Organic matter content (% dry weight)		53±43 ^a	85±5 ^a	79±11 ^a
P _{lime}		4.9±1.1 ^{ab}	4.5±0.2 ^a	3.9±0.4 ^b
C/N		16±0 ^a	20±3 ^a	20±3 ^a
N _t (% dry weight)		1.92±1.62 ^a	2.59±0.46 ^a	2.32±0.65 ^a
PO ₄ (% dry weight)		0.14±0.07 ^{ab}	0.07±0.03 ^a	0.70±0.64 ^b
Vegetation (<i>n</i>)		(5)	(11)	(5)
Standing crop				
Phanerogams (g m ⁻²)		983±315 ^a	248±46 ^c	345±396 ^b
Cryptogams (g m ⁻²)		0	226±93 ^a	314±167 ^a
Limitation		N (<i>n</i> =1), none	N (<i>n</i> =2), P (<i>n</i> =1)	N (<i>n</i> =1)
Number of species (<i>n</i> [10 m] ⁻²)		12±5 ^b	28±7 ^a	22±4 ^a

Figure 13.6 integrates eco-hydrological patterns in two typical cross-sections, one for the Upper Basin and one for the Lower Basin. In Biebrza, electro-conductivity (EC_{25}) was a suitable parameter to distinguish rainwater from groundwater and river water, the latter two having higher solute concentrations. We measured EC_{25} values at every 10-cm depth and at horizontal intervals ranging from a few meters to 50 m, depending on the differences in values between adjacent sites. For this, we used a probe allowing for measurement of EC_{25} values at every desirable depth in water-saturated peat (Van Wirdum 1984). EC_{25} patterns were validated with water quality analyses of samples taken from surface water and from piezometers with filters at several depths (see Wassen et al. 1992). The groundwater flow pattern in the Biebrza Upper Basin shows groundwater discharge at the foot of the moraine and slight groundwater flow fed by infiltrating rainwater further away from the upland (Fig. 13.6A). EC_{25} values are fairly homogeneous over large distances in both cross-sections, showing that the gradient in water quality from the valley edge to the river is fairly gradual. There is little dilution at the surface, except for the shallow rainwater lens in the Upper Basin, where groundwater is recharged by infiltrating rainwater. In the Upper Basin, there is no river flooding (Fig. 13.6A). The larger part of the peatland in the Lower Basin is flooded annually by the river (see also Okruszko 1990). In the Lower Basin (Fig. 13.6B), groundwater discharges originate from the dune complex, which borders the peatland here. These dunes consist of leached sand (Wassen et al. 1996), resulting in low EC_{25} values in the groundwater coming from these dunes. In the direction of the river, EC_{25} values are increasing, which is ascribed to the river floods and exchange of solutes from sedimentary loam (Wassen et al. 1992). In both the Upper and Lower Basins, a number of mesotrophic species (species of moderate nutrient-rich conditions) are exclusively restricted in their distribution to the groundwater discharge zone: *Carex diandra* and *C. lasiocarpa* (depicted in Fig 13.6A) are representative for a larger number of species, e.g. *Parnassia palustris*, *C. lepidocarpa*, *C. panicea*, and *Pedicularis palustris*. A number of species which tolerate slightly more nutrient-rich conditions are present along almost the entire cross-section: *Menyanthes trifoliata*, *Caltha palustris*, *Equisetum fluviatile*. Some species are only present in the mineral-poor rainwater infiltration belt in the Upper Basin: *Betula humilis*, *Drosera rotundifolia*, *Oxycoccus palustris*, *Ledum palustre*. Eutrophic species (species of nutrient-rich habitats) tolerant for inundation are only present in the Upper Basin along the river bank (*Carex cespitosa*), whereas in the Lower Basin, these are arranged in wide zones according to decreasing flood tolerance (respectively *Glyceria maxima*, *C. acuta*, *C. elata*; Fig. 13.6B).

From a dynamic 3-D model based on the MODFLOW code (Janssen 2000; Batelaan and Kuntohadi 2002) the percent contribution of water fluxes to the rooted peat top-layers were estimated for some vegetation communities (Table 13.4). In addition to rain water, the vegetation zones close to the river

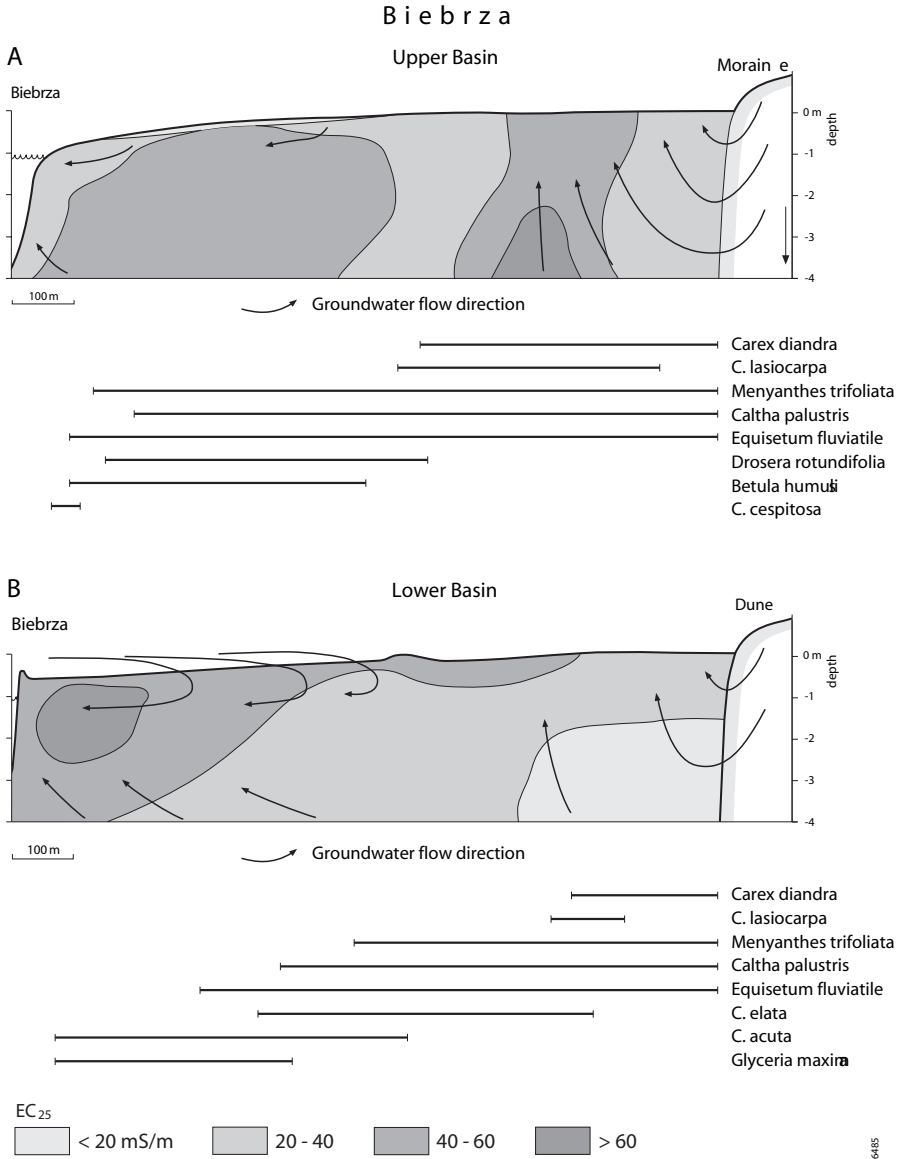


Fig. 13.6 Cross-sections of the Biebrza valley (A Upper Basin, B Lower Basin) from the upland (right) to the river (left). Arrows show schematic groundwater flow pattern (simulated with FLOWNET), gray shades show electro-conductivity (EC₂₅) of the groundwater, horizontal lines below the cross-sections show approximate distribution of some characteristic fen plant species (after Wassen et al. 1992, 1996)

Table 13.4 Attribution of different water sources to major vegetation types in the Biebrza wetlands

Vegetation type	Attribution (%) of water fluxes to the root zone ^a		
	Ground-water	River water	Overland flow
Reedland (<i>Scirpo-Phragmitetum</i>)	0	23	0
Tall grasses (<i>Glycerietum maximae</i>)	1	12	2
Tall sedges (<i>Caricetum acutae</i>)	7	8	0
Tall sedges (<i>C. elatae</i>)	29	0	0
Sedge grassland (<i>Calamagrostietum strictae</i> type a ^b)	37	0	0
Sedge grassland (<i>C. strictae</i> type b ^b)	46	0	0
Moss sedgeland (<i>Caricetum limoso-diandrae</i>)	76	0	0
Scrub-moss-sedgeland (<i>Betuletum humilis</i>)	45	0	0

^a The rest of the water flux consists of precipitation water (after Janssen 2000; Batelaan, unpublished data).

^b Refers to two types of *Calamagrostietum strictae* vegetation (see Wassen et al. 2002).

(*Scirpo-Phragmitetum*, *Glycerietum maximae*) receive substantial amounts of river water in flood periods, while zones at a greater distance from the river (*Caricetum elatae*, *Calamagrostietum strictae*) are supplied with groundwater and rainwater. Especially, the rich-fen type *Caricetum limoso-diandrae* is dominated by discharging groundwater, while in contrast, the moderately rich-fen type *Betuletum humilis* receives mainly rainwater.

13.5 Productivity and Nutrient Limitation of Marsh and Fen Vegetation

Species richness-productivity relationships for threatened species in wetlands show hump-shaped patterns, with a narrow hump at low productivity (Moore et al. 1989, Wheeler and Shaw 1991; Olde Venterink et al. 2003). The narrow hump indicates that these species are sensitive to productivity increases, and hence to increased availabilities of nutrients which limit plant growth. Nitrogen, phosphorus, and potassium availability limit biomass production in most wetlands. Although many freshwater wetlands seem to be limited by nitrogen, phosphorus limitation can also occur in fens with high inputs of iron-, aluminium- and/or calcium-rich waters (Boyer and Wheeler 1989; Boeye and Verheyen 1994; Wassen et al. 1992) and in nitrogen-enriched fens where annual mowing depletes the soil phosphorus pool relatively faster than the nitrogen pool (Verhoeven and Schmitz 1991). The Biebrza floodplain

marshes are highly productive and growth is limited by nitrogen, if limited by nutrients at all (Table 13.3). The groundwater-fed rich fens were in two cases limited by nitrogen and in one case growth was phosphorus-limited, whereas the moderate rich fen was nitrogen-limited.

In the Biebrza Upper Basin, productivity and nutrient availability were analyzed along a gradient from rich fen to moderately rich fen (see Fig. 13.6A). The traditional mowing regime has been abandoned here for some decades and Schmidt et al. (2000) observed a invasion of *Betula pubescens* in the rich fen. El-Kahloun (2004) investigated possible shifts in nutrient limitation in this fen by analyzing peat and water and, in 2003, repeating measurements of nitrogen/phosphorus ratios in vascular plant tissue, as done earlier by Wassen et al. in 1992 (published by Wassen et al. 1995, 1998). The main objective of this comparison was to analyze whether the observed changes in vegetation composition (especially the invasion of *Betula pubescens*) during the past ten years were related to changing nutrient availabilities.

It appeared that, in 2003, water tables and phosphorus concentrations in water and peat were lower than in 1992 in both fen types, whereas pH values were higher than in 1992 (Table 13.5). Nitrogen and phosphorus concentrations in above-ground plant material declined. Nitrogen/phosphorus ratios indicated nitrogen limitation in 1992 (for critical values, see Güsewell and Koerselman 2002; Olde Venterink et al. 2003). In 2003, nitrogen/phosphorus ratios were higher than in 1992, both in the rich fen and in the moderately rich fen. In the rich fen, the nitrogen/phosphorus ratios of 2003 clearly indicate phosphorus-limited growth (Table 13.5).

An explanation for this shift in limitation from nitrogen to phosphorus limitation could be an increase in external eutrophication. However, from the actual lower nutrient concentrations in groundwater in comparison with data from 1992, we can infer that no external eutrophication through the groundwater has occurred, which is in line with earlier observations by Wassen et al. (1990, 1992). We have found no indications that atmospheric nitrogen deposition has increased. We therefore conclude that external eutrophication is limited and has not increased since the study of Wassen et al. (1990). Present groundwater levels are lower compared with the levels measured in the period from 1987 to 1993 (Wassen et al. 1996). We suggest a lowering of the groundwater table as a possible cause for the lowered availability of phosphorus and the shift from nitrogen to phosphorus limitation in the rich fen. Lower water tables may have enhanced co-precipitation of phosphorus with aluminum and iron hydroxides under oxic conditions (Patrick and Khaled 1974; Boeye and Verheyen 1994). The development of trees may have lowered the groundwater table by increasing evapotranspiration (Wassen and Joosten 1996). This hypothesis is supported by observations by El-Kahloun et al. (2003). They observed a very low water table in summer when evapotranspiration rates were high, while water levels in spring were close to the mire surface, as in 1992. These observations suggest not only that the removal of biomass by hay-

Table 13.5 Water tables, peat water quality, nutrient content in peat and in standing crop, and above-ground biomass production in two major fen types of the Biebrza Upper Basin, in 1992 and 2003. Values are average \pm SD (number of observations given in parentheses). Water levels were measured relative to the peat surface. Standing crop was harvested at the height of the growing season (July). See Wassen et al. (1995, 1998) and El-Kahloun et al. (2003, 2005) for sampling and analyzing methods

	Rich fen		Moderately rich fen	
	1992	2003	1992	2003
Water table (cm above peat surface)	April: 0 ± 3 (51) July: -33 ± 6 (17)	April: -7 ± 1.7 (3) July: -55 ± 1 (3)	April: 2 ± 4 (51) July: -24 ± 4 (17)	April: 1.3 ± 5.0 (3) July: -50 ± 2 (3)
Peat water quality (mg l^{-1})				
PO ₄	0.31 ± 0.26 (3)	0.02 ± 0.02 (4)	7.09 ± 6.53 (3)	0.01 ± 0.0 (4)
NH ₄	0.34 ± 0.24 (4)	0.89 ± 0.06 (4)	0.41 ± 0.13 (3)	0.48 ± 0.5 (4)
NO ₃	0.39 ± 0.51 (4)	0.22 ± 0.3 (4)	2.28 ± 3.94 (3)	0.00 ± 0.0 (4)
Ca	75.0 ± 3.0 (4)	89.2 ± 19.9 (4)	58.0 ± 13.0 (3)	98.9 ± 32.6 (4)
pH	6.17 ± 0.09 (4)	6.95 ± 0.4 (4)	6.52 ± 0.20 (3)	7.01 ± 0.1 (4)
Nutrients in peat (% dry weight)				
N _{tot}	1.84 ± 0.28 (6)	2.05 ± 0.28 (4)	2.74 ± 0.69 (5)	2.89 ± 0.62 (4)
P _{tot}	0.08 ± 0.01 (6)	0.07 ± 0.03 (4)	0.49 ± 0.23 (5)	0.10 ± 0.04 (4)
Nutrients in above-ground biomass (mg g^{-1} dry weight)				
N	14.3 ± 2.3 (5)	10.61 ± 1.5 (4)	16.7 ± 1.0 (5)	9.45 ± 0.4 (4)
P	1.06 ± 0.23 (5)	0.43 ± 0.1 (4)	3.43 ± 0.4 (5)	0.82 ± 0.4 (4)
N/P	13.7 ± 2.37 (5)	24.16 ± 1.3 (4)	4.86 ± 0.15 (5)	12.81 ± 5.9 (4)
Above-ground biomass (g dry weight m ⁻²)	534 ± 198 (9)	496.4 ± 69 (4)	660 ± 453 (9)	394 ± 105 (4)

making influences nutrient availabilities directly by exporting nutrients but also that abandonment of this management practice may exert an indirect influence on nutrient availability via evapotranspiration and water tables. We did not find large differences in productivity, neither in space nor in time. Still, the type of nutrient limitation has changed and may possibly affect the species composition of the fens. In 2003, five threatened species (*Viola persicifolia*, *Linum catharticum*, *Dactylorhiza incarnata*, *Carex flava*, *Briza media*) which were not present in the species list of Wassen et al. (1992) were found along the cross-section. These species are common in phosphorus-limited sites (Wassen et al. 2005) and likely possess adaptations enabling them to obtain the limited phosphorus resources.

13.6 Discussion and Conclusions

We found a number of clear hydrological and ecological patterns in the Biebrza valley.

Hydrology in the Upper Basin was very different from the Lower Basin. In the Upper Basin groundwater discharge was dominant, whereas in the Lower Basin inundation was the predominant phenomenon. The hydro-chemistry of the mire water was governed by three principal sources of water: precipitation, groundwater seeping to the surface, and river floods. Vegetation zoning and productivity were related to the dominance of these water types in the mires and floodplains. In the river flood zone, nutrient availability and productivity was governed by the river, which provided the vegetation with nutrients dissolved in river water as well as attached to sedimentary loam and silt. The relationship between nutrient availability, productivity, and species composition outside the river flood zone in the Upper Basin was more complicated and its dynamics seemed to be related to succession and management. Generally speaking, the present situation in the Biebrza Upper Basin and in the Lower Basin, outside the reach of the river floods, allows for the study of processes in so-called through-flow fens (*Durchströmungsmoore*; cf. Succow 1988) without the disturbing effects of raised atmospheric nitrogen deposition, heavy drainage or eutrophication of groundwater (see Wassen and Joosten 1996). The same holds for the floodplains in the Biebrza Lower Basin, which in contrast to most European river marginal floodplains, are still flooded over vast areas. Even more fascinating, the floodplain interacts with a vast topogenous mire inundated in spring by atmospheric water and groundwater. Here we can learn how the interaction between river water, discharging groundwater, and atmospheric water (Chormanski 2003) establishes a biomass gradient with peat-forming vegetation and marsh vegetation arranged in a zoning pattern parallel to the river. Water fluxes, water level dynamics, water chemistry, and mineralization rates seem key factors determining these vegetation gradients (De Mars et al. 1997; Wassen et al. 2003).

In Western Europe and North America human, interference in hydrological systems led to changes in the distribution and size of water systems, causing fragmentation which in turn led to changes in the distribution of plant species and communities (Van Diggelen et al. 1991; Mitsch and Gosselink 1993; Stromberg 1993b; Barendregt et al. 1995; Wassen et al. 1996). Hydrological processes such as groundwater discharge and rainwater and surface water recharging the groundwater are of course still active in disturbed landscapes, but the place where they occur, their intensity, and their water quality has changed (Giller and Wheeler 1988; Wassen et al. 2003). For instance, deterioration of ecosystems in the Vecht river plain is partly due to poor water quality (Barendregt 1993) and drainage (De Mars 1996) but the fragmented distribution of ecosystems in the Vecht river plain is caused by hydrological

fragmentation; and restoration should thus try to re-enforce larger regional water systems. The fairly undisturbed hydrology at Biebrza allowed us to assess how vegetation was fed by different water sources. Moreover, it became apparent that, where large regional water systems meet, gradual spatial differences in water fluxes facilitate the hydrological conditions for large-scale vegetation gradients. Such gradients cannot exist in a hydrologically fragmented landscape. Bootsma et al. (2000) compared the Drentse Aa valley with Biebrza; and Bootsma and Wassen (1996) compared three large fen wetland areas in the Netherlands with Biebrza. They concluded that the Drentse Aa valley was not as severely disturbed as the other Dutch areas. The eutrophication problem was especially severe in the Vecht river plain, whereas acidification of fens was an especially serious problem in the Wieden and Weerribben.

In using Biebrza as a reference for other areas, we should consider that Biebrza is a lowland river of intermediate size (average annual discharge in the upper course ca. $5 \text{ m}^3 \text{ s}^{-1}$ and in the lower course ca. $30 \text{ m}^3 \text{ s}^{-1}$) running through a flat valley filled with peatlands and marshes and surrounded by a post-glacial landscape with ice-pushed hills, moraines, and outwash plains. Its origin, geomorphology, and topography in northeastern Poland is similar to that in northern Germany, parts of Denmark and the United Kingdom, and the northern half of the Netherlands. The present-day climate shows differences: the above-mentioned western European countries have an Atlantic climate with mild winters and a precipitation surplus of ca. 300 mm year^{-1} , whereas the sub-continental climate of northeastern Poland shows colder winters and an annual precipitation surplus of only 150 mm . However, these climatic differences do not appear to have a predominant influence on the flora. Although the flora of Biebrza contains continental and sub-boreal elements, 96 % of the plant species present in the Biebrza valley also belong to the Dutch flora (Bootsma 2000). Thus, we conclude that Biebrza can be used as a reference example for lowland rivers, floodplains, and fens in western and central Europe, such as the rivers Peene and Ems in Germany, Drentse Aa, Vechtstreek, Wieden and Weerribben in the Netherlands, Zwarte Beek in Belgium, and the Norfolk Broads in Britain (see also Van Wirdum 1991; Grootjans and Van Diggelen 1995; Wheeler and Shaw 1995).

We should also realize that a far-reaching objective will automatically add uncertainty to knowledge from a reference area applied in the area that is to be restored. Wassen (2005) discerns the following objectives of reference studies: (a) to discover the relationship between natural key processes and ecosystem functioning, (b) to estimate the degree of degradation of areas to be restored, (c) to set targets for nature conservation and to define conditions necessary for (re-)establishment of target species and communities, and (d) to design restoration measures in restoration projects. We conclude that the first two objectives are feasible by using information from a reference wetland. However, when the aim of the reference study is to set targets for nature conservation, or to define environmental standards, or specific

restoration measures necessary for (re-)establishment of target species and communities, we also have to deal with added uncertainty related to recovery processes. This leads us to the fundamental question: Can we predict recovery? Knowledge from reference areas in itself does not enable us to predict the potentials for recovery of disturbed and stressed ecosystems, since recovery does not necessarily follow the same path as deterioration and also the rate of recovery may differ from the rate of deterioration. Hysteresis occurs in both abiotic and biotic processes. Drainage may lead to irreversible decomposition of peat (Okruzsko 1995). Also, the redox status of peat may irreversibly change following drainage (De Mars and Wassen 1999) and the nutrient dynamics is strongly impacted by drying and re-wetting (Olde Venterink et al. 2002). Restoration projects aiming at counterbalancing acidification show that pH and base saturation of the soil recover very slowly (Beltman et al. 2001). Also, high atmospheric deposition and poor water quality may prevent full recovery of nutrient-poor conditions (Bakker and Berendse 1999). For this reason, Van Diggelen (1998) is more optimistic about the restoration prospects of eutrophic floodplains than those of mesotrophic fens and fen meadows. In this respect, it is also important to note that re-establishment of the desired species is hampered if they are absent in the actual vegetation and the seed-bank. Regeneration of the vegetation depends in such cases on dispersion possibilities, which are unfavorable for many wetland species in the present-day fragmented landscape (Bakker et al. 1996; Poschlod and Bonn 1998; Van Diggelen 1998). Additionally, above- and belowground communities influence each other through a variety of direct and indirect interactions (Wardle 2002). Time lags needed by soil organisms to respond to change lead to different selection pressures, for example as exerted by above- and belowground herbivores and pathogens (Van der Putten et al. 2001). De Deyn et al. (2003) showed that a strong linkage exists between succession in vegetation and soil community composition. This linkage is often overlooked in restoration projects in which either only soil fertility is reduced or aboveground vertebrate grazers are introduced. The slow recovery of belowground communities might be a factor responsible for the disappointing recovery of ecosystems after restoration measures were applied to former agricultural fields.

What these examples (in which time lags, feedbacks, unpredictable recovery processes, and hysteresis occur) demonstrate is that they are all potential reasons for slow or incomplete recovery. The conclusion should be that information from reference areas is very useful to demonstrate the general potential for restoration or rehabilitation, but it has to be treated with care in order not to raise too high an expectation for the outcome of restoration projects (Wassen 2005). We can never guarantee success for a resource manager or a landscape planner in his restoration attempt, when using solely the knowledge obtained in reference areas. Research in reference areas undoubtedly has invaluable importance for conservation and restoration. Therefore if we fail to

protect or if we should lose these unspoilt areas, we are automatically cut off from a source which enables us to gain knowledge and information needed for restoration elsewhere.

Acknowledgements We thank Vincent Roodenburg for correcting the English and Ton Markus for drawing the figures.

References

- Baird AJ, Wilby RL (1999) *Eco-hydrology*. Routledge, London
- Bakker JP, Berendse F (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol Evol* 14:63–68
- Bakker JP, Poschod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot Neerl* 45:461–490
- Barendregt A (1993) *Hydro-ecology of the Dutch polder landscape*. PhD thesis, Utrecht University, Utrecht
- Barendregt A, Wassen MJ, Schot PP (1995) Hydrological systems beyond a nature reserve, the major problem in wetland conservation of Naardermeer (the Netherlands). *Biol Conserv* 72:393–405
- Batelaan O, Kuntohadi T (2002) Development and application of a groundwater model for the Upper Biebrza River basin. *Ann Warsaw Agric Univ SGGW Land Reclam* 33:57–69
- Beltman B, Van den Broek T, Barendregt A, Bootsma MC, Grootjans AP (2001) Rehabilitation of acidified and eutrophied fens in The Netherlands: effects of hydrologic manipulation and liming. *Ecol Eng* 17:21–31
- Boeye D, Verheyen RF (1994) The relation between vegetation and soil chemistry gradients in a groundwater discharge fen. *J Veg Sci* 5:553–560
- Bootsma MC (2000) *Stress and recovery in wetland ecosystems*. PhD thesis, Utrecht University, Utrecht
- Bootsma MC, Wassen MJ (1996) Water quality of fen vegetation types in three European lowland mires. *Vegetatio* 127:173–189
- Bootsma MC, Wassen MJ, Jansen AJM (2000) The Biebrza-valley as an ecological reference for Dutch stream valleys (in Dutch with English summary). *Landschap* 17:113–130
- Boyer MLH, Wheeler BD (1989) Vegetation patterns in spring-fed calcareous fens: Calcite precipitation and constraints on fertility. *J Ecol* 77:597–609
- Byczkowski A, Kicinski T (1984) Surface waters in the Biebrza drainage basin. *Pol Ecol Stud* 10:271–299
- Cellot B, Dole-Olivier MJ, Bornette G, Patou G (1984) Temporal and spatial environmental variability in the Upper Rhone river and its floodplain. *Freshwater Biol* 31:311–325
- Chormanski J (2003) *Methodology of the flood extent determination*. PhD thesis Warsaw Agricultural University, Warsaw
- Cirujano S, Casado C, Bernues M, Camargo JA (1996) Ecological study of Las Tablas de Daimiel National Park (Ciudad Real, central Spain): differences in water physico-chemistry and vegetation between 1974 and 1989. *Biol Conserv* 75:211–215
- De Deyn GB, Raaijmakers CE, Zoomer HR, Berg MP, De Ruiter PC, Verhoef HA, Bezemer TM, Van der Putten WH (2003) Soil invertebrate fauna enhances grassland succession and diversity. *Nature* 422:711–713

- De Mars H (1996) Chemical and physical dynamics of fen hydro-ecology. PhD thesis, Utrecht University, Utrecht
- De Mars H, Wassen MJ (1999) Redox potentials in relation to water levels in different mire types in the Netherlands and Poland. *Plant Ecol* 140:41–51
- De Mars H, Wassen MJ, Olde Venterink H (1997) Flooding and groundwater dynamics in fens in eastern Poland. *J Veg Sci* 8:319–328
- Dyrzc A, Zdunek W (1993) Breeding statistics of the Aquatic warbler on the Biebrza marshes, NE Poland. *J Ornithol* 134:317–323
- Dyrzc A, Okulewicz J, Witkowski J (1985) Bird communities on natural eutrophic fen mires in the Biebrza river valley, N.E. Poland. *Vogelwarte* 33:26–52
- El-Kahloun M (2004) Vegetation dynamics in P-limited rich fens. PhD thesis, Antwerp University, Antwerp
- El-Kahloun M, Verhagen B, Van Haesebroeck V, Verhagen B (2003) Differential recovery of above- and belowground fen vegetation following fertilization. *J Veg Sci* 14:451–458
- El-Kahloun M, Gerard M, Meire P (2005) Phosphorus and nitrogen cycling in fen vegetation along different trophic conditions in the Biebrza valley, Poland. *Ecohydrol Hydrobiol* 5:68–79
- Giller KE, Wheeler BD (1988) Acidification and succession in a floodplain mire in the Norfolk Broadland, U.K. *J Ecol* 76:849–866
- Girel J (1994) Old distribution procedure of both open water and matter fluxes in floodplains of Western Europe: impact on present vegetation. *Environ Manage* 18:203–221
- Grootjans AP, Van Diggelen R (1995) Assessing the restoration prospects of degraded fens. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) *Restoration of temperate wetlands*. Wiley, Chichester, pp 73–90
- Güsewell S, Koerselman W (2002) Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspect Plant Ecol* 5:37–61
- Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46:7–43
- Janssen A (2000) Modeling groundwater flow in a floodplain in the lower Biebrza catchment with the MODFLOW three dimensional finite differences code. (Report of the Department of Physical Geography) Utrecht University, Utrecht
- Jongman RGH (1998) Rivers: key elements in European ecological networks. In: Nienhuis PH, Leuven RSEW, Ragas AMJ (eds) *New concepts for sustainable management of river basins*. Backhuys, Leiden, pp 53–67
- Kossowska-Cezak U (1984) Climate of the Biebrza ice-marginal valley. *Pol Ecol Stud* 10:253–270
- Kubrak J, Okruszko T (2000) Hydraulic model of the surface water system for the central Biebrza basin. In: Mioduszewski W, Wassen MJ (eds) *Some aspects of water management in the Valley of the Biebrza River*. Institute of Land Reclamation and Grassland Farming, Falenty, pp 83–90
- Large ARG, Prach K, Bickerton, MA, Wade PM (1994) Alteration of patch boundaries on the floodplain of the regulated river Trent, U.K. *Regul Rivers* 9:71–78
- McCollin D, Moore L, Sparks T (2000) The flora of a cultural landscape: environmental determinants of changes revealed using archival sources. *Biol Conserv* 92:249–263
- Mioduszewski W, Querner EP (eds) (2002) *Hydrological system analysis in the valley of Biebrza River*. Institute of Land Reclamation and Grassland Farming, Falenty
- Mioduszewski W, Wassen MJ (eds) (2000) *Some aspects of water management in the valley of the Biebrza river*. Institute of Land Reclamation and Grassland Farming, Falenty
- Mitsch WJ, Gosselink JG (1993) *Wetlands*, 2nd edn. Van Nostrand Reinhold, New York
- Moore DRJ, Keddy PA, Gaudet CL, Wisheu IC (1989) Conservation of wetlands: do infertile wetlands deserve a higher priority. *Biol Conserv* 47:203–217

- Okruszko H (1990) Wetlands of the Biebrza valley; their value and future management. Polish Academy of Sciences, Warsaw
- Okruszko H (1995) Influence of hydrological differentiation of fens and their transformation after dehydration and on possibilities for restoration. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 113–119
- Okruszko T, Wasilewicz M, Dembek W, Rycharski M, Matuszkiewicz A (2003) Analysis of the changes in water, soil and plant conditions in Bagno Lawki in the Lower Biebrza Basin. (Report 3-1) Institute of Land Reclamation and Grassland Farming, Falenty, pp 107–128
- Olde Venterink H, Davidsson TE, Kiehl K, Leonardson L (2002) The impact of drying and re-wetting on N, P and K dynamics in a wetland soil. *Plant Soil* 243:119–130
- Olde Venterink H, Wassen MJ, Verkroost AWM, De Ruiter PC (2003) Species richness-productivity patterns differ between N, P and K limited wetlands. *Ecology* 84:2191–2199
- Pajnowska H, Pozniak R, Wienclaw E (1984) Groundwater of the Biebrza valley. *Pol Ecol Stud* 10:301–311
- Palczyński A (1984) Natural differentiation of plant communities in relation to hydrological conditions of the Biebrza valley. *Pol Ecol Stud* 10:347–385
- Palczyński A, Stepa T (1991) Biomass production in main plant associations of the Biebrza valley with respect to soil conditions. *Pol Ecol Stud* 17:53–62
- Patrick WH, Khaled RA (1974) Phosphate release and sorption by soil and sediments: effect of anaerobic and anaerobic conditions. *Science* 186:53–55
- Poschlod P, Bonn S (1998) Changing dispersal perspectives in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? *Acta Bot Neerl* 47:27–44
- Rich TCG, Woodruff ER (1996) Changes in vascular plant floras of England and Scotland between 1930–1960 and 1987–1988: the BSBI monitoring scheme. *Biol Conserv* 75:217–229
- Schmidt A, Piórkowski H, Bartoszek H (2000) Remote sensing techniques and geographic information systems for wetland conservation and management: monitoring scrub encroachment in Biebrza National Park. Report Alterra, Wageningen
- Stromberg JC (1993a) Instream flow models for mixed deciduous riparian vegetation within a semiarid region. *Regul Rivers* 8:225–235
- Stromberg JC (1993b) Riparian mesquite forests: a review of their ecology, threats, and recovery potential. *J Ariz Nev Acad Sci* 27:111–124
- Stromberg JC (2001) Biotic integrity of *Platanus wrightii* riparian forests in Arizona: first approximation. *Forest Ecol Manage* 142:251–266
- Stromberg JC, Tiller R, Richter B (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecol Appl* 6:113–131
- Succow M (1988) Landschaftsökologische Moorkunde. Borntraeger, Berlin
- Succow M, Jeschke L (1986) Moore in der Landschaft. Urania, Leipzig
- Swiatek D, Okruszko T, Chormanski J (2002) Surface water system analysis. In: Mioduszewski W, Querner EP (eds) Hydrological system analysis in the Valley of Biebrza River. Institute of Land Reclamation and Grassland Farming, Falenty, pp 39–80
- Toner M, Keddy P (1997) River hydrology and riparian wetlands: a predictive model for the ecological assembly. *Ecol Appl* 7:236–246
- Trémolières M, Roeck U, Klein JP, Carbiener R (1994) The exchange processes between river and groundwater on the central Alsace floodplain (eastern France): the case of a river with functional floodplain. *Hydrobiologia* 273:19–36
- Van der Putten WH, Vet LEM, Harvey JA, Wäckers LA (2001) Linking above- and below-ground multitrophic interactions of plants, herbivores, pathogens and their antagonists. *Trends Ecol Evol* 16:547–554

- Van Diggelen R (1998) Moving gradients; assessing restoration prospects of degraded brook valleys. PhD thesis, University of Groningen, Groningen
- Van Diggelen R, Molenaar W, Casparie WA, Grootjans AP (1991) Paläoökologische Untersuchungen als Hilfe der Landschaftsanalyse im Gorecht-gebiet. *Telma* 21:57–73
- Van Urk G (1984) Lower Rhine–Meuse. In: Whitton BA (ed) *Ecology of European rivers*. Blackwell, Oxford, pp 437–468
- Van Wirdum G (1984) Development of techniques for ecohydrological research. (Annual report 1983) Research Institute for Nature Management, Leersum
- Van Wirdum G (1991) Vegetation and hydrology of floating rich fens. PhD thesis, University of Amsterdam
- Verhoeven JTA, Schmitz MB (1991) Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry* 12:135–148
- Verhoeven R, Banasik R, Swiatek D, Chormanski J, Okruszko T (2004) Surface water modeling of the Biebrza River network. In: *River flow*. Balkema, Rotterdam, pp 1057–1063
- Wardle DA (2002) *Communities and ecosystems: linking the aboveground and below-ground components*. Princeton University, Princeton
- Wassen MJ (2005) The use of reference areas in the conservation and restoration of riverine wetlands. *Ecohydrol Hydrobiol* 5:41–49
- Wassen MJ, Grootjans AP (1996) Ecohydrology: an interdisciplinary approach for wetland management and restoration. *Vegetatio* 126:1–4
- Wassen MJ, Joosten JHJ (1996) In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza Upper Basin (Poland). *Vegetatio* 124:191–209
- Wassen MJ, Barendregt A, Palczynski A, De Smidt JT, De Mars H (1990) The relationship between fen vegetation gradients, groundwater flow and flooding in an undrained valley mire at Biebrza, Poland. *J Ecol* 78:1106–1122
- Wassen MJ, Barendregt A, Palczynski A, De Smidt JT, De Mars H (1992) Hydro-ecological analysis of the Biebrza mire, Poland. *Wetland Ecol Manage* 2:119–134
- Wassen MJ, Olde Venterink H, De Swart EOAM (1995) Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *J Veg Sci* 6:5–16
- Wassen MJ, Van Diggelen, R, Wolejko L, Verhoeven JTA (1996) A comparison of fens in natural and artificial landscapes. *Vegetatio* 126:5–26
- Wassen MJ, Van der Vliet RE, Verhoeven JTA (1998) Nutrient limitation in the Biebrza fens and floodplain (Poland). *Acta Bot Neerl* 47:241–253
- Wassen MJ, Bleuten W, Bootsma MC (2002) Linking hydrology to ecology; Biebrza as a geographical reference. *Ann Warsaw Agric Univ* 33:27–34
- Wassen MJ, Peeters WHM, Olde Venterink H (2003) Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. *Plant Ecol* 165:27–43
- Wassen MJ, Olde Venterink H, Lapshina ED, Tanneberger F (2005) Endangered plants persist under phosphorus limitation. *Nature* 437:547–550
- Wheeler BD, Shaw SC (1991) Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J Ecol* 79:285–301
- Wheeler BD, Shaw SC (1995) A focus on fens – Controls on the composition of fen vegetation in relation to restoration. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) *Restoration of temperate wetlands*. Wiley, Chichester, pp 49–72
- Zalewski M (2000) Eco-hydrology – the scientific background to use ecosystem properties as management tools toward sustainability of water resources. *Ecol Eng* 16:1–8
- Zurek S (1984) Relief, geologic structure and hydrography of the Biebrza ice-marginal valley. *Pol Ecol Stud* 10:239–251