Unravelling hydrological mechanisms behind fen deterioration in order to design restoration strategies

De hydrologische oorzaken van de achteruitgang van laagveengebieden ontrafeld

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De hydrologische oorzaken van de achteruitgang van laagveengebieden ontrafeld

(met een samenvatting in het Nederlands)

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1 Introduction

1.1 Scope

Wetlands are areas of land whose soil is permanently or seasonally saturated with groundwater and, in some cases, covered by water. The ecosystems found in wetlands comprise, among others, bogs, swamps and fens. Fens are the most biologically diverse type of wetland ecosystem. They used to be widespread in the temperate regions of Western Europe, but, like in the rest of the world, have strongly declined in number and size due to anthropogenic pressure on environmental resources (Millennium Ecosystem Assessment, 2005; Succow and Joosten, 2001). In addition, many fen plant species are near extinction despite national and international legislation and agreements on the conservation of biodiversity for future generations (e.g. Council of Europe, 2000). In order to reverse the deterioration of fens, ambitious efforts have been undertaken in The Netherlands to reduce the impact of anthropogenic activities on low-productive fens. The effectiveness of such restoration projects, however, has been variable (Jansen et al., 2000; Lamers et al., 2002). Two of the numerous causes of this variable effectiveness have attained wide interest in literature, namely (1) the inability of target species to re-establish themselves at successfully restored sites (Bischoff, 2002; Bossuyt and Honnay, 2008; Plassman et al., 2009; Soons et al., 2005; Van Dijk et al., 2007) and (2) the increased availability of nutrients upon rewetting (Koerselman et al., 1993; Lamers et al., 1998; Olde Venterink et al., 2002; Smolders et al., 2006; Van Dijk et al., 2004). Another possible cause of the limited success of fen restoration projects is insufficient rewetting with unpolluted groundwater. This latter cause has, however, only been studied in a descriptive manner (Jansen et al., 2004; Jansen et al., 2000; Kemmers et al., 2003; Lamers et al., 2002; Van der Hoek and Sykora, 2006), and the underlying hydrological processes have not yet been unravelled. Knowledge of these hydrological processes is important for fen restoration and conservation, particularly because of the high costs and the significant social impact that hydrological fen restoration measures may have.

The purpose of this thesis is to enhance insight into the hydrological constraints of, and requirements for, successful fen restoration in regions with an anthropogenically controlled hydrology. The focus is on low-productive fens. This fen type has significant conservation value in many countries because of its high species diversity and the presence of endangered plant species (Moore et al., 1989; Verhoeven and Bobbink, 2001; Wheeler and Shaw, 1991).

1.2 Low-productive fens

Low-productive fens are permanently wet, alkaline, quite infertile ecosystems with a biomass production ranging from 200 to 600 g/m^2 (Moore et al., 1989; Wheeler and Shaw, 1991). Plant species belonging to the alliances *Caricion davallianae* and *Caricion lasiocarpae* are well-adapted to fen habitat conditions and are often abundant in low-productive fens (Wheeler and Proctor, 2000); plant species typical of bogs and some shrubs and trees may also be present. Compared to typical faithful fen plants, these latter species, however, form a minority in fen ecosystems. Only when habitat conditions have been modified for a longer period due, for example, to an altered hydrology associated with a rise in surface level by peat accumulation, will bogs and eventually forests permanently replace low-productive fens. The reversal of this successional change only occurs when external forces (like climate change) reset the abiotic conditions typical of low-productive fens.

Successional change in low-productive fens can occur in three principle directions, distinguished by distinct changes in vegetational composition and abiotic conditions (Wheeler and Proctor, 2000). The first successional direction is characterised by the establishment of bogs, i.e., permanently wet, acidic ecosystems, and is associated with rainwater accumulation (Van Diggelen et al., 1996; Van Wirdum, 1995; Wheeler and Proctor, 2000). The second successional direction is a shift towards more productive fens (covered with grasses, reed, shrubs or forest), and is associated with increased nutrient availability or abandonment of land use (Fojt and Harding, 1995; Moore et al., 1989; Wheeler and Proctor, 2000; Wheeler and Shaw, 1991). Finally, the third successional direction of low-productive fens is characterised by the establishment of litter fens or fen meadows, and is associated with a drop in summer water tables due to increased drainage (Wheeler and Shaw, 1995).

Despite their tendency to change successionally, low-productive fens can persist for several centuries in a natural setting if external forces, like climate, are stable (Grootjans et al., 2006; Succow, 1988; Wassen and Joosten, 1996). Under these conditions, succession of low-productive fens is slowed by the supply of alkaline groundwater (Van Diggelen et al., 1996; Van Wirdum, 1995). The supply of groundwater causes shallow water levels throughout the year, and thus prevents the succession of low-productive fens along the water level gradient (Van Wirdum, 1995). Moreover, the permanent supply of alkaline ions transported by groundwater flow to the fen surface provides a near-neutral pH to fen root zones. This prevents the succession of low-productive fens to acidic bogs (Van Diggelen et al., 1996). Finally, the supply of groundwater and solutes often controls internal nutrient cycling in fens by (1) chemically binding phosphate to calcium or iron (Boomer and Bedford, 2008; Boyer and Wheeler, 1989), and (2) promoting the conversion of nitrate into N_2 gas by means of denitrification under permanently water-saturated conditions (De Mars and Wassen, 1999; Olde Venterink et al., 2002). For these reasons, the permanent supply of groundwater and solutes to fens may also prevent the succession of low-productive fens to more productive fens. As a result of these controls on successional change, species that are typical of late-successional stages (bogs, shrubs and trees) are usually outcompeted soon after their establishment in a fen by the fen plants that are better adapted to minerotrophic ("groundwater-like") conditions. This competition continues until the fen surface has been raised to a certain level due to peat accumulation that rainwater accumulates in the fen soil. From this moment on, bog species become more abundant at the expense of fen plant species, which disappear permanently after a certain time.

1.3 Fen deterioration

In this thesis, fen deterioration is defined as (1) the reduction of an area containing vegetation types typical of low-productive fens and (2) the threat to species that are members of these vegetation types as a result of land reclamation and environmental degradation. Fen deterioration may therefore operate on both a vegetation level and a species level (Fig. 1.1). Both aspects of fen deterioration are discussed below.

1.3.1 Fen deterioration at the vegetation level

Fen deterioration at the vegetation level is an example of successional change resulting in the replacement of vegetation types typical of low-productive fens by more productive vegetation types or by vegetation types that are typical of bogs or forested mires. Evidence exists that low-productive fens in an anthropogenically dominated setting (i.e., managed fens) are more susceptible to successional

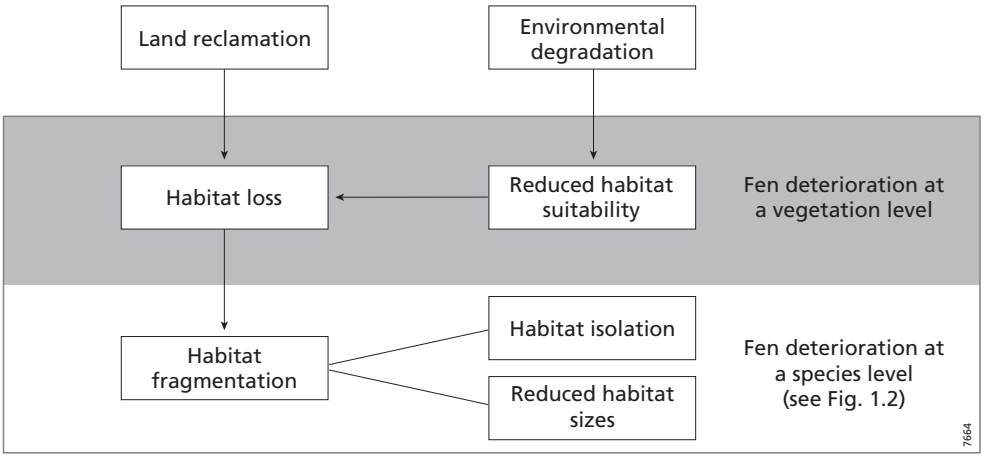

Figure 1.1: The concept of fen deterioration at two levels as defined in this thesis. Land reclamation and environmental degradation have an impact at the vegetation level, whereas habitat fragmentation (due to habitat loss) affects the population viability of species. Note that environmental degradation contributes to habitat loss if habitat conditions have become unsuitable for fen plants.

change than fens in a natural setting (i.e. natural fens). In The Netherlands and the United Kingdom, for example, the persistence of low-productive fens after restoration ranges from a few to several tens of years (Fojt and Harding, 1995; Grootjans et al., 2006; Van Diggelen et al., 1996; Van Wirdum, 1995), while, as noted above, natural fens can exist for centuries. The accelerated successional change of managed fens compared to natural fens is often attributed to environmental degradation, which can be triggered by water management actions that reduce the supply of alkaline groundwater to fen root zones. A reduced supply of groundwater may cause a lowering of the water table. It also enhances the infiltration of surface water and local precipitation into fens. The infiltration of surface water, which in densely populated regions is often contaminated by nutrients and sulphate, is reported to enhance nutrient cycling in fens (Lamers et al., 1998). As a result, abiotic conditions in fens often shift along the productivity gradient (Wassen and Barendregt, 1992). The infiltration of precipitation leaches ions from the fen root zone (Almendinger and Leete, 1998) and causes a shift from anoxic to oxic conditions. The latter is caused (1) by the halted groundwater supply of electron donors and the simultaneously increased supply of electron acceptors via local precipitation (Boomer and Bedford, 2008) and (2) by the aeration of the fen soil as a result of a lowering of the water table (De Mars and Wassen, 1999). Depending on management, these shifts in process directions can trigger succession along the productivity or the acidic gradient, together with succession along the water level gradient (Fojt and Harding, 1995; Mälson et al., 2008; Van Wirdum, 1991; Verhoeven and Bobbink, 2001).

1.3.2 Fen deterioration at the species level

Fen deterioration at the species level refers to an increased risk of local extinction and a reduced probability of the re-establishment of low-productive fen plant species due to habitat loss and fragmentation (Fig. 1.2). Rare fen plant species that are dependent on very limited ranges of abiotic conditions are particularly susceptible to these altered population dynamics (Ewers and Didham, 2005), given the following theoretical considerations.

Habitat loss (consisting of land reclamation and severe environmental degradation) causes a reduced geographical distribution of individuals, which results in a higher vulnerability of remnant populations to environmental and demographical stochasticity (Gaggiotti and Hanski, 2004), and hence an increased risk of local extinction (Fig. 1.2). Moreover, a reduced number of individuals in a population impoverishes the genetic diversity of remnant populations (Hooftman et al., 2004), which may lead to a decreased fitness of individuals in the long term due to genetic drift or inbreeding. As a result, the competitive strength of rare species may weaken compared to that of more common species, which increases the risk of local extinction of the rare species. This effect is further enhanced by habitat fragmentation, i.e., a reduced habitat connectivity and small habitat sizes, if gene flows between remnant populations are reduced (Hooftman et al., 2003; Newman and Tallmon, 2001; see Fig. 1.2).

In addition to the increased risk of local extinction, habitat fragmentation may lead to a reduced success of seed dispersal via wind (Soons et al., 2005), water (Soomers et al., 2009), animal migration (Soons et al., 2008) and management activities (Klimkowska et al., 2007), hence delaying the re-establishment of rare species in abandoned habitat patches. Furthermore, edge effect on small habitat patches may become significant, because the increased nutrient input from surrounding agricultural fields, for example, (Saunders et al., 1991) makes the edges of the habitat patches less suitable for fen plants. This

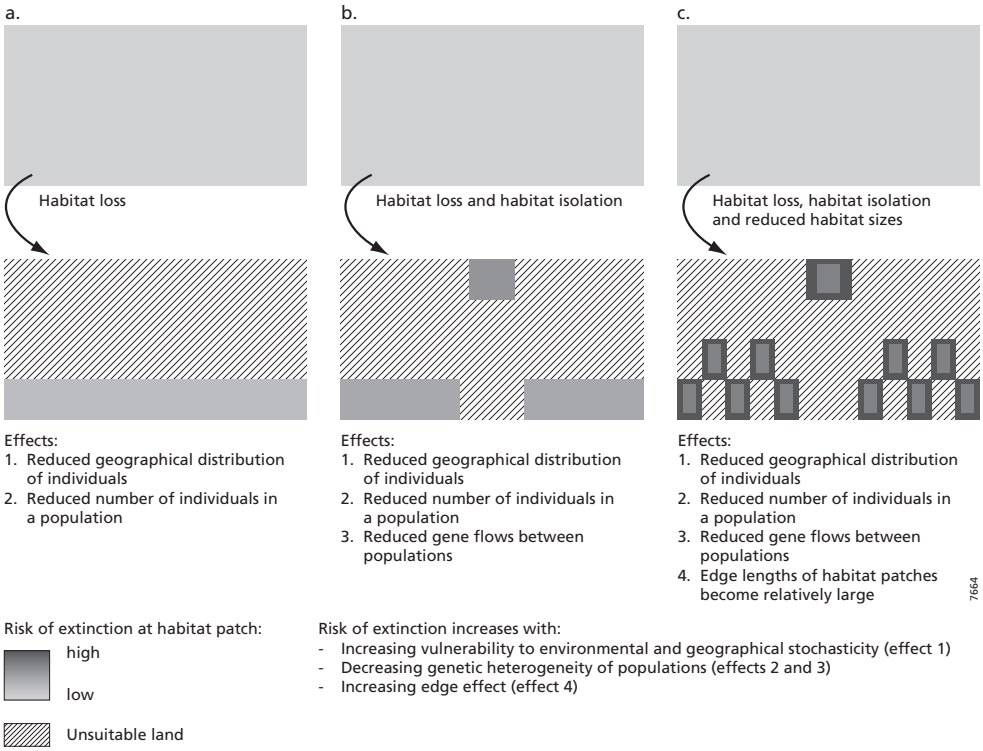

Figure 1.2: Conceptual relationship between habitat loss and extinction risk of fen plant species for different degrees of habitat fragmentation. The degree of habitat fragmentation increases from a through c, while the total amount of habitat loss is the same for a, b and c.

further reduces the success of seed dispersal, while imposing a higher risk of local extinction on fen plant species that are dependent on very limited ranges in abiotic conditions (Bender et al., 1998; Ewers and Didham, 2005; Fig. 1.2).

1.4 Problem definition, objectives and research questions

Keeping the above-mentioned causes of fen deterioration in mind, the sustainable conservation of low-productive fen plant populations in anthropogenically dominated regions requires the restoration of habitat conditions suitable for low-productive fen plants in such a configuration that both habitat loss and fragmentation are counteracted. Vegetation types typical of low-productive fens can then become more abundant, while the probability that these species can re-establish themselves at successfully restored sites is increased. Given the hydrological controls on successional change, the combination of these requirements for successful fen restoration implies that vast areas receive alkaline groundwater in the root zone, as observed in natural fens. However, currently utilized hydrological fen restoration projects have reported variable success in rewetting managed fens with groundwater (Jansen et al., 2004; Jansen et al., 2000; Kemmers et al., 2003; Lamers et al., 2002; Van der Hoek and Sykora, 2006). A possible cause of this limited restoration success is that the underlying strategies were based on a biased perception of the hydrological mechanisms behind fen deterioration due to an incomplete knowledge of groundwater flow under natural conditions. For example, Wassen et al. (1996) used a geographical reference area to study anthropogenic hydrological interferences of an intensively managed fen. Yet, conclusions based on studies of geographical reference areas are rather speculative because geo-hydrological or climatic conditions may differ between reference and managed areas (Wassen, 2005). Schot and Molenaar (1992) used models to obtain site-specific hydrological reference data of an intensively managed fen in order to study the long-term changes in groundwater flow towards fens. Their models, however, only provided qualitative results and lacked a thoroughly underpinned reconstruction of past geo-hydrological conditions. Succow and Joosten (2001) studied anthropogenically induced hydrological changes in managed fens by analysing the botanical composition of peat cores. This method, however, only provided a qualitative proxy of past hydrological conditions and its applicability to intensively managed fens is limited as most of the peat had already been excavated or oxidized from these fens. Note that a general limitation of the existing hydrological reference data is that the information has most often been obtained during transect studies, whereas groundwater flow is typically a three-dimensional phenomenon. In order to overcome these methodological limitations, a quantitative, spatially explicit and site-specific approach is needed to analyse the effects of anthropogenic hydrological interferences with groundwater flow.

The objective of this thesis is to enhance insight into the hydrological requirements of successful fen restoration in regions with an anthropogenically controlled hydrology. These requirements consist of effective measures, including their spatial planning, to reverse fen deterioration by creating opportunities to regenerate low-productive fens and restore habitat configurations that support the re-establishment of fen plant species by natural dispersal. Both site-specific, quantitative reference data and geographical reference data were collected from an intensively managed fen in The Netherlands in order to determine these requirements and to answer the following research questions:

1. Which hydrological mechanisms underlie the groundwater supply of persistent fens in a natural setting?

2. How do individual anthropogenic hydrological interferences affect the groundwater supply of fens and consequently contribute to fen deterioration?

3. How can currently utilized hydrological fen restoration strategies be improved in order to preserve fen plant populations for the future?

1.5 Hydrological mechanisms behind fen deterioration: state of the art

In order to effectively answer the research questions raised in Section 1.4, a literature search was conducted regarding (1) mechanisms that may underlie the groundwater supply of persistent fens (research question 1), and (2) anthropogenic hydrological interferences that may have caused fen deterioration (research question 2). The results of this review are outlined below. In Chapters 2, 3 and 4, new data is presented with regard to these research questions and the implications for hydrological fen restoration are discussed (research question 3). Research question 3 is answered more explicitly in Chapter 5 by analysing the effectiveness of a number of hydrological fen restoration strategies.

1.5.1 Mechanisms behind the groundwater supply of persistent fens

Two conceptual models of groundwater flow in persistent fens in a natural setting have been described that may support the existence of vast areas of groundwater supply: the exfiltration model and the throughflow model (Fig. 1.3).

The exfiltration model assumes an upward transport of groundwater on a landscape scale, which leads to regional groundwater exfiltration at the fen surface (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006). Local precipitation is either discharged by surface runoff or stored in the fen soil, while it mixes with exfiltrating groundwater. In this model, lateral flow is limited to the local scale (Drexler et al., 1999) and fen plants are confined to the exfiltration zones. Two variants of the exfiltration model have been proposed in literature. The first variant assumes that permanent groundwater exfiltration is essential to maintain shallow groundwater levels and permanently alkaline conditions in the fen root zone (Almendinger and Leete, 1998; Komor, 1994). These conditions may prevail in regions where (semi-confined) aquifers gradually lose groundwater due to hydrostatic pressure exerted by the mounding water table in the adjacent uplands. The second variant assumes that fen plants can persist at sites that only periodically receive exfiltrating groundwater (Fraser et al.. 2001; Glaser et al., 1990; McNamara et al., 1992), if locally infiltrated precipitation is sufficiently mixed with deep alkaline groundwater to provide minerotrophic conditions in the fen root zone. This mixing process can be driven by the upward transport of groundwater to compensate for groundwater losses by intense evapotranspiration during the growing season, and it may be relevant in vast fen areas that are distant from recharge areas. As a result, vast patches of fen habitat can be sustained even at sites that receive most of their water from local precipitation instead of from exfiltrated groundwater.

The throughflow (i.e., durchströming cf. Succow, 1988) model assumes that groundwater exfiltrates at the upstream margins of fens, and that the high exfiltration rates cause a surplus of groundwater in the shallow subsurface, which is then discharged by lateral flow through the loosely structured root zone, i.e. throughflow (Schipper et al., 2007; Succow, 1988; Wassen and Joosten, 1996). In this model, throughflow redistributes exfiltrated groundwater mixed with local precipitation through the fen root zone on a regional scale, hence preventing rainwater accumulation in the soil profile. As a result,

throughflow may provide abiotic conditions suited for fen plants outside the exfiltration zones. Note that throughflow can also prevail in the absence of groundwater discharge, but only if the precipitation surplus is sufficiently high to cause a water surplus in the shallow subsurface that is not drained by creeks or rivers. These latter conditions do not lead to the establishment of minerotrophic fens, but rather to the establishment of ombrotrophic bogs (Succow and Joosten, 2001).

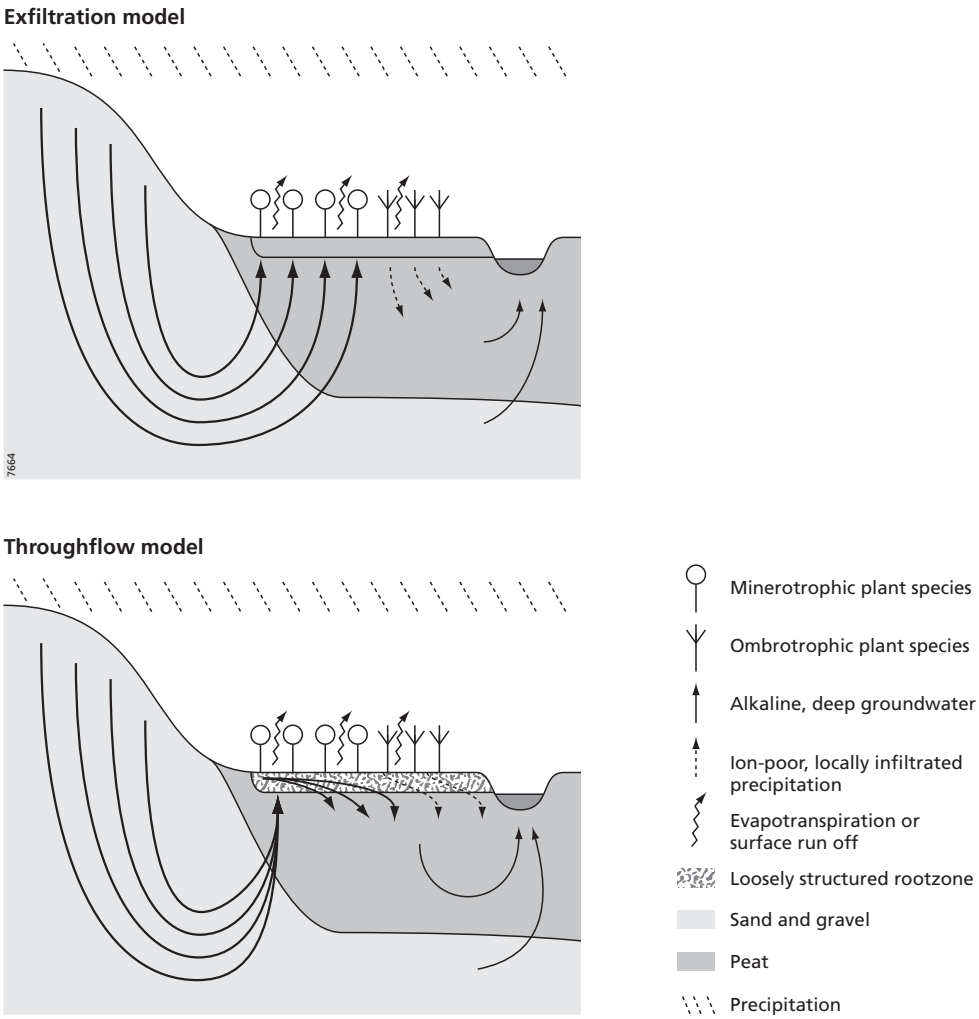

Figure 1.3: Two conceptual models of groundwater flow in natural fens: the exfiltration model and the throughflow model. The exfiltration model assumes groundwater exfiltration on a regional scale as a result of permanent or periodic upward groundwater flow (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006). The throughflow model assumes intense groundwater exfiltration at the upstream fen margins, causing a surplus of groundwater in the shallow subsurface that is discharged by lateral flow through the loosely structured root zone, i.e., throughflow (Schipper et al., 2007; Succow, 1988; Wassen and Joosten, 1996).

1.5.2 Anthropogenic hydrological interferences that may lead to fen deterioration

Anthropogenic hydrological interferences that may lead to fen deterioration consist of (1) water management actions that reduce the volume of groundwater discharge into fens, (2) the establishment of systems of polders with distinctly different surface elevations and individually controlled surface water levels, which affects the regional configuration of groundwater discharge patterns and (3) drainage networks that diffusively intercept exfiltrating groundwater that is otherwise supplied to the fen root zone. Each of these anthropogenic hydrological interferences can lead to a reduction in area size and a fragmented configuration of suitable fen habitat, and thus may contribute to fen deterioration. These anthropogenic effects are discussed below in more detail.

Numerous authors (e.g., Almendinger and Leete, 1998; Fojt, 1994; Schot et al., 1988; Witmer, 1989) have demonstrated that fen deterioration may be caused by a reduced volume of groundwater being discharged into low-productive fens. A reduction in the volume of groundwater discharge may result

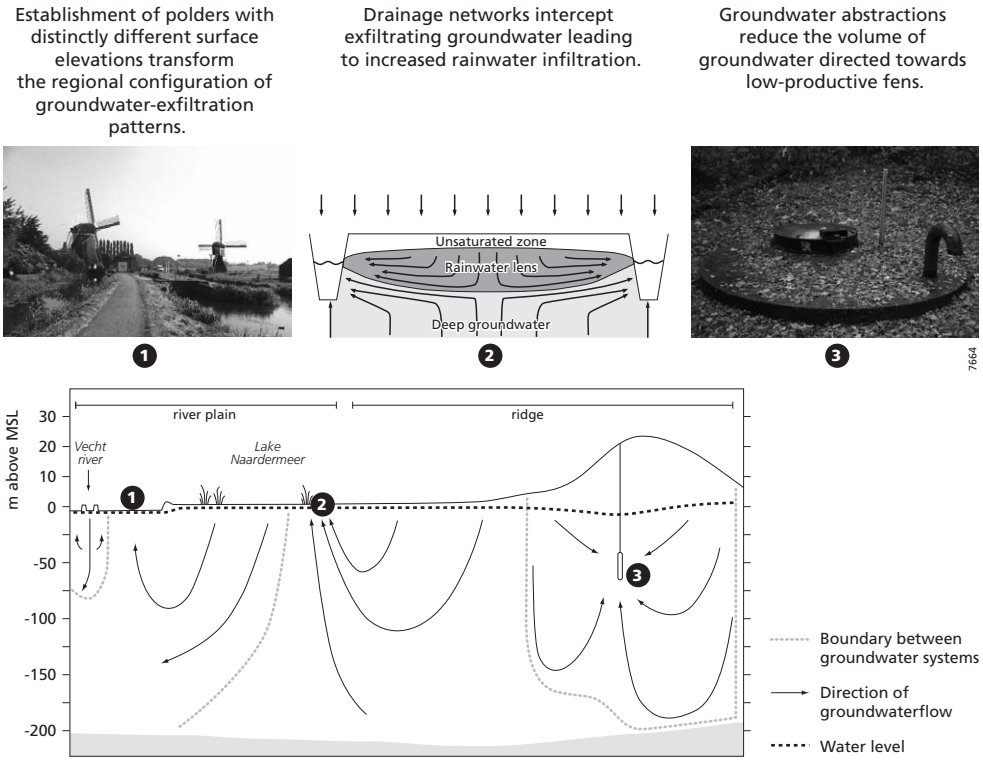

Figure 1.4: Impact of anthropogenic hydrological interferences on the groundwater supply of low-productive fens (modified from Schot and Van der Wal, 1992; Schot et al., 2004). These interferences include (1) the establishment of systems of polders with distinctly different surface elevations and individually controlled surface water levels, which affect the regional configuration of groundwater discharge patterns, (2) drainage networks that diffusively intercept exfiltrating groundwater that is otherwise supplied to the fen root zone and (3) water management actions, like groundwater abstractions, that reduce the volume of groundwater discharge into fens.

from the redirection of groundwater flow towards abstraction wells or deep agricultural polders, or from a reduced groundwater recharge in the source area due to an anthropogenic change in land cover (Fig. 1.4). As a result, parts of the managed fens that were supplied by exfiltrating groundwater under natural conditions can have become dominated by rain water infiltration and thus be less suitable for fen plants.

The establishment of systems of polders with distinctly different surface elevations has transformed the configuration of groundwater exfiltration patterns by interfering with regional groundwater flow patterns. As a result, large groundwater exfiltration zones may be transformed into fragmented groundwater exfiltration zones associated with nested groundwater systems (Fig. 1.4). These nested groundwater systems developed with the degradation of the surface morphology (Schot and Molenaar, 1992; Wassen et al., 1996) and the management of surface water levels in polders. Regions where groundwater exfiltration is interrupted, i.e., the newly established recharge zones, have become entirely supplied by local precipitation and are unsuitable for fen plants as a result. This may reduce the area in which fen plants can grow.

Finally, drainage networks may cause fen deterioration as they are thought to intercept and discharge exfiltrating groundwater from fens that otherwise would have entered the fen root zone (Grootjans et al., 1988; Schot et al., 2004; Wassen et al., 1990, Fig. 1.4). As a result, the infiltration of local precipitation into drained fens is enhanced, which leads to the development of rain water lenses, i.e., parcel-scale groundwater systems. This causes drained fens to be supplied by local precipitation, irrespective of whether or not they are situated in groundwater discharge areas, and hence reduces the area potentially suitable for fen plants.

1.6 Methodology and thesis outline

1.6.1 Study area

The research questions raised in Section 1.4 were studied using the Gooi- and Vechtstreek district (The Netherlands) as the study area. This geographic region was selected, because (1) many endangered fen plant species still grow there as remnant populations of naturally occurring populations, thus making the area's conservation of international importance, (2) intense water management currently limits the availability of groundwater to low-productive fens and thus largely determines the potential for successful fen restoration (Schot et al., 1988; Wassen et al., 1990), and (3) the long history of water management in the area is well-documented and sufficient scientific knowledge and information are available to collect site-specific hydrological reference data. Further details on the study area are provided in the individual chapters of this thesis.

1.6.2 Methodological framework and thesis outline

The methodological framework used to find the answers to the research questions posed in Section 1.4 comprises four case studies, each considering a different range of anthropogenic hydrological interference (Fig. 1.5). The core of the methodological framework consists of a palaeo-hydrological reconstruction of the Gooi- and Vechtstreek area (Chapter 2). The purpose of this reconstruction is to analyse the evolution of groundwater systems driven by natural and anthropogenic developments, thus providing site-specific insight into the hydrological mechanisms behind fen deterioration (research questions 1 and 2). Then, the hydrological mechanisms behind the supply of groundwater to natural

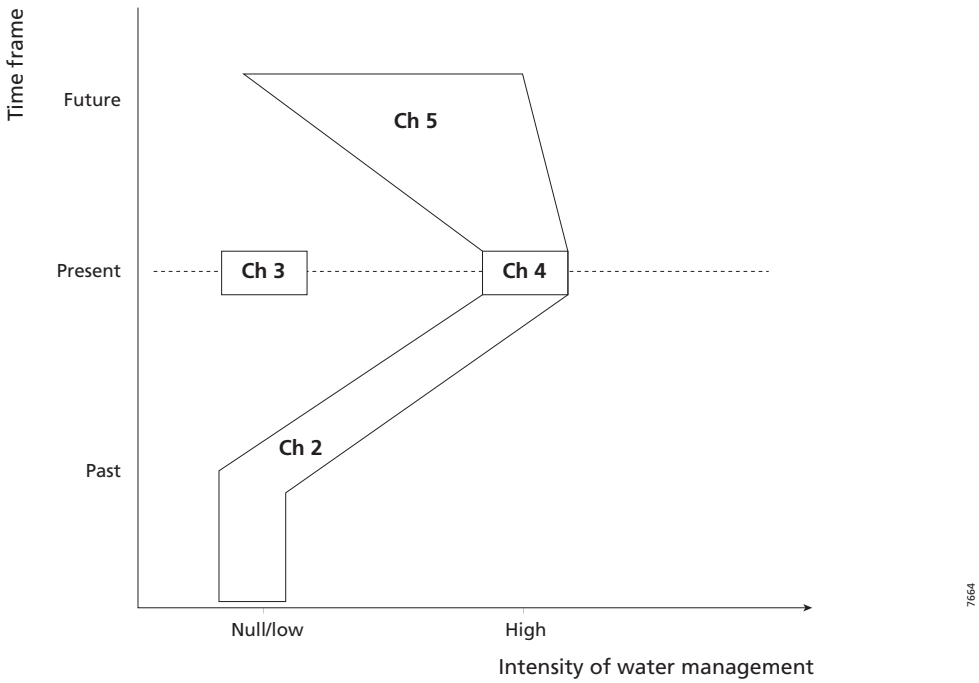

Figure 1.5: Scope of the chapters in this thesis with respect to time frame and intensity of water management.

fens (research question 1) are explained in more detail using empirical data and models (Chapter 3). For this purpose, the near-natural Biebrza River valley (Poland) is used as a geographical reference of intensively managed fens. The main focus of this chapter is to test whether exfiltrated groundwater is likely to be laterally redistributed through natural fen root zones by throughflow, hence providing abiotic conditions suitable for fen plants outside the exfiltration zones. The impact of water management actions (particularly drainage) on the hydrological mechanisms behind the supply of groundwater to fens (research question 2) is then examined in more detail in Chapter 4. For this purpose, groundwater flow in a poorly drained fen and in an anthropogenically drained fen is studied at a parcel scale using groundwater models and empirical data. The main focus of this chapter is to analyse to what extent anthropogenic drainage networks interfere with natural hydrological processes, because drainage networks are thought to increase rainwater infiltration at a landscape level. Chapter 5 aims to translate the findings of Chapters 2-4 into recommendations for hydrological fen restoration (research question 3). To do this, a habitat suitability model is linked with a seed dispersal model to analyse the effectiveness of a number of restoration strategies on the regeneration of fen habitat configurations that support the re-establishment of target species by natural seed dispersal. Finally, in Chapter 6, answers to the research questions raised in Section 1.4 are formulated using the results of the Chapters 2 through 5 and suggestions for future research are provided.

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2 Palaeo-hydrological reconstruction of a managed fen area in The Netherlands

A.H. van Loon, P.P. Schot, J. Griffioen, M.F.P. Bierkens and M.J. Wassen, 2009. Palaeo-hydrological reconstruction of a managed fen area in The Netherlands, Journal of Hydrology, 378, 205-217 (with appendix).

Abstract
Knowledge of the anthropogenic impact on the hydrology of low-productive fens that are subject to environmental degradation is essential to improve currently utilized hydrological fen restoration strategies. We analyse the naturally and anthropogenically driven evolution of groundwater systems in an intensively managed fen area in The Netherlands using a series of three-dimensional palaeo-groundwater models at a high spatial and temporal resolution. These palaeo-models are representative for five time slices of the time-frame 0 to 2000 AD (Anno Domini), which are defined according to the timing of the natural and anthropogenic developments that had major impacts on the groundwater system configuration. For each time slice, palaeo-geo-hydrological conditions are reconstructed, which allowed for the calculation of groundwater discharge patterns, water balances and groundwater flow patterns.

Contrary to former studies on the evolution of groundwater systems, our palaeo-hydrological reconstruction indicates that current groundwater discharge flux into managed fens may exceed the late-natural groundwater discharge flux. The increased groundwater discharge flux relates to the development of additional groundwater systems in the river valley with the establishment of polders since 1350 AD. Notably, more recent redirections of groundwater flow due to the reclamation of lakes and the establishment of abstractions wells, as well as the decreased groundwater recharge by anthropogenic land cover change, reduced the groundwater discharge flux only to a minor extent. This finding opposes the hypothesis that a decreased groundwater flux to fens underlies the environmental degradation of fens in intensively managed regions. The palaeo-hydrological reconstruction provides evidence that it is mainly the changes in the spatial configuration and the shift in the predominant groundwater discharge mechanism that underlies the environmental degradation of managed low-productive fens. We discuss the consequences of these hydrological changes for the suitability and availability of fen habitat sites.

2.1 Introduction

Many fen plant species have become endangered due to worldwide land reclamation and environmental degradation of fens (Millennium Ecosystem Assessment, 2005). Environmental degradation of fens consists of acidification, eutrophication and desiccation. These processes are often induced by anthropogenic interferences with the regional hydrology of fens (Lamers et al., 2002). Counteraction of these interferences by active water management aims at sustainable conservation of the remaining populations of endangered fen plant species and the re-establishment of fen plants in areas where they have disappeared. However, hydrological restoration strategies have not been particularly effective so far, possibly due to insufficient knowledge of the human impact on the hydrology of managed fens. The present study aims at enhancing insight into the long-term hydrological changes of a managed fen area in The Netherlands.

Most endangered fen plants are typically found in nutrient-poor fens, which have a low biomass production (Wheeler and Shaw, 1991). These so-called low-productive fens develop at minerotrophic, acid-buffered and moderately nutrient-rich sites (Bedford et al., 1999; Sjörs and Gunnarsson, 2002). These sites are usually associated with areas of groundwater discharge for two reasons. Firstly, areas of groundwater discharge receive excessive amounts of water, i.e., groundwater and precipitation, which results in shallow groundwater tables and reduced conditions in the shallow subsurface (Boomer and

Bedford, 2008; De Mars and Wassen, 1999). Secondly, weathering products dissolved during flow are transported with the groundwater to the fen surface. Both reduced conditions and the presence of weathering products in the shallow subsurface, are essential for buffering the acidity at a near-neutral pH level (Almendinger and Leete, 1998) and limiting nutrient availability for plant growth (Boyer and Wheeler, 1989; Olde Venterink et al., 2002).

Many of the processes underlying the environmental degradation of low-productive fens are reinforced or induced by a decrease of the groundwater supply of fens (Barendregt et al., 1995; Fojt and Harding, 1995; Lamers et al., 2002). A decrease of the groundwater supply of fens may cause desiccation if the consequent water deficits are not counterbalanced by an increased supply of precipitation (Schot et al., 2004) or surface water (Van Wirdum, 1991). However, these shifts in the origin of water supply affect the biogeochemical processes determining the acidity and nutrient availability in fens (Almendinger and Leete, 1998) and may cause acidification or eutrophication of fens (Beltman et al., 2000; Smolders et al., 2006). Therefore, the restoration of groundwater flow to low-productive fens is thought to be a prerequisite for the preservation of threatened fen plant species in intensively managed areas (Fojt and Harding, 1995; Wassen et al., 1990).

The design of effective hydrological fen restoration strategies requires insight into the causal relation between water management and the evolution of groundwater systems. Numerous studies have been performed on the evolution of groundwater systems in the past by analysing (Lamentowicz et al., 2007) or reconstructing (Pons and Oosten, 1974) botanical peat deposits, performing groundwater model exercises (Schot and Molenaar, 1992) and comparing intensively managed areas with near-natural areas (Wassen et al., 1996). These studies suggest that the groundwater supply of managed fens decreased with anthropogenic developments. However, none of these studies provided a quantitative analysis on the evolution of groundwater systems driven by natural and anthropogenic developments. Obtaining this lacking knowledge may enhance insight into the anthropogenic impacts on the hydrological key-processes that underlie the environmental degradation of low-productive fens in intensively managed regions like The Netherlands.

In this chapter, we analyse the naturally and anthropogenically driven evolution of groundwater systems that discharge into an intensively managed fen in The Netherlands using a series of three-dimensional palaeo-groundwater models at a high spatial and temporal resolution. These palaeo-groundwater models are based on a thoroughly underpinned and complete reconstruction of geo-hydrological conditions in the past. The purpose of this model exercise is to analyse past shifts in the groundwater supply of fens and to disentangle the effects of subsequent natural and anthropogenic developments on the groundwater supply of fens.

2.2 Study area and its historical development

The palaeo-hydrological reconstruction was performed for the Gooi- and Vechtstreek area in The Netherlands (52°03`N – 52°20`N and 5°00`E – 5°18`E; Fig. 2.1). The study area was selected because (1) sufficient geo-scientific knowledge and data is available to perform a reconstruction of past geo-hydrological conditions on a high spatial resolution and (2) human domination of the current hydrology of the studied fen area is large, due to a series of hydrological changes that have occurred in the past.

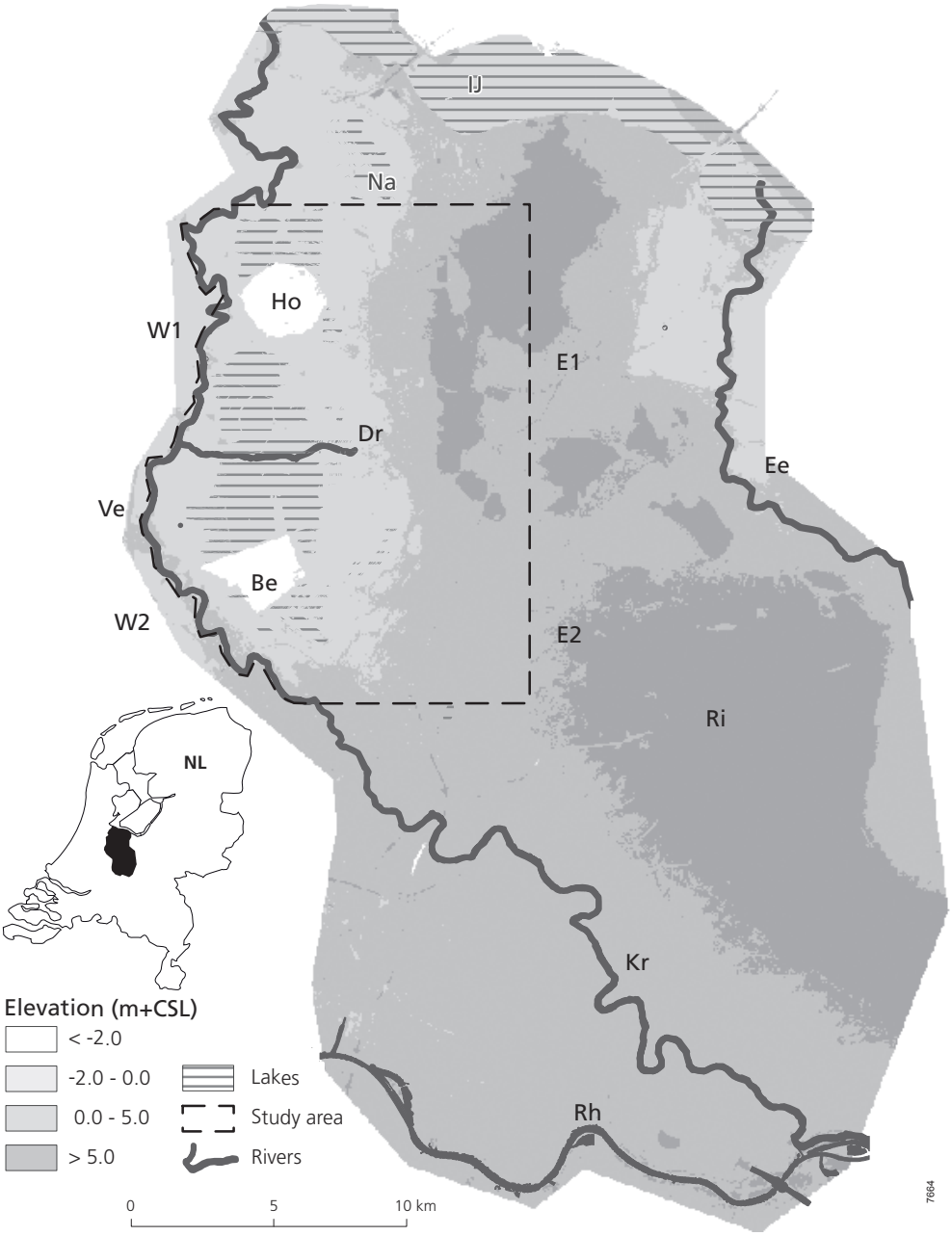


Figure 2.1: Gooi- and Vechtstreek area (The Netherlands) with major topographical features. Elevation denotes current ground surface elevation (m + CSL). Two transects that were studied in more detail are signified by E1 and W1 and E2 and W2. Other abbreviations refer to: IJ – Lake IJsselmeer, formerly known as inland Sea Zuyderzee and Lake Flevo; Na – Lake Naardermeer; Ho – Polder Horstermeer; Dr – peat creek Drecht; Ve – River Vecht, Be – Polder Bethune; Kr – River Kromme Rhine; Rh – River Rhine; Ri – Ice-pushed ridge and Ee – River Eem.

The naturally and anthropogenically driven landscape-hydrological developments of the Gooi- and Vechtstreek area since 0 AD are listed in Table 2.1.

The eastern border of the study area is the ice-pushed ridge Het Gooi. This ridge consists of elongated hills of sandy fluvial deposits pushed-up by glaciers during the Saalien glaciation. In the west, the study area is bordered by the River Vecht, which discharges into Lake IJsselmeer situated north of the study area. Surface elevations of the ice-pushed ridge vary between 0 and 30 m + CSL (Current Sea Level) and surface elevations of the river valley vary between – 5 and 0 m + CSL. Due to this difference in surface elevation, regional groundwater flow is directed from the ice-pushed ridge to the river valley (Schot, 1989; Witmer, 1989).

The river valley harbours many fen reserves, which are remnants of extended groundwater-fed fens that developed under natural conditions before 800 AD (Borger, 1992; Pons and Oosten, 1974; Wassen et al., 1996). Due to land reclamation and peat excavation, the majority of these extended fens have been transformed into agricultural fields or turf ponds. Turf ponds originally had a size of a few hectares,

Table 2.1: Natural and anthropogenic developments affecting the hydrology of the Gooi- and Vechtstreek area, The Netherlands.

Year (AD)	Natural and anthropogenic developments	Ref
< 0	Peat accumulation, Holocene sea transgression	1, 2
0-650	River Vecht partly silted up	3,4
650-850	Peat accumulation in the lakes along River Vecht	5
700-750	First inhabitants migrated into Vecht River valley	6,7
800-850	Peat accumulation stagnated due to local reclamation activities	7
1000	Inland Lake Flevomeer transformed into inland Sea Zuyderzee; peat and ice-pushed ridge were partly eroded	8,2
1100-1150	Systematic reclamation of Vecht River valley was initiated	7,8
1122	River Rhine was forced into its current channel by damming of River Kromme Rhine	9
1300-1400	Diking of River Vecht and inland sea Zuyderzee	8
1400-1500	First windmill was introduced and extended turf ponds developed due to peat excavation and wind erosion	6,7
1400-1900	Heather lands and bare soils developed on the ice-pushed ridge	7,10
1437	First dam construction in River Vecht	11
1500-1550	Initiation of dredging of peat from turf ponds	7
1629-1854	Attempts to reclaim Lake Naardermeer	12
1674-1823	Sand excavations at ice-pushed ridge	5,10
1878-1885	Development of the deep agricultural polders Horstermeer and Bethune	12,13
1888	Initiation groundwater abstraction from ridge	14
1900-1950	Planting of pine plantations and expanding urban areas on ice-pushed ridge	13
1932	Inland sea Zuyderzee was transformed into Lake IJsselmeer	
1968	Reclamation of Lake IJsselmeer: polder Flevoland developed	
1970-1980	Peat excavation ends	15
> 1990	Hydrological restoration measures	

References: [1] Van der Plassche et al. (2005), [2] Zagwijn (1986), [3] Weerts (2002), [4] Bos et al. (2009), [5] Van der Linde (1954), [6] Lagers and Strating (1998), [7] Borger (1992), [8] Bakker et al. (1976), [9] Berendsen and Stouthamer (2000), [10] Knol et al. (2004), [11] Haartsen and Ten Oever-Van Dijk (2000), [12] Van Zinderen Bakker (1942), [13] Anonymous (1990), [14] Witmer (1989), [15] Haartsen and Brand (2005).

but uncut peat baulks were eroded by wind, leading to the development of large lakes since 1400 AD (Borger, 1992). One of these lakes and a natural lake, have been reclaimed in the 1880s. These reclaimed lakes are currently known as the deep agricultural polders Bethune and Horstermeer. Both polders, i.e., water management districts, drain large amounts of groundwater and surface water from the river valley. During the long history of water management, the river valley has gradually transformed into a polder system with intensively controlled groundwater levels.

Land cover at the ice-pushed ridge transformed from natural oak-beech forests (Zagwijn, 1986) into urban areas, heather lands and pine forests. In addition, numerous abstraction wells currently withdraw up to 15 million m^3 groundwater per year for drinking water production. Both land cover change and groundwater abstractions are thought to contribute to the reduced groundwater supply of the fens in the river valley.

Groundwater flows through unconsolidated aquifers composed of fluvial deposits that vary in texture from fine to coarse sand (Van de Meene et al., 1988). The ice-pushed ridge consists of coarse sand intercalated with sloping clay sheets in the east. The hydrological base of the aquifers is formed by early Pleistocene clays of marine origin at -150 to -250 m + CSL. The aquifers are separated by discontinuous resistance layers consisting of fluvial clay (Fig. 2.8). In the Vecht river valley, a semi-confining peat layer is present (Fig. 2.8). This peat layer accumulated in response to groundwater level rise by Holocene sea transgression and gradually expanded in the direction of the ice-pushed ridge. Near the River Vecht, the peat layer is intercalated by fluvial clay and sand, which were deposited into the flood plain of the River Vecht until 650 AD (Bos et al., 2009). Peat excavation and peat mineralization associated with drainage have reduced the thickness and spatial extent of this semi-confining peat layer since 1100 – 1150 AD (Borger, 1992).

2.3 Palaeo-hydrological modelling

2.3.1 General

Five time slices were defined according to the timing of natural and anthropogenic developments that were expected to underlie the major transformations of the groundwater system configuration in the past (Fig. 2.2). From a comparison of these five time slices, insight into the evolution of the groundwater systems in response to natural and anthropogenic developments was deduced.

For each time slice, groundwater flow was simulated with a stationary groundwater model based on the MODFLOW-code (McDonald and Harbaugh, 1988). Initially a groundwater model for the most recent time slice was constructed and calibrated using annual mean heads observed in 659 observation wells (Fig. 2.3, page 33). The calibrated parameters were groundwater recharge, transmissivities and hydraulic conductivities of surface waters. After calibration, the difference between modelled and mean observed heads was less than 0.2 m for 47 % of the reference cells and less than 0.5 m for 75 % of the reference cells (Table 2.2). Deviations between modelled and observed heads that exceeded 0.5 m relate either to the presence of abstraction wells, or to heterogeneous clay sheets in the eastern part of the ice-pushed ridge (Fig. 2.3).

Groundwater models for the past time slices on the other hand, were constructed by transformation of the calibrated groundwater model for the most recent time slice. For this purpose, we considered

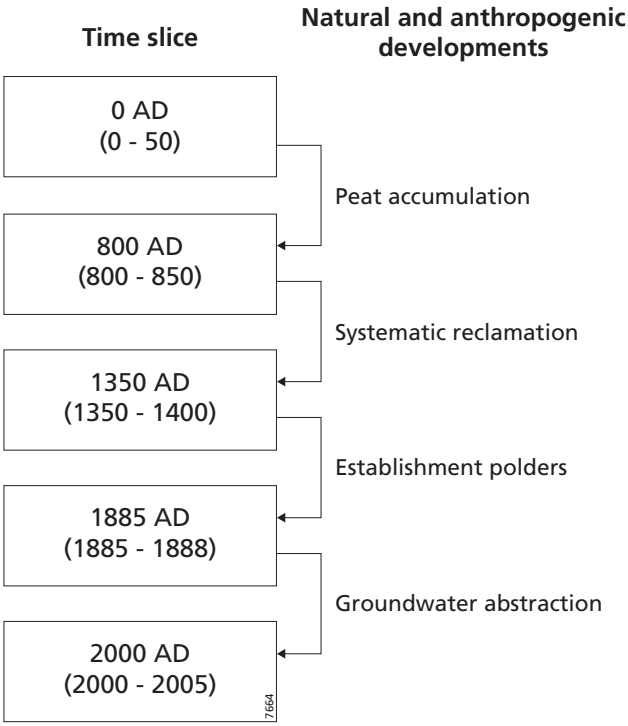


Figure 2.2: Time slices and natural and anthropogenic developments characterising major states in groundwater system configuration for the Gooi- and Vechtstreek area, The Netherlands.

Table 2.2: Performance of the calibrated groundwater model of the Gooi- and Vechtstreek area, The Netherlands, for the most recent time slice. *dH* refers to the difference between modelled and mean observed heads.

Model layer	*n*	**|*dH*|< 0.2 m (%)**	**|*dH*|< 0.5 m (%)**	R^2
1	86	66	91	0.96
2	394	51	76	0.91
3	60	33	68	0.90
4	72	28	68	0.93
5	30	37	73	0.95
6	17	18	47	0.91
All	659	47	75	0.91

geo-hydrological properties either as permanent or transient. Permanent properties were the hydraulic properties of pre-Holocene geological deposits, i.e., the properties of all geological deposits except for the semi-confining peat layer. Corresponding transmissivities and hydraulic resistances were derived from a national geological database (Vernes et al., 2005) and anisotropy factors for the ice-pushed ridge were derived from Gehrels (1995). Transient properties were groundwater recharge, drainage intensity, surface water level, ground surface elevation, hydraulic properties of the semi-confining layer and groundwater abstractions. Transient geo-hydrological properties for the past time slices

were established by reconstruction if quantitative data was not available. This reconstruction was preferentially performed by transforming model parameters in inverse chronological order, starting with the most recent time slice. For example, trends in hydraulic properties of the semi-confining layer due to excavation and oxidation of peat were determined by increasing the current thickness of peat layers. However, if the transformation of model parameters in inverse chronological order was not possible, then transient geo-hydrological properties were reconstructed from knowledge provided in literature as outlined in the following sections. In order to test the robustness of the models for the past time slices against uncertainty in palaeo-geo-hydrological conditions, we performed a sensitivity analysis of (1) hydroclimatic variability, (2) hydraulic resistance of the semi-confining peat layer and (3) palaeo-geographical conditions of the river valley for time slice 800 AD.

All groundwater models were based on a common conceptual model that consists of:

- Six confined layers represented by transmissivities, hydraulic resistances and anisotropy factors.
- The Recharge-package, for modelling groundwater recharge with a spatially variable flux into the upper model layer.
- The Drain-package, for modelling topographic control of groundwater tables by overland flow.
- The River-package, for modelling groundwater-surface water interactions. Drainage was allowed for all surface waters, whereas infiltration was restricted to surface waters in polders with intensively controlled water levels.
- The Well-package, for modelling groundwater abstraction from wells with a spatially variable flux.
- No-flow conditions defined for the southern model boundary by the River Rhine, the western model boundary by the River Vecht and the northern model boundary by Lake IJsselmeer (Fig. 2.1). The eastern model boundary was defined at a sufficient distance from the ice-pushed ridge so that a negligible influence on the groundwater flow from the ice-pushed ridge to the river valley was exerted.

The model was constructed on a 50 by 50 m grid and covered an area of 32.2 by 45.6 km counting 2.3 $\times 10^6$ model cells.

For each time slice, flow paths were mapped by means of a particle tracking analysis based on the MODPATH-code (Pollock, 1994), in order to identify trends in the position of the recharge area of the fen. The porosity was set at 0.32 (-) for all model layers and particles were intercepted from sink cells that discharged at least 90 % of the groundwater flux into the cell.

2.3.2 Groundwater recharge

The MODFLOW Recharge-package assigns a user-defined flux into the upper model layer for modelling groundwater recharge. Groundwater recharge was set equal to the precipitation surplus, which was calculated with interception factors, f_i (-) and crop factors, f_M (-), according to:

$$R = (1 - f_i) \cdot P - f_M \cdot E_M \qquad \text{(Eq. 1)}$$

where R denotes the precipitation surplus (m/d), P the precipitation (m/d) and E_M the Makkink reference evapotranspiration (m/d) (Winter et al., 1995). Crop factors and interception factors were derived from Gehrels (1995) and Spieksma et al. (1995). Groundwater recharge of each land cover unit was calculated using the average precipitation and reference evapotranspiration for the period 2000 – 2005 (Table 2.3). Although decadal precipitation in Europe may have varied up to 20 % since 1500 AD (Pauling

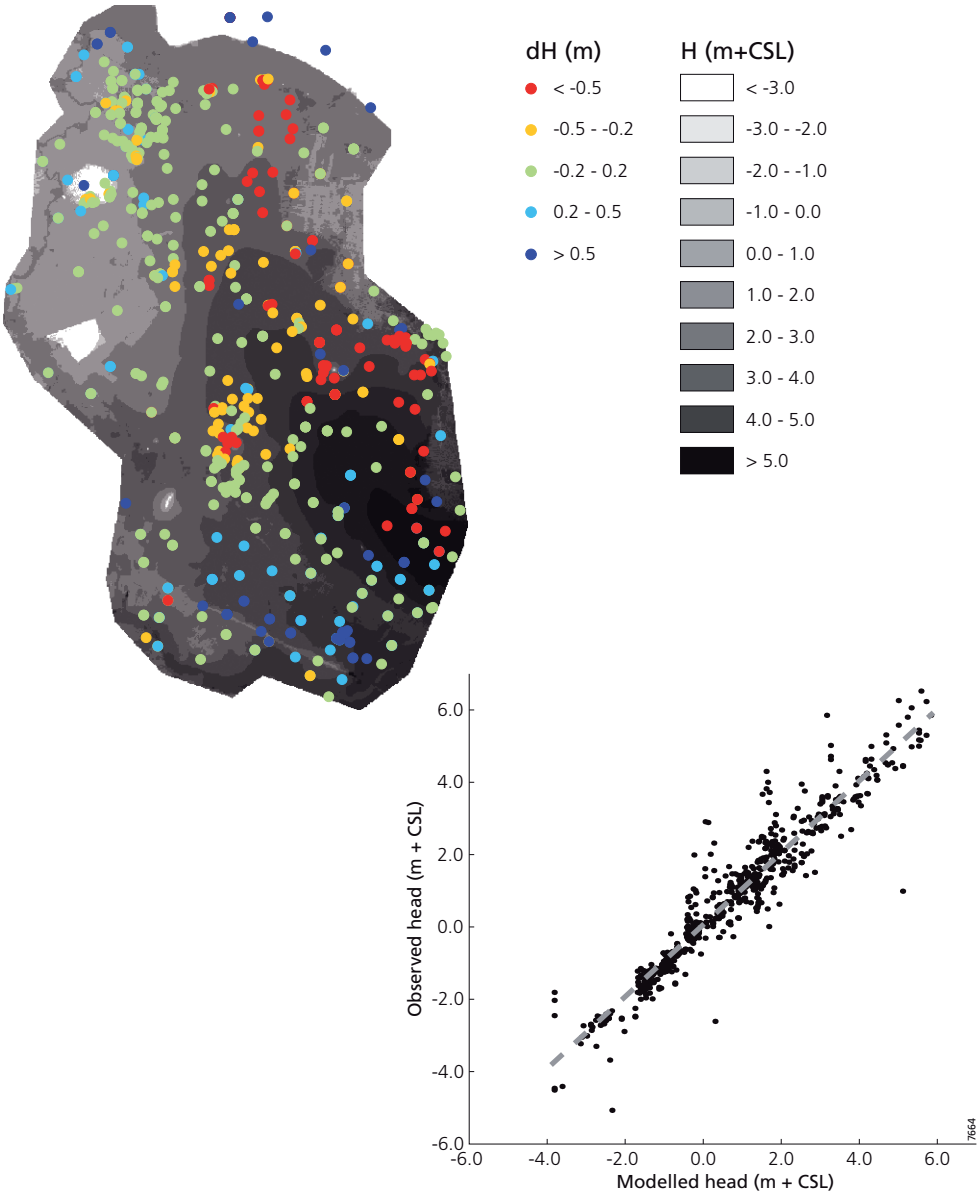


Figure 2.3: Performance of the calibrated groundwater model of the Gooi- and Vechtstreek area, The Netherlands, for the most recent time slice. (a) Differences between modelled heads and mean observed heads (dH = modelled head – observed head) plotted on top of modelled hydraulic heads (H) in the upper model layer; (b) Modelled vs. mean observed heads.

et al., 2006), we considered precipitation as permanent for all time slices, because no quantitative or proxy data of precipitation variability in The Netherlands was available. Reference evapotranspiration was also considered as permanent, because solar radiation, i.e., the energy that is potentially available

Table 2.3: Land cover and groundwater recharge calculated according to the Makkink reference evapotranspiration (Winter et al., 1995) under Dutch meteorological conditions (Gehrels, 1995; Spieksma et al., 1995).

Land cover	Groundwater recharge mm/d	Land cover	Groundwater recharge mm/d
Grass	0.74	Deciduous forest	0.65
Maize	0.75	Pine forest	0.53
Potato	0.81	Water	0.46
Beet	0.77	Urban areas	0.62
Cereals	0.85	Bare soil	1.68
Other crops	0.85	Heather land	0.74
Orchard	0.51	Other nature	0.71

for evapotranspiration, varied less than 0.5 % since 800 AD (Cubasch et al., 1997; Pongratz et al., 2009). Changes in groundwater recharge were thus considered only as a function of land cover change. Land cover was reconstructed using land use maps and literature by the following approach. Note that the magnitude of added uncertainty due to ignored hydroclimatic variation is explored by a sensitivity analysis hereafter.

For time slice 2000 AD, the spatial distribution of 14 land cover units was derived from a 25 by 25 m resolution land use map (De Wit and Clevers, 2004). For time slice 1885 AD, the spatial distribution of 9 land cover units was derived from a 50 by 50 m resolution historical land use map (Knol et al., 2004). For time slice 1350 AD, no quantitative data was available about the land cover of the modelled area, though anthropogenic impact on the land cover was considerable (Borger, 1992). Therefore, land cover was estimated by transformation of the land cover map for time slice 1885 AD. Turf ponds and urban areas in the Vecht River valley were transformed into grass and urban areas at the ice-pushed ridge were transformed into deciduous forests. For time slice 800 AD, deciduous forests were considered the dominant land cover at the ice-pushed ridge, because succession triggered by Holocene climate change has approached its climax-state in The Netherlands prior to 0 AD (Westhoff et al., 1970; Zagwijn, 1986). Marshes were the dominant land cover in the river valley (Borger, 1992). Reference evapotranspiration of the marshes was set to equal that of grass. And lastly, land cover for time slice 0 AD was reconstructed using the same method as that for time slice 800 AD, however, reference evapotranspiration of the lakes along the River Vecht (Bos et al., 2009) were set to equal that of surface water.

2.3.3 Drainage intensity and surface water levels

The MODFLOW River-package calculates fluxes, Q_{riv} (m^3/d), between groundwater and surface water according to hydraulic head differences established by user-defined surface water levels, H_{riv} (m), and calculated hydraulic heads, H_{cell} (m):

$$Q_{riv} = k_{riv} \cdot D \cdot (H_{riv} - H_{cell}) \qquad \textit{(Eq. 2)}$$

where k_{riv} denotes the specific hydraulic conductivity of the river bed (1/d) and D the drainage intensity (m^2), i.e., the total area of surface water within a grid cell (McDonald and Harbaugh, 1988). The specific hydraulic conductivity of the river bed was obtained from calibration of the groundwater model for

most recent time slice and was considered as permanent. Drainage intensities and surface water levels were considered as transient.

Drainage intensities were derived from a topographical map for the most recent time slice and from a historical topographical map and literature (Borger, 1992; Berendsen and Stouthamer, 2000; Pons and Oosten, 1974; Bos et al., 2009) for past time slices.

For the most recent time slice, surface water levels in polders were derived from water management maps, which provide target polder levels for the winter period. Surface water levels in drainage ditches at the ice-pushed ridge were derived from a 5 by 5 m resolution digital elevation model (Van Heerd et al., 2000). For time slice 1885 AD, surface water levels were either derived from literature (Van der Plassche et al., 2005; Lagers and Strating, 1998; Van Zinderen Bakker, 1942), or reconstructed from current surface water levels and land subsidence rates (see section 3.4). For time slice 1350 AD, surface water levels were reconstructed by setting a constant hydraulic head gradient at the River Vecht of 4 cm/km towards former inland sea Zuyderzee. This hydraulic head gradient approaches the current hydraulic head gradient of the River Rhine. Surface water levels of the former inland sea Zuyderzee were derived from Van der Plassche et al. (2005). For time slice 800 AD and time slice 0 AD, surface water levels were reconstructed with the same approach as used for time slice 1350 AD. However, for time slice 0 AD, surface water levels of the lakes along the River Vecht were set horizontal.

2.3.4 Surface elevation

Topographic control of groundwater levels by overland flow was modelled with the MODFLOW Drain-package. The MODFLOW Drain-package calculates drainage fluxes, Q_{drn} (m^3/d), according to hydraulic head differences established by user-defined drain elevations, d_{drn} (m) and calculated hydraulic heads, H_{cell} (m):

$$Q_{drn} = C_{drn} \cdot (d_{drn} - H_{cell}) \qquad \textit{(Eq. 3)}$$

where C_{drn} denotes the drain conductance (m^2/d) (McDonald and Harbaugh, 1988). The drain conductance was set to an arbitrarily high value to avoid unrealistic heads above the ground surface (Batelaan and De Smedt, 2004) and user-defined drain elevations were set to equal ground surface elevations for each time slice.

For time slice 2000 AD, ground surface elevations were derived from a 5 by 5 m Digital Elevation Model (DEM) (Van Heerd et al., 2000). For time slice 1885 AD, ground surface elevations were reconstructed by compensating the DEM of the most recent time slice for land subsidence and filling-in of peat excavations and sand excavations by performing a nearest neighbour interpolation. Land subsidence, $S(x,y)$ (m) was calculated with:

$$S(x,y) = \alpha \cdot f_{peat}(x,y) \cdot \Delta T \qquad \textit{(Eq. 4)}$$

where α denotes the subsidence rate of reclaimed peat lands (m/y), $f_{peat}(x,y)$ is the spatially variable peat fraction of the unsaturated zone (-) and ΔT the time span (y). The subsidence rate was set at 2 mm/y, which corresponds with observed subsidence rates in Dutch polders (Schothorst, 1982; Van Asselen et al., 2009; Van der Meulen et al., 2007) and agrees reasonably with associated lowering of the polder levels during the last century (Lagers and Strating, 1998). Peat fractions of the unsaturated zone were

derived from a 250 × 250 × 0.5 m resolution lithological model for the most recent time slice (Weerts et al., 2005). For time slice 1350 AD, ground surface elevations were reconstructed by compensating the DEM of the pre-development state, i.e., time slice 800 AD (see below), for land subsidence at the reclaimed areas (Borger, 1992) using Eq. 4.

For time slice 800 AD, ground surface elevations were reconstructed using a series of logical expressions applied to the current geological properties of the river valley along east-west cross-sections. The first logical expression sets the ground surface elevation of the floodplain at 0.4 m above the reconstructed surface water level of the River Vecht. The second logical expression sets a constant ground surface elevation gradient of 0.1 m/km for peat lands and it sets the expansion of the peat lands according to the morphology of the ice-pushed ridge. The reconstructed expansion of the peat lands is indicative for areas with groundwater tables at or near the surface and roughly agrees with the current drainage pattern. The last logical expression superimposes bog domes upon the peat lands by setting a constant surface elevation gradient of 0.02 m/km for bog domes. The topographic position of the bog domes was derived from Pons and Oosten (1974). For time slice 0 AD, the ground surface elevations were reconstructed with the same approach as used for time slice 800 AD.

2.3.5 Hydraulic properties of the semi-confining layer

Hydraulic properties of the semi-confining layer were modelled with spatially variable transmissivities and hydraulic resistances. Transmissivities, *kD* (m²/d) and hydraulic resistances, *c* (d), were assessed from the lithological composition of the semi-confining layer according to:

$$kD = d \cdot \sum_{l=1}^{l=6} p(l) \cdot k_h(l) \qquad \text{(Eq. 5)}$$

$$c = d \cdot \sum_{l=1}^{l=6} p(l) \cdot \frac{1}{k_v(l)} \qquad \text{(Eq. 6)}$$

where d denotes the thickness of the semi-confining layer (m) (see Fig. 2.8), $p(l)$ the fraction of lithological class l in the semi-confining layer (-), $k_h(l)$ the horizontal permeability (m/d) and $k_v(l)$ the vertical permeability (m/d) of lithological class l. Horizontal and vertical permeabilities of the six lithological classes (l = 6) used in this study are listed in Table 2.4.

Transmissivities and hydraulic resistances were reconstructed for all time slices by considering horizontal and vertical permeabilities of the lithological classes as permanent and by considering the lithological composition of the semi-confining layer as transient. For the most recent time slice, the lithological

Table 2.4: Horizontal and vertical permeabilities of six lithological classes in the Gooi- and Vechtstreek area, The Netherlands (derived after Bierkens, 1996).

Lithological class	Horizontal permeability m/d	Vertical permeability m/d
Clay	0.005	0.005
Sandy clay	0.04	0.04
Peat	0.5	0.05
Fine sand	9	4
Medium fine sand	11	6
Coarse sand	40	20

composition of the semi-confining layer was derived from a 250 × 250 × 0.5 m lithological model (Weerts et al., 2005). Dating methods to identify the presence of peat deposits in the past (Berendsen and Stouthamer, 2000) were not applicable for the reconstruction of the lithological composition of the semi-confining layer for the past time slices, because majority of the peat that was deposited after 0 AD has been excavated or oxidized (Bos et al., 2009). Alternatively, we reconstructed the lithological composition of the semi-confining layer by intersecting the lithological model of the most recent time slice with the reconstructed ground surface elevation for each past time slice (see section 2.3.4). Deposits that were situated above the reconstructed ground surface were eliminated from the semi-confining layer, whereas peat was added to the semi-confining layer if the reconstructed ground surface elevation exceeded the ground surface elevation for the most recent time slice.

2.3.6 Groundwater abstractions

Groundwater abstractions were modelled with the Modflow Well-package, which forces groundwater flow according to a user-defined flux from the model. For time slice 2000 AD, groundwater discharge fluxes from abstraction wells were obtained from time series of abstraction rates exceeding 10 m^3/d. The well package was inactive for the past time slices, because systematic groundwater abstractions were not yet in practice.

Table 2.5: Discharge areas, vertical fluxes between the semi-confining layer and the upper aquifer and water balances of the fen area for subsequent time slices. Units are 10^3 m^3/d if not specified. Phases correspond to Fig. 2.4. Fen refers to the fen area, excluded the deep agricultural polders Horstermeer and Bethune, which are signified by Polder. The recharge flux is indicative for groundwater flow within the river valley. Positive fluxes across the east-boundary relate to groundwater flow from the ice-pushed ridge to the river valley. Note that (1) the fen area expanded due to peat accumulation between time slice 0 AD and 800 AD, but remained permanent after time slice 800 AD and (2) the west-boundary of the fen area coincides with a no-flux model boundary.

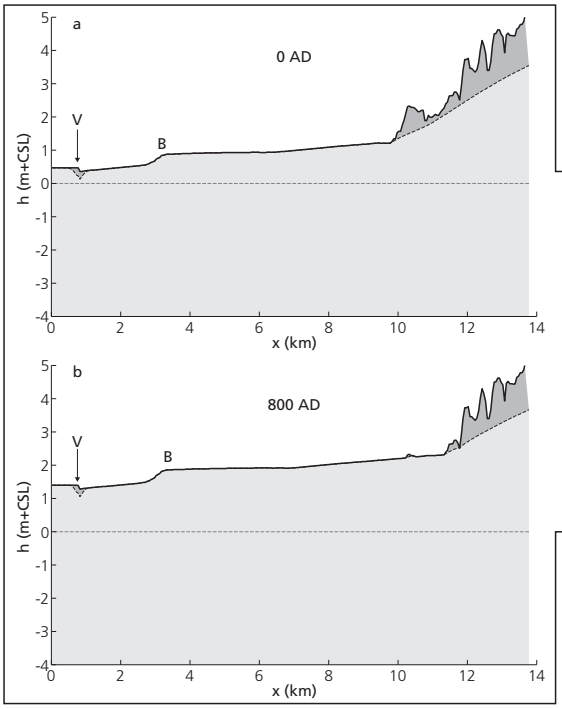
Phase	**Accumulation**		**Stagnation**	**Degradation**	
Time slice	**0 AD**	**800 AD**	**1350 AD**	**1885 AD**	**2000 AD**
Discharge area and vertical fluxes					
Discharge area (km^2) – Fen	83	93	92	59	60
Discharge area (km^2) – Polder	0	0	0	11	11
Discharge flux – Fen	56	50	63	141	108
Discharge flux – Polder	0	0	0	85	100
Recharge flux upper aquifer	23	22	27	185	205
Water balance					
Precipitation surplus	121	172	132	118	118
Infiltration surface water	0	0	0	220	262
Drainage – Fen	-21	-15	-21	-208	-185
Drainage – Polder	0	0	0	-90	-106
Overland flow – Fen	-133	-185	-147	-54	-52
Overland flow – Polder	0	0	0	-27	-39
Abstraction	0	0	0	0	-26
North boundary	1	0	1	4	4
East boundary	26	24	28	33	21
South boundary	6	6	7	14	13

2.4 Results

The results of the palaeo-hydrological reconstruction are depicted in Table 2.5 and Figs. 2.4 – 2.8. Reconstructed geo-hydrological conditions, i.e., groundwater recharge, drainage intensity and hydraulic resistance of the semi-confining peat layer, for subsequent time slices are presented in Appendix A to provide further information on the hydrological evolution of the study area. We distinguish three phases of landscape development according to the evolution of geo-hydrological properties of the river valley (Fig. 2.4): the accumulation phase, the stagnation phase and the degradation phase. Below we describe the co-evolution of geo-hydrological properties and groundwater systems during these phases.

2.4.1 Accumulation phase

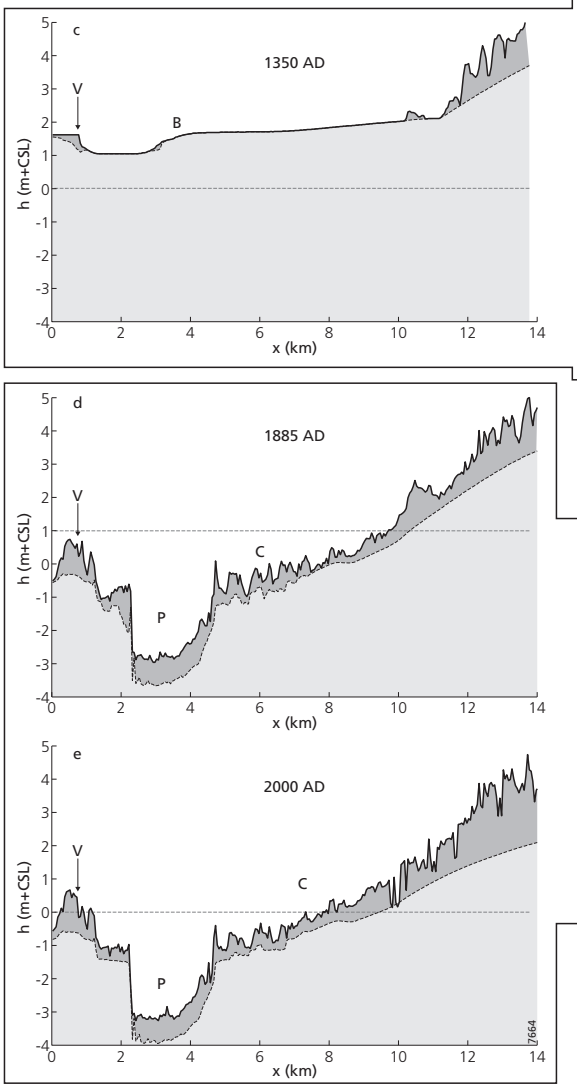
During the accumulation phase, ground surface levels of the river valley increased by approximately 0.6 m due to the accumulation of peat (Figs. 2.4 and 2.6). Peat accumulation was triggered by the continuous rise in the sea level during the Holocene and silting up of the lakes along the River Vecht (Fig. 2.5). Notably, groundwater supplied to the river valley mainly originated from the ice-pushed ridge (Table 2.5). This groundwater discharged at high intensity (> 0.1 mm/d) in the upstream margins of the river valley and at low intensity (< 0.001 mm/d) across the river valley (Figs. 2.7 and 2.8). Except for the slightly elevated bog domes, groundwater in the river valley was rather stagnant, due to the small hydraulic gradients determined by the flat ground surface of the river valley (Fig. 2.8). Both, groundwater fluxes from the ice-pushed ridge and groundwater fluxes within the river valley, slightly decreased during the accumulation phase (Table 2.5). Groundwater and precipitation were mainly discharged from the river valley by overland flow, whereas drainage fluxes into the River Vecht and peat creek Drecht were relatively low.



Accumulation phase

Peat accumulation triggered ground surface level rise and associated groundwater level rise

Geo-hydrological characteristics river valley:
- Surface water levels and ground surface levels above current sea level.
- Regional drainage basis situated at the River Vecht (V).
- Flat topography, with major topographical gradients associated to the bog domes (B).
- Groundwater tables at or near the surface



Stagnation phase

Groundwater level rise triggered by Holocene sea transgression is counterbalanced by anthropogenic drainage, which resulted into stagnation of the ground surface level ris

Geo-hydrological characteristics river valley:

- Surface water levels and ground surface levels above current sea level.
- Regional drainage basis situated at the River Vecht (V) and anthropogenic drainage ditches (D).
- Flat topography, with major topographical gradients associated to the reclaimed areas
- Groundwater tables at or near the surface

Degradation phase

Peat excavation and anthropogenic drainage induced a lowering of ground surface levels and groundwater levels

Geo-hydrological characteristics river valley:

- Surface water levels and ground surface levels below current sea level.
- Regional drainage basis situated at the deep agricultural polders (P).
- Topography is dominated by cascades of polders (C) with relatively large topographical gradients.
- Groundwater tables are anthropogenically controlled at 0.5 a 1 m below the ground surface.

Figure 2.4: (left page and above) Co-evolution of ground surface elevations and hydraulic heads in the semi-confining layer for subsequent time slices and definition of phases of landscape development. The cross-section is marked with W2 and E2 in Fig. 2.1. Solid lines represent surface levels and dashed lines represent groundwater levels.

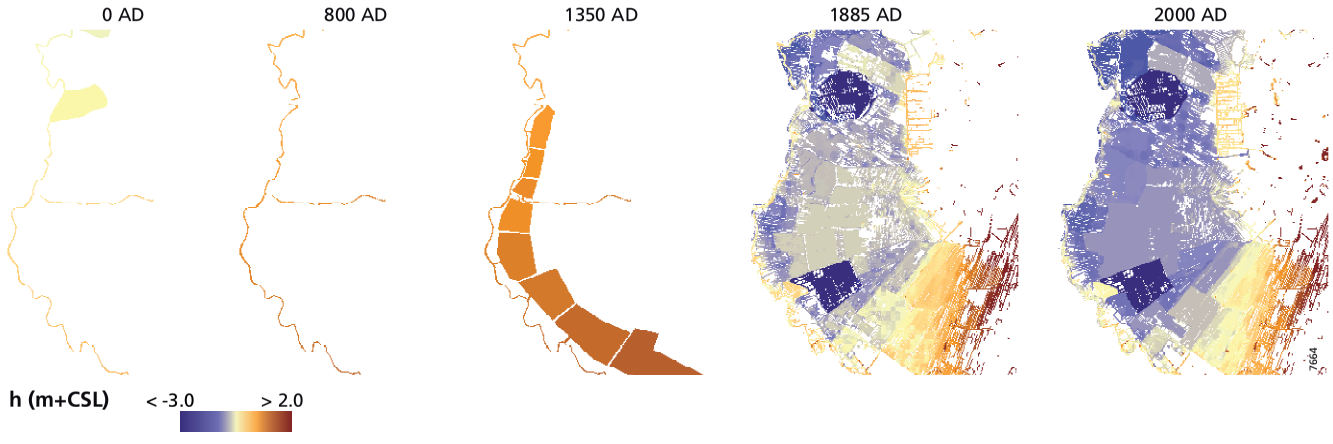


Figure 2.5: Reconstructed surface water levels for subsequent time slices.

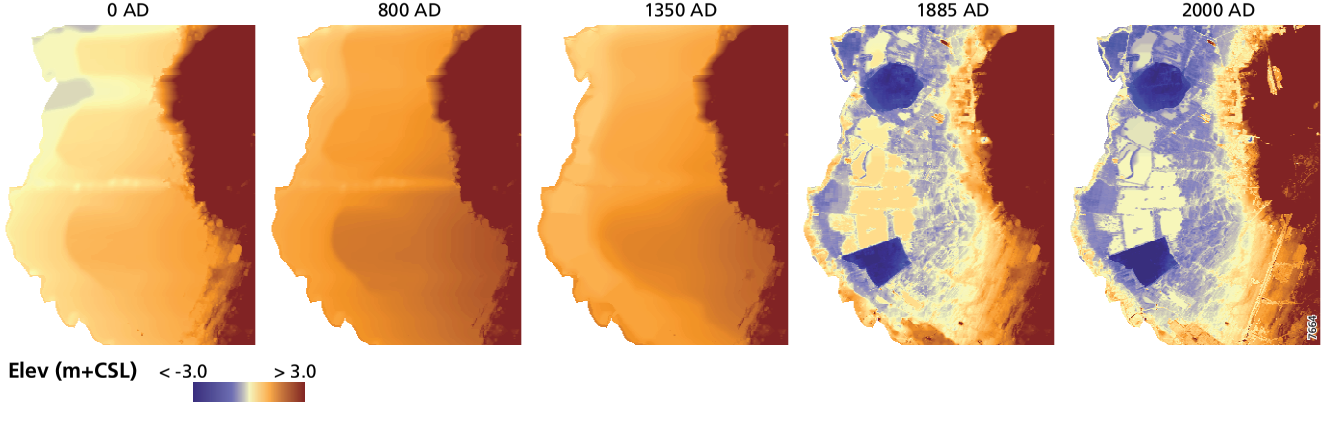


Figure 2.6: Reconstructed ground surface elevations for subsequent time slices.

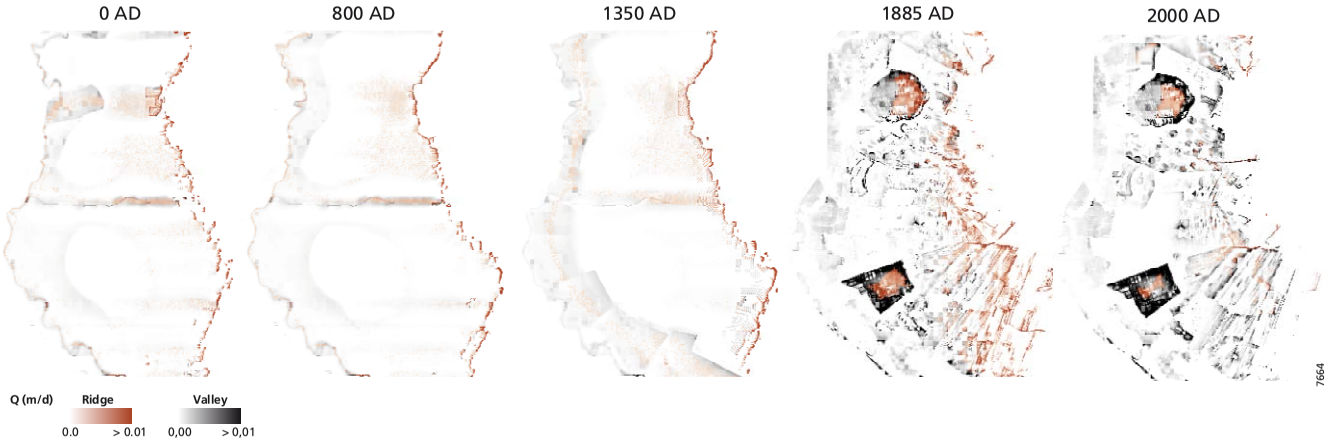


Figure 2.7: Reconstructed groundwater discharge intensities related to groundwater that is recharged at the ice-pushed ridge and that is recharged at the river valley for subsequent time slices.

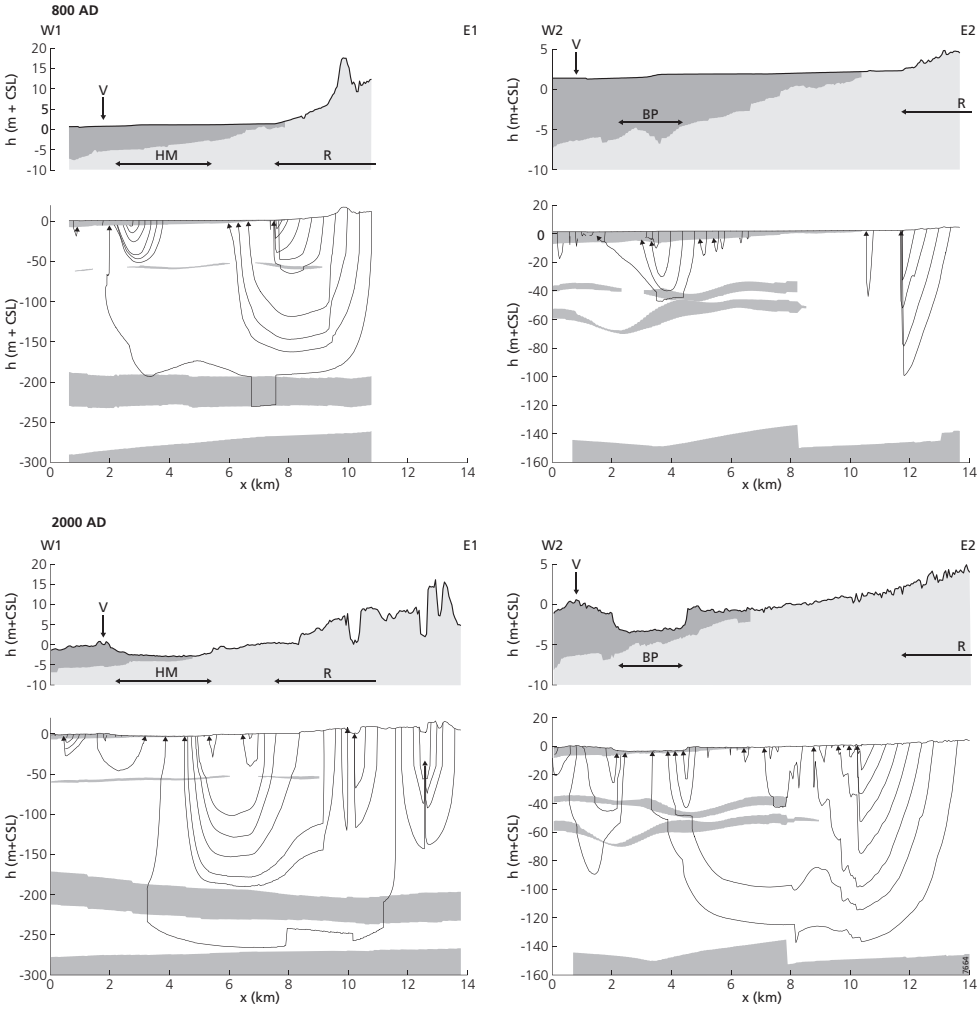


Figure 2.8: Groundwater flow paths modelled along two west-east cross-sections through the deep agricultural polders Horstermeer (HM) and Bethune (BP) for time slices 800 AD and 2000 AD. The positions of the cross-sections are signified by W1-E1 and W2-E2 respectively in Fig. 2.1. The River Vecht is signified by V and the ice-pushed ridge by R. The position and thickness of the semi-confining layer and resistance layers are indicated by the shaded areas.

2.4.2 Stagnation phase

During the stagnation phase, peat accumulation and associated ground surface level rise stagnated (Figs. 2.4 – 2.6) as a result of anthropogenic drainage, which counterbalanced the effects of Holocene sea level rise. In the anthropogenically drained areas, land subsidence was initiated due to enhanced mineralization of peat, following the local lowering of the groundwater level. Here, ground surface levels decreased by approximately 0.4 m (Fig. 2.6). The decreased groundwater discharge into the river valley during the accumulation phase transformed into an increased groundwater discharge during the stagnation phase (Table 2.5), because (1) groundwater flow from the ice-pushed ridge to the river valley

was enhanced with the stagnation of the ground surface levels of the river valley and the ongoing Holocene sea level rise (Figs. 2.5 and 2.6) and (2) groundwater flow within the river valley was enhanced by the increased hydraulic gradients within the river valley caused by the reclamation of peat lands (Table 2.5). However, groundwater discharge patterns were hardly transformed (Figs. 2.7 and 2.8) and groundwater and precipitation were still predominantly discharged by overland flow (Table 2.5).

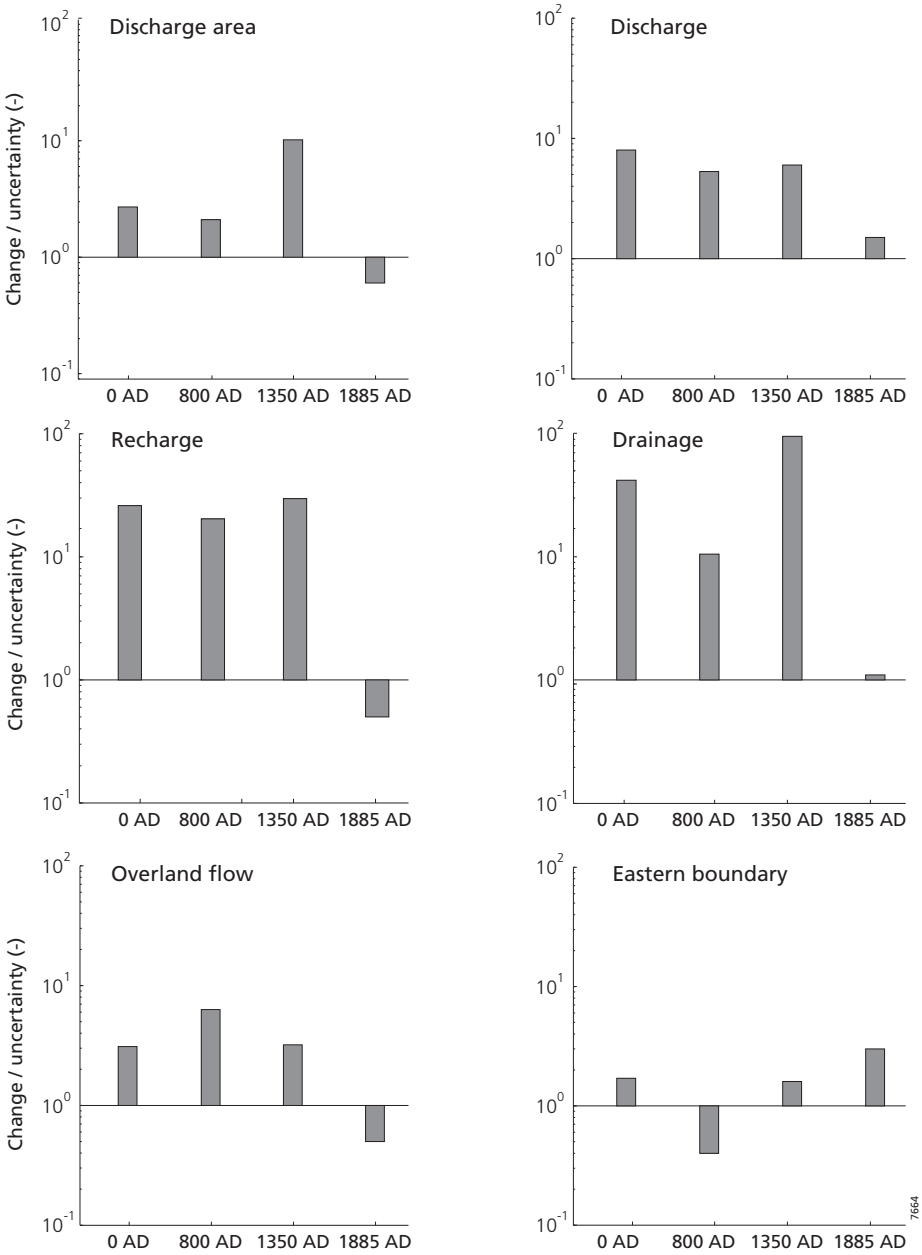
2.4.3 Degradation phase

During the degradation phase, ground surface levels of the river valley decreased by several meters due to peat excavation and anthropogenic drainage of the peat lands (Figs. 2.4 – 2.6). The increased groundwater discharge into the river valley during the stagnation phase continued during the degradation phase (Table 2.5) for three reasons. Firstly, groundwater flow from the ice-pushed ridge to the river valley was further enhanced (Table 2.5), due to the establishment of polders in the river valley with ground surface elevations below sea level (Figs. 2.4 and 2.6). Secondly, groundwater flow within the river valley was further enhanced (Table 2.5), due to a further increase of the hydraulic gradients within the river valley by the establishment of polders with distinctly different ground surface elevations (Figs. 2.4 – 2.6). And lastly, groundwater recharge fluxes in the river valley increased due to infiltration from anthropogenically controlled surface waters, including the River Vecht, which are supplied by alien surface water to prevent desiccation of crops and nature in summer. The effects of these hydrological changes on the groundwater supply of the fen were partly counterbalanced during the last century by (1) the redirection of groundwater flow to the deep agricultural polders and to abstractions wells (Table 2.5) and (2) the decreased groundwater flux from the ice-pushed ridge due to the decreased precipitation surplus (Table 2.5) related to land cover change (planting of pine plantations and expanding urban areas). These hydrological changes transformed the more contiguous groundwater discharge pattern in 1350 AD into a dispersed groundwater discharge pattern after 1885 AD, which is associated with the development of nested groundwater systems in the river valley (Figs. 2.7 and 2.8). Moreover, the dominant groundwater discharge mechanism transformed from regional overland flow to local drainage (Table 2.5) during the process of land reclamation, which was particularly intense from 1400 AD until 1800 AD.

2.5 Discussion and conclusion

2.5.1 Methodological approach

In this study, we analyzed the naturally and anthropogenically driven evolution of groundwater systems using a series of three-dimensional palaeo-groundwater models. Similar to many palaeo-groundwater models such as presented by Sanford and Buapeng (1996), Piotrowski (1997) and Van Weert et al. (1997), the palaeo-models presented in this chapter could not be validated, because quantitative reference data is only available for the last few decades and not for the past time slices. Nevertheless, we consider the palaeo-groundwater models presented in this chapter of sufficient quality for providing a conceptual representation of the evolution of groundwater systems in the Gooi- and Vechtstreek area for two reasons. Firstly, the palaeo-groundwater models for past time slices were constructed by transformation of a calibrated groundwater model for the current condition, that reproduced the observed patterns in hydraulic heads across the catchment of the studied fen area. Secondly, an uncertainty analysis of hydroclimatic variability, hydraulic resistance of the semi-confining layer and (for time slice 800 AD) palaeo-geographical features of the river valley demonstrated that the palaeo-models were robust against uncertainty (Fig. 2.9). As shown in Figure 2.9, the modelled trends in groundwater discharge


Discharge area
Discharge
Recharge
Drainage
Overland flow
Eastern boundary
Change / uncertainty (-)
10^2
10^1
10^0
10^{-1}
0 AD
800 AD
1350 AD
1885 AD
7664

area, vertical fluxes between the semi-confining layer and the upper aquifer and most terms of the water balance, exceed uncertainty in these values by several orders of magnitude for all past time slices except for time slice 1885 AD. Uncertainty exceeds the change in hydrological characteristics for this time slice, because differences between 1885 AD and the current groundwater systems are small. Note that the spatial configuration of groundwater discharge areas was also robust against uncertainty, which further confirms the suitability of the palaeo-models for studying the evolution of groundwater systems.

Compared to the previously mentioned palaeo-groundwater models, the series of palaeo-groundwater models presented in this chapter is representative for a relatively short time span in the nearby past and it describes the evolution of groundwater systems on a relatively high spatial resolution, i.e., a regional instead of a supra-regional spatial scale. Owing to this high temporal and spatial resolution, the series of palaeo-groundwater models provides an eco-hydrologically relevant representation of the evolution of groundwater systems for two reasons. Firstly, the considered time span and the temporal resolution of the series of palaeo-models coincide with the rate of anthropogenically driven evolution of groundwater systems. For this reason, the series of palaeo-models can be used to disentangle the natural and anthropogenic drivers of hydrological changes that may underlie environmental degradation of fens. Secondly, the spatial scale of the palaeo-models coincides with the dimensions of regional groundwater systems discharging into fens. This high spatial resolution is required for analysing anthropogenic interferences with the regional hydrological key-processes underlying fen development at a landscape scale, which is not possible when using palaeo-models constructed at a supra-regional spatial scale.

The palaeo-groundwater models provide convincing evidence that the natural evolution of groundwater systems is characterised by small transformations of groundwater flow patterns, whereas the anthropogenically driven evolution of groundwater systems is characterised by large transformations of groundwater flow patterns. The minor evolution of groundwater systems under natural conditions agrees with the presence of thick sedge-peat beds in natural fens, which developed by the accumulation of organic matter produced by plants that have a preference for minerotrophic (groundwater-like) site conditions (Succow, 1988; Wassen and Joosten, 1996) during the last five to ten centuries. In contrast to natural processes, anthropogenic activities have accelerated the evolution of groundwater systems

Figure 2.9: (see left page) Robustness of the modelled changes in groundwater discharge area and fluxes since each past time slice against uncertainty in modelled groundwater discharge areas and fluxes for each past time slice. Robustness was quantified by change-uncertainty ratios, by considering uncertainty in hydroclimatic variability (Recharge multiplied with 0.8 and 1.2), hydraulic resistance of the semi-confining layer (leakance factors multiplied with 0.5 and 2.0) and palaeo-geographical conditions of the river valley (only for time slice 800 AD). The range of considered palaeo-geographical conditions consisted of (1) an increased size of the bog domes, (2) elimination of the bog domes, (3) an increased ground surface elevation gradient of the bog domes to 0.1 m/km, (4) elimination of peat creek Drecht, (5) implementation of three peat creeks, (6) a decreased elevation of the flood plain to equal that of the surface water level in the River Vecht and an increased elevation of the flood plain to 1 m above the surface water level in the River Vecht, (7) a decreased ground surface elevation gradient of the fen to 0.05 m/km and an increased ground surface elevation gradient to 0.1 m/km and (8) a decreased surface water level gradient of the River Vecht to 0.02 m/km and an increased surface water level gradient to 0.06 m/km. Change-uncertainty ratios exceeding 1 thus indicate that the change since a past time slice exceeds uncertainty, whereas ratios below 1 indicate that the change is lower than uncertainty.

towards their current state, which highly deviates from natural groundwater system configurations. This finding agrees with former studies on the anthropogenic impact on regional groundwater systems and the associated consequences for the spatial patterns in groundwater supply of fens (Schot and Molenaar, 1992; Wassen et al., 1996).

2.5.2 Groundwater supply of fens

The basic premise of the present study was the assertion that the groundwater flux to managed fens has decreased with increasing anthropogenic interferences with the regional hydrology. This assertion is invalidated by our palaeo-hydrological reconstruction, which shows that current groundwater discharge flux into the studied fen area exceeds the late-natural groundwater discharge flux. The groundwater discharge flux increased after the initiation of water management due to the development of additional groundwater systems in the river valley with the establishment of polders since 1350 AD. Note that groundwater in the river valley was rather stagnant during natural conditions. Furthermore, the additional groundwater systems in the river valley became increasingly recharged by surface water, which is abundantly available as a result of the anthropogenic supply of alien surface water to polders to prevent desiccation of crops and nature areas during summer. The increase of the groundwater discharge flux into the fen since 1350 AD still counterbalances more recent effects of (1) redirections of groundwater flow as a result of both the reclamation of two lakes and the establishment of abstraction wells for drinking water production and (2) the decreased precipitation surplus due to anthropogenic land cover change from deciduous forest into pine forest and urban areas. Anthropogenic developments since 1885 AD, in particular groundwater abstractions, reduced the groundwater discharge into the fen only to a minor extent compared to the former increase of the groundwater discharge by the establishment of polders.

2.5.3 Conclusion

The results of the present study provide new insights into the impact of anthropogenic hydrological interferences with the groundwater supply of fens on a regional scale. The finding of an increased groundwater discharge flux into managed fens after the initiation of water management opposes the hypothesis that a decreased groundwater flux to fens underlies the environmental degradation of fens in intensively managed regions (Barendregt et al., 1995; Fojt, 1994). Instead, the palaeo-hydrological reconstruction provides evidence that it is mainly the decreased area of groundwater discharge and the shift in the predominant groundwater discharge mechanism from regional overland flow to local drain discharge, that underlie the environmental degradation of managed fens. Despite of an increased groundwater discharge flux into the river valley, the area of groundwater discharge decreased during the anthropogenically driven evolution of groundwater systems. This decrease in potentially suitable fen area relates to an increased convergence of groundwater flow paths by the establishment of polders. A more important factor that reduced the potentially suitable fen area may be that the dominant groundwater discharge mechanism of the fen transformed from regional overland flow to local drain discharge. Groundwater discharge by overland flow implies that groundwater is laterally redistributed across fens and may re-infiltrate into the fen root zone before it is discharged from the fen. The conditioning effect of this lateral redistribution of groundwater on fen development has been reported for natural fens in Poland (Wassen and Joosten, 1996), Siberia (Schipper et al., 2007) and Germany (Succow, 1988). In these fens, groundwater discharges into a narrow belt adjacent to the regional groundwater recharge area in a comparable pattern as modelled for the present study area during the pre-development state. Fen plants, however, are not confined to the zones of groundwater discharge in these natural fens, but also prevail at sites that are supplied with groundwater by lateral

flow. Contrary to overland flow, groundwater discharge via drainage ditches implies that groundwater is prevented from entering the root zone of fens, because it is intercepted by drainage ditches (Schot et al., 2004) and it is subsequently discharged from the fen by surface water flow. By consequence, locally infiltrated precipitation instead of discharging groundwater drives the abiotic conditions in managed fens (Wassen et al., 1990), which causes sites to become less suitable for the establishment and survival of fen plants on a long-term (Grootjans et al., 2005; Mälson et al., 2008). For these reasons we believe that environmental degradation of fens more likely relates to a shift in the predominant discharge mechanism from regional overland flow to local drain discharge, rather than to a decreased groundwater discharge flux into fens.

Finally, we note that a shift in the origin of groundwater supply of fens may also underlie the environmental degradation of managed fens. The results of this study indicate that most of the groundwater that discharged into the fen under natural conditions originated from the regional groundwater recharge area, whereas groundwater increasingly originated from the fen area itself with increasing anthropogenic hydrological interferences. This shift in the origin of groundwater supply may increase the acid buffering capacity of fens, as groundwater recharged at organic soils often has a higher alkalinity compared to groundwater recharged at mineral soils (Schot and Wassen, 1993), i.e., sandy upland areas. This may be beneficial for fen plants. However, the shift in the origin of groundwater supply may also induce eutrophication of fens, because mineralization of organic soil compounds and groundwater recharge by polluted surface water, are thought to increase the nutrient availability for plants (Schot and Wassen, 1993; Beltman et al., 2000; Smolders et al., 2006). The hydrochemical and ecological consequences of anthropogenically induced shifts in the origin of groundwater supply of fens are not yet sufficiently understood to assess the full impact of these processes on the suitability of fen habitat sites, though this knowledge is essential for improving currently utilized fen restoration strategies.

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3 Throughflow as a determining factor for habitat contiguity in a near-natural fen

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Abstract
Knowledge of the hydrological mechanisms that underlie persistent plant communities within natural fens is essential for the improvement of current fen restoration and conservation strategies. In this study, steady-state groundwater modelling was performed to quantify the impact of throughflow mechanisms on the presence of exfiltrated, alkaline groundwater across a near-natural fen in the Biebrza River catchment (Poland). Alkaline groundwater is considered essential for the existence of low-productive fen plants. The results indicate that throughflow redistributes exfiltrated groundwater, mixed with locally infiltrated precipitation, in various concentrations across the fen. The throughflow model provides an explanation for the major patterns in the plant alliances that have a preference for minerotrophic or ombrotrophic habitat conditions. These patterns could not be reproduced with groundwater models that did not account for the existence of throughflow on a regional scale. We conclude that throughflow (1) enables a spatially contiguous supply of exfiltrated groundwater across fens and thereby (2) facilitates abiotic conditions suitable for fen plants outside the zones that are directly supplied by exfiltrated groundwater. Throughflow mechanisms are argued to be relevant for fens in natural lowland river valleys. These new insights into landscape hydrological mechanisms that drive abiotic conditions within natural fens necessitate the re-prioritization of current hydrological fen restoration strategies.

3.1 Introduction

Many fen plant species are currently threatened by worldwide land reclamation, environmental degradation and associated habitat fragmentation (Millennium Ecosystem Assessment, 2005). Habitat fragmentation is the reduction of vast, contiguous habitat patches into multiple small habitat patches, which negatively affects the viability of remnant populations (Ewers and Didham, 2005; Hooftman et al., 2003). For this reason, the sustainable restoration of fen plant populations in intensively managed fens requires the restoration of vast, contiguous populations. However, as the hydrological mechanisms that underlie the presence of vast plant populations in natural fens are not yet sufficiently understood, fen restoration projects are frequently trial-and-error processes with unpredictable results (Jansen et al, 2000; Lamers et al., 2002). The goal of the present study is to contribute to the knowledge that is available on the hydrological mechanisms that mediate abiotic conditions for fen plants under natural conditions.

In particular, fen plants with a low biomass production that are typical of nutrient-poor conditions have become threatened. These so-called low-productive fens usually develop at sites that are supplied by exfiltrated, alkaline groundwater and local, weakly acid precipitation (Amon et al., 2002). This excessive supply of water causes shallow water tables and reduced conditions in the shallow subsurface throughout the year (Boomer and Bedford, 2008; De Mars and Wassen, 1999). In addition, dissolved minerals are supplied to the fens via exfiltrating groundwater. Both the shallow water tables and the supply of dissolved minerals maintain the acidity of these fens at a near-neutral pH level (Almendinger and Leete, 1998; Kemmers et al., 2003) and limit the availability of nutrients for plant growth if phosphorous is chemically bound to Ca, Fe or Al (Bedford et al., 1999; Boomer and Bedford, 2008; Boyer and Wheeler, 1989), or nitrogen is removed from the soil as N2-gas due to denitrification (Olde Venterink et al., 2002).

Environmental degradation of low-productive fens includes desiccation, acidification and eutrophication (Lamers et al., 2002). These degradation processes may be reinforced or induced by a decreased supply of exfiltrated groundwater. This may result either in the lowering of water tables triggering desiccation, or in the enhancement of infiltration of local precipitation or surface water (Van Wirdum, 1991). These shifts in the origin of the water supply often induce acidification (Almendinger and Leete, 1998; Kemmers et al., 2003) or eutrophication (Beltman et al., 2000; Smolders et al., 2006). The restoration of groundwater exfiltration at fens, therefore, is thought to be a prerequisite for the restoration and conservation of fens in managed areas (Barendregt et al., 1995; Fojt, 1994).

The restoration of vast fen plant populations in managed areas relies, amongst others, on the restoration of a spatially contiguous supply of exfiltrated groundwater comparable to that observed in many natural fens (Succow, 1988; Glaser et al., 1990; Wassen and Joosten, 1996; Almendinger and Leete, 1998; Schipper et al., 2007). The establishment of a spatially contiguous supply of exfiltrated groundwater can be explained by two conceptual models of groundwater flow in natural fens: the exfiltration model and the throughflow model (Fig. 3.1). The exfiltration model assumes that groundwater exfiltrates on a regional scale as a result of permanent or periodic (evapotranspiration-driven) upward groundwater flow (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006). In this model, lateral flow is limited to the local scale (Drexler et al., 1999) and fen plants are confined to the exfiltration zones. The throughflow model assumes that groundwater exfiltrates at the upstream margins of fens, while the high exfiltration rates cause a surplus of groundwater in the shallow subsurface which is discharged by lateral flow through the loosely structured root zone, i.e. throughflow (Schipper et al., 2007; Succow, 1988; Wassen and Joosten, 1996). In this model, throughflow redistributes exfiltrated groundwater on a regional scale and provides abiotic conditions for fen plants outside the exfiltration zones. The relevance of throughflow for the provision of abiotic conditions for fen plants is however uncertain, because (1) the transport distances of exfiltrated groundwater by throughflow have not been quantified yet and (2) throughflow may be composed of any mixture of locally infiltrated precipitation and exfiltrated groundwater.

The objective of this study is to analyse the relevance of the exfiltration model and the throughflow model for a near-natural fen in Poland by comparison of observed patterns in plant alliances with modelled patterns in exfiltrated groundwater.

3.2 Study area

The study area is situated along the upper reach of the left bank of the Biebrza River (N.E. Poland, 22°30` – 23°60`E, 53°30` – 53°75` N, Fig. 3.2). This area was selected because (1) both its hydrology and vegetation composition are still near-natural (Palczynski, 1984; Wassen and Joosten, 1996) and (2) vegetation patterns are reported to be closely related to spatial gradients in the supply rates of locally infiltrated precipitation and exfiltrated groundwater (Wassen et al., 1992).

The morphology of the Biebrza River catchment is characterized by a 1-3 km wide ice-marginal valley, surrounded by morainic uplands in the south, east and west and by an outwash plain in the north. The valley and the lower parts of the outwash plain are covered by 3-6 m peat. This peat layer is locally incised by the Biebrza River (Oswit, 1994). Ground surface elevations of the Biebrza River valley range from 100 to 130 m amsl (above mean sea level), while those of the morainic uplands and the outwash

plain range from 130 to 170 m amsl (Zurek, 1984; see Fig. 3.2). As a result of this gradient in elevation, the morainic uplands function as a regional groundwater recharge area and groundwater flow is directed from the morainic uplands towards the river valley (Pajnowska and Wienclaw, 1984).

Groundwater flows through unconsolidated aquifers composed of fluvial and fluvioglacial gravels and sands. The base of these aquifers is formed by Tertiary marls found at approximately 0-40

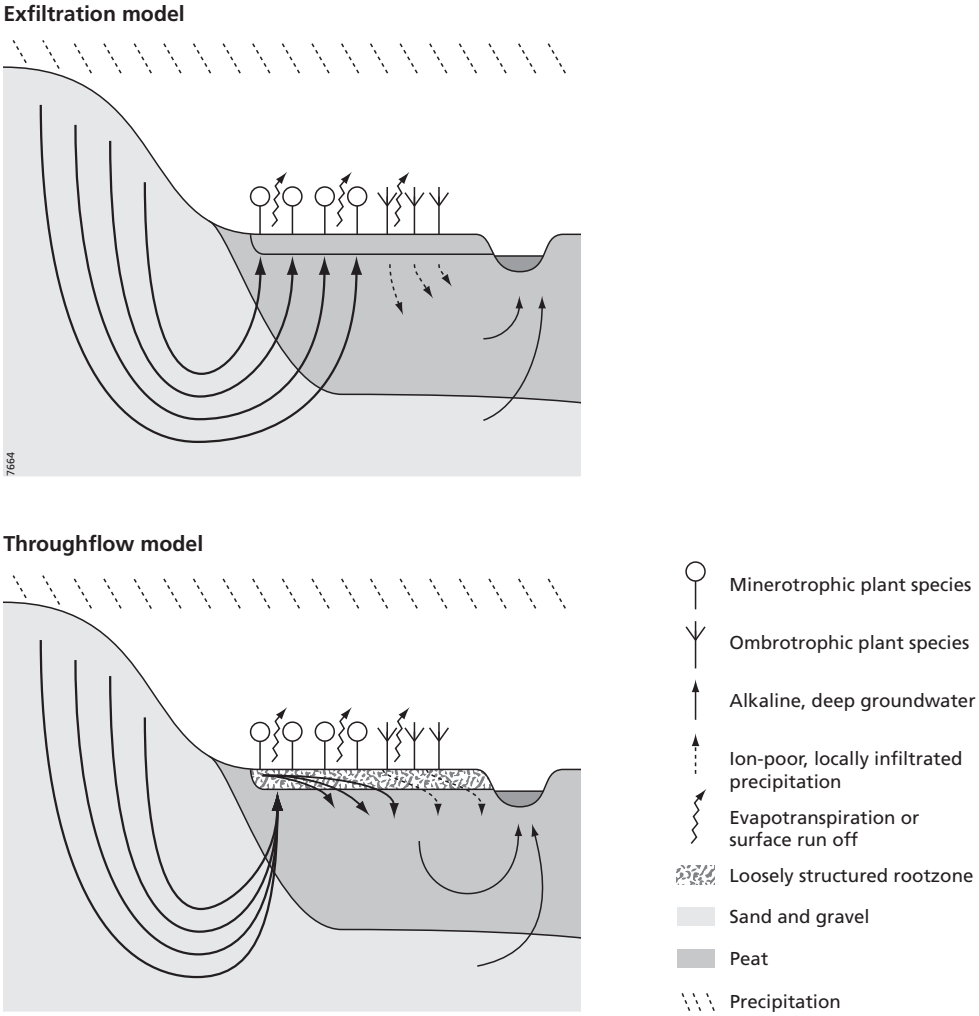

Figure 3.1: Two alternative conceptual models of groundwater flow in natural fens: the exfiltration model and the throughflow model. The exfiltration model assumes that groundwater exfiltrates on a regional scale as a result of permanent or periodic, evapotranspiration-driven, upward groundwater flow (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006). The throughflow model assumes that intense groundwater exfiltration at the upstream fen margins causes a surplus of groundwater in the shallow subsurface, which is discharged by lateral flow through the loosely structured root zone, i.e., throughflow (Schipper et al., 2007; Succow, 1988; Wassen and Joosten, 1996).

m amsl (Malinowski et al., 1970). The aquifers are separated by glacial tills with a thickness ranging from 0.1 to 20 m (Ber, 2005; Pajnowska and Wienclaw, 1984). Glacial tills, or boulder clays, are largely heterogeneous glacial deposits composed of sand, gravel and boulders. As a result, hydraulic permeabilities of glacial tills vary by 10^5 orders of magnitude. Glacial tills within the Biebrza catchment act as confining layers for groundwater flow (Pajnowska and Wienclaw, 1984). A semi-confining layer composed of compacted peat is found in the river valley. The uppermost 0.2 – 0.5 m of the semi-confining peat layer is loosely structured and thus highly permeable.

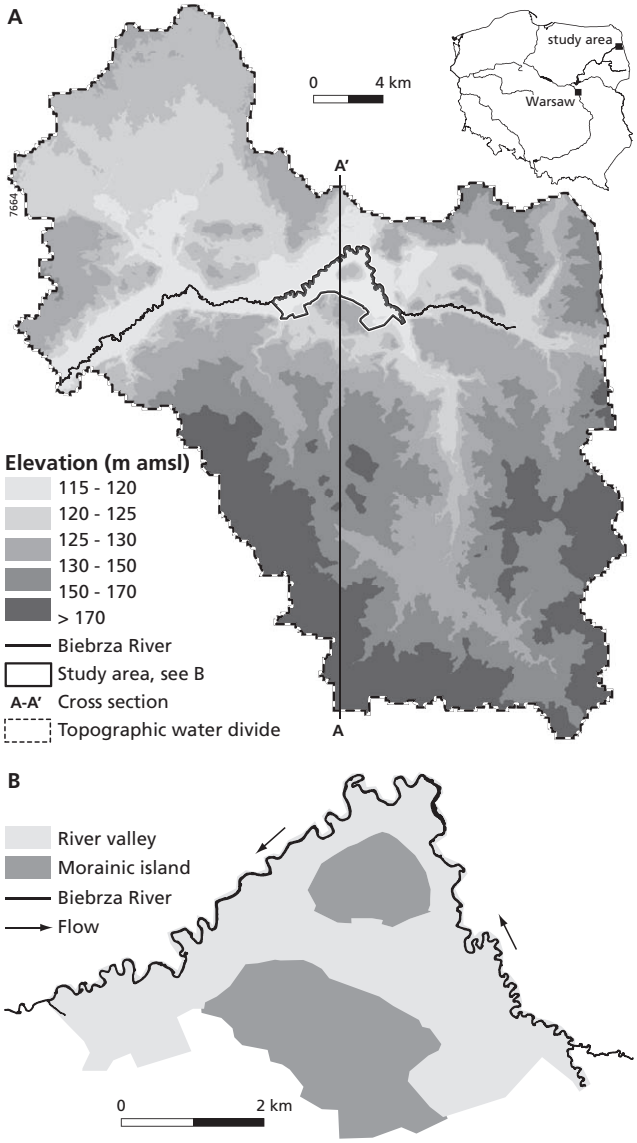

Figure 3.2: Topographic position and geographic features of the study area. (a) Ground surface elevations of the Biebrza River catchment; (b) Morphological features of the study area.

Current land cover in the morainic uplands consists mainly of arable fields and remnants of the natural oak-beech forests. Approximately 750 m^3 groundwater per day is abstracted from a few wells for the production of drinking water. Groundwater is also abstracted from numerous domestic wells. Given the low population density of the study area, however, abstractions from domestic wells are expected to harvest only a minor fraction of the mean annual precipitation, which is estimated at 545 mm/d for the period 1965-2000. The mean annual evapotranspiration is approximately 470 mm/y.

Large fens developed within the river valley during the Holocene. Although these low-productive fens are still abundant (Oswit, 1994; Wassen and Joosten, 1996), succession has resulted in the development of some forests (Palczynski, 1985). Moreover, a recent transition towards bog has occurred at the centre of the river valley. This fen-bog transition is thought to be initiated by enhanced infiltration of local precipitation following either a subtle lowering of the surface water level of the Biebrza River by weir construction, or enhanced evapotranspiration by shrub encroachment in response to a lack of mowing since World War II (Wassen and Joosten, 1996). Tolerance to flooding is not decisive for the vegetation composition across this fen, because flooding of the river valley is limited to a few tens of metres from the river bank during the winter season. For these reasons, groundwater flow and succession are determining mechanisms underlying the zoning of vegetation types within the Biebrza River valley (Palczynski, 1984).

3.3 Method

3.3.1 General approach

The relevance of the exfiltration model and the throughflow model was analysed by comparison of observed patterns in plant alliances with modelled patterns in groundwater supply for both the exfiltration model and the throughflow model (Fig. 3.1) in five methodological stages.

Firstly, we arranged the plant alliances that are present in the study area into three classes. The first class comprises plant alliances that have a preference for minerotrophic, groundwater-like, conditions. The second class comprises plant alliances that have a preference for ombrotrophic, rainwater-like, conditions. The third class comprises plant alliances that are indifferent or ambiguous for minerotrophic and ombrotrophic conditions. Minerotrophic plant alliances were used as indicators for the presence of exfiltrated groundwater and ombrotrophic plant alliances were used as indicators for the absence of exfiltrated groundwater, i.e. for the sole presence of locally infiltrated precipitation. Plant alliances that are indifferent or ambiguous for minerotrophic and ombrotrophic conditions were excluded from this analysis, because their existence is not determined by the origin of groundwater supply.

Secondly, regional groundwater flow within the Biebrza River catchment was modelled using a steady-state groundwater model that was based on the MODFLOW-1988 code (McDonald and Harbaugh, 1988). Two versions of the groundwater model were developed; one that is conceptualised with the exfiltration model and one that is conceptualised with the throughflow model. These models differed by the hydraulic conductivity that was assigned to the fen root zone. For the exfiltration model, the hydraulic conductivity of the fen root zone was set to equal that of the semi-confining peat layer, i.e. 0.34 m/d, in order to disable throughflow on a regional scale. For the throughflow model, the hydraulic conductivity of the root-zone layer was set at a higher value of 50 m/d and was increased stepwise

(see below), to enable throughflow of exfiltrated groundwater and locally infiltrated precipitation on a regional scale.

Thirdly, the fraction of exfiltrated groundwater (FEG) in the fen root zone was quantified for both the exfiltration model and the throughflow model through analysis of the fluxes derived from the groundwater models. The fraction of exfiltrated groundwater was defined as the relative contribution of exfiltrated groundwater to the total water supply of each model cell within the fen root zone, the latter being the sum of exfiltrated groundwater and locally infiltrated precipitation. Groundwater exfiltration was defined as the upward groundwater flow from the semi-confining peat layer into the root-zone layer.

Fourthly, the relevance of both the exfiltration model and the throughflow model was analysed for a range of parameter settings by comparison of the calculated FEG to the observed patterns in plant alliances. For the exfiltration model, we calculated FEG for a realistic range of river bed conductivities, surface water levels and hydraulic conductivities of the semi-confining peat, while the hydraulic conductivity of the fen root zone was set at fixed value. For the throughflow model, we calculated FEG for a realistic range of hydraulic conductivities of the fen root zone, while setting other model parameters at a fixed value. In other words, parameter values were altered within a realistic range, to test whether FEG could be fitted to the observed patterns in plant alliances. For this purpose, we assumed that minerotrophic plant alliances can occur in cells that receive any mixture of exfiltrated groundwater and locally infiltrated precipitation (FEG > 0), whereas ombrotrophic plant alliances occur in cells that exclusively receive locally infiltrated precipitation (FEG = 0).

Finally, if the modelled patterns in groundwater supply could be successfully fitted to the observed patterns in plant alliances, we evaluated the performance of the groundwater model by comparison of the modelled FEG with observed patterns in groundwater composition.

3.3.2 Mapping plant alliances

Patterns in plant alliances were derived from a vegetation map of the Biebrza River valley (Matuszkiewicz et al., 2000). This map is based on the classification of plant associations described by Palczynski (1984). We defined plant alliances that have a preference for minerotrophic conditions by the presence of plant species that persist exclusively at (slightly) minerotrophic sites and by the absence of plant species that persist exclusively at ombrotrophic sites. Likewise, plant alliances that have a preference for ombrotrophic conditions were identified by plant species that persist exclusively at ombrotrophic sites and by the absence of plant species that persist exclusively at (slightly) minerotrophic sites. Four plant alliances within our study area had a preference for minerotrophic conditions and one had a preference for ombrotrophic conditions (Table 3.1). The plant alliances that were indifferent to minerotrophic and ombrotrophic conditions consisted mainly of forests, rushes and bushes, which have developed through plant succession (Palczynski, 1985). Plant alliances were defined as ambiguous for minerotrophic and ombrotrophic conditions if the map units were poorly defined (e.g. "mosaic of sedge-moss communities").

3.3.3 Groundwater modelling

The exfiltration model and the throughflow model both consist of six layers represented by transmissivities for horizontal flow and leakance factors for vertical flow. The uppermost model layer represents the fen root zone. In order to obtain model convergence, the saturated thickness of this

Table 3.1: Classification of plant alliances by indicator species for minerotrophic and ombrotrophic conditions.

Class[1]	Plant alliance	Indicator species[2]	Indicated conditions	Topographic position
Minerotrophic	Calamagrostion neglectae	Drepanocladus aduncus Bryum pseudotriquetrum Calliergon giganteum	Alkaline, mesotrophic to eutrophic	Upstream and downstream margins of the river valley
Minerotrophic	Caricion demissae	Fissidens adianthoides Utricularia intermedia	Neutral, oligotrophic to mesotrophic	Adjacent to the morainic uplands
Minerotrophic	Caricion diandrae	Carex diandra Caltha palustris Galium palustre	Neutral, oligotrophic to mesotrophic	Across the river valley, but mostly adjacent to the morainic uplands
Minerotrophic	Magnocarion	Iris pseudacorus Carex acutiformis Lysimachia vulgaris	Neutral, eutrophic to mesotrophic	Adjacent to the flood plains of the Biebrza River
Ombrotrophic	Sphagnetalia fusci	Sphagnum magellanicum Sphagnum rubellum Andromeda polifolia	Acid, oligotrophic	Centre of the river valley
Indifferent	Forests, rushes or bushes		Late successional stage	Across the river valley, but not adjacent to the morainic uplands
Indifferent	Filipendulion ulmaraie	Filipendula ulmaria Veronica longifolia	Late successional stage, dynamic groundwater level	Upstream margins of the river valley, often at pastures
Indifferent	Carici-Betulion pubescentis-verrucosae	Betula pubescens Betula verrucosa Alnus glutinosa	Late successional stage	Centre of the river valley
Indifferent	Molinion	Molinia caerulea	Dynamic groundwater level	Upstream margins of the river valley, often at pastures
Indifferent	Phragmition	Glyceria maxima	Flooding	At flood plains of the Biebrza River
Indifferent	Aquatic plants		Surface water	In the Biebrza River

References: (Palczynski, 1984; Van Wirdum, 1991; Wassen et al., 1992; Wheeler and Shaw, 1995)
[1]Ambiguous plant alliances are not listed as these correspond to poorly defined map units.
[2] At most three indicator species are listed.

root-zone layer was not established interactively with the groundwater level by means of an unconfined modelling approach. Instead, the saturated thickness of the root-zone layer was set at a fixed value of 0.3 m based on field observations. The configuration and composition of the five model layers below the root-zone layer (Fig. 3.3) were determined by a schematisation of geological cross-sections by Malinowski et al. (1970). The semi-confining peat layer is represented by the second model layer, which has a uniform thickness of 4 m. In areas where peat is absent, this layer is composed of glacial or peri-glacial sand and gravel. The upper most glacial till is represented by the third layer, which has a thickness of up to 40 m. This layer is composed of sand at the river valley and the outwash plain. The fourth layer represents a homogeneous aquifer composed of sand and gravel and with a thickness ranging from 20 to 70 m. The fifth layer is a homogeneous glacial till with a uniform thickness of 20 m. The sixth model layer is a homogeneous aquifer with a uniform thickness of 30 m. We assume that horizontal hydraulic conductivities were 10 times larger than vertical hydraulic conductivities to account for anisotropy of the geological deposits. The hydraulic conductivities of these layers are established

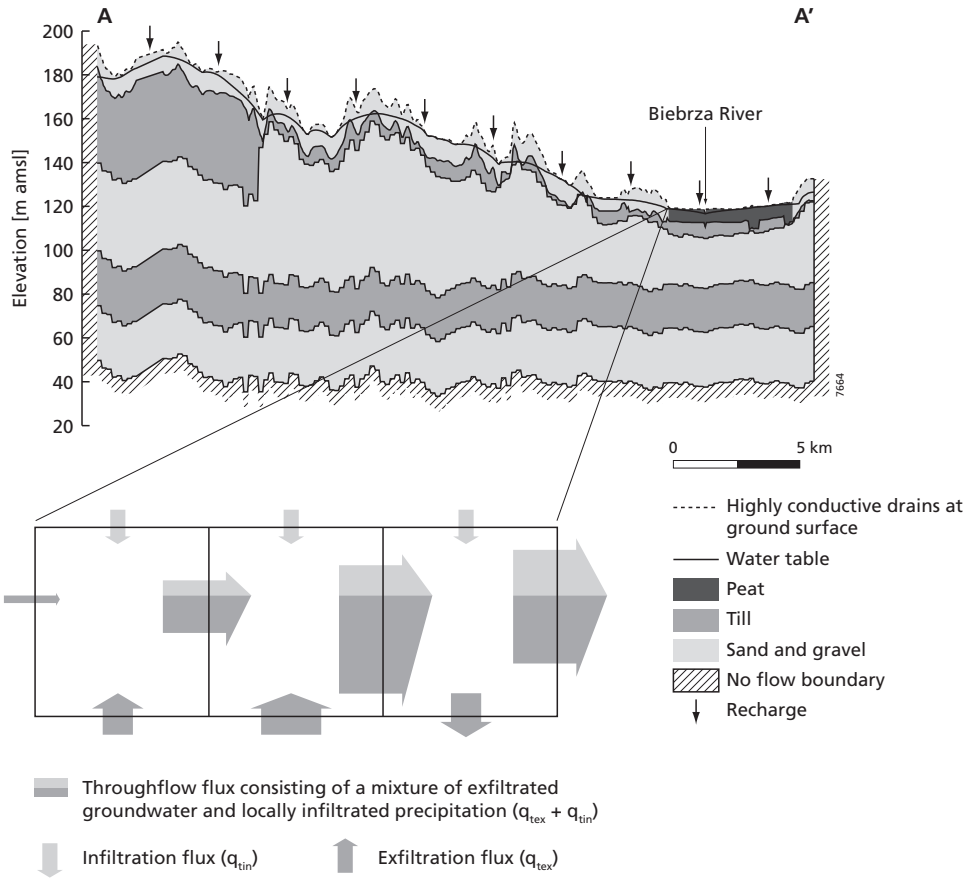

Figure 3.3: Vertical cross section through the model domain. (a) Model layer configuration and boundary conditions; (b) Throughflow model of the subsurface transport of locally infiltrated precipitation and exfiltrated groundwater in relation to modelled fluxes across each cell face of the root-zone layer.

by model calibration (Table 3.2) using water levels observed in 52 domestic wells, with measured levels from September 1999, May 2000, May 2001, December 2001 and April 2002. No-flow boundaries were set at the topographic water divide of the Biebrza River catchment (Fig. 3.2 and 3.3). The model was constructed using a uniform resolution of 50 by 50 m grid cells and comprises an area of 37 by 43 km, resulting in 2.0×10^6 model cells.

Groundwater-surface water interaction was modelled using the MODFLOW RIVER Package. Surface water levels of the Biebrza River were derived from a hydraulic model (Okruszko et al., 2006), whereas those of the tributaries and of the drainage ditches were related to the ground surface elevation. River conductivities were calculated using drainage intensities, i.e., the total area of surface water within a model cell, and specific hydraulic conductivities of the river bed (McDonald and Harbaugh, 1988). Drainage intensities were derived from topographic maps by calculation of the cumulative length of all river reaches within each model cell and by estimation of the width of each river reach based on field knowledge. The specific hydraulic conductivity of the river bed was set at 1 d^{-1}.

Table 3.2: Hydraulic conductivities (m/d) of the exfiltration model for different geomorphological units within the Biebrza River catchment established by calibration of the model using water levels observed in 52 domestic wells at September 1999, May 2000, May 2001, December 2001 and April 2002. The considered range of hydraulic conductivities was derived from the listed references. Note that the hydraulic conductivity of layer 1 was set at 500 m/d at the river valley for the throughflow model.

Layer	Geomorphological unit			Geological feature
	River valley	Outwash plain	Moraine	
1	0.34[a,b]/500	0.1[c]	1.0[c]	Loosely structured peat or loamy sands
2	0.34[a,b]	0.1[c]	1.0[c]	Peat or loamy sands
3	20.0[c]	0.0013[c]	0.0015[c]	Glacial till incised by Biebrza River
4	1.0[b]	1.0[b]	1.0[b]	Sands and gravels
5	0.0018[b]	0.0018[b]	0.0018[b]	Glacial till
6	40.0[c]	40.0[c]	40.0[c]	Sands and gravels

[a] Bleuten and Schermers (1994) [b] Slesicka et al., (2002) [c] Liwski (1994)

Topographic control of groundwater levels leading to diffuse discharge was modelled using the MODFLOW DRAIN Package. Drain elevations were derived from a 50 by 50 m digital elevation model based on digitised contour lines and integrated GPS – total station surveys. Drain conductivities were set at a high value in order to minimize unrealistic water tables above the ground surface (Batelaan and De Smedt, 2004).

Groundwater abstractions were modelled with the MODFLOW WELL Package. Abstractions for public drinking water production were incorporated as time-averaged abstraction rates at the wells from the aquifer underneath the semi-confining peat layer.

Groundwater recharge was modelled using the MODFLOW RECHARGE Package. Spatially variable groundwater recharge fluxes were estimated with the shallow subsurface water balance model WetSpass (Batelaan and De Smedt, 2007), using

$$R = P - I - S - T \qquad \textit{(Eq. 7)}$$

where R is the groundwater recharge (m/y), P the precipitation (m/y), I the interception (m/y), S the surface runoff (m/y) and T the actual transpiration (m/y). Precipitation was set at 583 mm/y (Kossowska-Cezak, 1984). Interception was a constant fraction of precipitation depending on land cover. Surface runoff was a constant fraction of the precipitation that is not lost by interception, i.e., P – I. Runoff fractions were derived from lookup tables, whose values are dependent on the slope, soil type, land use and precipitation intensity relative to the infiltration capacity of the soil. Actual transpiration was calculated using the Penman open water evaporation, vegetation coefficients and a reduction function that describes the availability of soil water and groundwater based on soil type and plant rooting depths. The availability of soil moisture is not limiting evapotranspiration in those model cells in which plant rooting depths exceed the groundwater level, assuming that fen plants are physiologically able to cope with near-saturated conditions. For a more detailed description of the equations and parameter values used to quantify interception, surface runoff and actual evapotranspiration we refer to Batelaan and De Smedt (2007). The WetSpass model was calibrated using the base flow of the Biebrza River as a quantitative indicator of the long-term groundwater recharge of the catchment area. The base flow of

the Biebrza River was established by a HYSEP analysis (Sloto and Crouse, 1996) of the daily Biebrza River discharge from 1951 to 1994 (Batelaan and Kuntohadi, 2002).

3.3.4 Quantification of the fraction of exfiltrated groundwater

For all model cells representing the fen root zone, FEG was calculated as:

$$FEG = \frac{q_{ex} + \sum_{c=1}^{c=4} q_{tex}(c)}{q_{ex} + \sum_{c=1}^{c=4} q_{tex}(c) + q_{in} + \sum_{c=1}^{c=4} q_{tin}(c)} \qquad \text{(Eq. 8)}$$

where q_{ex} (m³/d) is the exfiltration flux, q_{tex} (m³/d) is the throughflow flux of exfiltrated groundwater originating from adjacent cells, q_{in} (m³/d) is the infiltration flux, q_{tin} (m³/d) is the throughflow flux of locally infiltrated precipitation originating from adjacent cells and c is the vertical cell face between adjacent cells (Fig. 3.3b). Note that Eq. 8 only considers positive fluxes, which corresponds to the assumption of steady-state convective transport. q_{ex} and q_{in} in Eq. 8 equal the fluxes across respectively the lower cell face and the upper cell face of the root-zone layer as calculated by the MODFLOW-model. q_{tex} and q_{tin}, however, may consist of a mixture of locally infiltrated precipitation and exfiltrated groundwater (Fig. 3.3b). For this reason, we calculated $q_{tex}(c)$ and $q_{tin}(c)$ by separating the modelled lateral cell-to-cell fluxes ($q_{lat}(c)$, m³/day), using

$$q_{tex}(c) = f_{tex}(c) \cdot q_{lat}(c) \qquad \textit{(Eq. 9)}$$

$$q_{tIN}(c) = f_{tin}(c) \cdot q_{lat}(c) \qquad \textit{(Eq. 10)}$$

where $f_{tex}(c)$ and $f_{tin}(c)$ are fractions of the modelled lateral cell-to-cell flux across cell face *c* for, respectively, exfiltrated groundwater and locally infiltrated precipitation. The fractions of the modelled lateral cell-to-cell fluxes (f_{tex} and f_{tin}) were determined by tracking flow paths representative of both origins of water supply and are defined as

$$f_{tex}(c) = \frac{\sum_{j=1}^{j=m} w_{tex}(c,j)}{\sum_{j=1}^{j=m} w_{tex}(c,j) + \sum_{i=1}^{i=n} w_{tin}(c,i)} \qquad \text{(Eq. 11)}$$

$$f_{tin}(c) = \frac{\sum_{i=1}^{i=n} w_{tin}(c,i)}{\sum_{i=1}^{i=n} w_{tin}(c,i) + \sum_{j=1}^{j=m} w_{tex}(c,j)} = 1 - f_{tex}(c) \qquad \text{(Eq. 12)}$$

where $w_{tex}(c,j)$ is the weight of the jth flow path of exfiltrated groundwater intersecting cell face c, m the total number of flow paths of exfiltrated groundwater intersecting cell face c, $w_{tin}(c,i)$ the weight of the ith flow path of locally infiltrated precipitation intersecting cell face c and *n* the total number of flow paths of locally infiltrated precipitation intersecting cell face c. The weight of each particle was set equal to the flux across the cell face from which the particle was released. These weights represent groundwater loads when considering a relative concentration of 1 for exfiltrated groundwater and a relative concentration of 0 for locally infiltrated precipitation.

Flow paths were determined by a particle tracking analysis based on the MODPATH code (Pollock, 1994). Flow paths of exfiltrated groundwater were identified by particles released at the bottom of the root-zone layer and flow paths of locally infiltrated precipitation were identified by particles released at the ground surface. In order to obtain representative fractions for the separation of modelled lateral cell-to-cell fluxes, 16 evenly distributed particles were released at the bottom of each root zone cell. The same number of particles was released from the ground surface. In total, 2.5×10^5 particles were released. Particles were intercepted at strong sinks, i.e., the particles were allowed to flow through the root-zone layer until they entered a river cell or drain cell that discharged the entire groundwater flux out of the model, or until the model boundaries were intersected.

3.3.5 Evaluation by groundwater composition

The performance of the groundwater model that was successfully fitted to observed patterns in plant alliances was evaluated by comparing modelled FEG with observed patterns in groundwater composition. Electrical Conductivity (EC) was considered as a quantitative indicator of exfiltrated groundwater with distinctly higher values than the EC of locally infiltrated precipitation. Because our modelling approach assumed a mixing of exfiltrated groundwater and local precipitation in the fen root zone, we quantified the performance of our groundwater model as the explained variance (R^2) obtained from linear regression between modelled FEG and the observed EC.

The ECs across the river valley were measured in 110 groundwater samples collected from piezometers that were installed at depths of 10 cm, 20 cm or 30 cm below the peat surface. The piezometers consisted of polyethylene tubes with a screen length of 10 cm. The piezometers were installed along a transect across the river valley in April 1992 (n = 21) and April 1993 (n = 44) and within a 300 m wide zone along the moraine in May 2007 (n = 45). Observation wells were emptied once before sampling and ECs were measured directly after sampling using a field electrode that automatically compensates for temperature effects.

3.4 Results

3.4.1 Comparison of the exfiltration model and the throughflow model

Both the exfiltration model and the throughflow model indicated that groundwater exclusively exfiltrates into the upstream fen margins and into the Biebrza River. Due to the different ability of the exfiltration model and the throughflow model to redistribute groundwater across the fen root zone, however, the modelled zones of groundwater supply differed widely among the models (Fig. 3.4). This causes a different ability of the models to reproduce patterns in plant alliances. The exfiltration model indicated that groundwater is only supplied to the exfiltration zones at the upstream fen margins, whereas minerotrophic plant alliances also occur near the centre of the fen (Fig. 3.4). Although a change in the river bed conductivity, surface water level or the hydraulic conductivity of the semi-confining peat layer causes a slight change in the modelled patterns of groundwater supply, the exfiltration model could not be fitted to the observed patterns in plant alliances. In contrast, the throughflow model indicated that groundwater is redistributed across the fen by throughflow, which causes a larger area to be supplied with exfiltrated groundwater compared to the exfiltration model. Owing to this feature, the throughflow model could be reasonably fitted to the observed patterns in plant alliances (Fig. 3.4). By setting the hydraulic conductivity of the fen root zone at 500 m/d, the modelled zones of groundwater supply included the entire fen, except for the site covered with ombrotrophic plant

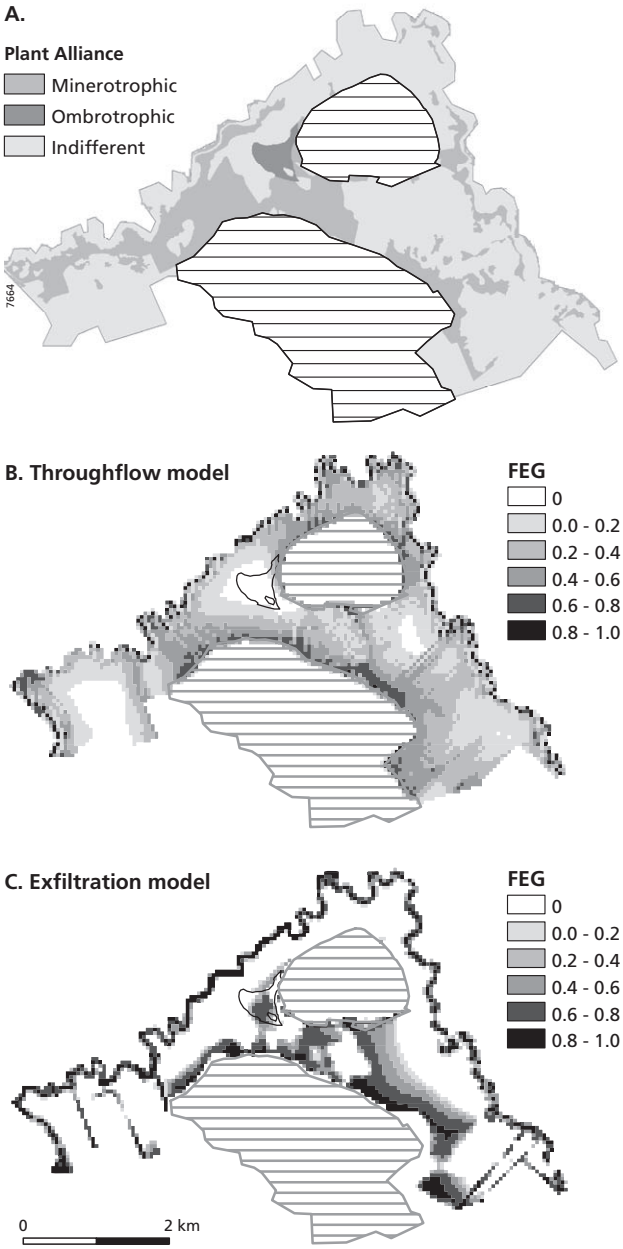

Figure 3.4: Comparison between patterns in plant alliances and modelled fractions of exfiltrated groundwater for the fitted throughflow model and the exfiltration model. (a) Minerotrophic and ombrotrophic plant alliances; (b) Fraction of exfiltrated groundwater (FEG) for the fitted throughflow model; (c) FEG for the exfiltration model. Note that the hatched areas represent the morainic uplands. The solid line in Figs. 3.4b and 3.4c signifies the position of the ombrotrophic plant alliances that are indicated in Fig. 3.4a. Indifferent refers to plant alliances that are indifferent or ambiguous for minerotrophic and ombrotrophic conditions.

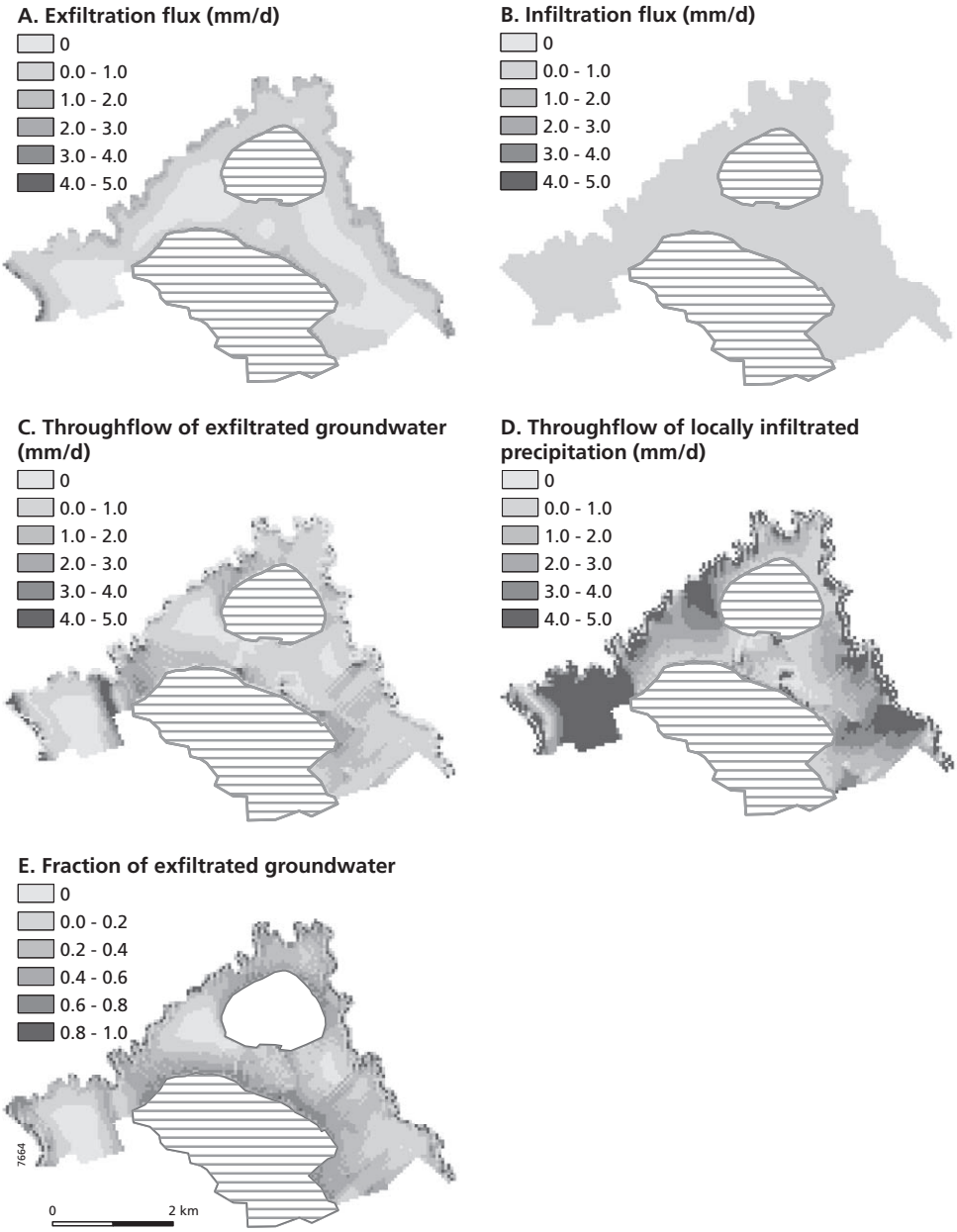

Figure 3.5: Modelled groundwater fluxes generated by the throughflow mechanisms and modelled fractions of exfiltrated groundwater in the fen root zone across the Biebrza River valley for the fitted throughflow model. Exfiltrated groundwater was absent at a site near the centre of the fen which is occupied with ombrotrophic plants. Note that (1) Fig. 3.5e is identical to Fig. 3.4b and (2) the hatched areas represent the morainic uplands.

alliances. A comparable hydraulic conductivity of poorly decomposed peat in natural fens and bogs was previously established by Hoag and Price (1995), Reeve et al. (2000) and Rosa and Larocque (2008).

The exfiltration model indicated an exfiltration flux into the river valley exceeding 0.35 mm/d for the considered range of parameter settings. This is slightly less than the exfiltration flux of 0.43 mm/d calculated with the fitted throughflow model. As groundwater recharge at the river valley was estimated at 0.36 mm/d, both models thus indicate that groundwater recharge and exfiltration cause a water surplus exceeding 0.7 mm/d in the fen root zone. Field observations indicated that the storage of superfluous water by inundation of the ground surface only prevails in response to snowmelt during early spring. This implies that the water surplus in the root-zone layer is mainly discharged by throughflow and subsequently re-infiltrates into the deeper peat. This contradicts with the exfiltration model, because it does not account for throughflow as a discharge mechanism of superfluous groundwater.

3.4.2 Near-surface flow mechanisms driving throughflow

The fitted throughflow model indicated that both exfiltrated groundwater and locally infiltrated precipitation are laterally redistributed across the fen by throughflow (Fig. 3.5c and d). Throughflow fluxes of exfiltrated groundwater yield up to 4 mm/d at the upstream margins of the fen, which relates to the prevalent high exfiltration fluxes that range from 1.0 to 3.5 mm/d (Fig. 3.5a). Towards the centre of the fen, the throughflow fluxes of exfiltrated groundwater gradually decrease, while the throughflow fluxes of locally infiltrated precipitation gradually increase (Fig. 3.5c and d). This change in the composition of throughflow results from the reinfiltration of exfiltrated groundwater downstream of the exfiltration zones, while local precipitation is uniformly supplied to the fen. The spatially variable fluxes generated by the throughflow mechanisms induce high fractions of exfiltrated groundwater between 0.7 and 0.9 at the upstream fen margins, whereas exfiltrated groundwater does not reach two sites at the centre of the fen (Fig. 3.5e). These sites are exclusively supplied with locally infiltrated precipitation, supporting the establishment of ombrotrophic site conditions.

3.4.3 Evaluation of the throughflow model by observed EC patterns

The performance of the fitted throughflow model was evaluated using linear regression between modelled fractions of exfiltrated groundwater and observed ECs at shallow depths. This linear regression explained 69 % of the variance in the EC at a depth of 10 cm and less than 5% of the variance at depths of 20 cm and 30 cm (Fig. 3.6). We attribute this difference in explained variance with depth to soil chemical processes acting during downward flow through the root zone resulting in increasing EC with depth. In particular, the dissolution of calcite has been reported to provide a groundwater-like composition to locally infiltrated precipitation (Komor, 1994; Schot and Wassen, 1993). For this reason, we only considered ECs in the uppermost 10 cm to be representative of the possible infiltration of precipitation. Following this reasoning, the high explained variance of observed ECs at 10 cm depth obtained by linear regression confirms the suitability of our modelling approach of the throughflow mechanisms across the fen.

3.4.4 Groundwater supply of plant alliances

According to the fitted throughflow model, minerotrophic plant alliances occur most frequently at sites with fractions of exfiltrated groundwater between 0 and 0.5 (Fig. 3.7). Within this range, minerotrophic plant alliances seem to be indifferent for the amount of groundwater supply. However, they rarely occur

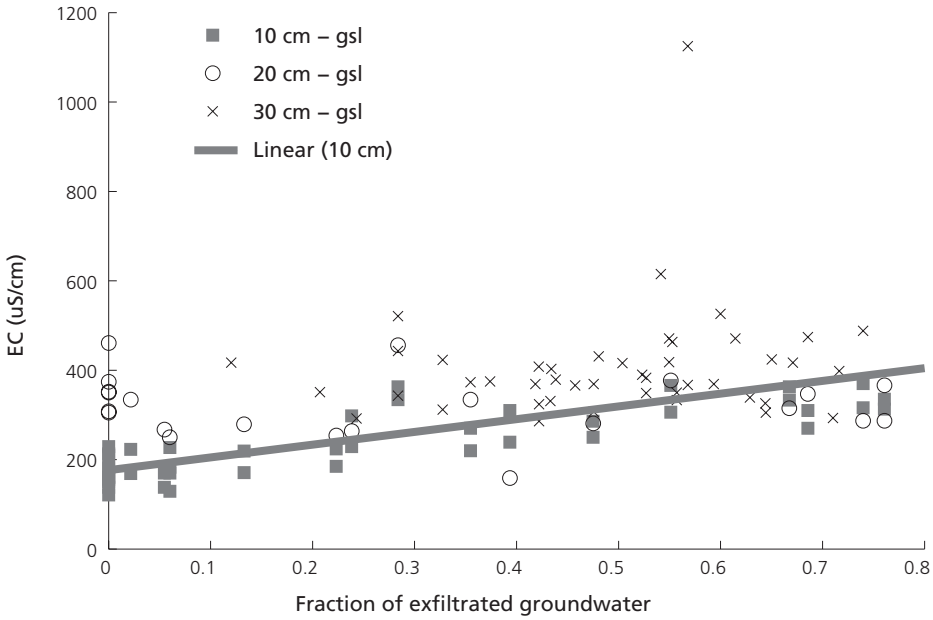

Figure 3.6: Evaluation of the fitted throughflow model by comparison of the modelled fractions of exfiltrated groundwater with observed ECs in shallow groundwater. The linear regression line (R^2 = 0.69) is only plotted for the EC observed at 10 cm depth. R^2 = 0.008 for the EC at 20 cm depth and R^2 = 0.02 for the EC at 30 cm depth.

at sites that are not supplied with exfiltrated groundwater. Interestingly, sites with fractions of exfiltrated groundwater exceeding 0.7 make up less than 5% of the total habitat of these plant alliances.

Ombrotrophic plant alliances are confined to one single patch in the centre of the river valley. According to our model, 85% of this patch is situated outside the influence of exfiltrated groundwater and is supplied exclusively with locally infiltrated precipitation (Figs. 3.5 and 3.7). The fraction of exfiltrated groundwater in the remaining 15% of this patch ranges from 0.05 to 0.45 (Fig. 3.7).

3.5 Discussion and conclusion

3.5.1 Methodological approach

In this study, we analysed how throughflow mechanisms involved in the transport of locally infiltrated precipitation and exfiltrated groundwater impact gradients of abiotic conditions across a near-natural fen. We modelled throughflow using a shallow model layer with a homogeneous thickness and a high hydraulic conductivity. Our approach did not account for the dependency of throughflow fluxes on the groundwater level or saturated thickness of the root-zone layer, as observed by Hutchinson and Moore (2000). As groundwater levels near the Biebrza River become increasingly controlled by drainage rather than by topography (Wassen and Joosten, 1996), our throughflow model likely overestimates the throughflow fluxes near the river. However, the established homogeneous thickness of the root-zone layer is a reasonable assumption for the upstream margins of the river valley, where most of the

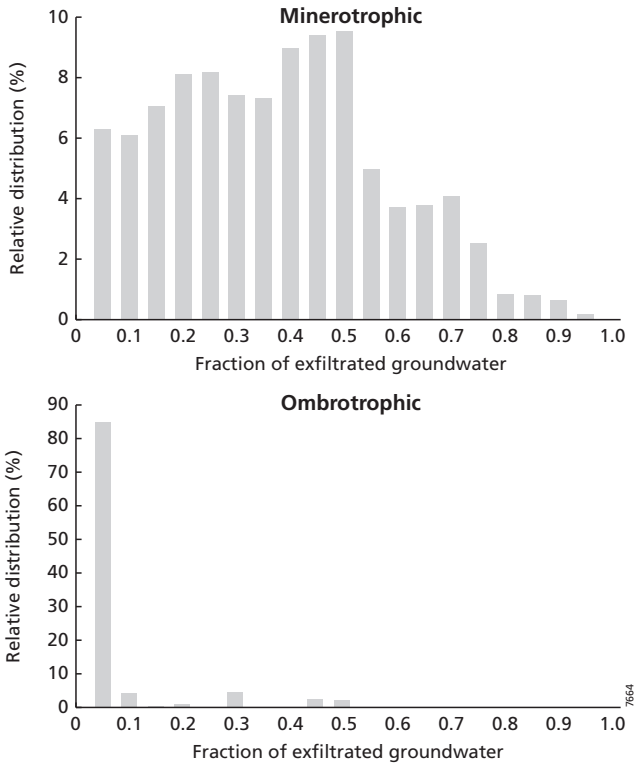

Figure 3.7: Relative distribution of plant alliances typical of minerotrophic and ombrotrophic conditions over the modelled fractions of exfiltrated groundwater for the fitted throughflow model.

fen plants grow and shallow water tables prevail at these locations not directly drained by the Biebrza River (Wassen and Joosten, 1996). As the purpose of this study was to analyse whether groundwater exfiltration or throughflow is the predominant mechanism behind the groundwater supply of natural fen plant communities, this justifies our modelling approach to analyse the near-surface flow mechanisms that determine the origin of water supply of the fen.

3.5.2 Hydrological mechanisms behind fen contiguity

The fitted throughflow model indicates that exfiltrated groundwater and locally infiltrated precipitation are laterally redistributed in varying concentrations across the fen. The resulting pattern of exfiltrated groundwater reasonably agrees with patterns in groundwater composition and plant alliances and could explain the presence of vast, contiguous fen habitat patches found in the near-natural Biebrza River valley. In contrast, the exfiltration model fails to reproduce patterns in plant alliances for the considered range of parameter settings and indicates a water surplus in the fen root zone that could not be discharged in a realistic way. Based on these findings, we conclude that throughflow (1) enables a spatially contiguous supply of exfiltrated groundwater across the near-natural fen and (2) facilitates abiotic conditions suitable for fen plants outside the zones that are directly supplied by exfiltrating groundwater. For this reason, our study provides evidence that habitat contiguity within natural fens is facilitated by throughflow of exfiltrated groundwater, that originates from elongated exfiltration zones adjacent to regional groundwater recharge areas.

The groundwater models presented in this study indicate that the zones of groundwater exfiltration are confined to the upstream fen margins, whereas minerotrophic conditions in the shallow subsurface are observed across most of the fen. Although the models are only representative for average geo-hydrological conditions, these results confirm in a deterministic and quantitative way the conclusions of many authors that minerotrophic conditions in natural fens can prevail outside the zones that are permanently supplied with exfiltrating groundwater (Fraser et al., 2001; Glaser et al., 1990; Wassen and Joosten, 1996). Minerotrophic conditions at these sites are thought to result from mixing of deep groundwater with local precipitation, which can be explained by both the throughflow model and the exfiltration model (Fig. 3.1). The results of the present study, however, provide evidence that these conceptual models may each be relevant for different landscape settings. In fens, like the one presented here, where focused groundwater exfiltration causes a water surplus in the fen root zone throughout most of the year, throughflow of exfiltrated groundwater probably exerts a more dominant effect on abiotic conditions than periodic groundwater exfiltration driven by evapotranspiration in summer seasons. As indicated by falling water tables in summer (Wassen and Joosten, 1996), only prolonged periods of intense evapotranspiration can interrupt the establishment of a water surplus by groundwater exfiltration needed to enable throughflow across the fen. Solutes may then be transported towards the fen surface by upwelling groundwater that is used for plant transpiration instead of by throughflow. However, the relative importance of these hydrological mechanisms behind the solute supply of fens is probably not only determined by the water balance of the fen, but also by the hydraulic conductivities of the fen root zone and the semi-confining peat layer. The higher the contrast between these hydraulic conductivities the more preferential the root zone may be for transporting groundwater throughout the fen and the less groundwater will re-infiltrate from the root zone into the deeper peat. For these reasons, we expect the throughflow model to be applicable to narrow, gently sloping fens situated within lowland river valleys that receive large volumes of exfiltrating groundwater compared to evapotranspiration and where the permeability of the root zone is several orders of magnitude higher than that of the deeper peat.

In contrast, vast fens that are not permanently connected to a regional groundwater system, like those in the Glacial Lake Agassiz Peatlands (USA) studied by amongst others Reeve et al. (2006), derive their water surpluses to a larger extent from local precipitation. In the absence of a permanent supply of groundwater, high evapotranspiration rates during the growing season cause falling water tables and temporally redirect groundwater flow towards the fen surface (Fraser et al., 2001). These vertical groundwater flow reversals are thought to mix deep and shallow groundwater (Fraser et al., 2001; Glaser et al., 1990; McNamara et al., 1992) and may increase the upward transport of solutes by transverse dispersion generated by lateral groundwater flow through the aquifers (Reeve et al., 2006; Reeve et al., 2001). As these mixing mechanisms are only relevant for providing minerotrophic conditions at sites distant from groundwater exfiltration areas (Reeve et al., 2001), we expect the exfiltration model to be applicable to vast fens.

3.5.3 Implications for hydrological fen restoration

Knowledge of the hydrological mechanisms that underlie persistent plant communities within natural fens is essential to improve currently utilized hydrological restoration strategies of managed fens. Managed fens often have an anthropogenically controlled hydrology to accommodate multiple land uses like housing and agriculture. Tile drains and ditches (Schot et al., 2004; Van Loon et al., 2009a) and groundwater abstractions (Fojt, 1994), for example, intercept groundwater that is potentially directed to

the fen surface and prevent the available groundwater from entering the fen root zone. Furthermore, drainage elements accelerate the discharge of groundwater from fens via surface water and often prevent the reinfiltration of groundwater into the fen root zone (Wassen et al., 1990). For these reasons, anthropogenic hydrological interferences are thought to underlie the reduction of spatially contiguous zones of groundwater supply during natural conditions, into multiple smaller zones of groundwater supply during managed conditions (Van Loon et al., 2009b). This may have contributed to the loss and fragmentation of habitat of many low-productive fen plants. In order to mitigate the negative effects that habitat fragmentation has on the viability of fen plant populations (Ewers and Didham, 2004), contiguous fen plant populations as seen in natural fens need to be restored. The demonstrated importance of the lateral redistribution of exfiltrated groundwater by throughflow for sustaining contiguous fen plant populations implies that restoration measures should ensure both the transport of available groundwater towards the fen surface and the conservation of exfiltrated groundwater in the shallow subsurface. We conclude that instead of measures that enhance groundwater flow to fens, like closing down abstraction wells, the elimination of drainage elements requires the highest priority in fen restoration projects.

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4 Local and regional impact of anthropogenic drainage on fen contiguity

A.H. van Loon, P.P. Schot, M.F.P. Bierkens, J. Griffioen and M.J. Wassen, 2009. Local and regional impact of anthropogenic drainage on fen contiguity, Hydrology and Earth System Sciences, 13, 1837-1848.

Abstract
Knowledge of the hydrological mechanisms behind habitat fragmentation of fen plant communities in intensively managed regions like The Netherlands is essential to improve currently utilized fen restoration and conservation strategies. In this study, we analysed the local and regional impact of anthropogenic drainage on the groundwater supply of fens. For this purpose, we developed fine-scale groundwater models and collected empirical data to analyse (1) the differences in groundwater supply between an anthropogenically drained fen and a poorly drained fen in The Netherlands and (2) the local and regional effects of the elimination of drainage ditches on the groundwater supply of both fens. Our results consistently indicated the presence of recently infiltrated precipitation on top of upwelling groundwater across the anthropogenically drained fen and a mixing gradient of recently infiltrated precipitation and upwelling groundwater across the poorly drained fen. Furthermore, our results showed that the elimination of drainage ditches from the anthropogenically drained fen increased the area and the flux of groundwater supply of both the anthropogenically drained fen and the poorly drained fen. We conclude that anthropogenic drainage not only causes a lowering of groundwater tables, but also (1) enhances the infiltration of local precipitation across fens while simultaneously preventing upwelling groundwater from entering the fen root zone and (2) reduces the groundwater supply of adjacent fens by intercepting groundwater that is potentially directed to downstream regions. These insights support the need to reconsider the current priorities in hydrological fen restoration strategies.

4.1 Introduction

Although the sustainable conservation and restoration of endangered plant species in Europe has been internationally agreed upon since the early 1990s (Council of Europe, 2000), only modest progress has been made to counteract the negative effects of land reclamation and environmental degradation on fens. One of the reasons is that currently utilized fen restoration strategies are often ineffective in the counteraction of habitat fragmentation of the remaining fen plant populations (Klimkowska et al., 2007). Habitat fragmentation is disadvantageous for species if ecological barriers prevent seed dispersal or the genetic exchange between populations (Ozinga et al., 2009; Hooftman et al., 2003). For low-productive fens, these ecological barriers may consist of zones of ceased groundwater supply, as these zones are thought to be less suitable for the establishment and survival of most fen plant species (Sjörs and Gunnarsson, 2002). The hydrological mechanisms behind the development of zones of ceased groundwater supply are still poorly understood; however, this knowledge is essential to improve currently utilized fen restoration strategies. In this chapter, we analyse how anthropogenic drainage affects the groundwater supply of fens.

Particularly ambitious efforts to conserve and restore low-productive fens have been undertaken in The Netherlands, because these fens usually accommodate a high diversity of plant species, many of which have a threatened status (Lamers et al., 2002). Low-productive fens are typical of sites with a low nutrient availability (Bedford et al., 1999) and a near-neutral pH (Sjörs and Gunnarsson, 2002). These site factors are usually conditioned by the supply of both upwelling groundwater and local precipitation (Amon et al., 2002). The excessive water supply causes shallow groundwater tables and anaerobic conditions in the shallow subsurface (De Mars and Wassen, 1999; Boomer and Bedford, 2008b). In addition, dissolved minerals are transported by the groundwater to the fen surface. Both the shallow groundwater tables and the supply of dissolved minerals maintain the acidity of fens at a near-neutral pH level (Kemmers et al., 2003; Almendinger and Leete, 1998) and limit nutrient availability for plant

growth provided the sulphate concentration of the groundwater is low (Boomer and Bedford, 2008a; Lamers et al., 1998).

Environmental degradation of low-productive fens may consist of desiccation, acidification or eutrophication (Lamers et al., 2002). These degradation processes are often triggered by a shift in the origin of groundwater supply as a result of water management practices. In particular, drainage (Schot et al., 2004) and groundwater abstractions (Fojt, 1994) are thought to prevent groundwater from entering the fen root zone, because they intercept groundwater that is potentially directed to the fen surface. This decreased supply of groundwater may cause a fall in groundwater tables and enhances the infiltration of local precipitation and surface water (Van Wirdum, 1991). As the chemical compositions of precipitation and surface water deviate from that of groundwater, an increase of these infiltration rates are thought to cause abiotic conditions that are less suitable for fen plants (Wassen et al., 1990; Fojt and Harding, 1995).

Since exfiltrating groundwater mediates abiotic conditions that are suitable for fen plants (Klijn and Witte, 1998), habitat fragmentation of low-productive fens may be related to the development of zones of ceased groundwater supply, i.e., the disintegration of spatially contiguous zones of groundwater supply. Spatially contiguous zones of groundwater supply are common in natural fens, including those in Poland (Van Loon et al., 2009b), Germany (Succow and Joosten, 2001) and Siberia (Schipper et al., 2007). In managed fens, however, these zones have become dispersed as a result of regional changes in groundwater flow caused by anthropogenic developments (Van Loon et al., 2009a). Furthermore, it is hypothesized that the interception and subsequent discharge of groundwater by drainage ditches may further reduce the area and thus the contiguity of zones of groundwater supply. This hypothesis is supported by 2D groundwater flow and transport models (Schot et al., 2004) and hydrochemical field surveys at numerous drained fens (Grootjans et al., 1988; Wassen et al., 1990; Bootsma et al., 2002). These studies indicate that anthropogenically drained fens are not supplied with groundwater, but with locally infiltrated precipitation. None of these studies, however, provide a spatially explicit analysis of the impact of anthropogenic drainage on the groundwater supply of fens. This knowledge is essential for the improvement of the current perception of the hydrological mechanisms behind fen deterioration.

This chapter presents an analysis of the impact that anthropogenic drainage has on the groundwater supply of fens. We not restricted ourselves to on-site, local effects, but we also analysed how changes in water management on a local scale affect downstream regions, i.e., exert effects on a regional scale. For this purpose, we developed fine-scale groundwater models and collected empirical data to analyse (1) the differences in groundwater supply between an anthropogenically drained fen and a poorly drained fen and (2) the effects of the elimination of drainage ditches on the local and regional groundwater supply of fens. We hypothesize that anthropogenic drainage (1) directs local groundwater flow to the drainage ditches and thus prevents upwelling groundwater from entering the fen root zone (Schot et al., 2004) and (2) intercepts groundwater that is potentially directed toward downstream regions and thus reduces the groundwater supply of adjacent fens.

4.2 Study area

The Naardermeer is a polder in the centre of The Netherlands (52°17′N and 5°8′W) that is comprised of fens, a number of lakes and pastures (Fig. 4.1a). The Naardermeer is bordered to the east by the

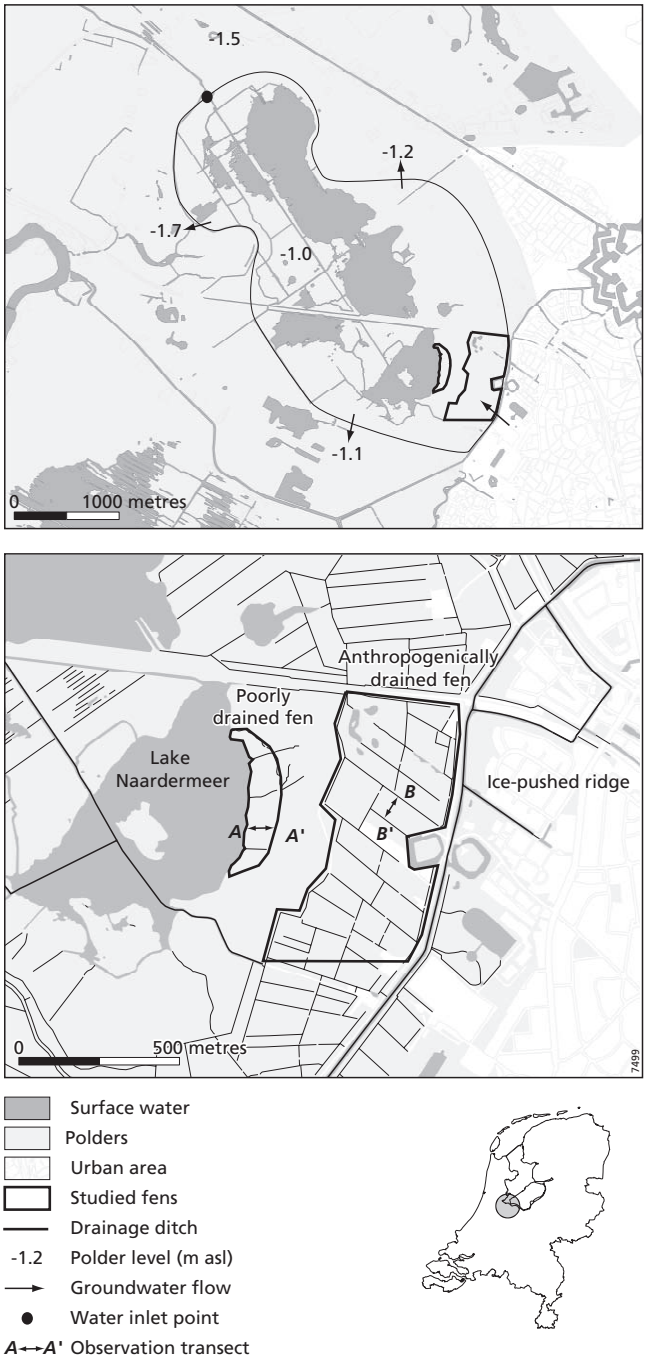

Figure 4.1: Topographic maps of (a) the Naardermeer, The Netherlands and (b) the anthropogenically drained fen and the poorly drained fen.

ice-pushed ridge Het Gooi. This ridge consists of elongated hills of sandy fluvial deposits that had been pushed up by glaciers during the Saalien glaciation. Owing to its relatively high topography (0-30 m asl), the ice-pushed ridge functions as a regional groundwater recharge area (Schot, 1989). Land cover of the ridge consists of urban areas, heaths and forests. Groundwater abstractions for drinking water production were removed from the ridge during the 1990s in order to enhance groundwater flow to the fens in the Naardermeer.

The Naardermeer is bordered to the north, south and west by other polders (Fig. 4.1a). Polders are water management districts from which excessive water is drained by means of dense ditch networks and discharged by pumping. In periods of water deficit, however, the ditch networks are used to irrigate the polders with alien surface water that is pumped in to acquire optimal conditions for agricultural crop production. Owing to their low topography (-1.7 to -1.1 m asl), these polders form the regional drainage basis of the Naardermeer, implying that infiltration conditions prevail at the downstream margins of the Naardermeer (Schot et al., 1988). Water losses caused by infiltration and evapotranspiration are compensated for by the supply of alien surface water to the north-western lake of the Naardermeer during the summer season (Barendregt et al., 1995).

The anthropogenically drained fen in the eastern part of the Naardermeer comprises a 500 m wide zone adjacent to the ice-pushed ridge Het Gooi (Fig. 4.1b). This fen is drained by parallel drainage ditches that are 0.4-1.0 m deep and spaced 30-60 m apart. These drainage ditches are relicts of the former agricultural use of this fen. The fen has now become an extensively managed buffer zone to protect the downstream fens and Lake Naardermeer from eutrophication (Barendregt et al., 1995). The surface water levels in the drainage ditches are anthropogenically controlled at 0.4-0.7 m below ground surface by means of weir constructions and a supply of alien surface water via the ditches during periods of water deficit in summer. Ground surface elevations of the anthropogenically drained fen range from -1.0 to 0.0 m asl. As a result of this relatively low topography, groundwater flow is directed from the ice-pushed ridge to the fen (Schot, 1989).

The poorly drained fen is situated along one of the lakes in the Naardermeer (Fig. 4.1b). This fen is drained not only by the lake, but also by few shallow drainage ditches. The impact of these draining elements on groundwater flow through the fen is limited, however, as the fen is only slightly elevated above the lake level (Wassen et al., 1989). Alien surface water supplied to Lake Naardermeer does not reach the lake bordering the poorly drained fen. Owing to its low topography (-1.0 to -0.5 m asl), the poorly drained fen is supplied with both groundwater recharged at the ice-pushed ridge and brackish palaeo-groundwater (Wassen et al., 1989; Schot et al., 1988) that originates from early Holocene sea water intrusions (Post et al., 2003).

Groundwater flow to and within the Naardermeer is through aquifers consisting of unconsolidated, fluvial deposits. The hydrological base of the study area consists of early Pleistocene clays of marine origin at -250 to -150 m asl. Discontinuous resistance layers consisting of fluvial clays interfinger the aquifers laterally. The ice-pushed ridge consists of coarse sands that are partly intercalated with sloping clay sheets in the east. A semi-confining peat layer with a thickness up to 0.8 to 1.0 m is present in the Naardermeer. This peat layer is not present at the ice-pushed ridge.

4.3 Method

4.3.1 Groundwater modelling

Groundwater exfiltration patterns across both the anthropogenically drained fen and the poorly drained fen were established using a 3D groundwater model. This groundwater model consisted of six model layers that were defined according to the geological stratigraphy of the catchment of the Naardermeer. The horizontal resolution of the model was 5 by 5 m. This high horizontal resolution corresponds to the resolution of the most detailed digital elevation model available (Van Heerd et al., 2000) and serves to accurately establish groundwater exfiltration patterns on a local scale. The groundwater model was based on the MODFLOW code (McDonald and Harbaugh, 1988) and was developed in three successive stages. Initially, we developed a regional steady-state groundwater model of the catchment of the Naardermeer and its surroundings (for details of the model set-up see Van Loon et al., 2009a). The model grid size was 50 by 50 m. Transmissivities were calibrated using time-averaged hydraulic heads observed in 659 monitoring wells between 2000 and 2005. Then, the steady-state groundwater model was modified into a transient groundwater model representative for 2006. Transient behaviour was determined by temporally varying groundwater recharge, groundwater abstractions and surface water levels. Transient equilibrium was accomplished by resuming the model run using the modelled heads at December 2006 as starting heads for January 2006, until stable starting heads were obtained. Finally, the transient groundwater model was refined at the Naardermeer through telescopic mesh refinement. The boundary fluxes of the local groundwater model were obtained from the regional groundwater model, however, no feedback was established between these models. Changes in water storage within the studied fens as a result of this missing feedback (Mehl et al., 2006) were prevented by (1) defining the model boundaries a few kilometres from the studied fens and (2) accomplishing transient equilibrium for the refined model. Except for ground surface elevations, surface water levels and drain conductivities, the resolution of the input data was the same for both the local and the regional groundwater models.

4.3.2 Corroboration with empirical data

The methods that are available to observe hydraulic heads were not sufficiently accurate to establish hydraulic head gradients on the small spatial scale of this study. Therefore, we corroborated the modelled groundwater exfiltration patterns using chemical and physical properties of water in order to identify patterns in source waters. The source waters considered in this study were (1) locally infiltrated precipitation, (2) upwelling fresh groundwater, (3) upwelling brackish palaeo-groundwater and (4) alien surface water. These source waters were identified using the indicators chloride (Cl), electrical conductivity (EC) and tritium (^3H). Observed gradients in the Cl, EC and ^3H concentrations were visualised with isolines that were established by Kriging interpolation using a linear variogram model.

Chloride was used as an indicator of alien surface water in the anthropogenically drained fen, because (1) the Cl concentration of alien surface water is usually relatively high compared to that in the other source waters (Table 4.1) and (2) Cl behaves conservatively during flow, i.e., Cl is not involved in any chemical or biological process that may alter its concentration in the groundwater during flow. Based on the ion concentrations of the source waters (Table 4.1), we used Cl concentrations exceeding 20 mg/l as indicators of alien surface water.

Chloride was used as an indicator of upwelling brackish palaeo-groundwater for the poorly drained fen: concentrations exceeding 300 mg/l were used as indicators of brackish palaeo-groundwater,

Table 4.1: Chloride, EC and tritium in the water sources of the Naardermeer.

	Cl (mg/l)	EC (μS/cm)	^{3}H (TU)
Precipitation	< 10[a]	< 50[a]	> 11 TU[b]
Alien surface water	> 100[c]	590[c]	45[b,1]
Upwelling fresh groundwater	< 20[c]	240[c]	0[d]
Upwelling brackish groundwater	> 300[c]		0[d]

[a] RIVM, 2005, [b] Knetsch, 2007, [c] Schot and Wassen, 1993, [d] Robertson and Cherry, 1989.
[1]average concentration in surface water observed at Lobith (East Netherlands) and Maassluis (West Netherlands) in 2006. Note that ^{3}H in surface water at these locations ranged between 26 and 81 TU during 2006 and between 15 and 161 TU during 2005.

concentrations below 20 mg/l as indicators of the absence of brackish palaeo-groundwater and concentrations between 20 mg/l and 300 mg/l as indicators of mixtures of brackish palaeo-groundwater and source waters that contained low amounts of Cl (Table 4.1).

The indicator we used to establish patterns of locally infiltrated precipitation was EC, because (1) the EC of precipitation clearly deviates from the EC of the fens' other source waters (Table 4.1) and (2) compared to individual ion concentrations, the EC is less sensitive to the hydrochemical evolution of infiltrated precipitation that may acquire a groundwater signature during flow. We used ECs below 200 μS/cm as indicators of recently infiltrated precipitation. Electrical conductivities exceeding 200 μS/cm are not ambiguous for any of the source waters as high ECs may relate to the presence of (1) chemically evolved, locally infiltrated precipitation, (2) upwelling groundwater, or (3) infiltrated alien surface water.

In order to identify patterns of locally infiltrated precipitation and upwelling fresh or brackish groundwater, ^{3}H was used as an indicator of groundwater-residence time. We defined ^{3}H signatures of groundwater using ^{3}H concentrations in groundwater at the sampling date as a function of the year of infiltration (see Fig. 4.2). These were calculated from time series of ^{3}H in precipitation in The Netherlands (compiled from Meinardi, 1994 and Knetsch, 2002, 2007) and by considering first-order decay of ^{3}H. Note that ^{3}H signatures established by this approach may underestimate groundwater residence times

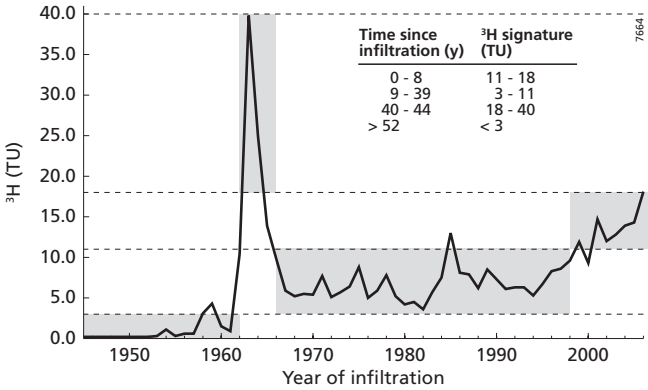

Figure 4.2: Calculated ^{3}H concentration in groundwater for 2006 as a function of the year of infiltration by considering first-order decay of ^{3}H. Tritium signatures of groundwater are indicted by the gray bars and they are listed above the graph.

in the presence of alien surface water, because a high ^3H load in alien surface water caused by industrial activities in the Rhine catchment (Table 4.1) can mask the presence of pre-modern groundwater, which is poor in ^3H.

Chloride, EC and ^3H concentrations in groundwater and surface water were determined across both the anthropogenically drained fen and the poorly drained fen. Samples were collected from observation wells at depths ranging from 0.25 to 2.0 m below the ground surface. The observation wells were installed in clusters of 2 or 4 and they were positioned along transects parallel to the expected direction of groundwater flow. The distance between observation clusters was at most 10 m. A total of 42 observation wells was installed for this study, 20 at the anthropogenically drained fen and 22 at the poorly drained fen. The observation wells consisted of polyethylene tubes with a screen length of 5 cm and a diameter of 1.6 cm. This small diameter was used to minimise the amount of extracted groundwater needed to obtain a representative groundwater sample, i.e., to minimise interference with the hydrochemical patterns across the fens that can be caused by sampling.

Samples were analysed for Cl in November 2005, April 2006, May 2006, August 2006 and November 2006. They were filtered using 0.45 μm filters, stored in polyethylene bottles at 4°C and analysed within three days after sampling using ion chromatography in conformity with the instructions of the Laboratory of Geosciences (Utrecht University, The Netherlands). Electrical conductivities were measured using a field electrode every 4-6 weeks from November 2005 to April 2007 directly after sampling. In November 2006, 12 samples from both the anthropogenically drained fen and the poorly drained fen (total = 24) were analysed for ^3H. The samples were conserved in glass bottles according to the instructions of the Centre of Isotope Research (University of Groningen, The Netherlands). The samples were then artificially enriched by distillation and electrolysis to obtain the lowest detection limit of 0.2 tritium units (1 TU = 1 ^3H atom per 10^{18} H atoms).

4.3.3 Numerical experiment

The local and regional effects of anthropogenic drainage on the groundwater supply of fens were analysed with a numerical experiment consisting of the elimination of drainage ditches from the anthropogenically drained fen. Local effects of anthropogenic drainage were defined as changes in groundwater level, exfiltration pattern and water balance of the anthropogenically drained fen. Regional effects of anthropogenic drainage were defined as changes in groundwater level, exfiltration pattern and water balance of the poorly drained fen.

4.4 Results

4.4.1 Anthropogenically drained fen

The groundwater model indicates permanent groundwater exfiltration into the drainage ditches in the anthropogenically drained fen due to the maintenance of low surface water levels throughout the year (Fig. 4.3a). Outside the drainage ditches, however, groundwater only exfiltrates into the fen root zone when plant transpiration causes falling water tables during the periods of precipitation deficit (i.e., evapotranspiration exceeds precipitation, see Fig. 4.3b). During periods of precipitation surplus (i.e., precipitation exceeds evapotranspiration), groundwater infiltrates into the deeper soil due to the redistribution of excessive water by groundwater flow. As a result of this temporally varying groundwater exfiltration, the relative area of groundwater exfiltration outside the drainage ditches can

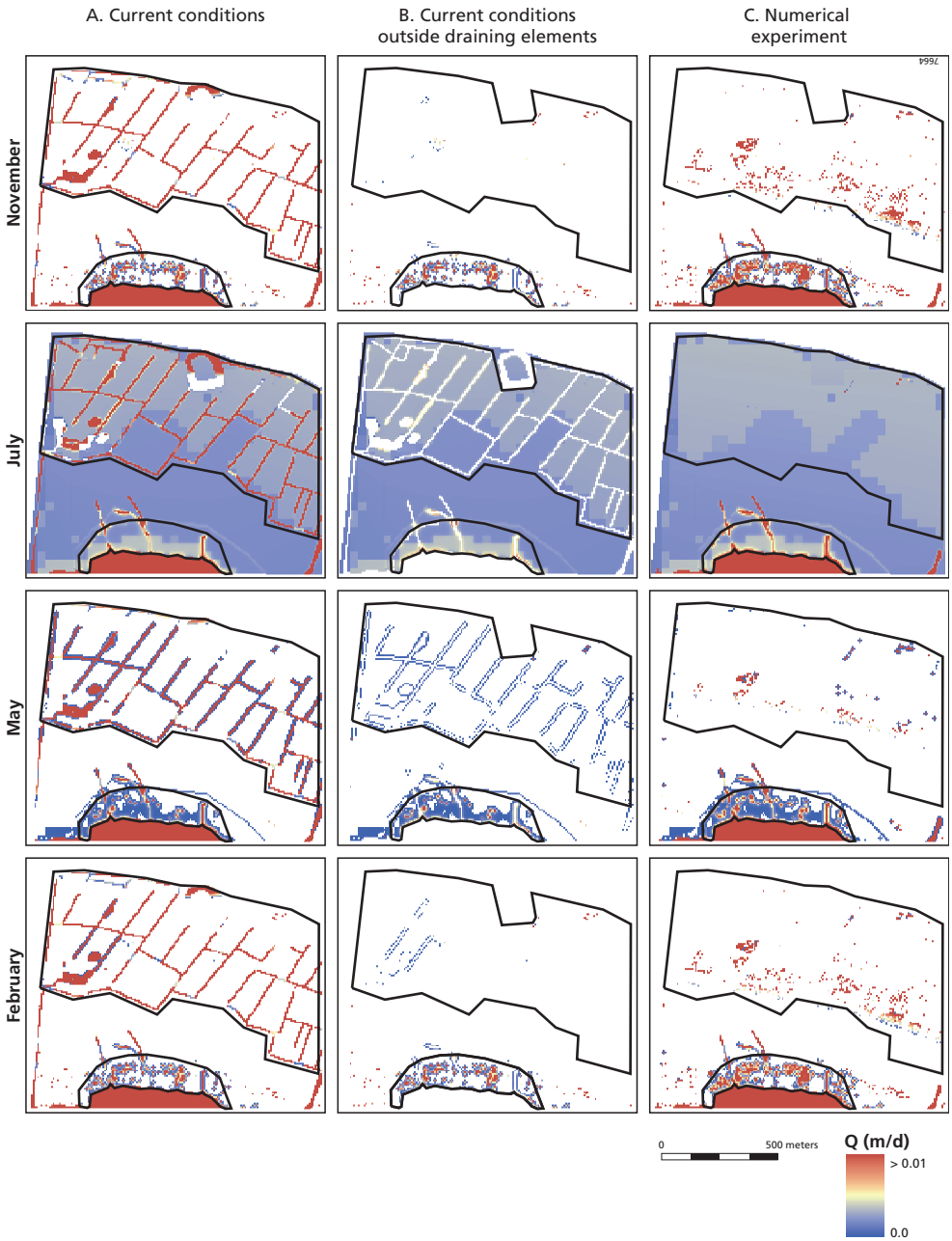

Figure 4.3: Groundwater exfiltration fluxes (Q, m/d) across the Naardermeer modelled for February, May, July and November 2006. (a) Current conditions for the entire fen area; (b) Current conditions outside the drainage elements; (c) Numerical experiment consisting of the elimination of drainage ditches from the anthropogenically drained fen. Note that groundwater infiltration fluxes are not plotted in this figure in order to highlight differences in groundwater exfiltration patterns.

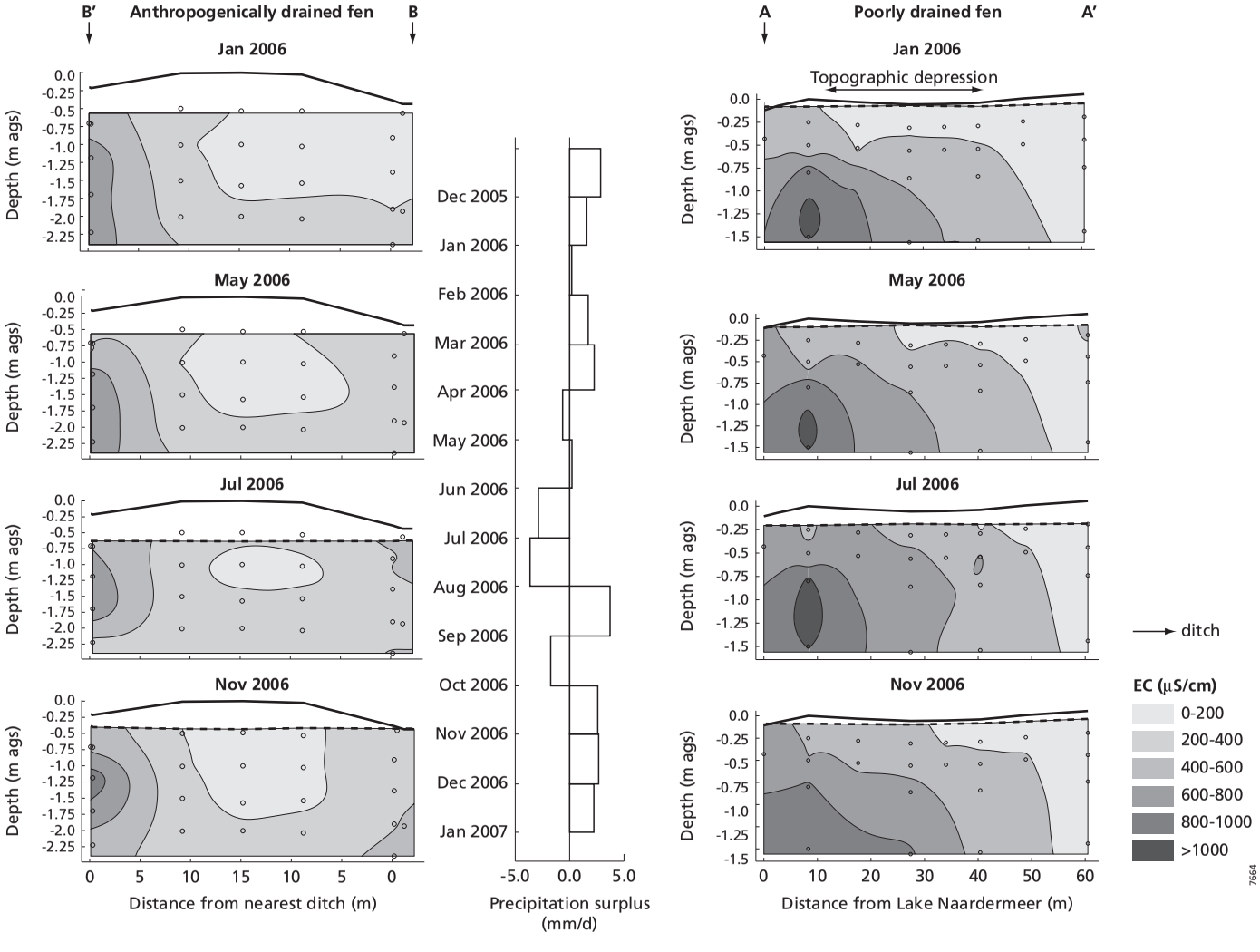
B'
Anthropogenically drained fen
B
Jan 2006
May 2006
Jul 2006
Nov 2006
Depth (m ags)
0.0
-0.25
-0.5
-0.75
-1.0
-1.25
-1.5
-1.75
-2.0
-2.25
0
5
10
15
10
5
0
Distance from nearest ditch (m)
Dec 2005
Jan 2006
Feb 2006
Mar 2006
Apr 2006
May 2006
Jun 2006
Jul 2006
Aug 2006
Sep 2006
Oct 2006
Nov 2006
Dec 2006
Jan 2007
-5.0
0.0
5.0
Precipitation surplus
(mm/d)
A
Poorly drained fen
A'
Topographic depression
0
10
20
30
40
50
60
Distance from Lake Naardermeer (m)
ditch
EC (µS/cm)
0-200
200-400
400-600
600-800
800-1000
>1000
7664

Figure 4.4: (left page) ECs (µS/cm) observed across the anthropogenically drained fen and the poorly drained fen in January, May, July and November 2006. A-A' and B-B' signify the positions of the observation transects in Fig. 4.1. Low ECs (< 200 µS/cm) indicate the presence of locally infiltrated precipitation. The high ECs across the poorly drained fen correspond to a mixing gradient of brackish palaeo-groundwater and locally infiltrated precipitation.

Table 4.2: Effects of the elimination of drainage ditches on the groundwater supply of the anthropogenically drained fen and the poorly drained fen: relative area of groundwater exfiltration and exfiltration flux outside the draining elements. Arrows are directed from the lowest to the highest value of corresponding areas or fluxes.

	Prec sur (mm/d)	Relative area of groundwater exfiltration (%)						Total exfiltration flux (m^3/d)					
		Anthropogenically drained			Poorly drained			Anthropogenically drained			Poorly drained		
		Current conditions		Ditches eliminated	Current conditions		Ditches eliminated	Current conditions		Ditches eliminated	Current conditions		Ditches eliminated
February	1.71	1.0	→	3.8	46.1	→	63.4	19	→	541	73	→	160
May	0.22	11.3[a]	←	2.6	63.1	→	77.4	18	→	191	40	→	77
July	-3.64	100.0	↔	100.0	100.0	↔	100.0	715	→	918	104	→	115
November	2.67	0.4	→	4.4	42.6	→	59.8	23	→	684	79	→	171

[a] Temporal increase of the area of groundwater exfiltration, as a result of the attenuation of local head gradients within the anthropogenically drained fen by the raised surface water levels on May 1st (see Fig. 4.3).

yield 100 % during dry summer months, whereas it is less than 5% during wet winter months (Table 4.2). Despite a slight precipitation surplus in May 2006, the modelled area of groundwater supply for this month is relatively large compared to those for the other months of precipitation surplus. This is caused by groundwater exfiltration into narrow zones parallel to the drainage ditches (Fig. 4.3b) due to the temporary attenuation of local head gradients by the anthropogenically raised surface water levels on May 1, 2006.

The modelled temporally varying groundwater exfiltration outside the drainage ditches is confirmed by the ECs observed across the anthropogenically drained fen (Fig. 4.4). The low ECs (< 200 μS/cm) at the centre of the fen indicate the presence of a permanent rainwater lens of at least 1 m in depth. This rainwater lens expands in a vertical direction when there is a net infiltration of local precipitation during periods of precipitation surplus and shrinks when locally infiltrated precipitation evaporates during periods of precipitation deficit. The shrinking of the rainwater lens is accompanied by a lowering of the groundwater table and by a shift from groundwater infiltration to exfiltration. This shift is indicated by the increased ECs at the centre of the fen from May 2006 to July 2006. Because of the permanently low Cl concentration in the groundwater (Cl < 20 mg/l, see Fig. 4.5), these increased ECs result from

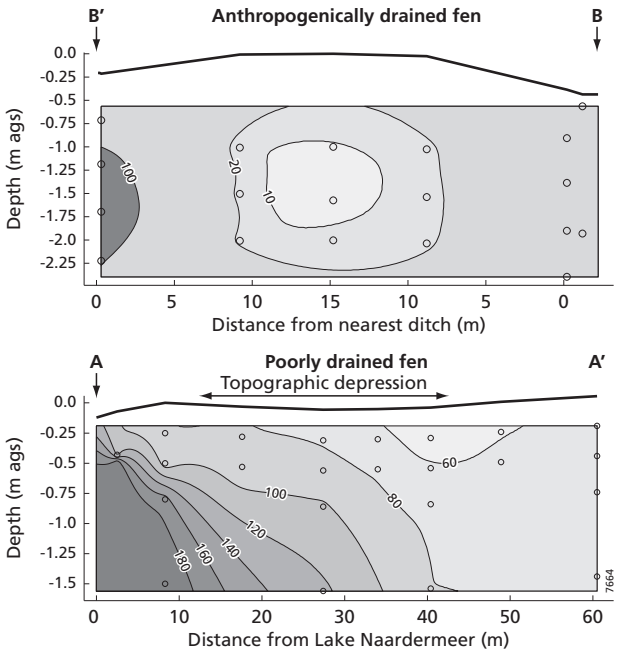

Figure 4.5: Time-averaged Cl concentration (mg/l) observed across the anthropogenically drained fen and the poorly drained fen. A-A' and B-B' signify the positions of the observation transects in Fig. 4.1. Vertical arrows denote draining elements and horizontal arrows topographic depressions. Cl samples were collected in November 2005, March 2006, May 2006, August 2006 and November 2006. A low Cl concentration (Cl < 20 mg/l) indicates the absence of infiltrated surface water in the anthropogenically drained fen. The high Cl concentrations in the poorly drained fen correspond to a mixing gradient of brackish palaeo-groundwater and locally infiltrated precipitation.

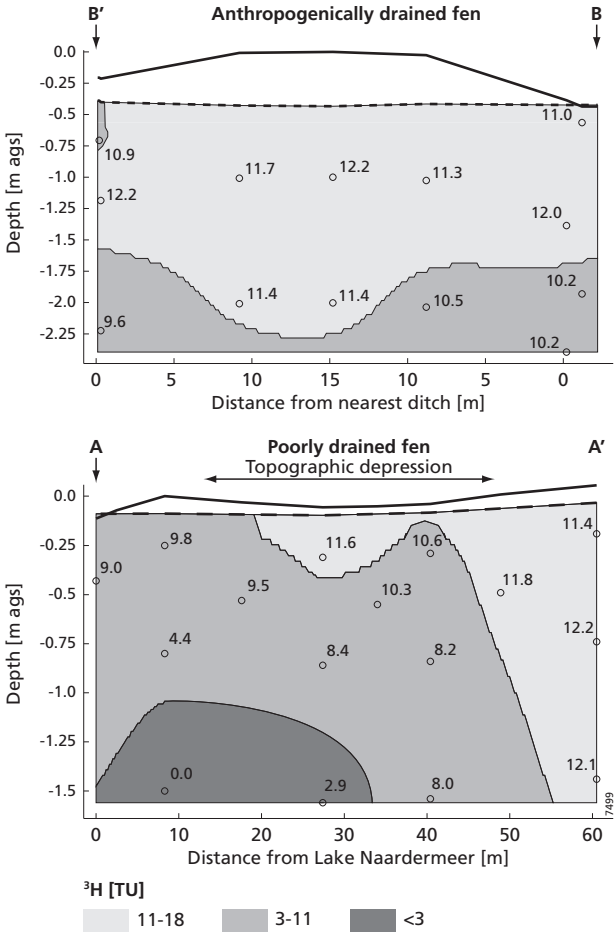

Figure 4.6: Tritium concentrations (TU) observed across the anthropogenically drained fen and the poorly drained fen in November 2006. A-A' and B-B' signify the positions of the observation transects in Fig. 4.1. Vertical arrows denote draining elements and horizontal arrows topographic depressions. The ^{3}H-isolines correspond to the ^{3}H signatures defined in Fig. 4.2.

upwelling fresh groundwater and not from the lateral redistribution of infiltrated surface water from the ditches.

The observed ^{3}H concentrations provide further evidence of the presence of locally infiltrated precipitation (^{3}H > 11 TU) on top of older groundwater (3 TU < ^{3}H < 11 TU) in the anthropogenically drained fen (Fig. 4.6). The observed ^{3}H pattern strongly resembles that of the EC and confirms the presence of a rainwater lens of at least 1 m in depth. The relatively low ^{3}H concentrations (indicating infiltration before 1999 AD) in the groundwater under the drainage ditches confirm the modelled exfiltration into the drainage ditches; however, no pre-modern groundwater (infiltrated before 1962 AD) signified by ^{3}H concentrations below 3 TU was found in the anthropogenically drained fen. As the Cl concentration near the drainage ditches permanently exceeded 20 mg/l (Fig. 4.5), the presence

of pre-modern groundwater might have been masked by ^{3}H enrichment of the groundwater by the infiltrated alien surface water (Table 4.1).

4.4.2 Poorly drained fen

The groundwater model indicates permanent groundwater exfiltration into the topographic depressions near the centre of the poorly drained fen (Fig. 4.3). This relates to the relatively low water levels that become established by the immediate discharge of excessive water by surface runoff. Outside the topographic depressions, i.e., at the topographic mounds near the fen margins, groundwater only exfiltrates in response to falling water tables by plant transpiration during periods of precipitation deficit (Fig. 4.3). During periods of precipitation surplus, however, groundwater levels raise at the topographic mounds, which locally causes the infiltration of local precipitation and its subsequent redistribution from the topographic mounds to the topographic depressions by groundwater flow. As a result of the temporally varying groundwater exfiltration, the relative area of groundwater exfiltration into the poorly drained fen can yield 100 % during dry summer months and ranges from 40 to 65% during wet winter months (Fig. 4.3a and b, Table 4.2).

Observed ^{3}H concentrations across the poorly drained fen (Fig. 4.6) confirm the infiltration of ^{3}H-rich precipitation at the topographic mounds and the exfiltration of ^{3}H-poor, pre-modern groundwater at the topographic depressions. The increasing ^{3}H age with increasing depth and from the topographic mounds to the topographic depressions, corresponds to a mixing gradient of brackish palaeo-groundwater and locally infiltrated precipitation. Evidence for this mixing gradient is provided by the permanently high Cl concentrations (Cl > 20 mg/l) that increase along the same direction as the ^{3}H age does (Fig. 4.5). The absence of indicators of locally infiltrated precipitation (ECs < 200 μS/cm and Cl concentrations < 20 mg/l, see Figs. 4.4 and 4.5 respectively) indicates that precipitation mixes with upwelling brackish palaeo-groundwater immediately after infiltration into the fen soil. The observed ECs (Fig. 4.4) further suggest that brackish palaeo-groundwater disperses through the fen during periods of precipitation deficit to compensate for groundwater losses by plant transpiration and that brackish palaeo-groundwater in the shallow subsurface is diluted by locally infiltrated precipitation during periods of precipitation surplus.

4.4.3 Effects of the elimination of drainage ditches

The numerical experiment indicates that the elimination of drainage ditches from the anthropogenically drained fen causes the reallocation of on-site, permanent groundwater exfiltration zones from the drainage ditches to the topographic depressions as seen in the poorly drained fen (Fig. 4.3). At the topographic mounds, however, groundwater exfiltration remains temporally variable with the precipitation surplus (Fig. 4.3). Due to the rather irregular surface morphology, i.e., the absence of vast topographic depressions as seen in the poorly drained fen, the relative area of groundwater exfiltration outside the drainage ditches remains small compared to that of the poorly drained fen (Table 4.2). Nevertheless, the model results indicate the establishment of hydrological conditions similar to those of the poorly drained fen, as exfiltration fluxes outside the drainage ditches increase by several orders of magnitude (Table 4.2) and surface runoff, instead of drain discharge, become the dominant discharge mechanism (Fig. 4.7). The latter implies that a larger amount of local precipitation discharges from the fen before entering the fen root zone and that exfiltrated groundwater may disperse across the fen and re-infiltrate at downstream regions.

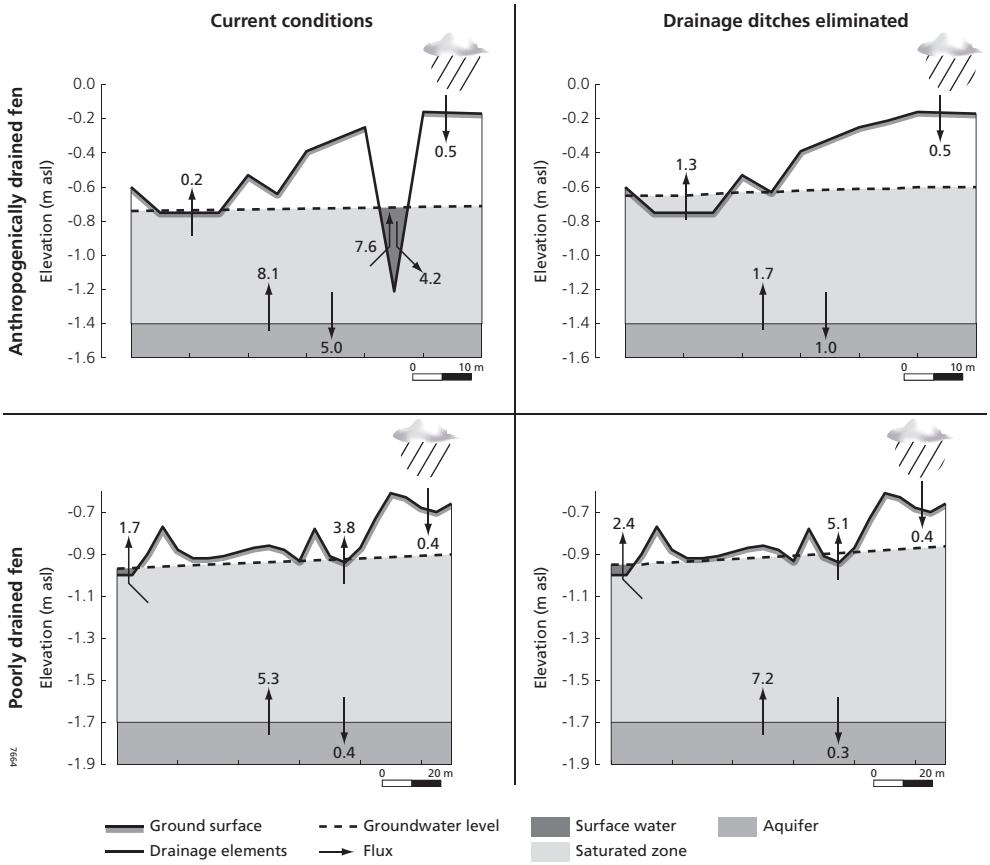

Figure 4.7: Effects of the elimination of drainage ditches on the water balance (mm/d) of the anthropogenically drained fen and the poorly drained fen. Note that part of the groundwater that is currently directed to the anthropogenically drained fen becomes redirected to the poorly drained fen.

Although the elimination of drainage ditches from the anthropogenically drained fen only increased the on-site groundwater level with at most a few tens of centimetres, the consequences for regional groundwater flow were rather large. Part of the groundwater that is currently directed to the anthropogenically drained fen was redirected to areas outside the fen, in which the water levels remained permanent. Part of this redirected groundwater exfiltrated into the poorly drained fen, causing an increase in the exfiltration flux (Fig. 4.7). As a result, the relative area of groundwater exfiltration into the poorly drained fen increased (Fig. 4.3 and Table 4.2), as did the groundwater level and discharge flux by surface runoff (Fig. 4.7). These hydrological changes indicate that the elimination of drainage ditches at the anthropogenically drained fen also enhanced the groundwater supply of the poorly drained fen.

4.5 Conclusion and discussion

4.5.1 Local impacts on fen deterioration

The groundwater model and the empirical data of chemical and physical properties of groundwater consistently indicated the presence of locally infiltrated precipitation on top of upwelling groundwater across the anthropogenically drained fen and a mixing gradient of locally infiltrated precipitation and upwelling groundwater across the poorly drained fen. In addition, the numerical experiment showed that the elimination of drainage ditches from the anthropogenically drained fen caused the establishment of hydrological conditions similar to those of the poorly drained fen. These results confirm the hypothesis postulated by, for example, Schot et al. (2004) that anthropogenic drainage does not only cause a lowering of the groundwater table, but also enhances the infiltration of local precipitation across fens. Simultaneously, it prevents upwelling groundwater from entering the fen root zone, as a result of the immediate discharge of exfiltrated groundwater as surface water. These local hydrological consequences of anthropogenic drainage may have far-reaching consequences for the suitability of fen habitat sites, because (1) base cations become leached from fens, instead of supplied to fens, when locally infiltrated precipitation percolates through the fen soil (Almendinger and Leete, 1998) and (2) oxic conditions, instead of anoxic or sub-oxic conditions, become established across the shallow subsurface when the groundwater supply of electron donors has ceased (Boomer and Bedford, 2008a) and aeration of the fen soil is enhanced (De Mars and Wassen, 1999). As the cumulative effects of these shifts in supply rates are thought to contribute to the acidification (Van Diggelen et al., 1996) and eutrophication (Fojt and Harding, 1995; De Mars et al., 1996) of fens, the hydrological consequences of anthropogenic drainage may underlie the loss of fen plant species observed at drained fens in The Netherlands (Grootjans et al., 2005; Van der Hoek and Sykora, 2006) and Sweden (Mälson et al., 2008). Moreover, we think that a continuous loss of fen plant species will occur across intensively managed regions like Western Europe during the next decades or centuries as anthropogenically drained fens further deteriorate because of the depletion of the soil chemical buffering capacity caused by the permanent leaching of minerals.

4.5.2 Regional impacts on fen deterioration

In addition to the above mentioned local hydrological effects of anthropogenic drainage, the results of our study indicate that drainage ditches intercept groundwater that is potentially directed toward downstream regions. This regional hydrological impact of anthropogenic drainage may further reduce the availability of suitable fen habitat sites, as infiltration rates of precipitation will increase at these downstream regions to compensate for the reduced groundwater supply (Van Wirdum, 1991). Although the regional consequences of anthropogenic drainage for the suitability of fen habitat sites may not be as severe as the local consequences, the increased infiltration of precipitation into fens may accelerate plant succession towards species poorer fens or bogs compared to plant succession under more natural conditions (Van Diggelen et al., 1996), especially if large quantities of phosphorous are released from the soil (Kooijman and Paulissen, 2006). For these reasons, anthropogenic drainage may cause fen deterioration on a spatial scale that is larger than one may expect from previous studies that focused only on the local hydrological effects of anthropogenic drainage (Schot et al., 2004; Holden et al., 2004).

4.5.3 Hydrological fen restoration

Knowledge of the hydrological mechanisms behind habitat fragmentation of the remaining fen plant communities in intensively managed regions like The Netherlands is essential to improve currently

utilized fen restoration and conservation strategies. These strategies often include measures to restore individual fen reserves e.g. by removing abstraction wells from recharge areas as suggested by, amongst others, Fojt (1994), or by lowering the ground surface of fen reserves by means of top-soil removal as suggested by Van der Hoek and Heijmans (2007). In order to counteract habitat fragmentation of low-productive fens, however, a spatially coherent hydrological fen restoration strategy is required that is also suitable to restore zones of ceased groundwater supply outside fen reserves, as these zones are thought to be less suitable for the establishment of most fen plants (Sjörs and Gunnarsson, 2002) and thus may form barriers against fen plant dispersal. In other words, in order to overcome the negative effects of limited dispersal of fen plants in fragmented landscapes (Ozinga et al., 2009), the restoration of spatially contiguous zones of groundwater supply that are common in natural fens (Van Loon et al., 2009b; Succow and Joosten, 2001; Schipper et al., 2007) may be required. Based on knowledge of the hydrology of a near-natural fen in Poland, Van Loon et al. (2009b) have speculated that the elimination of drainage ditches from fens should be given high priority in fen restoration projects in order to re-establish spatially contiguous zones of groundwater supply in fragmented fens. This statement was primarily based on the findings of Schot et al. (2004), who used 2D groundwater flow and transport models to illustrate that drainage ditches prevent upwelling groundwater from entering fen root zones. The results presented in this chapter convincingly demonstrate that the removal of drainage ditches is indeed an effective measure to rewet drained fens with exfiltrating groundwater, even though the on-site exfiltration fluxes may also decrease due to the redirection of groundwater flow to areas outside the drained fen area where the water levels are not altered. This chapter further showed that the elimination of drainage ditches from fens may enhance the lateral redistribution of exfiltrated groundwater by surface runoff, which potentially increases the availability and contiguity of fen habitat sites like in natural fens (Van Loon et al., 2009b; Succow and Joosten, 2001). In order to enhance the supply of exfiltrated groundwater to fragmented fens by surface runoff, however, additional measures to reduce the re-infiltration of exfiltrated groundwater may be required. This is because the infiltration conditions across managed fens are thought to prevail on a larger spatial scale than those across natural fens (Wassen et al., 1996; Van Loon et al., 2009a). Potentially suitable measures to reduce infiltration across fens include the inundation of polders and the closing of abstraction wells in fens.

Earlier ecohydrological analyses of the present study area indicated that endangered fen plant communities in the poorly drained fen recently declined in number and size due to succession towards plant communities that are more common in Western Europe (Barendregt et al., 1995; Wassen et al., 1989). This development was mainly attributed to the decreased supply of groundwater originating from the ice-pushed ridge, which enhanced the infiltration of precipitation and induced the upward movement of brackish palaeo-groundwater (Wassen et al., 1989; Schot, 1989) stored below the lake bordering the fen (Schot, 1989). Based on these findings, water management authorities closed the abstraction wells at the ice-pushed ridge in the late 1990s, with the goal of re-establishing the supply of fresh groundwater to the poorly drained fen. Although this measure has certainly increased the amount of fresh groundwater that is available for regional groundwater flow to the fen (Schot, 1989), our empirical data provide evidence that brackish palaeo-groundwater instead of fresh groundwater is still the major source of water for the fen. In other words, the fresh groundwater supply that is required to sustainably conserve the endangered fen plant communities in this area has not become re-established, even though groundwater fluxes from the ice-pushed ridge have increased over the past 10 years. One explanation for this insufficient fresh groundwater supply is that the replacement of brackish palaeo-groundwater by fresh groundwater may be delayed compared to the redirection of groundwater flow. The results of our study indicate, however, that the lack of a fresh groundwater

supply may also be due to the interception of groundwater by the drainage ditches that are situated about half a kilometre upstream of the poorly drained fen. This latter explanation would imply that most of the redirected groundwater is lost by drain discharge instead of becoming available for fen plants. This renders measures that enhance groundwater flow to fens ineffective when nearby drainage ditches have not been eliminated first. As most fens in Western Europe have been reclaimed by means of the installation of drainage networks (Succow and Joosten, 2001), this is probably a commonly encountered problem that limits the effectiveness of regional hydrological fen restoration measures. For this reason, we suggest that regional measures that enhance groundwater flow to fens be assigned a lower priority than local measures that support the transport of available upwelling groundwater up to the fen surface. For practical reasons, however, it can be more convenient to plan restoration measures in another sequence, but resource managers should then be aware that costly investments to improve the regional hydrology of fen reserves only have effect after measures have been implemented in the direct vicinity of the fens targeted at preventing diffuse loss of groundwater via drainage ditches.

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5 Linking habitat suitability and seed dispersal models in order to analyse the effectiveness of hydrological fen restoration strategies

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Abstract

Integration of the knowledge of processes determining abiotic habitat suitability and seed dispersal may be beneficial to design restoration measures for counteracting habitat loss and fragmentation of endangered plant species. In this study, a linked habitat suitability and seed dispersal model was developed to predict potential species distribution as a function of water management actions, dispersal infrastructure, species-specific dispersal traits and the current species distribution. This novel method was applied to analyse the effectiveness of hydrological restoration strategies in the restoration of viable fen plant populations in an intensively managed region in The Netherlands.

With the aid of the linked model, we were able to optimise the spatial planning of restoration measures, taking into account both the constraints of water management practices on abiotic restoration and the effects of habitat fragmentation on dispersal. Moreover, we could demonstrate that stand-alone habitat suitability models, which assume unlimited dispersal, may considerably overestimate restoration prospects. For these reasons, we believe the presented modelling approach may serve as a basis for future attempts to improve the predictive ability of habitat suitability models, and thus provide a valuable tool for resource managers to design cost-effective fen restoration measures.

The results of our strategy analysis provide new insights into spatially optimised and more cost-effective fen restoration. These insights may necessitate the reconsideration of planned ecosystem networks in drained fens and they may help preserve viable fen plant populations in areas of planned wetland reclamation by means of smart spatial planning of the reclaimed areas.

5.1 Introduction

The sustainable conservation of endangered plant species and the restoration of their habitats were agreed upon internationally in the early 1990s (Millennium Ecosystem Assessment, 2005). A recent analysis of Northwest Europe, however, showed only modest progress in the reduction of the negative effects that habitat loss and fragmentation have on the viability of endangered vascular plant species (Ozinga et al., 2009). Habitat fragmentation, i.e., the breaking apart of large contiguous habitat patches into multiple smaller ones, is disadvantageous for both plant and animal populations, because it results in reduced population sizes, increased edge-effect and reduced habitat connectivity (Ewers and Didham, 2005). Habitat fragmentation, in particular reduced habitat connectivity, may also hinder plants from re-establishing at successfully restored habitat patches due to the limited success of seed dispersal by wind (Soons et al., 2005), water (Boedeltje et al., 2003; Soomers et al., 2009), animal migration (Soons et al., 2008) or anthropogenic activities (Klimkowska et al., 2007). For these reasons, nature restoration strategies should aim at the restoration of habitats in such a way that habitat patches can be reconnected (Hooftman et al., 2004; Ozinga et al., 2009).

Low-productive fens are endangered, species-rich ecosystems (Wheeler and Shaw, 1991) that are typical for sites with a low nutrient availability (Bedford et al., 1999), a near-neutral pH (Sjörs and Gunnarsson, 2002) and permanently groundwater-saturated conditions. These site factors are usually associated with a supply of alkaline, nutrient-poor water, i.e., groundwater or unpolluted surface water (Van Wirdum, 1991). Since unpolluted surface water is rarely available in densely populated regions, low-productive fens usually rely on the supply of exfiltrating groundwater (Schot et al., 1988; Wassen and Barendregt,

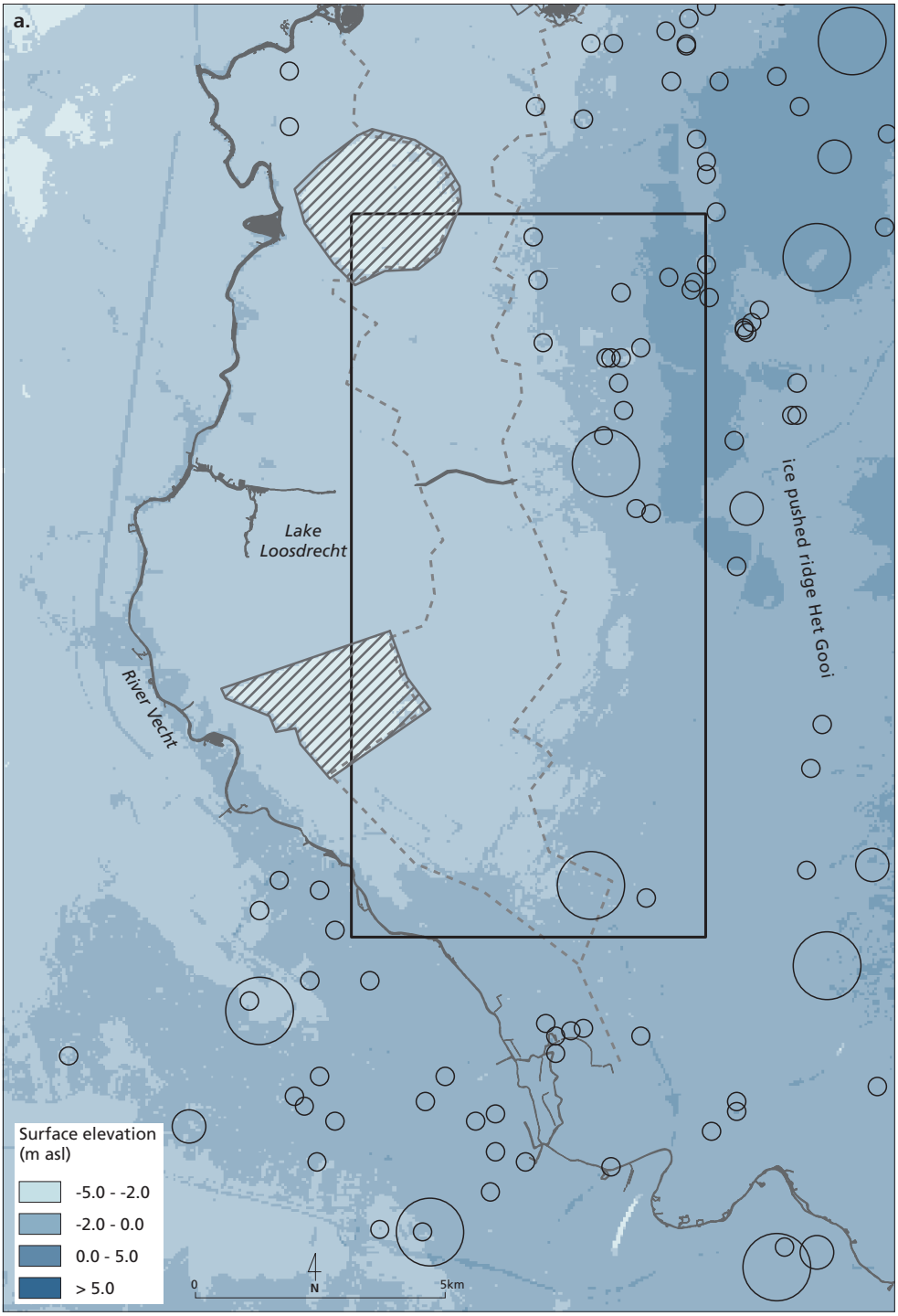
1992). Exfiltrating groundwater carries dissolved minerals to the fen surface (Almendinger and Leete, 1998) and forms the surplus of water that causes shallow groundwater tables and anaerobic conditions in fen root-zones (Boomer and Bedford, 2008). These conditions contribute to the maintenance of a near-neutral pH (Almendinger and Leete, 1998) and control the availability of nutrients for plant growth (Boomer and Bedford, 2008; Boyer and Wheeler, 1989).

Water management practices, such as drainage and groundwater abstraction, cause a lowering of water tables, and may enhance the infiltration of precipitation and polluted surface water into fens (Van Loon et al., 2009a; Van Wirdum, 1991). As the chemical compositions of precipitation and polluted surface water differ from that of groundwater, these hydrological changes often cause environmental degradation (Fojt and Harding, 1995; Wassen et al., 1990). This degradation process is spatially differentiated due to the complex groundwater flow patterns that established during past anthropogenic hydrological interference (Van Loon et al., 2009c). Under natural conditions, groundwater was redistributed from the exfiltration zones by lateral flow through the fen root-zone, i.e., throughflow (Van Loon et al., 2009b). With intensifying water management, however, the spatial configuration of the exfiltration zones changed and exfiltrating groundwater became increasingly intercepted by drainage networks (Van Loon et al., 2009c). This contributes to a fragmented distribution of habitat remnants within a matrix unsuitable for fen plants.

The variable effectiveness of hydrological fen restoration measures (Jansen et al., 2000; Lamers et al., 2002) demonstrates that our present knowledge of the effects of water management on fen deterioration, and how fen deterioration can be reversed, is incomplete. In restoration ecology, habitat suitability and meta-population models can be helpful, because they predict changes in species distribution for varying scenarios. Habitat suitability models describe the probability of plant species occurrence by using tables or regression methods in which habitat conditions serve as the explaining variables and plant species as the dependent variables (Olde Venterink and Wassen, 1997; Schröder et al., 2008; Segurado and Araújo, 2004). When the explaining input variables are derived from physical or chemical speciation models, the effectiveness of abiotic restoration measures can be predicted (Van Ek et al., 2000). However, habitat suitability models usually overestimate species distribution, because they assume that dispersal is unlimited; i.e., they ignore the effects of limited dispersal on species distribution in fragmented landscapes (Ozinga et al., 2005).

Meta-population models, in contrast, describe population dynamics and viability by solving the dynamic equilibrium between dispersal and local extinction mathematically, using (among others) habitat maps as the input variables (Fagan and Lutscher, 2006; Hanski, 2008; Purves and Dushoff, 2005). Since these habitat maps are derived from field observations and not from physical or chemical speciation models, meta-population models lack the flexibility to predict ecosystem responses to hydrological restoration measures.

To overcome the constraints of both modelling approaches, recent studies have linked habitat suitability and dispersal models in order to evaluate the effects of climate change scenarios on the potential distribution of tree species at either a supra-regional or a regional scale (Engler and Guisan, 2009; Iverson et al., 2004; Scheller and Mladenoff, 2008). To our knowledge, however, linked habitat suitability and dispersal models have not yet been used to analyse the effectiveness of regional hydrological fen restoration measures. Such linkage would effectively combine knowledge of the hydrological processes determining fen habitat suitability with that of seed dispersal processes, and


a.
Lake
Loosdrecht
River Vecht
ice pushed ridge Het Gooi
Surface elevation
(m asl)
-5.0 - -2.0
-2.0 - 0.0
0.0 - 5.0
> 5.0
0
5km
N

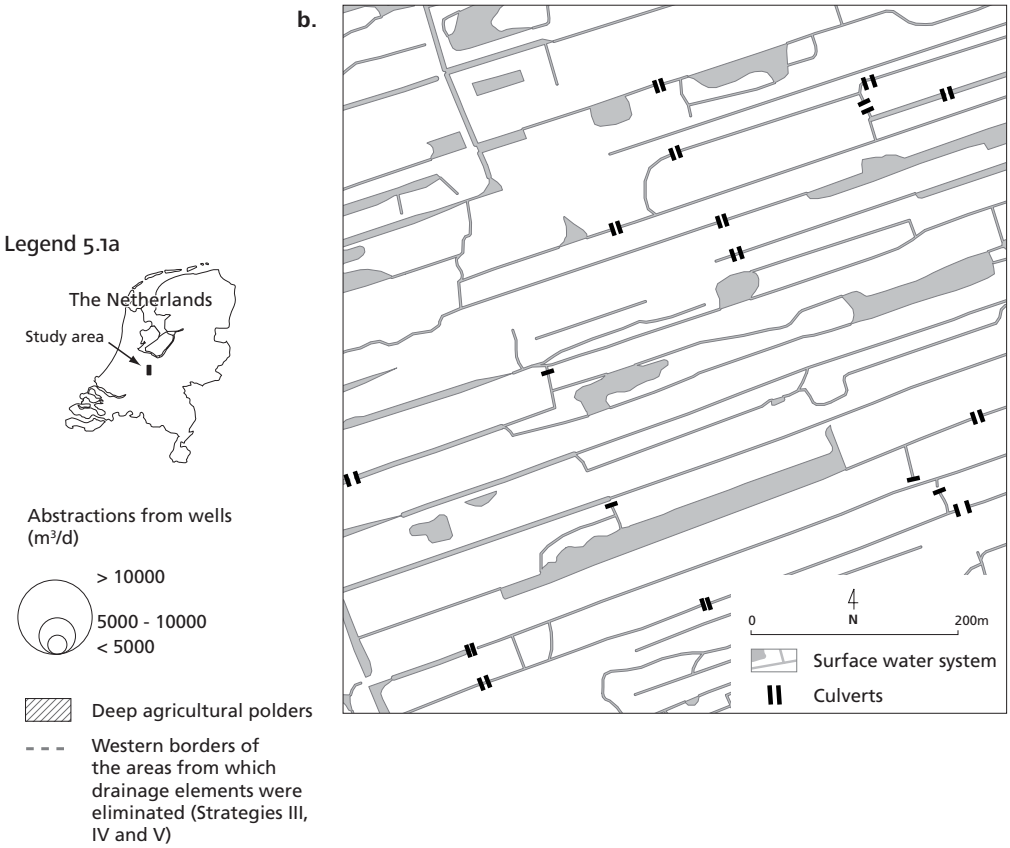


Figure 5.1: Topographic features of the Gooi- and Vechtstreek area (The Netherlands). (a) Surface elevation and spatial aspects of the restoration strategies (left page); (b) Impression of the network of drainage ditches that provides an infrastructure for hydrochorous dispersal.

thus provides the opportunity to optimise hydrological fen restoration measures for the restoration of both suitable fen habitats and sufficient connectivity between habitat patches for viable fen plant populations.

This paper presents a linked habitat suitability and seed dispersal model that predicts potential species distribution as a function of water management actions, dispersal infrastructure, species-specific dispersal traits and current species distribution. The habitat suitability part of the model consists of a deterministic groundwater model to assess the fen habitat configuration for a number of restoration strategies. The seed dispersal part is a two-dimensional, integrated anemochorous-hydrochorous seed dispersal model that is empirically parameterised for a real species. The two sub-models were developed at the regional scale and linked to the local scale in order to integrate the effects of regional groundwater flow and local dispersal on potential species distribution. The objective of this study was to demonstrate that the linked habitat suitability and dispersal model is a powerful tool to optimise the design and spatial planning of nature restoration and conservation measures, in particular for low-productive fens.

5.2 Study area

The strategy analysis was performed for part of the Vechtstreek area in The Netherlands (52°10'N and 5°10'E; Fig. 5.1, page 97). This study area was selected, because (1) remnant populations of low-productive fen plant species persist in fragmented nature reserves, and (2) intensive water management of the river valley and its surroundings reduces the availability of groundwater for fen plants, and thus limits the availability of fen habitat.

The Vechtstreek area was a vast lowland mire until the Middle Ages, when it was reclaimed through the installation of drainage networks. Subsequent land subsidence has resulted in the current ground surface levels being below sea level (Fig. 5.1a). Nowadays, the Vechtstreek area comprises agricultural fields, urban areas, lakes and fen reserves. Fen reserves are comprised of floating fens and terrestrial fens. Floating fens are early-successional stages of terrestrial ecosystems that prevail in ponds with minimal wave action and receive sufficient groundwater to mediate minerotrophic (groundwater-like), nutrient-poor conditions (Schaminée et al., 1995). Terrestrial fens with a nutrient-poor, organic topsoil can have a species composition comparable to that of floating fens, provided that they receive groundwater. Both types of low-productive fens can be maintained for up to several decades if succession is slowed by mowing (Van Diggelen et al., 1996).

Water levels in the Vechtstreek area are intensively controlled to accommodate multiple land uses. Intensively drained water management districts, called polders, have been established for this purpose. The surface water levels of these polders can be controlled independently from each other. During dry summer periods, surface water is supplied from the River Vecht via the ditch network to the polders in order to irrigate crops and nature reserves. During wet periods, superfluous water is drained from the polders into the River Vecht.

The western boundary of the study area is formed by Lake Loosdrecht and the deep agricultural polders Horstermeer and Bethune (Fig. 5.1). The lake level is maintained at -1 m asl (above sea level) by means of active water management. The deep agricultural polders Horstermeer and Bethune are reclaimed lakes with surface elevations ranging from -3 to -4 m asl. Due to their low topographic position, both polders drain large amounts of groundwater and surface water from the river valley (Schot and Molenaar, 1992; Wassen et al., 1990). Because of the intensive agricultural activities in these two polders, nutrients have accumulated in the soils, making them unsuitable for low-productive fen plants.

The study area is bordered to the east by the ice-pushed ridge Het Gooi. This ridge consists of elongated sandy hills that have a high permeability. The surface elevation of the ridge ranges from 0 to 30 m asl. Because of the ridge's relatively high topographic position, groundwater flows from the ice-pushed ridge towards the river valley (Van Loon et al., 2009c). Numerous wells abstract in total 15 million m^3 groundwater per year for the production of drinking water, which reduces the supply of groundwater to the fen reserves in the river valley.

Groundwater flows through unconsolidated, sandy aquifers (Van de Meene et al., 1988; for a cross-section see Van Loon et al., 2009c). The hydrological base of the study area consists of early Pleistocene clays of marine origin at -250 to -150 m asl. Discontinuous resistance layers consisting of fluvial clays intercalate the aquifers laterally. The ice-pushed ridge consists of coarse sands that are partly

intercalated with sloping clay sheets in the east. A semi-confining peat layer with a thickness of 0.8 to 1.0 m is present in the river valley. Peat is not present in the ice-pushed ridge.

5.3 Method

5.3.1 General approach

We linked groundwater and seed dispersal models in order to predict the potential distribution of fen plant species as a function of water management actions. The groundwater model was used to determine the configuration of potential fen habitat. Potential fen habitat was defined as permanently wet, groundwater-fed sites with a morphology that allows for the development of a low-productive fen. By this definition, potential fen habitat consists of ponds that receive exfiltrating groundwater and terrestrial areas that are permanently wet because of groundwater surplus either by exfiltration or by throughflow. We assumed that drainage ditches do not provide habitat for fen plants because the development of a floating fen is prevented by annual mowing or removal of aquatic plants from the ditches. The seed dispersal model was used to identify which habitat patches can be potentially colonised by target species via seed dispersal from existing populations.

The linked models were used to analyse the effectiveness of hydrological restoration strategies for increasing the current viability of endangered fen plant species in the Vechtstreek area. For this purpose, we considered species viability to increase with (1) an increasing total area of subpopulations, (2) increasing subpopulation sizes and (3) decreasing edge effect on subpopulations, i.e., an increasing area with regard to edge-length of subpopulations. These general indicators of habitat loss and fragmentation (Fahrig, 2003) were determined by modelling the potential distribution of *Carex diandra*. *C. diandra* was selected as the focal species, because (1) it is one of the fen species that is greatly affected by water management practices due to its preference for minerotrophic, wet habitat patches (Van Wirdum, 1991; Wassen et al., 1992; Wheeler and Shaw, 1995), (2) it persists in only 34 highly fragmented remnant populations across the study area (Wassen et al., 1990) and (3) sufficient data are available to compile an area-covering, parcel-scale species distribution map (unpublished data Provinces of Utrecht and North Holland).
The hydrological restoration strategies that were considered are (1) Strategy I: inundation of the deep agricultural polders Horstermeer and Bethune in order to redirect part of the 100 x 10^3 m^3/d groundwater that currently discharges into these polders towards the fen surface; (2) Strategy II: closure of all abstraction wells in the river valley and the ridge in order to redirect part of the 40 x 10^3 m^3/d groundwater that is currently intercepted by wells towards the fen surface; (3) Strategy III: elimination of all drainage elements from the upstream fen margins, i.e., a 0.5 – 2 km wide belt adjacent to the ridge; (4) Strategy IV: elimination of all drainage elements across the river valley (both Strategies III and IV aim at reducing diffuse groundwater losses by drainage); and (5) Strategy V: all measures mentioned in the Strategies I – IV. Details of these strategies are provided in Figure 5.1.

5.3.2 Groundwater modelling

Groundwater flow was modelled for each restoration strategy using 3-dimensional, steady-state groundwater models based on the MODFLOW-1988 code (McDonald and Harbaugh, 1988). First, a groundwater model for the current condition was constructed at a 50 x 50 m resolution. The model was calibrated using time-averaged heads of 659 observation wells. For details of the model configuration and parameter estimation the reader is referred to Van Loon et al. (2009c). Next, the

model was refined to a resolution of 25 x 25 m and a highly conductive root-zone layer was added to enable the modelling of throughflow of exfiltrated groundwater (cf. Van Loon et al., 2009b). Throughflow patterns of exfiltrated groundwater were determined using a MODPATH particle tracking analysis (Pollock, 1994). Finally, the modelled zones with groundwater supply (by direct exfiltration or by throughflow) were down-scaled to a resolution of 2.5 x 2.5 m by assigning exfiltration fluxes to surface water elements within the model cell, or by distributing them evenly over the fen surface in the absence of surface water elements. The restoration strategies were simulated by adjusting the groundwater model according to the related changes in hydrological characteristics.

5.3.3 Seed dispersal modelling

Both anemochorous and hydrochorous seed dispersal of *C. diandra* were modelled for each restoration strategy using a 2-dimensional stepping-stone model that considered a successive number of dispersal stages (Fig. 5.2). In the first dispersal stage, the seed shadows of the current populations of *C. diandra* were calculated and new populations were assumed to be established at habitat patches in the seed shadow. The second and following dispersal stages repeated this procedure, with seed shadows being calculated from each new population. New dispersal stages were initiated until seed dispersal no longer resulted in the establishment of new populations.

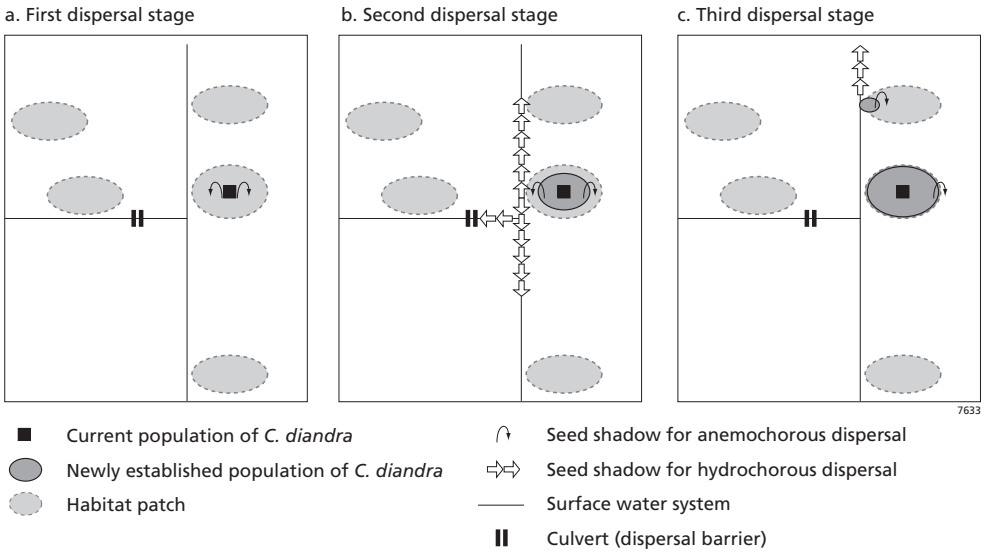


Figure 5.2: Conceptual model of integrated anemochorous-hydrochorous dispersal of *C. diandra* for three dispersal stages. Dispersal is a function of the current species distribution, species-specific dispersal traits, the dispersal infrastructure (i.e., the surface water system) and the configuration of habitat patches. Anemochorous dispersal distances of *C. diandra* ranged from 0 to 10 m and hydrochorous dispersal distances ranged from 0 to 500 m. Anemochorous and hydrochorous dispersal was allowed in any direction. New dispersal stages were initiated until seed dispersal no longer resulted in the establishment of new populations, implying that time is not limiting the success of seed dispersal.

Anemochory

Anemochory is the dispersal of seeds by wind. Like other *Carex* species, *C. diandra* has plumeless seeds that are not specifically adapted to long distance anemochory. However, plumeless seeds can disperse over distances varying from several metres to several kilometres, depending mainly on wind velocity and species-specific dispersal traits, i.e., seed terminal velocity and release height (Soons, 2006). Seeds with a terminal velocity greater than 2 m/s generally do not exceed distances of several metres when dispersing via wind (Soons, 2006). More specifically, the 95% percentile dispersal distance of plants that have dispersal traits comparable to that of *C. diandra* does not exceed 10 m, even if the wind speed approaches that of severe storms (Soons et al., 2004). We calculated the terminal velocity of the seeds of *C. diandra* using the gravitational acceleration, drop height and drop time. Drop time was determined for 20 seeds (cf. Soons and Heil, 2002) randomly selected from 5 populations situated in the study area. Since the average terminal velocity was calculated to be 2.58 m/s (standard deviation: 0.47), we set the maximum dispersal distance via wind at 10 m. We assumed that the seeds could disperse in any direction from a population, because wind direction is variable. This implied that habitat patches could become colonized by *C. diandra* via anemochorous dispersal if they were situated within a distance of 10 m from a population. Because we also assumed that time does not limit the success of seed dispersal, habitat patches became entirely colonised by *C. diandra* as soon as they overlapped with a seed shadow of a neighbouring population.

Hydrochory

Hydrochory is the dispersal of seeds or (parts of) plants by water. Like many other *Carex* species, *C. diandra* is characterised by a relatively high seed buoyancy of ca. 100 days (Van den Broek et al., 2005), i.e., 50% of the seeds still float in stagnant water after ca. 100 days. This potentially enables long-distance dispersal via the surface water system. However, dispersal barriers, such as aquatic plants or helophytes, rather than seed buoyancy seem to limit hydrochorous dispersal distances in anthropogenically drained fens in The Netherlands (Soomers et al., 2009). In these fens, dispersal distances of 500 m along surface water elements have been observed for seeds of *Carex* species (Beltman et al., 2005; Soomers et al., 2009). Because wind stress on the water surface, not water flow, is the principle driver of hydrochorous seed dispersal via surface water elements in stagnant or slow-flowing water (Soomers et al., 2009), we assumed that seeds could be dispersed over a distance of 500 m in any direction via surface water elements. We further assumed that seeds could neither pass culverts (Soomers et al., 2009) nor disperse from one polder to the other, because the polders were not directly connected via surface water elements. The dispersal infrastructure for hydrochory, i.e., the configuration of the surface water system, was derived from a high-resolution topographical map (see example in Fig. 5.1b), gridded to a resolution of 2.5 × 2.5 m, and combined with the modelled water levels to identify inundated areas.

5.4 Results

5.4.1 Current condition

The groundwater model for the current condition showed that most of the groundwater that exfiltrates into the river valley is intercepted by the deep agricultural polders and agricultural drainage ditches outside the deep polders (Table 5.1) and is inaccessible to fen plants as a result. This hinders the establishment of contiguous fen habitat patches (Fig. 5.3a) and consequently limits the success of anemochorous dispersal of *C. diandra* as indicated by the small number of subpopulations that can

potentially establish via this dispersal mechanism (Fig. 5.4a). The effect of habitat fragmentation on the hydrochorous dispersal of *C. diandra* is less severe, even though only half of the habitat patches can be colonised by means of seed dispersal via the surface water system (Fig. 5.4a). Due to limited dispersal and the small sizes of the fen habitat patches, the populations of *C. diandra* have a rather low viability given the small number, area, sizes and area to edge-length ratios of the modelled subpopulations (Fig. 5.4).

5.4.2 Inundation of deep agricultural polders (Strategy I)

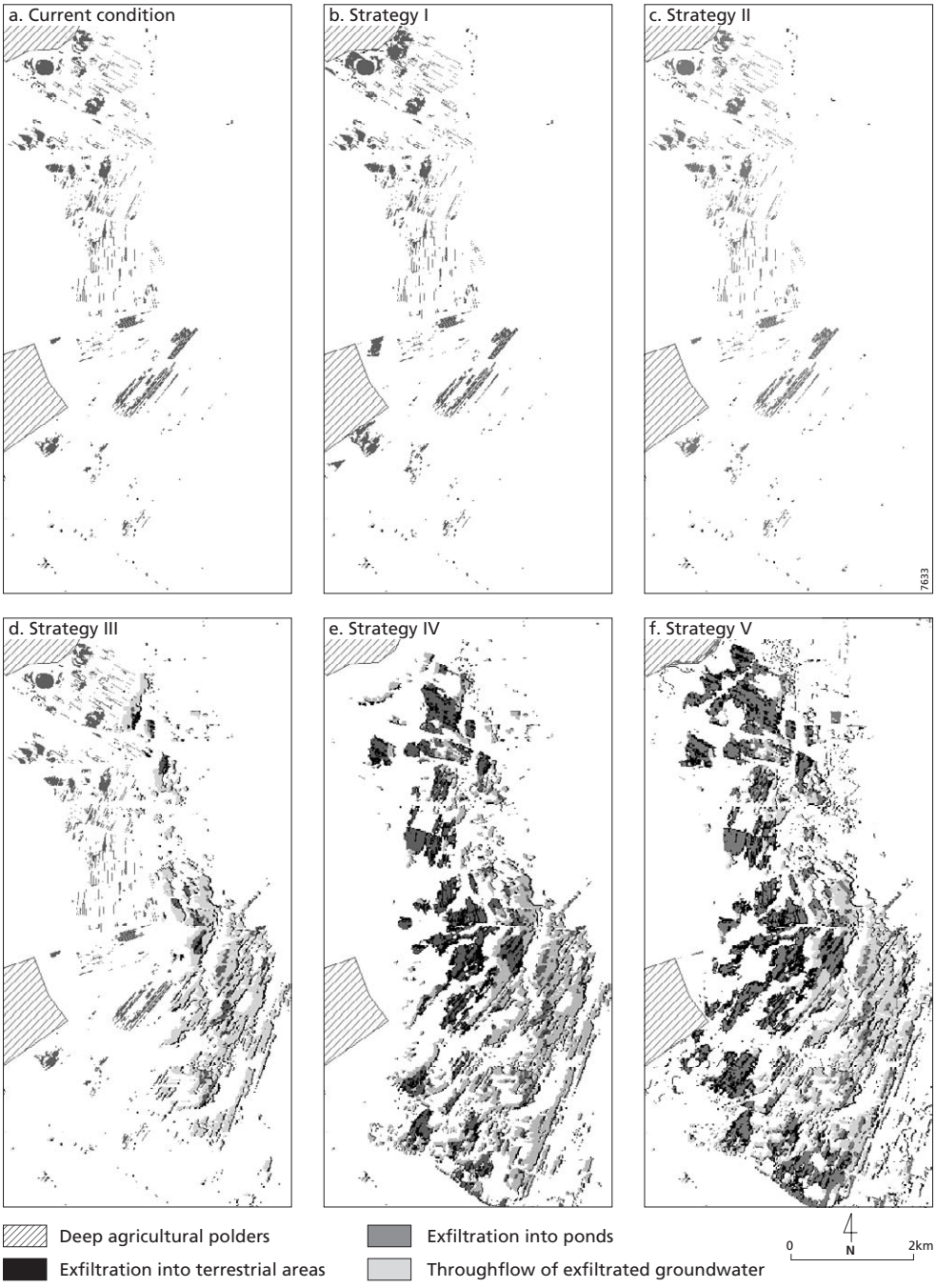
Inundation of the deep agricultural polders Horstermeer and Bethune (Strategy I) would redirect most of the groundwater that currently discharges into the deep polders towards the drainage ditches across the river valley (Table 5.1). As drainage ditches do not provide suitable habitat for low-productive fen plants, this strategy only has minor effects on the habitat configuration of *C. diandra* (Fig. 5.3b). As a result, the dispersal success of *C. diandra* is not improved as indicated by the unchanged number of subpopulations of *C. diandra* (Fig. 5.4a). Moreover, the total area, sizes and area to edge-length ratios of subpopulations of *C. diandra* is hardly increased compared to the current condition (Fig. 5.4).

Table 5.1: Modelled groundwater exfiltration fluxes into the unsuitable matrix and into potential fen habitat patches for the current condition and five hydrological fen restoration strategies. The unsuitable matrix consists of deep agricultural polders, anthropogenic drainage ditches and deep lakes. Potential fen habitat consists of shallow lakes, inundated areas and terrestrial areas.

	Modelled exfiltration fluxes (× 10^3 m^3/d)				
	Unsuitable matrix		**Potential fen habitat**		**Total**
Current condition or restoration strategy	**Deep agricultural polders**	**Drainage ditches and deep lakes**	**Shallow lakes and inundated areas**	**Terrestrial areas**	
Current condition	100	204	22	2	328
I. Inundation of deep agricultural polders	6	215	26	2	249[a]
II. Closure of abstraction wells	100	243	23	2	368
III. Drainage elements eliminated from upstream fen margins	100	122	30	10	262[a]
IV. Drainage elements eliminated across river valley	79	88	29	13	209[a]
V. All measures implemented	9	113	60	22	204[a]

[a] Total exfiltration flux decreases compared to the current condition due to a reduction of the volume of surface water that recharges the aquifer under the river valley in response to a decreased head gradient in the river valley (strategy I and V) or the interrupted ability to supply alien surface water to polders (strategy III, IV and V).

Figure 5.3: (see right page) Configuration of potential fen habitat provided by groundwater exfiltration into terrestrial areas, groundwater exfiltration into shallow lakes and inundated areas and throughflow of exfiltrated groundwater. (a) Current condition; (b) Strategy I: Inundation of deep agricultural polders; (c) Strategy II: Closure of abstraction wells; (d) Strategy III: Draining elements eliminated from upstream fen margins; (e) Strategy IV: Draining elements eliminated across the river valley; (f) Strategy V: All measures implemented. See Fig. 5.1 for details of the restoration strategies.


a. Current condition
b. Strategy I
c. Strategy II
d. Strategy III
e. Strategy IV
f. Strategy V
7633
Deep agricultural polders
Exfiltration into terrestrial areas
Exfiltration into ponds
Throughflow of exfiltrated groundwater
0
N
2km

5.4.3 Closure of abstraction wells (Strategy II)

By closing the abstraction wells (Strategy II), most of the groundwater that is currently directed towards the abstraction wells would be redirected towards the drainage ditches across the river valley (Table 5.1). Like Strategy I, this strategy only has a minor effect on the fen habitat configuration (Fig. 5.3c). Also, as the dispersal infrastructure for *C. diandra* is not improved, the viability of *C. diandra* is only improved to a minor extent (Fig. 5.4).

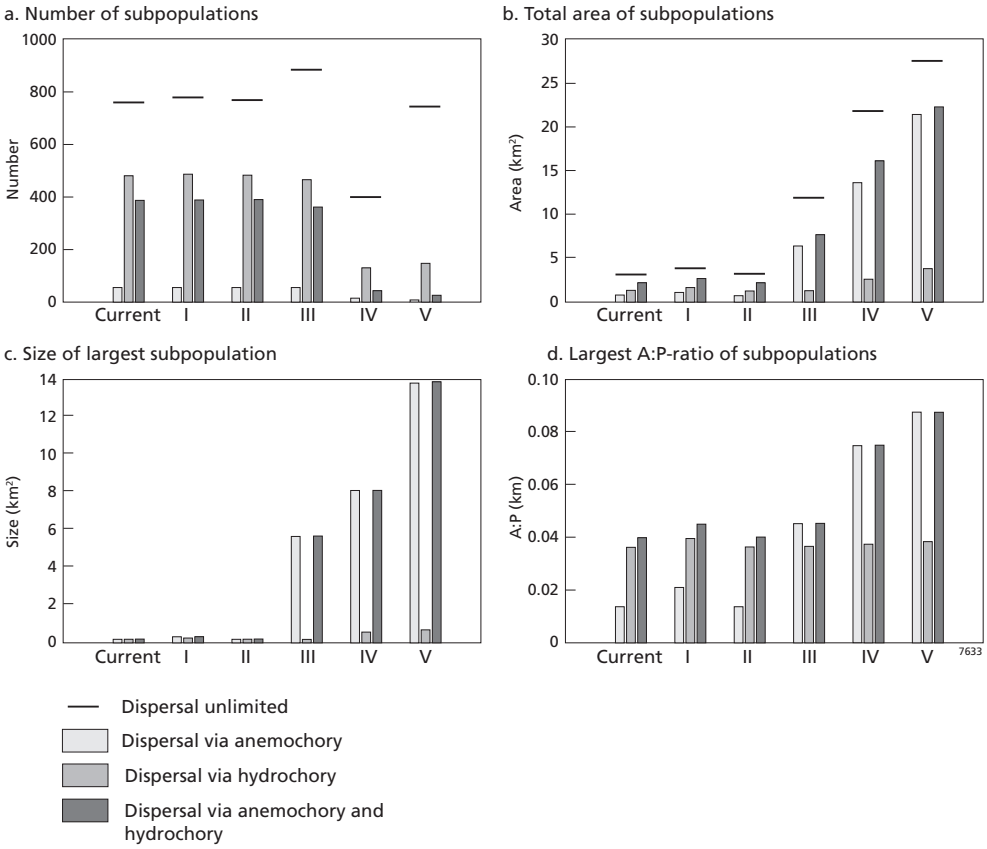


Figure 5.4: Spatial characteristics of potential subpopulations of *C. diandra* calculated using anemochorous, hydrochorous and coupled anemochorous-hydrochorous dispersal models for the current condition and for the restoration strategies. (a) Number of subpopulations; (b) Total area of subpopulations; (c) Size of largest subpopulation; (d) Largest area to edge-length ratio (A:P ratio) of subpopulations. The coupled anemochorous-hydrochorous dispersal model integrates the effects of both dispersal mechanisms on the colonisation of abandoned fen habitat patches (see Fig. 5.3). The x-axis refers to the restoration strategies I – V (see Table 5.1), including the current condition (denoted by C). Note that the number of subpopulations for the hydrochorous dispersal model exceeds the number of subpopulations for the coupled anemochorous-hydrochorous dispersal model (Fig. 5.4a), because the small subpopulations that can establish via solely hydrochorous dispersal are merged together via subsequent anemochorous dispersal.

5.4.4 Drainage elements eliminated from upstream fen margins (Strategy III)

The elimination of drainage elements from the upstream fen margins (Strategy III) would cause a decrease in the total groundwater exfiltration flux into the study area compared to the current condition (Table 5.1). This decrease relates to the interrupted ability to supply alien surface water to the upstream polders, which causes a reduction in the volume of surface water that recharges the aquifer under the river valley. According to the groundwater model, strategy III has spatially differentiated effects on the habitat configuration of *C. diandra* (Fig. 5.3d). In the north, the elimination of drainage elements would not result in the restoration of fen habitat, because groundwater is redirected towards the maintained drainage ditches and the deep agricultural polders instead of towards the ponds or the terrestrial areas. In the south, most of the groundwater that is currently directed towards the drainage elements would be redirected towards ponds or terrestrial areas (Fig. 5.3d, Table 5.1). As a result, superfluous groundwater is not discharged via the drainage network, but is laterally redistributed by throughflow (Fig. 5.3d). This results in contiguous fen habitat patches at the upstream fen margins, which can become effectively colonised by *C. diandra* via anemochorous dispersal, leading to an increase in the number, area, sizes and area to edge-length ratios of potential subpopulations (Fig. 5.4). Note that hydrochorous dispersal has become less effective, because its dispersal infrastructure is lost when the upstream drainage ditches are eliminated (Fig. 5.4).

5.4.5 Drainage elements eliminated across valley (Strategy IV)

Compared to Strategy III, the elimination of the drainage elements across the river valley (Strategy IV) would cause a further decrease in the total groundwater exfiltration flux into the study area (Table 5.1). This relates to the interrupted ability to supply alien surface water to the study area. Nevertheless, the volume of groundwater that is available for fen plants would increase compared to Strategy III, because of the reduced interception of groundwater by drainage ditches and the deep agricultural polders (Table 5.1). Moreover, the area and contiguity of habitat patches is further increased by enhanced throughflow at the upstream fen margins and the development of groundwater-fed ponds near the centre of the study area (Fig. 5.3e). As a result, the success of anemochorous and hydrochorous dispersal is increased, supporting an increase in the total area, sizes and area to edge-length ratios of subpopulations of *C. diandra* (Fig. 5.4).

5.4.6 All measures implemented (Strategy V)

Finally, Strategy V, which consists of all of the measures discussed in Strategies I – IV, would cause an even further increase of the availability of groundwater for fen plants compared to Strategy IV (Table 5.1, Fig. 5.3f). The larger volume of groundwater that is redirected towards the ground surface in the study area causes an expansion of both the groundwater-fed ponds and the throughflow zone (Fig. 5.3f). As a result, contiguous habitat patches can establish that are easily colonised via anemochorous and hydrochorous dispersal. This would result in a further increase in the viability of C. diandra compared to the other strategies (Fig. 5.4).

5.5 Discussion

5.5.1 Methodological approach

In this study, we used a linked habitat suitability and seed dispersal model to analyse the effectiveness of a number of hydrological fen restoration strategies to counteract habitat loss and fragmentation of low-productive fens. Compared to stand-alone habitat suitability models, the added value of the

linked approach is that the effects of restoration strategies are not quantified by changes in potentially suitable habitat, but by changes in potentially colonisable habitat. Potentially colonisable habitat is a more relevant indicator of the restoration prospects of fragmented ecosystems, because habitat fragmentation reduces the dispersal success of plants (Soons et al., 2005) and may consequently hinder the colonisation of habitat patches by target species (Bischoff, 2002; Ozinga et al., 2005). Our model showed that, for each strategy, 20 – 35% of the potentially suitable habitat could not be colonized by *C. diandra*, indicating that habitat suitability models that ignore the effects of limited dispersal on colonisation may considerably overestimate the prospects for fen restoration. For this reason, we believe the presented modelling approach may serve as an example for future attempts at improving the predictive ability of habitat suitability models.

Habitat suitability models have been employed in a number of studies to predict ecosystem responses to hydrological fen restoration measures (Olde Venterink and Wassen, 1997; Van Ek et al., 2000). These studies considered habitat suitability on an interval or continuous scale in order to quantify the probability of plant species occurrence as a function of multiple predictors, like ion concentrations in shallow groundwater, soil characteristics and management actions. In the current study, we simplified the habitat suitability concept by considering fen habitat to be either suitable or unsuitable. Moreover, we ignored the effects of non-hydrological management actions, e.g. mowing (Fojt and Harding, 1995), and soil-chemical processes (Lamers et al., 1998) on habitat suitability. These simplifications are justified because our goal was to compare the effectiveness of hydrological fen restoration strategies using predicted potential species distributions. However, in order to better predict ecosystem responses to hydrological restoration measures, additional habitat suitability models that use our results as a basis are needed.

Numerous studies have used dispersal models to analyse population dynamics (Engler and Guisan, 2009; Scheller and Mladenoff, 2008) or species viability (Soons et al., 2005) in relation to climate change or habitat fragmentation. These studies used fitted or physically based dispersal kernels to model seed deposition as a function of the distance to the parent plant. In the present study, we used uniform dispersal kernels for anemochorous and hydrochorous dispersal. These simplified dispersal kernels hinder a sound assessment of the time to colonisation and habitat connectivity. However, this approach allows for an assessment of the potential species distribution under the assumption that long-distance dispersal by animals (Soons et al., 2008) or man (Klimkowska et al., 2007) does not contribute to the colonisation of suitable patches. It also provides sufficient information to assess the effectiveness of restoration strategies, because the frequency and success rate of long-distance dispersal events are uncertain, unless seeds are actively dispersed by management activities (Klimkowska et al., 2007). Further progress in the development of more realistic dispersal models on the regional scale is required to enhance the predictive ability of species distribution models.

A general constraint of habitat suitability and meta-population models is the lack of reference data to evaluate predicted responses to external changes. For this reason, species distribution models can only be evaluated using independent (or re-sampled) reference data for the current condition (Guisan and Thuiller, 2005). In our case, we could evaluate the linked habitat suitability and seed dispersal model by comparing the modelled realised habitat for the current condition with the actual distribution of *C. diandra* derived from presence/absence data projected on a cadastral map. According to our analysis, 20 (i.e., 59%) of the 34 parcels inhabited by *C. diandra* could be explained by the linked model. This limited fit between predictions and observations may be related to our method for downscaling the

Table 5.2: Robustness of the total area of subpopulations of *C. diandra* (km²) against uncertainty in anemochorous and hydrochorous dispersal distances. *Ane* refers to anemochorous dispersal distance and *Hyd* refers to hydrochorous dispersal distance. See Fig. 5.1 for further details on the restoration strategies.

	***Ane*[1] = 10 (m)**		***Ane* = 5 (m)**	
Current condition or restoration strategy	***Hyd*[1] = 500 (m)**	***Hyd* = 250 (m)**	***Hyd*[1] = 500 (m)**	***Hyd* = 250 (m)**
Current condition	2.09	2.06	1.53	1.50
I. Inundation of deep agricultural polders	2.57	2.45	1.89	1.86
II. Closure of abstraction wells	2.11	2.08	1.54	1.51
III. Drainage elements eliminated from upstream fen margins	7.64	7.62	7.11	7.09
IV. Drainage elements eliminated across river valley	16.10	16.10	16.09	16.09
V. All measures implemented	22.26	22.26	22.26	22.26

[1] Default values

modelled zones with groundwater supply by assigning exfiltrating groundwater to drainage elements within model cells. As a result, floating fens bordering drainage ditches may not have been identified as suitable habitat, because the entire volume of exfiltrating groundwater was assigned to the drainage ditches, while part of this groundwater may, in reality, have been directed to these floating fens. Given the absence of open water in the direct vicinity of these fens, succession may soon cause the loss of fen habitat (Verhoeven and Bobbink, 2001). In this case, 10 of the 14 parcels inhabited by *C. diandra* but not explained by the linked model, will render unsuitable conditions for fen plants in the nearby future.

Uncertainty in the modelled distribution of *C. diandra* under the restoration strategies relates (among others) to changes in the dispersal ability of plants in response to changes in the hydraulic properties of the surface water system (Soomers et al., 2009) or the vegetation structure (Soons et al., 2004). We tested the robustness of the model against changes in the dispersal ability of *C. diandra* by means of a sensitivity analysis of anemochorous and hydrochorous dispersal distances. For this purpose, these distances were multiplied with a factor 0.5 or 2.0. Uncertainty in the modelled population area of *C. diandra* ranged from 25 to 30% for the current condition and for the strategies in which the drainage ditches were maintained, whereas uncertainty was less than 1% for the strategies in which the drainage ditches were eliminated (Table 5.2). More importantly, trends in the modelled results were robust against uncertainty in dispersal ability of *C. diandra*. This justifies our method of comparing hydrological restoration strategies using empirical-based seed dispersal models to predict species distributions. However, given the inability to evaluate the predictions and the simplified habitat suitability model used, the model results have no absolute value.

5.5.2 Model results

The strategy analysis indicated that both the inundation of polders and the closure of abstraction wells would cause an increase in the volume of groundwater that is directed towards the area where fens are present, but that most of this groundwater is intercepted by drainage ditches. As drainage ditches do not provide habitat for low-productive fen plants, these measures only restore small habitat patches, while leaving the unsuitable matrix largely unaltered. Consequently, the dispersal success and viability of *C. diandra* improve only slightly. These results provide further support for the hypothesis postulated by, among others, Schot et al. (2004) and Van Loon et al. (2009a): i.e., measures that enhance

groundwater flow towards drained fens are by themselves not effective in improving the viability of fen plant populations. However, these measures can contribute to improving the quality of surface water, as the increased availability of groundwater in the fen area provides opportunities to reduce the amount of polluted surface water that is supplied to polders during the growing season. This could be particularly beneficial for aquatic species, but also for the regeneration of floating fens that are currently polluted by alien surface water (Lamers et al., 1998).

Measures that include the elimination of drainage elements have been demonstrated to be effective in increasing the volume of groundwater available for fen plants. Moreover, the elimination of drainage elements supports a more efficient supply of groundwater to fen root zones by throughflow as found in natural fens (Van Loon et al., 2009c). This leads to the establishment of contiguous habitat patches in the upstream fen margins, even if drainage networks are maintained near the centre of fens and groundwater continues to be abstracted through wells. Although a rather effective infrastructure for hydrochorous dispersal is lost with the elimination of drainage ditches (Soomers et al., 2009), dispersal is not a bottleneck for successful fen restoration provided that contiguous habitat patches are established, because these patches can be easily colonised via anemochorous dispersal. Given the small transport distances of seeds dispersed by wind, the time lag between restoration and colonization of habitat patches may be considerable though.

5.6 Conclusion and implications for fen restoration

Hydrological fen restoration is often constrained by the presence of anthropogenic land uses that have opposite demands for water management than are desirable for fen restoration. Likewise, abiotic restoration of sites that have a low probability for re-colonisation by target species is not cost-effective. Our linked habitat suitability and dispersal model is capable of identifying these constraints and therefore forms a valuable tool for resource managers to design cost-effective fen restoration measures and to optimise the spatial planning of such measures. Further progress is needed in the development of dispersal models of multiple target species in order to increase the representativeness for restoration objectives.

The linked groundwater and dispersal model was used to predict the potential distribution of *C. diandra* for a number of hydrological fen restoration strategies. The results suggest that regional measures that enhance groundwater flow to drained fens are, by themselves, not effective in increasing the viability of fen plant populations except when combined with the elimination of drainage elements at a regional scale. As the potential for fen restoration is highest at the upstream fen margins – even if intense water management is practiced near the centre of fens – the elimination of drainage elements can best be utilized in a spatially coherent way, starting at the edge of regional groundwater recharge areas and working in a downstream direction. This new insight into spatially optimised and more cost-effective fen restoration measures may necessitate the reconsideration of planned ecosystem networks in drained fens across temperate regions. Likewise, it may help conserve viable fen plant populations in areas of planned wetland reclamation by smart spatial planning of the reclaimed areas.

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6 Innovation, conclusions and recommendations for future research

6.1 Introduction

Low-productive fens have deteriorated severely in many anthropogenically dominated regions due to anthropogenic pressure on environmental resources (Millennium Ecosystem Assessment, 2005; Succow and Joosten, 2001). This pressure is comprised of, among others, a reduced groundwater supply caused by anthropogenic interference with hydrology (Fojt and Harding, 1995; Van Wirdum, 1995). A reduced groundwater supply results in either a lowering of the groundwater level, which may lead to desiccation, or an increased infiltration of local precipitation or polluted surface water, which may lead to acidification (Almendinger and Leete, 1998) or eutrophication (Lamers et al., 1998). When either happens, the abiotic conditions in fens can become less suitable, or even incompatible, for fen plants and the area containing vegetation types typical of low-productive fens can decrease in size (Fojt and Harding, 1995; Mälson et al., 2008; Van Wirdum, 1991; Verhoeven and Bobbink, 2001). The latter, in turn, can cause habitat fragmentation, i.e., the breaking apart of large contiguous habitat patches into multiple smaller ones, which further increases the risk of local extinction of endangered fen plant species that depend on very limited ranges in abiotic conditions (Ewers and Didham, 2005; Hooftman et al., 2003).

The sustainable conservation of low-productive fen plant populations in anthropogenically dominated regions requires the restoration of habitat conditions suitable for fen plants in a configuration that supports the counteraction of both habitat loss and fragmentation. Given the hydrological control of abiotic conditions in fens, this means that anthropogenic hydrological interference with the hydrology of fens must be sufficiently reduced in order to restore groundwater supply on a regional scale. Anthropogenic hydrological interference consists of (1) groundwater abstractions that reduce the volume of groundwater directed towards areas where low-productive fens are situated (Almendinger and Leete, 1998; Fojt, 1994; Schot et al., 1988; Witmer, 1989), (2) water level control in systems of management districts (i.e., polders) with distinctly different surface elevations, which transforms regional groundwater flow patterns (Schot and Molenaar, 1992; Wassen et al., 1996) and (3) water level control through the maintenance of drainage networks that intercept exfiltrating groundwater that would otherwise enter the fen root zone (Grootjans et al., 1988; Schot et al., 2004; Wassen et al., 1990). Measures to counteract these possible hydrological causes of fen deterioration, however, have shown variable effectiveness in the rewetting of low-productive fens with unpolluted groundwater (Jansen et al., 2000; Lamers et al., 2002). This demonstrates that our present knowledge of the effects of water management on fen deterioration, and how fen deterioration can be reversed, is incomplete.

One possible cause of our incomplete knowledge of the effects of water management on fen deterioration is the limited reference data on natural hydrological conditions in intensively managed fens (Wassen, 2005). Currently available reference data have been obtained from geographical reference areas (Schipper et al., 2007; Wassen and Joosten, 1996), palaeo-modelling exercises (Schot and Molenaar, 1992) and analyses of the botanical peat composition of managed fens (Succow and Joosten, 2001). According to these (and comparable) studies, low-productive fens in a natural setting can be supplied with alkaline groundwater by either regional groundwater exfiltration (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006) or the lateral redistribution of exfiltrated groundwater by near-surface flow mechanisms (i.e., throughflow; Schipper et al., 2007; Succow and Joosten, 2001; Wassen and Joosten, 1996). The relevance of these conceptual models of groundwater flow for intensively managed fens is debatable, however, because the methods used to obtain these reference data are either not site-specific, strongly simplified or only of qualitative value. These methodological

limitations hamper the identification of the hydrological mechanisms behind fen deterioration, which may in turn constrain the design of new and effective hydrological fen restoration strategies.

The objective of this thesis is to enhance insight into the hydrological requirements for effective fen restoration in regions with an anthropogenically controlled hydrology. In order to reach this objective, the hydrological mechanisms behind fen deterioration were unravelled using both site-specific, quantitative reference data and geographical reference data for an intensively managed fen in The Netherlands. This chapter will first present the innovative aspects of the applied methods. Then, the research questions raised in Chapter 1 will be answered using the results of the Chapters 2 through 5. Finally, a number of recommendations for future research will be discussed to enhance further progress in the restoration ecology of low-productive fens.

6.2 Innovative methodological aspects

The hydrological mechanisms behind fen deterioration were unravelled by analysing, from a historical perspective, the impact of water management actions on near-surface groundwater flow in fens. This was achieved by comparing the current hydrological state of an intensively managed fen area in The Netherlands with past hydrological states, including that under natural conditions. Past hydrological states were investigated using a series of palaeo-groundwater models (Chapter 2) and a present-day near-natural fen in East Poland as a geographical reference of natural hydrological conditions in intensively managed fens (Chapter 3). Significant progress in gaining insight into the natural hydrology of intensively managed fens was made with this approach.

In contrast to the strongly simplified, 2D palaeo-modelling exercise performed by Schot and Molenaar (1992), the palaeo-groundwater models presented in Chapter 2 provide a quantitative, 3D representation of four hydrological palaeo-states of the managed fen area, based on a complete reconstruction of geo-hydrological conditions. These palaeo-groundwater models provide additional insight into natural hydrological conditions and into the hydrological changes that the fen has undergone with intensifying water management. Although the palaeo-groundwater models could not be validated due to a lack of reference data, the validity of the approach for studying anthropogenically induced changes in groundwater flow was confirmed by the robustness of the modelled trends in hydrological states against changes in parameter values. Nevertheless, the applicability of palaeo-groundwater models in the study of the hydrological mechanisms behind the supply of groundwater of fens under natural conditions is limited, because palaeo-groundwater models are typically developed for a regional scale.

Groundwater flow in a near-natural fen was studied (Chapter 3) in order to improve the reference data of natural hydrological conditions obtained with the palaeo-groundwater models. Near-natural fens have been used in the past as geographical reference areas for intensively managed fens, because they allow the accumulation of empirically verified hydrological reference data of past conditions (Wassen, 2005). So far, the applicability of this method has been debatable, because the representativeness of geographical reference areas for managed areas elsewhere is doubtful due to the incompatibility of geo-hydrological and climatic conditions. In this thesis, however, the representativeness of the geographical reference area could be confirmed by the close correspondence between the modelled hydrological properties of the near-natural fen and those of the intensively managed fen prior to the start of anthropogenic hydrological interference. Accordingly, the combined results of the palaeo-groundwater

models and the case study of the near-natural fen provided a quantitative, site-specific and empirically verified reference of natural groundwater flow for an intensively managed fen.

New insights into past hydrological conditions in relation to the modelled changes in groundwater flow in response to intensifying water management (Chapter 2) and the detailed analysis of current groundwater flow patterns in the Gooi- and Vechtstreek area (Chapter 4) provide the opportunity to unravel the hydrological mechanisms behind fen deterioration in anthropogenically dominated regions. A better understanding of these mechanisms is essential in order to identify the requirements for successful hydrological fen restoration (Wassen, 2005). The restoration of a more natural hydrology, however, may be limited by irreversibly changed geo-hydrological conditions (e.g., the degradation of the surface morphology of fens by peat excavation and land subsidence) or by the presence of land uses that have opposite demands on water management than would be desirable for fen restoration. For this reason, it is essential to design tailor-made hydrological fen restoration measures by using modelling software that can help predict ecosystem responses to water management actions. Numerous authors have employed habitat suitability models for this purpose (Olde Venterink and Wassen, 1997; Van Ek et al., 2000). These models are not, however, capable of predicting ecosystem responses at the species level because they ignore the impact of limited dispersal on colonization. To overcome this constraint, a linked habitat suitability and seed dispersal model was developed to effectively integrate the knowledge of hydrological processes that determine habitat suitability and seed dispersal processes that determine the availability of habitat for fen plants (see Chapter 5). Measures to enhance the viability of fragmented fen plant populations can be spatially optimised using this approach, by identifying areas that have a high potential for both abiotic restoration and recolonisation by target species.

6.3 Conclusions with respect to the research questions

In this section, conclusions are drawn with respect to the research questions raised in Section 1.4 and requirements are identified for successful hydrological fen restoration in anthropogenically dominated regions. First, the hydrological mechanisms that may underlie the groundwater supply of persistent fens in a natural setting are discussed using the results described in Chapters 2 and 3. Next, the impact of individual anthropogenic hydrological interferences with natural groundwater flow is analysed using the results from Chapters 2 and 4. Finally, the effectiveness of a number of hydrological restoration strategies is discussed using the results of Chapters 4 and 5 and management implications are formulated.

6.3.1 Which hydrological mechanisms underlie the groundwater supply of fens in a natural setting?

Two conceptual models of groundwater flow in natural fens have been proposed in the literature: the exfiltration model and the throughflow model. The exfiltration model assumes the upward transport of groundwater on a landscape scale, leading to regional groundwater exfiltration at the fen surface (Fraser et al., 2001; Glaser et al., 1990; Reeve et al., 2006). Local precipitation is either discharged by surface runoff or it is stored in the fen soil, while it mixes with exfiltrating groundwater as a result of vertical flow reversals that relate to dynamic meteorological conditions. In this model, lateral flow is limited to the local scale (Drexler et al., 1999) and fen plants are confined to the exfiltration zones. The throughflow model assumes that groundwater exfiltrates at the upstream margins of fens, and that the high exfiltration rates cause a surplus of groundwater in the shallow subsurface, which is then discharged by lateral flow through the loosely structured root zone, i.e., throughflow (Schipper et al.,

2007; Succow and Joosten, 2001; Wassen and Joosten, 1996). In this model, throughflow redistributes exfiltrated groundwater mixed with local precipitation through the fen root zone on a regional scale. As a result, throughflow may provide abiotic conditions suitable for fen plants outside the exfiltration zones. The suitability of these models to provide a hydrological reference of intensively managed fens like the one studied in this thesis is analysed below using the results of Chapters 2 and 3.

The palaeo-groundwater models of the Gooi- and Vechtstreek area that are representative of natural conditions (Chapter 2) indicated the presence of a narrow zone at the upstream fen margins that receives large volumes of exfiltrating groundwater. Towards the centre of the fen, groundwater was rather stagnant as shown by the small vertical flux rates (upward or downward) of 1×10^{-3} mm/d or less. These conditions impede the infiltration of exfiltrated groundwater and local precipitation into the fen, causing a water surplus in the shallow subsurface that was discharged by near-surface flow mechanisms. Comparable hydrological conditions prevail in the near-natural fen of the Biebrza River valley (Poland), as demonstrated in Chapter 3. Observed patterns in minerotrophic and ombrotrophic plant alliances in the near-natural fen could be related to the existence of throughflow comprising a mixture of exfiltrated groundwater and local precipitation. More specifically, patterns in habitat conditions suitable for fen plants are determined by the volume of groundwater that is supplied to the fen root zone and the rate of infiltration of shallow groundwater that is redistributed laterally by throughflow. Based on the above, throughflow is expected to be particularly relevant for fens situated in gently sloping lowland river valleys that receive large volumes of exfiltrating groundwater and in which low-conductive peat is present that reduces the infiltration of shallow groundwater. Notably, the results of this study combined with the empirical data of the same near-natural fen (Wassen and Joosten, 1996) indicate that regional groundwater exfiltration only prevails in these fens during dry summer periods, when diffuse groundwater losses by evapotranspiration are compensated for by the upward transport of groundwater. It can be concluded, therefore, that throughflow is the key mechanism that underlies the groundwater supply of fens in natural lowland river valleys.

6.3.2 How do individual anthropogenic hydrological interferences affect the groundwater supply of fens?

So far, studies on the hydrology of intensively managed fens have revealed varying causes of fen deterioration as a result of anthropogenic interference with the groundwater supply of fens. Almendinger and Leete (1998), Fojt (1994), Schot et al. (1988) and Witmer (1989), for example, argued that water management actions that reduce the volume of discharging groundwater in managed fens may cause fen deterioration. Schot and Molenaar (1992) and Wassen et al. (1996) showed that systems of polders with distinctly different surface elevations interfere with regional groundwater flow and consequently cause a diverged pattern of groundwater exfiltration zones. Finally, Grootjans et al. (1988), Schot et al. (2004) and Wassen et al. (1990) demonstrated that drainage ditches cause diffuse losses of exfiltrated groundwater by means of interception and subsequent discharge, thus preventing the exfiltrated groundwater from becoming available for fen plants. None of these studies, however, provided complete insight into the hydrological mechanisms behind fen deterioration, because they underrated the importance of throughflow in providing habitat conditions suitable for fen plants and ignored the impact of water management actions on throughflow mechanisms. The impact of individual water management actions on throughflow mechanisms is discussed below from a historical perspective, using the results presented in Chapters 2 and 4.

Water management actions that reduce the volume of groundwater discharge into fens
The series of palaeo-groundwater models of the Gooi- and Vechtstreek area presented in Chapter 2 confirm the findings of Almendinger and Leete (1998), Fojt (1994), Schot et al. (1988) and Witmer (1989) that abstraction wells, deep agricultural polders and (to a lesser degree) anthropogenic changes in land cover are major sinks of groundwater that is otherwise directed towards fen areas. Yet, the modelled long-term trends in the water balance of the fen area suggest that the reduced volume of groundwater discharge into the fen area caused by these water management actions has only prevailed during the last century. Before then, the throughflow mechanisms must have already been interrupted by anthropogenic hydrological interferences, given the strongly reduced volume of groundwater discharge at the fen surface. Moreover, prior interference, particularly the establishment of systems of polders with distinctly different surface levels, increased the volume of groundwater discharge into the fen area due to the development of additional groundwater systems in the river valley. As a result, the current volume of groundwater that is potentially available for throughflow still exceeds that of natural conditions, while throughflow mechanisms are not operational in intensively managed fens. Based on these findings, it can be concluded that water management actions that reduce the volume of groundwater discharge into intensively managed fens have not interrupted natural throughflow mechanisms, and thus are not the major cause of fen deterioration in anthropogenically dominated regions.

Systems of polders with distinctly different surface elevations
The series of palaeo-groundwater models presented in Chapter 2 confirm the findings of Schot and Molenaar (1992) and Wassen et al. (1996) that the establishment of systems of polders with distinctly different surface elevations has transformed regional groundwater flow patterns, thus leading to diverged zones of groundwater discharge. In fact, the area of groundwater discharge has decreased by 35% since the start of water management. This has particularly affected hydrological conditions near the centre of the fen, where distinct infiltration conditions associated with the stepwise elevation differences between polders have replaced the stagnant groundwater associated with the smooth surface morphology of the fen under natural conditions. As a consequence, the zones of groundwater exfiltration and infiltration have become situated within a relatively short distance of each other, which reduces the area that is potentially supplied with exfiltrated groundwater by throughflow. Moreover, outside the exfiltration zones, local precipitation is no longer discharged by near-surface flow mechanisms; it infiltrates into the fen soil, leading to the existence of ombrotrophic conditions that are less suitable for fen plants. Therefore, it can be concluded that systems of polders with distinctly different surface elevations reduce the spatial scale at which throughflow mechanisms can potentially operate.

Drainage networks
Calculated trends in the water balance of the fen area since the start of water management (Chapter 2) and the demonstrated interception of groundwater by drainage networks (Chapter 4) confirm the findings of Grootjans et al. (1988), Schot et al. (2004) and Wassen et al. (1990) that drainage networks prevent groundwater exfiltration at the fen surface and lead to enhanced rainwater infiltration across drained fens. In addition, drainage networks have been demonstrated (Chapter 4) to intercept groundwater that is otherwise directed towards nearby fens with a less disturbed hydrology. This can potentially cause the deterioration of fens in the vicinity of drainage networks. From a historical point of view, however, the impact of drainage networks on groundwater flow in fens is even more severe, as drainage networks interrupt the discharge of excess water by near-surface flow mechanisms. The

accelerated discharge of exfiltrating groundwater via drainage ditches hampers the lateral redistribution of exfiltrated groundwater across fen root zones, as found in natural fens. Likewise, the delayed discharge of local precipitation as a result of focused groundwater flow towards the drainage ditches causes the infiltration and storage of local precipitation in the fen soil on a landscape scale. Given these interferences with the throughflow mechanisms, it can be concluded that drainage networks are the major cause of fen deterioration in intensively managed fens, because they cause a regional shift in the supply of source water to fens from exfiltrated groundwater to local precipitation.

6.3.3 How can currently utilized hydrological fen restoration strategies be improved?

Currently utilized hydrological fen restoration strategies consist of the elimination of drainage ditches from fen reserves, the installation of poorly drained buffer zones, the reduction of groundwater abstractions and increased surface water levels in polders (Jansen et al., 2000). So far, these measures have not been particularly effective in rewetting fen reserves with unpolluted, alkaline groundwater (Jansen et al., 2000). According to our results, this limited effectiveness is probably due to the maintenance of drainage networks in the vicinity of fen reserves that need to be restored. Drainage networks effectively intercept exfiltrating groundwater, which consequently does not become available for fen plants, even if regional measures are implemented to redirect regional groundwater flow towards fen areas (Chapters 4 and 5). For this reason, hydrological restoration strategies are only effective if they include the elimination of drainage elements on a regional scale. Using this strategy, the volume of groundwater that is available for fen plants is effectively increased, even though groundwater is partly redirected outside the restored area. Moreover, if drainage elements are eliminated from upstream fen margins, geo-hydrological conditions can be restored that support the lateral redistribution of exfiltrated groundwater by throughflow mechanisms, as found in natural fens (Chapters 4 and 5). As a result, contiguous zones of groundwater supply can be restored even if drainage networks are maintained near the centre of the fen and groundwater continues to be abstracted via wells. Although complementary restoration measures (like sod-cutting to remove excess nutrients from fen root zones) may be required to successfully restore habitat conditions suitable for fen plants, this restoration strategy also supports the re-establishment of fen plants at successfully restored habitat patches by natural dispersal. As demonstrated in Chapter 5, contiguous habitat patches at upstream fen margins can be effectively colonised by fen plants via wind dispersal if remnant populations are present in the vicinity of the restored habitat patches. For these reasons, it can be concluded that the elimination of drainage elements from upstream fen margins is the most effective strategy to counteract fen deterioration caused by water management actions.

Management implications

In conclusion, in contrast to the frequently utilized ad-hoc strategy of restoring groundwater discharge to isolated fen reserves, a restoration strategy consisting of the elimination of drainage ditches from upstream fen margins (i.e., from the natural throughflow zone) has the highest potential to successfully restore habitat conditions in a configuration that supports connectivity between populations. For this reason, priority should be assigned to the elimination of drainage ditches in a spatially coherent manner, starting at upstream fen margins and proceeding in a downstream direction. Only if drainage is sufficiently impeded to allow the lateral redistribution of both exfiltrated groundwater and local precipitation by throughflow, can additional measures be implemented to reduce the reinfiltration of exfiltrated groundwater by raising surface water levels in the downstream regions where drainage ditches are conserved. Finally, lowest priority should be assigned to measures that enhance regional groundwater flow towards drained fen areas, as these measures do not improve conditions for a more

efficient supply of exfiltrated groundwater to fens. Although restoration measures can be planned in another sequence than the one suggested here for practical reasons, resource managers should be aware that costly investments to improve the regional hydrology of fen reserves only have effect after the diffuse loss of groundwater via drainage ditches has been sufficiently reduced.

6.4 Recommendations for future research

The results of this thesis provide new insights into the hydrological requirements for effective fen restoration in regions with an anthropogenically controlled hydrology. These insights were achieved by (1) analysing the hydrological mechanisms behind fen deterioration from a historical perspective and (2) predicting the effectiveness of a number of hydrological fen restoration strategies, taking into account hydrological processes determining habitat suitability and seed dispersal processes determining habitat availability for fen plants. The innovative aspects of the applied methods consist of the development and combination of regional groundwater and species distribution models that are representative of data-poor conditions, i.e., for the past (Chapter 2), the future (Chapter 5) and a near-natural geographical reference area (Chapter 3). Unfortunately, the modelled hydrological trends and responses to water management actions could not be validated in much detail because of the missing reference data. For this reason, further investigation is required on the effects of water management actions on fen deterioration and how fen deterioration can be reversed. In my opinion, future research should focus on (1) the prospects for the restoration of throughflow, (2) the need and effectiveness of complementary local hydrological fen restoration measures if the elimination of drainage elements on a regional scale is not feasible and (3) the improvement of the predictive ability of species distribution models. These recommended fields of future research are outlined below in more detail.

6.4.1 Prospects for the restoration of throughflow

The attributed importance of throughflow to provide habitat conditions suitable for fen plants in natural fens was mainly based on a regional groundwater model consisting of, among others, a highly conductive root zone layer (Chapter 3). By this approach, throughflow mechanisms were modelled interactively with regional groundwater flow. However, because the characteristic spatial and temporal scales of throughflow and groundwater flow widely differ and reference data to validate the groundwater model were scarce, our modelling approach only allows the investigation of throughflow mechanisms on a regional scale for average geo-hydrological conditions. In order to enhance insight into the importance of throughflow mechanisms for the mediation of habitat conditions suitable for fen plants, further empirical study of throughflow in natural fens is recommended. In particular, observations of hydraulic head gradients across fen root zones on varying spatial and temporal resolutions, combined with a sampling of environmental tracers (electrical conductivity, isotopes and macro-ions) in the shallow subsurface, may enhance insight into the hydrological mechanisms underlying the groundwater supply of natural fens under temporally varying geo-hydrological conditions. Likewise, the opportunities to restore throughflow in managed regions require further study by monitoring the effects of trial measures to see if the restoration prospects reported in this thesis are realistic.

6.4.2 Local hydrological fen restoration measures

According to the results of this thesis, the elimination of drainage networks from intensively managed fens has a relatively high potential to support the abiotic restoration of fens. If such a restoration strategy is not feasible (e.g., due to a high demand for land or limited financial resources), resource

managers may decide to undertake less ambitious efforts to rewet fen reserves with unpolluted groundwater by implementing local measures to restore groundwater exfiltration at the fen surface. Based on our results, these measures should at least include the elimination of drainage ditches from the fen reserves that need to be restored. The effectiveness of this measure may be variable, however, because groundwater flow is partly redirected towards downstream regions (Chapter 4), particularly if the surface morphology of the fen does not support the discharge of local precipitation by surface runoff. This results in rainwater becoming stagnant and infiltrating the fen. To avoid this restoration failure, shallow trenches may need to be installed in poorly drained fens to enhance the discharge of local precipitation at the fen surface. However, practical experience with this measure is still limited and its effectiveness is often variable (Dekker et al., 2004; Jansen et al., 2000). The cause of this variable effectiveness is either the enhanced infiltration of local precipitation due to increased drainage or the focused discharge of exfiltrated groundwater at the trenches and its accelerated discharge from the fen as surface water. In order to improve the current insight into the constraints and opportunities of the installation of shallow trenches to support hydrological restoration of individual fen reserves, further investigation of groundwater flow near drainage elements with varying hydrological properties (depths, water level dynamics and drain density) is needed. For this purpose, groundwater flow near shallow trenches installed in rewetted fens should be investigated using environmental tracers, high-resolution head observations or groundwater models with a high spatial and temporal resolution, as these methods have been shown to be useful for analysing patterns and dynamics of the supply of exfiltrated groundwater and local precipitation to fens.

6.4.3 Predicting ecosystem responses

The demonstrated prospects for hydrological fen restoration by means of eliminating drainage ditches from the upstream fen margins necessitate the regional reorganisation of land use in intensively managed fens. For instance, it may be necessary to reallocate (or expand) planned ecosystem networks to the upstream fen margins, while agricultural activities are shifted to the downstream fen regions. Given the high demand for land in The Netherlands, the social impact and costs of such a strategy are undoubtedly considerable. Similarly, the implementation of restoration measures in regions that are isolated from existing populations is not cost-effective as these regions have a low probability of becoming recolonised by target species (Bischoff, 2002; Jansen et al., 2000; Klimkowska et al., 2007). For these reasons, predictive tools are needed that integrate knowledge of environmental processes determining habitat conditions and of dispersal processes determining the probability of colonisation. These tools can be helpful in the optimisation of restoration measures by means of clever spatial planning of land use functions and hydrological restoration measures. The linked habitat suitability and seed dispersal model presented in Chapter 5 is a first step towards the development of such a predictive tool. However, in order to improve the approach's representativeness of fen restoration goals, further progress is needed in modelling seed dispersal of multiple species on a landscape scale and in integrating these seed dispersal models in sophisticated habitat suitability models that are capable of predicting the response of multiple species to changes in habitat conditions.

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Appendix A

Reconstructed palaeo-geohydrological conditions in the Gooi- and Vechtstreek area for the time-frame 0-2000 AD

Figure A1: Reconstructed groundwater recharge (R) for subsequent time slices.

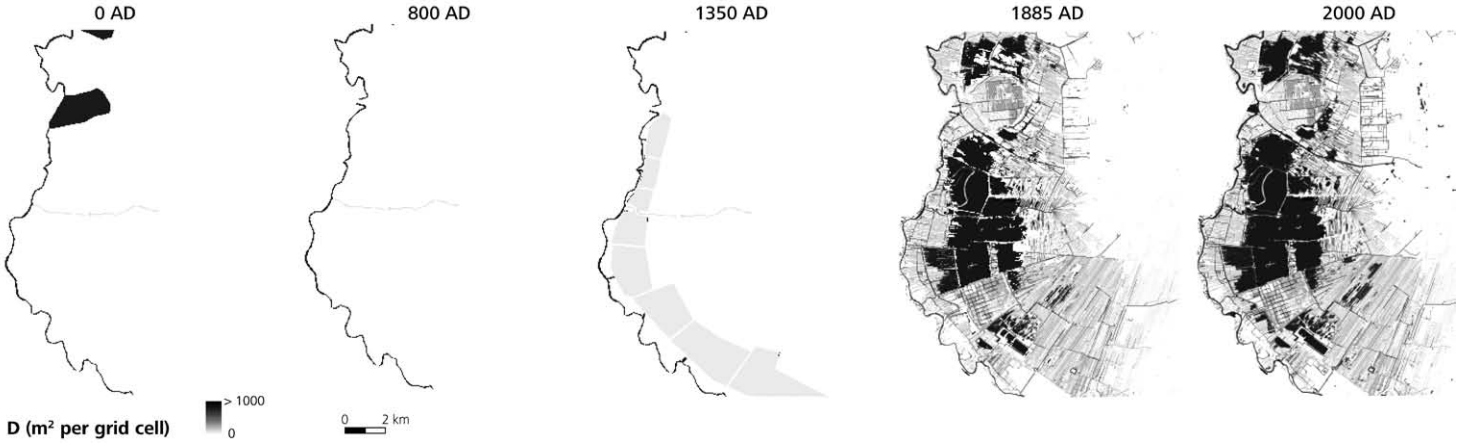

Figure A2: Reconstructed drainage intensity (D) for subsequent time slices.

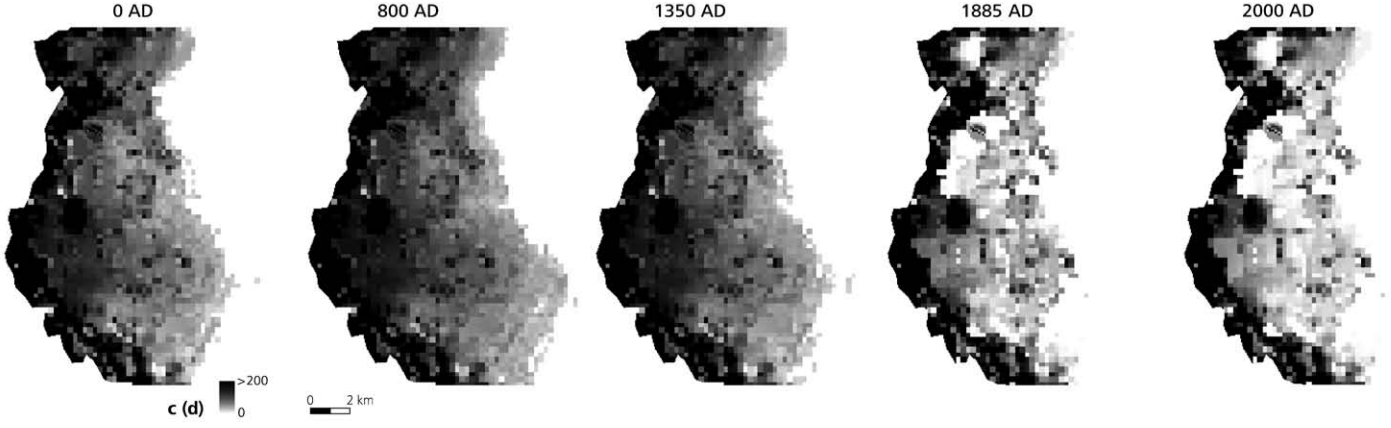

Figure A3: Reconstructed hydraulic resistance (c) of the semi-confining peat layer for subsequent time slices.

Abstract

Low-productive fens are wetland ecosystems that have strongly declined in number and size in temperate regions of Western Europe since World War II. This fen type has significant conservation value in many countries because of its high species diversity and the presence of endangered plant species. Along with the growing awareness of the importance of biodiversity in general, an interest has arisen to conserve fens for future generations. For this reason, ambitious efforts have been undertaken in The Netherlands to reverse fen deterioration by active nature and water management. However, the effectiveness of fen restoration schemes has so far been variable, partly because of inadequacy of measures to rewet fen reserves with unpolluted groundwater. A possible cause of this inadequacy is that currently utilized rewetting strategies are based on a biased perception of the hydrological mechanisms behind fen deterioration due to an incomplete knowledge of human impact on groundwater flow since the first water management actions. In this thesis, the hydrological mechanisms behind fen deterioration are studied from a historical perspective in order to identify the hydrological requirements for successful fen restoration in anthropogenically dominated regions.

A series of palaeo-groundwater models of the Gooi- and Vechtstreek area (The Netherlands) for the time-frame 0-2000 AD indicates that the volume of groundwater that discharges into the studied fen area increased with intensifying water management, except for a minor decrease since the start of groundwater abstraction by the end of the 19th century. Moreover, the models demonstrate that water management actions underlie the shift of the main groundwater discharge mechanism from regional throughflow to local drain discharge. The importance of throughflow for contiguous fen habitat patches in natural fens is demonstrated for the Biebrza River valley (Poland) by confronting modelled zones of groundwater supply with observed patterns in plant alliances and groundwater composition. Likewise, the impact of drainage networks on the groundwater supply of fens is demonstrated by high-resolution groundwater models and environmental tracers observed in a managed fen area. The results show that drainage networks diffusively intercept exfiltrating groundwater, enhance the infiltration of local precipitation on a landscape scale and interrupt the lateral redistribution of excess water by throughflow. A strategy analysis with a linked habitat suitability and seed dispersal model indicates that the elimination of drainage ditches from the upstream margins of fens, i.e., the natural throughflow zone, provides the best prospects for fen restoration. Using this strategy, both abiotic conditions suitable for fen plants and connectivity between habitat patches can be effectively restored.

The results of this thesis suggest that effective hydrological fen restoration requires the elimination of drainage ditches in a spatially coherent way, starting at the upstream fen margins and proceeding in a downstream direction. Only if drainage has been sufficiently impeded to restore natural throughflow mechanisms, additional measures, like raising surface water levels in polders, can further enhance fen restoration, by delaying the reinfiltration of exfiltrated groundwater. Lowest priority should be assigned to measures that enhance regional groundwater flow towards drained fen areas, like closing abstraction wells, because such measures do not contribute to a more efficient supply of exfiltrated groundwater to fens.

Samenvatting

De hydrologische oorzaken van de achteruitgang van laagveengebieden ontrafeld

Laagveengebieden hebben van nature een hoge soortenrijkdom. Behalve aansprekende vogelsoorten, zoals de purperreiger, het baardmannetje, de zwarte stern en de bruine kiekendief, komen er in laagveengebieden ook veel zeldzame plantensoorten voor. Vooral de plantensoorten die kenmerkend zijn voor relatief voedselarme omstandigheden maken laagvenen floristisch bijzonder. Een aantal van deze plantensoorten staat bovendien op de Rode Lijst van veel Europese landen, wat inhoudt dat ze sterk bedreigd zijn. Voorbeelden van bedreigde plantensoorten zijn de orchideeën moeraswespenorchis, sturmia, malaxis en welriekende nachtorchis. De bedreigde status van deze plantensoorten heeft een aantal oorzaken, waarvan de belangrijkste de grootschalige ontginning van laagveengebieden ten behoeve van de landbouw is. Daarnaast hebben ingrepen in de waterhuishouding, deels ook ten behoeve van landbouw, een negatief effect op de leefomstandigheden in laagveengebieden gehad. Zo hebben het bemalen van polders en het onttrekken van grondwater grote invloed op de hydrologie van intact gebleven laagveenrestanten. Deze invloed bestaat uit een daling van de grondwaterstand en een afname van de hoeveelheid toestromend grondwater. Dit laatste kan leiden tot verzuring, doordat o.a. opgeloste kalk niet meer met het grondwater naar de wortelzone wordt getransporteerd. Daarnaast kan de voedselrijkdom toenemen, doordat het veen mineraliseert, waarbij de in het veen opgeslagen koolstof ontwijkt naar de atmosfeer en voedingsstoffen vrijkomen die in het water oplossen. Het gevolg is dat op deze plaatsen de plantensoorten die karakteristiek zijn voor laagvenen verdwijnen, doordat ze weggeconcurreerd worden door plantensoorten die goed groeien van de vrijgekomen voedingsstoffen of onder zuurdere omstandigheden. Deze hydrologisch gestuurde veranderingen in de leefomstandigheden kunnen daarom leiden tot het lokaal uitsterven van laagveenplanten, wat tevens leidt tot versnippering van de overgebleven populaties van laagveensoorten. Populaties in een versnipperd landschap zijn relatief kwetsbaar voor uitsterven als het netwerk van met elkaar samenhangende subpopulaties zo klein is geworden dat planten zich nog maar moeizaam kunnen verspreiden. Tevens kan de vitaliteit van planten afnemen, doordat genetische uitwisseling tussen subpopulaties wordt bemoeilijkt.

Natuurbescherming in Nederland is begonnen met de aankoop van het Naardermeer in 1904 door Jac P. Thijsse en vrienden. Hiermee werd voorkomen dat deze schitterende laagveenplas met haar enorme vogel- en plantenrijkdom door de gemeente Amsterdam als vuilstort in gebruik werd genomen. Met de aankoop van het Naardermeer was de oprichting van de Vereniging Natuurmonumenten een feit. Nu, meer dan honderd jaar later, heeft deze vereniging 100.000 ha natuur verspreid over heel Nederland in eigendom. De maatschappelijke behoefte om de levende natuur te beschermen nam na de oorlog rechtevenredig toe met het tempo waarmee de landbouw intensiveerde en grootschaliger werd. De onderliggende reden was het verdwijnen van veel dier- en plantensoorten uit het landelijk gebied waar zij tot dan toe stand hielden ondanks de agrarische activiteiten. De laatste decennia is het steeds duidelijker geworden dat het voortbestaan van bedreigde laagveenplantensoorten afhankelijk is van de specifieke milieuomstandigheden die door toestromend grondwater bepaald worden. Dit grondwater is veelal afkomstig uit aangrenzende hoger gelegen zandgronden, zoals de Utrechtse heuvelrug, de Veluwe, het Drents Plateau en de Brabantse Wal. Het behoud van laagveensoorten vereist dus niet alleen beheersmaatregelen binnen de natuurreservaten, maar ook het afstemmen van het waterbeheer

op de natuurdoelstellingen voor natuurreservaten op regionale schaal. Concreet heeft dit in sommige gebieden aanleiding gegeven tot het verhogen van polderpeilen en het sluiten of verplaatsen van drinkwaterwinningen, zodat de hoeveelheid grondwater dat beschikbaar is voor natuur toe zou nemen. Echter, tot op heden hebben deze maatregelen niet altijd het gewenste effect gehad, ondanks de vaak kostbare investeringen die het vernatten van laagveengebieden met grondwater met zich meebrengt.

De gangbare vernattingsstrategieën van laagveengebieden zijn voornamelijk gebaseerd op kennis van het effect van waterbeheer op grondwaterstroming. Deze kennis is verkregen door wetenschappelijk hydrologisch onderzoek naar Nederlandse laagveengebieden waar al sinds mensenheugenis sprake is van waterbeheer. Deze kennis zou echter tekort kunnen schieten voor het herstellen van natuurwaarden, omdat inzicht ontbreekt in de omstandigheden van vóór die periode. Daardoor kan geen vergelijking worden gemaakt van de huidige omstandigheden met die onder natuurlijke omstandigheden en is het lastig om de effecten van verschillende vormen van waterbeheer op de waterhuishouding van laagveengebieden vast te stellen. Daarom heb ik in dit proefschrift de invloed van waterbeheer op de grondwatervoeding van laagveengebieden vanuit een historisch perspectief onderzocht. Dit heb ik gedaan door middel van een reconstructie van de hydrologische veranderingen die de Gooi- en Vechtstreek heeft ondergaan sinds het begin van het waterbeheer in de 9^{e} eeuw van onze jaartelling. Hiervoor heb ik een serie grondwatermodellen gemaakt die representatief zijn voor opeenvolgende stadia van waterbeheer. Daarnaast heb ik de waterhuishouding bestudeerd van een tamelijk ongestoord laagveengebied in Polen. De nieuwe kennis die dit opleverde over de natuurlijke waterhuishouding van laagveengebieden vormt de basis voor een analyse van de hydrologische veranderingen in de Gooi- en Vechtstreek ten gevolge van waterbeheer.

De resultaten van dit proefschrift laten zien dat de waterhuishouding van het laagveengebied in de Gooi- en Vechtstreek sterk aan verandering onderhevig is geweest gedurende de ontwikkeling van het waterbeheer de afgelopen 1000 jaar. Onder natuurlijke omstandigheden, voordat de mens het water beheerde, werd een relatief kleine zone aan de voet van de stuwwallen van het Gooi gevoed door grote hoeveelheden grondwater. Hierdoor was er in het bovenstrooms veengebied sprake van een wateroverschot bestaande uit grondwater en regenwater. Dit wateroverschot werd door laterale afstroming door de wortel zone en over het maaiveld oppervlakkig afgevoerd naar een systeem van kreken, dat afwaterde op de rivier de Vecht. Een vergelijkbaar stromingspatroon werd vastgesteld in het ongestoorde laagveengebied in het rivierdal van de Biebrza in Polen. Grondwatermodellen van dit laagveengebied laten zien dat grondwaterafhankelijke plantengemeenschappen voornamelijk gevoed worden door grondwater dat door laterale afstroming door de wortelzone ruimtelijke herverdeeld wordt over een groot gebied. Hierdoor is niet alleen de hoeveelheid uittredend grondwater, maar voornamelijk de snelheid van infiltratie van ondiep grondwater dat de omvang van grondwatergevoede gebieden bepaalt.

Menselijke ingrepen in de waterhuishouding van het veengebied in de Gooi- en Vechtstreek bestonden in eerste instantie (vanaf het jaar 1000) uit ontwatering ten behoeve van het verbouwen van voedselgewassen en het afgraven van veen dat gebruikt werd als brandstof. De winning van veen was vanaf de 14e eeuw zo wijdverbreid dat kleinere en grotere meren ontstonden. Twee meren, één natuurlijk meer (Horstermeer) en één door turfwinning ontstaan meer (de huidige Bethunepolder), zijn in de tweede helft van de 19e eeuw drooggelegd. Daarvoor dient tot op de dag van vandaag water met behulp van pompen uitgeslagen te worden. De toestroom van grondwater is zo sterk, dat bij het stopzetten van de pompen beide droogmakerijen binnen 24 uur weer volledig blank staan. Ondertussen

was ook in de omringende gebieden een complex poldersysteem ontstaan, waarmee de waterstanden per polder nauwkeurig konden worden afgestemd op de aanwezige landgebruiksfuncties: woningbouw, akkerbouw of veeteelt. Deze ingrepen hebben het vlakke veengebied veranderd in een veengebied met relatief grote variaties in topografische hoogten tussen de polders. De serie grondwatermodellen maken duidelijk dat in Gooi- en Vechtstreek de hoeveelheid grondwater dat naar het veengebied stroomt is toegenomen. Dit komt doordat met het ontstaan van grotere topografische verschillen in het veengebied meer regenwater in de bodem wordt opgenomen. Dit water wordt vervolgens door (relatief diepe) grondwaterstroming getransporteerd naar een lager gelegen polder. Door deze complexe stromingspatronen ontstonden nieuwe grondwatergevoede gebieden en nam de totale hoeveelheid grondwater dat naar en door het laagveengebied stroomde toe. Deze toename in de hoeveelheid toestromend grondwater in het laagveengebied is nog altijd groter dan de afname ten gevolge van drinkwaterwinningen in de stuwwallen van het Gooi sinds het einde van de 19e eeuw. Op dat moment was het afvoermechanisme van wateroverschotten echter al omgeslagen van oppervlakkige afstroming naar drainage door een netwerk van sloten.

In dit proefschrift zijn tevens gedetailleerde grondwatermodellen voor het in het noordelijke deel van de Vechtstreek gelegen Naardermeer gemaakt. Deze modellen en waargenomen patronen in de grondwatersamenstelling in het Naardermeer en omgeving laten duidelijk de effecten van regionale drainage op de waterhuishouding van laagveengebieden zien. Sloten die gegraven zijn om 'overtollig' water af te voeren blijken toestromend grondwater effectief af te vangen, zodat het toestromende grondwater de wortelzone van planten niet bereikt. Daarvoor in de plaats neemt zowel lokaal bij de sloten, als op de schaal van het veenlandschap als geheel, de voeding met regenwater toe. Drainage leidt dus niet alleen tot minder natte omstandigheden, maar ook tot een verschuiving van grondwater naar regenwater in de wortelzone. Doordat het ontstaan van wateroverschotten in de ondiepe ondergrond door drainagemiddelen worden voorkomen, en grondwater niet meer in de wortelzone kan uittreden, heeft het diffuus weglekken van toestromend grondwater naar drainagenetwerken tevens tot gevolg dat uittredend grondwater niet meer lateraal afgevoerd wordt, zoals onder natuurlijke omstandigheden het geval was. Daarom hebben drainagenetwerken een veel grotere invloed op de waterhuishouding van laagveengebieden dan tot nog toe werd gedacht.

Een analyse van mogelijke strategische hydrologische herstelmaatregelen laat tenslotte zien dat het verplaatsen van grondwaterwinningen en het verhogen van polderpeilen niet de meest effectieve maatregelen zijn voor het vernatten van gedraineerde laagveengebieden met grondwater. De uitgevoerde scenariostudie maakt duidelijk dat zulke ingrijpende (en dure) maatregelen niet verhinderen dat het meeste grondwater dat naar het veengebied stroomt via het drainagesysteem blijft weglekken. Hierdoor komt toestromend grondwater niet beschikbaar voor planten, maar wordt het versneld afgevoerd als oppervlaktewater. Daarentegen blijken herstelstrategieën waarbij sloten op regionale schaal worden gedempt of afgedamd wel effectief te zijn in het vernatten van laagveengebieden met grondwater. In het bijzonder het dempen of afdammen van sloten op de overgang van de stuwwallen van het Gooi en het aangrenzende laagveengebied blijkt een effectieve manier om het uittreden van grondwater aan het maaiveld te herstellen, zodat het grondwater vervolgens ruimtelijk herverdeeld kan worden door laterale afstroming zoals onder natuurlijke omstandigheden het geval was. Dit biedt kansen voor het herstel van grote, aaneengesloten leefgebieden van laagveenplantensoorten, zodat deze zich beter via natuurlijke zaadverspreiding kunnen verspreiden. Dit is zelfs het geval indien nog steeds een beperkte hoeveelheid grondwater wordt ontrokken uit de stuwwal en het poldersysteem

gehandhaafd wordt ten behoeve van landbouw in het benedenstrooms gebied. Dit zal dan wel een vorm van landbouw moeten zijn die op relatief vochtige grond kan plaatsvinden.

Dit proefschrift laat zien dat ingrepen in de waterhuishouding die resulteren in een afname van de hoeveelheid grondwater dat naar laagveengebieden stroomt (zoals grondwateronttrekkingen op de stuwwallen) niet de belangrijkste veroorzakers zijn van het verlies van natuurwaarden in laagveengebieden. Deze ingrepen hebben maar een beperkt effect op de laterale afstroming van het uitgetreden grondwater, dat onder natuurlijke omstandigheden bepalend was voor de omstandigheden die nodig zijn om bedreigde laagveenplanten te behouden. Het bemalen van polders heeft een groter effect op de waterhuishouding van laagveengebieden, doordat deze vorm van waterbeheer de infiltratie van regenwater en uitgetreden grondwater versnelt. Dit vermindert de oppervlakte die potentieel door laterale afstroming met grondwater gevoed kan worden. Het ontwateren van laagveengebieden door middel van grootschalige drainagenetwerken blijkt echter het grootste effect op de waterhuishouding van laagveengebieden te hebben. Drainagenetwerken veroorzaken niet alleen een verlaging van de grondwaterstand, maar ook het diffuus weglekken van toestromend grondwater, zodat laterale afstroming van regen- en grondwater wordt verhinderd. Dit hydrologische mechanisme, waarbij uittredend grondwater zich verspreid over een groter oppervlak, zorgt er in natuurlijke laagvenen voor dat een veel groter gebied dan de locatie waar het grondwater fysiek opkwelt wordt doordrenkt met kalkhoudend grondwater. Hierdoor komt kalkhoudend grondwater efficiënt beschikbaar voor planten. Intensieve drainage is hierdoor de belangrijkste oorzaak van het verloren gaan van de leefomstandigheden die geschikt zijn voor laagveensoorten.

Voor natuurbeheerders en waterschappen die zich inzetten om de laagveennatuur in oude glorie te herstellen levert deze studie overtuigend bewijs dat de gangbare ad-hoc strategie voor het vernatten van individuele natuurreservaten in intensief beheerde laagveengebieden niet effectief is. Het dempen of afdammen van sloten op de overgang van hoger gelegen zandgronden naar laagveengebieden is wel een veelbelovende maatregel voor natuurherstel van laagveengebieden. Daarom zou aan het afdammen van sloten op een ruimtelijk samenhangende manier de hoogste prioriteit moeten worden toegekend. Dit houdt in dat de ontwatering eerst beperkt dient te worden in de meest bovenstrooms gelegen gebieden door het dempen van sloten. Vervolgens kunnen gaandeweg in de richting van benedenstrooms gelegen gebieden sloten worden gedempt. Pas zodra voldoende sloten zijn gedempt voor het herstellen van de laterale verspreiding van uitgetreden grondwater, kunnen maatregelen worden getroffen voor het vertragen van de herinfiltratie van uitgetreden grondwater. Dit kan bijvoorbeeld door droogmakerijen te inunderen of polderpeilen te verhogen. Maatregelen om de hoeveelheid toestromend grondwater in gedraineerde laagveengebieden te verhogen, zoals het sluiten of verplaatsen van grondwateronttrekkingen op de hogere zandgronden, hebben een minder hoge prioriteit, omdat deze maatregelen niet bijdragen aan een efficiëntere grondwatervoorziening van laagveengebieden. Het kan zijn dat om praktische redenen vernattingsmaatregelen in een andere volgorde worden getroffen dan zoals hier voorgesteld. Dit geniet echter niet de voorkeur. Waterbeheerders moeten zich er in dat geval bewust van zijn dat kostbare investeringen in de vernatting van laagveengebieden alleen effect hebben nadat het diffuus weglekken van toestromend grondwater naar het drainagenetwerk voldoende is beperkt door het dempen of afdammen van sloten en andere drainage middelen.

Dankwoord

De laatste woorden van dit proefschrift wijd ik aan het bedanken van iedereen die direct of indirect heeft bijgedragen aan dit boekje. Allereerst zijn dat mijn promotoren en co-promotoren die mij na een sollicitatiegesprek in december 2004 de gelegenheid gaven om een carrière move te maken; ik verhuisde van Waterschap de Dommel naar de Universiteit Utrecht om de hydrologische oorzaken van habitat fragmentatie te onderzoeken. Aanvankelijk was ik nog wat onwennig in mijn nieuwe rol, maar gelukkig wisten jullie (vooral Paul!) me zover te krijgen om binnen 3 maanden een gestructureerd onderzoeksvoorstel te produceren. Al snel daarna was ik regelmatig in het veld te vinden om stromingspatronen in meer en minder gedraineerde natuurreservaten vast te stellen. Mede dankzij de praktische tips van Martin en Jasper is het bemonsteren van grondwater niet structureel verkeerd gegaan; ik had nog aardig wat te leren over filtreren, spoelen en conserveren van watermonsters. Ondertussen was ik al fanatiek in de weer met grondwatermodellen met als doel de hydrologische veranderingen in de Gooi- en Vechtstreek gedurende de afgelopen 2000 jaar te reconstrueren. Dit idee sprak mij van begin af aan enorm aan, maar de uitvoering bleek flink weerbarstig. Dankzij Marc en Jasper kon ik voor het modelleren gebruik maken van de faciliteiten, ervaring en databases van Deltares (voormalig NITG-TNO). En passant kreeg ik er tijdelijk een vijfde begeleider bij: Ype leerde mij in enkele maanden hoe met behulp van Fortran en ArcInfo gedetailleerde grondwatermodellen te maken die flexibel aan te passen zijn. Deze setting stelde mij in staat om de mooie modelresultaten van dit proefschrift te genereren, ook al ging het lang niet altijd vanzelf. Dankzij de modelervaring van Marc en de nuchtere becommentariëring van mijn bezigheden door Paul ("Doe nu niet meer dan wat nodig is; wat wil je nu precies weten?") kon ik de deelonderzoeken uit voeren en (belangrijker) tot afronding brengen.

Nog meer dan het modelleren, ging het schrijven van publicaties mij aanvankelijk op zijn zachtst gezegd niet gemakkelijk af. Ik zag daarom behoorlijk tegen deze klus op. Gelukkig hamerden Martin en (vooral) Paul er al snel op dat promoveren niet alleen het maken van modelletjes is, maar dat er vooral druk geschreven moest worden, en wel nu meteen. Schrijven was aanvankelijk een moeizaam proces, niet alleen omdat mijn schrijftalenten nog wat onderontwikkeld waren, maar ook omdat ik nog moest leren hoe met het commentaar van vier verschillende wetenschappers om te gaan. Gelukkig zag ik na een tijdje een patroon in jullie op- en aanmerkingen, zodat ik steeds vaker wist te voorkomen dat Paul nog los zou gaan op de structuur, Marc op de methodische details, Jasper op de beschreven implicaties voor abiotische omstandigheden en Martin op mijn interpretatie van de geleverde bijdrage aan de ecohydrologische literatuur. Het moet ook voor jullie leuk zijn geweest om te zien dat ik het schrijven steeds beter onder de knie kreeg. Natuurlijk zijn er meer leermomenten geweest dan ik hier beschrijven kan, maar de boodschap lijkt me duidelijk: dankzij jullie betrokkenheid met mijn werk heb ik een mooi proefschrift kunnen schrijven. Jullie waren (zijn!) een fijn en goed begeleidingsteam!

Ik heb de eer gehad om mijn promotieonderzoek bij zowel de vakgroep Milieunatuurwetenschappen van Universiteit Utrecht als het team Water- en bodemkwaliteit van Deltares uit te mogen voeren. Beide collega-groepen vormden een inspirerende omgeving, waar ik met veel plezier in heb gewerkt. Het schrijfwerk verrichtte ik meestal op de universiteit, waar ik met Hester een kamer deelde. Hester, wij zijn de afgelopen 5 jaar enorm naar elkaar toegegroeid. In eerste instantie leken onze onderzoeken nauwelijks raakvlakken te hebben; jij was bezig met zaadverspreiding en ik met palaeo-modellen.

Gaandeweg ontwikkelden wij het idee om onze data en modellen te combineren. Vervolgens heb jij het initiatief genomen om onze (nog wat vage) ideeën met Martin bespreken. Even leek onze moeite op niets uit te lopen, vast omdat we het te druk hadden met ons eigen onderzoek. Omdat mijn promotietijd ten einde liep heb ik de handschoen na een tijdje weer opgepakt. Uiteindelijk heeft dat geresulteerd in een gezamenlijk hoofdstuk waar ik erg trots op ben. Jouw werk was niet alleen essentieel om dit hoofdstuk te kunnen schrijven, ook jouw inzet om de tekst toegankelijk te maken voor ecologen waardeer ik enorm. Mijn herinneringen aan onze tijd in kamer 11.28 zijn natuurlijk niet beperkt tot onze samenwerking. Er is menig bakkie koffie (altijd door mij) en thee (altijd door jou) gedronken. We deelden onze hoogte en dieptepunten van ons promotieonderzoek, ook al vervloekte ik mijn vorderingen meestal hardop als jij er (even) niet was. Ondertussen volgden we jaarlijks het broedsucces van de scholeksters op het dak van het Educatorium, en wisten we wonder boven wonder 4 planten op onze kamer in leven te houden. Die uitdaging zul je vanaf nu zelf aan moeten gaan.

Omdat de kamer die ik met Hester deelde ingesloten zat tussen de kamers van Milieu-maatschappijwetenschappen, heb ik al die tijd goed contact gehad met Arnoud en Roos. Ik heb het erg gewaardeerd dat jullie zo nu en dan eens een praatje kwamen maken, vooral omdat ik zelf wat weinig initiatief nam om de rollen eens om te draaien. Om dezelfde reden ken ik mijn (directere) collega's van Milieunatuurwetenschappen vooral van de gezellige lunchpauzes, de vakgroepuitjes en de borrels ter gelegenheid van weer eens een mooie publicatie door een van ons. Ook heb ik goede herinneringen aan het EcoHydro-congres, vooral omdat ik daar volop de tijd had om met Paul over mijn en zijn onderzoek te praten en om volop grappen te maken. In deze week deelden Hugo, Max, Stefan, Paul en ik een appartement in het centrum van Wenen; een betere manier van teambuilding en inspiratie zoeken kan ik niet bedenken; lijkt me een goede tip om als vakgroep vaker te doen!

Als ik een modelleer klus te doen had, verkaste ik tijdelijk van de Universiteit naar Deltares, waar ik na verloop van tijd een kamer deelde met Geert en Jasper. Omdat jullie aardig wat aanloop hadden kreeg ik hier en daar nog wat mee van de ontwikkelingen in ons team en de ontvlechting van TNO en Deltares. Verder hield ik me afzijdig van deze ontwikkelingen, omdat ik me wilde focussen op mijn proefschrift en onderwijstaken bij de universiteit. Achteraf gezien stel ik vast dat ik jullie als team tekort heb gedaan; ik had er meer uit kunnen halen, door bijvoorbeeld zo nu en dan een teamoverleg bij te wonen. Daarom waardeer ik het des te meer dat ik erbij mocht zijn zodra het echt gezellig werd. De kerstdiners, teamuitjes, promoties, lunchwandelingen en de koffiepauzes: ik heb het altijd erg leuk gevonden om bij deze sociale activiteiten aanwezig te zijn.

Zo aan het begin van je promotietraject lijk je tijd genoeg te hebben. Daarom leek het mij een mooie gelegenheid om wat hobby's te beginnen. Met Ype en Chris kocht ik een Peugeot 404 van een jaar of 30 oud. Hier en daar de lak wat bijwerken en dat chassis, dat zouden we wel even met hulp van Martin (mijn broer) maken. Met succes begonnen we aan het repareren van de achterklep, zodat we vol goede moed aan de demontage van de rest van de auto begonnen. Helaas betekende dit dat de 404 al vrij snel op blokjes kwam te staan. Vervolgens was de roest niet meer te stoppen en starten zat er na 2 jaar ook niet meer in. Gelukkig hadden jullie het ondertussen ook wat te druk gekregen met banen of zo, zodat het minder opviel als ik de kantjes er vanaf liep. Niet dat dit het grootste probleem was, maar het is toch jammer dat we Parijs niet gehaald hebben… Ondertussen had ik samen met Bert, Chris en Ype mijn voetbalcarrière nieuw leven in geblazen. Elke woensdag trainen, althans dat was de bedoeling. Het lukte mij steeds minder vaak om tijd en energie te vinden voor de training. En dat kwam niet alleen door de belabberde instelling en prestaties van SKV-8, maar ook doordat mijn proefschrift steeds meer mijn

aandacht vereiste om het nog tot een goed einde te kunnen brengen. Uiteindelijk zijn de enige hobby's die het al die tijd gehouden hebben de (bijna-)wekelijkse etentjes (met Peter!) en bier drinken in de Zaaier. Regelmatiger waren de gezellige kopjes koffie die ik samen met Peter heb gedronken. Bedankt voor jullie belangstelling en de gezellige tijd die we samen hebben!

Oud-Parasietjes (voor de outsiders: De Parasiet was het gezelligste studentenhuis waar ik heb mogen wonen), ons contact is in de loop van de jaren wat onregelmatig geworden. We hebben het allemaal druk gekregen met een gezin of carrière. Onze Zaaier-bezoekjes zijn wat frequentie betreft niet meer wat het geweest is, maar als we elkaar zien is het meteen weer als vanouds. Flip (en Renate), Simon en Marieke, bedankt voor de relaxte tijd die we samen hebben!

De allereerste basis van dit proefschrift is gelegd tijdens mijn jeugd. Ik groeide met 5 broers en zussen op in Sprang-Capelle. Van kinds af aan had de "natuur"al een grote aantrekkingskracht op mij. Urenlang heb ik met de hengel in de hand langs het kanaal gezeten, regelmatig maakte ik omzwervingen door het natuurgebied Den Dulvert (pas een jaar of 15 later hoorde ik dat dit een van de natte natuurparels (!) van Brabant is) en sinds mijn 8^{e} verjaardag (ik kreeg een geit van mijn ouders) bouwde ik aan een kleine boerderij. Sprang-Capelle was een mooie plaats om op te groeien! Op de lagere school zat ik het liefst te rekenen; met taal redde ik het alleen dankzij het oneindige geduld van mijn moeder bij het helpen met mijn huiswerk. Tot mijn teleurstelling kreeg ik aan het einde van de lager school een MAVO-advies; liever wilde ik naar de brugklas HAVO-VWO. Gelukkig lieten mijn ouders het er niet bij zitten, kreeg ik een psychologische test (?) voor de kiezen, zodat ik alsnog de brugklas mocht gaan proberen. Zoals verwacht gingen de exacte vakken als vanzelf, maar de talen vraten energie, terwijl mijn vorderingen maar matigjes waren. Wederom was het schooladvies twijfelachtig; vwo zou (tot mijn teleurstelling) te hoog gegrepen zijn. Wederom hebben mijn ouders zich (met succes) ingezet om mij op het VWO te krijgen. Met de instelling dat je met hard werken veel kunt bereiken (die ik van huis uit heb meegekregen) en de aanmoedigingen van mijn ouders, broers en zussen haalde ik uiteindelijk zonder enig probleem mijn VWO-diploma. Vervolgens ben ik in Wageningen gaan studeren en ging ik op kamers. Lang bleef ik in de weekenden naar Sprang-Capelle komen om te werken, maar ook om op de hoogte te blijven van het leven van mijn broers en zussen. Het verbaast me nog steeds dat we op een of andere manier veel op elkaar lijken, maar dat we elk een heel ander beroep hebben gekozen, en dat we er nog best goed in zijn ook! Wat wij zeker delen is een goed gevoel voor humor en een voorliefde voor kamperen: de familieweekendjes van de afgelopen jaren waren stuk voor stuk toppers. Nu alleen nog met de fiets die Alpe d'Huez op!

Familie Top, wij kennen elkaar eigenlijk nog helemaal niet zo lang, maar dat wij elkaar kennen is voor mij al helemaal vanzelfsprekend. Misschien heeft het met mijn zwak voor goede koffie, wijn en eten te maken, maar waarschijnlijk veel meer met jullie openhartigheid, waardoor ik me al vanaf onze kennismaking bij jullie thuis voel. Elke keer als ik bij jullie kom voelt het alsof ik een klein beetje vakantie heb. Door jullie interesse in mijn werk heb ik me altijd enorm gesteund gevoeld.

Al lang voordat ik de eerste woorden van dit proefschrift op papier had staan, stond de inhoud van deze laatste paragraaf al vast. Marije, wij leerden elkaar een paar maanden voordat ik solliciteerde voor deze baan kennen. Ik woonde toen nog in Den Bosch, maar verhuisde al snel naar Carol's Paradise in Renkum. Dit oude herenhuis was veel te koud voor je, maar de grote tuin en leuke huisgenoten maakten het toch een fijne plaats om avonden en weekenden samen door te brengen. Na een jaar besloot ik om in een nog kouder studentenhuis in Wageningen te gaan wonen, terwijl jij al druk

bezig was met de aankoop van een appartement in de Groen van Prinstererstraat. We hadden toen nog niet de bedoeling om daar samen te gaan wonen, zodat je de verbouwing grotendeels zelf moest zien te regelen. Ik had namelijk naast een aantal nieuwe hobby's ook nog een proefschrift dat mijn aandacht en tijd opeiste. Gelukkig heb ik hier en daar wat tijd voor je vrij gemaakt om een muurtje uit je appartement te meppen of de stopcontacten te vervangen; ik beperkte me duidelijk tot de leuke klusjes. Na een jaar woonden we samen in dat heerlijke appartement met uitzicht op een prachtige kastanjeboom en de Grebbenberg. En dat samenwonen is essentieel geweest om elkaar regelmatig te kunnen blijven zien. Steeds vaker moest jij tegen je zin in voor je werk overnachten in Groningen. Ik vond dat niet perse heel erg, omdat ik dan ongemerkt wat extra uurtjes in mijn modellen kon stoppen. Als je dan na twee overnachtingen weer thuis kwam heb je regelmatig een golf van promotiefrustratie over je heen gekregen; het principe van promoveren heb je zodoende aardig mee gekregen, maar leuk was het vast niet altijd voor je. Terwijl jij de lange werk- en forenstijden zat werd en een nieuwe baan ging zoeken (en vond), ging ik steeds meer tijd in mijn proefschrift steken. Tijd had ik het afgelopen jaar nauwelijks meer voor je, ook niet in de weekenden. Daarom ging jij op zoek naar andere mensen die ('gelukkig' voor mij) wel mee naar Cuba of 'weekendjesweg' wilden. Uiteindelijk lukte het mij niet om mijn proefschrift op tijd af te krijgen, zodat ik na lang aandringen van jouw kant een uikering aanvroeg. Een baan die aan mijn hoge eisen voldeed zat er nog even niet in, zodat jij maandenlang de kostwinner was (bent). Marije, hoe had ik dit alles toch zonder jou kunnen doen?

Curriculum Vitae

Arnaut van Loon was born in Sprang-Capelle, The Netherlands, on May 26th, 1979. After finishing high school (VWO) at Willem van Oranje College in Waalwijk, he started his undergraduate studies in Soil, Water and Atmosphere at Wageningen University in 1997. Within the specialization Hydrology and Water management, he spent half a year at the University of Zululand (South Africa), working on groundwater flow in the St. Lucia wetlands under supervision of Prof. Bruce Kelbe. Next, he worked on an analytical solution to the linearised hillslope-storage Boussinesq equation for exponential hillslope-width functions under supervision of Prof. Peter Troch and dr. Emiel van Loon. He graduated from Wageningen University in 2003. In 2004, he started his professional career as a hydrological advisor at Waterboard De Dommel (The Netherlands). Subsequently, he started as a PhD-student at the department of Environmental Sciences (Utrecht University) under supervision of Prof. Martin Wassen, Prof. Marc Bierkens, Dr. Jasper Griffioen and Dr. Paul Schot. At the same department, he held a position of lecturer in Environmental Sciences (0.2 fte) from January until August 2008. The results of his research performed as a PhD-student are described in this thesis.