R. Bobbink B. Beltman J.T.A. Verhoeven D.F. Whigham (Eds.)

Wetlands: Functioning, Biodiversity Conservation, and Restoration

With 67 Figures, 6 in Color, and 21 Tables

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1 Wetland Functioning in Relation to Biodiversity Conservation and Restoration

ROLAND BOBBINK, DENNIS F. WHIGHAM, BOUDEWIJN BELTMAN, and JOS T.A. VERHOEVEN

1.1 Introduction

Wetland ecosystems are a natural resource of global significance. Historically, their high level of plant and animal (especially bird) diversity is perhaps the major reason why wetland protection has become a high priority worldwide, supported by international agreements such as the Ramsar Convention and the International Convention of Biological Diversity. More recently, a number of goods and services provided specifically by wetland ecosystems have been identified that may even outweigh biodiversity in terms of their importance for human welfare and sustainable natural resource management worldwide. Wetlands, as transitional zones between land and water, provide a natural protection against extreme floods and storm surges. They may also store freshwater to be used for drinking water preparation or for irrigation. Wetlands bordering streams, rivers and lakes have a water quality enhancement function that is increasingly recognized. Because riverine and lacustrine wetlands often provide a spawning habitat, their importance as a source of juvenile fish for adjacent aquatic ecosystems should not be underestimated. In addition to these local and regional benefits, wetlands as a global resource provide a net sink of carbon dioxide. The world's peatlands are the only type of terrestrial ecosystem with a long-term net carbon storage function. However, the large amounts of carbon that have accumulated historically in peatlands may be released as a result of degradation, such as drainage, excavation, or fertilization.

Wetlands do produce a striking variety of goods and services and it is no wonder that, more often than any other terrestrial ecosystem, they are used by environmental economists to illustrate ecosystem functions and their values to mankind. However, in spite of the high biodiversity and the high impor-

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tance of the goods and services of wetland ecosystems, their global status is poor and, in many situations, they are degrading at ever faster rates as a result of a wide variety of human impacts. Many wetlands, particularly river floodplains, deltas and estuaries, are especially impacted by human activities. Early civilizations have been successful particularly because of their utilization of wetland resources. Where agriculture has thrived, the natural fertility of the soils and transport has been favored by river channels and associated wetlands. In the industrial era, human impacts have become dramatically negative as a result of floodplain reclamation, poldering, construction of flood control structures, drainage for agriculture, excavation of peat for fuel and the modification and straightening of river channels in favor of navigation. Worldwide, more than 50 % of the wetland resource has been lost because of these reasons. In some densely populated regions in Europe, North America and East Asia, more than 80 % of the wetlands have been lost or severely degraded. This clearly stresses the urgent need to restore or (re)create wetlands ecosystems.

This volume presents an integrated account from several of the major symposia presented at the 7th INTECOL International Wetlands Conference (Utrecht, The Netherlands). In this introductory chapter, we will give an overview of recent advances in the comprehension of how plants and animal function in wetlands, the biodiversity conservation of wetland ecosystems and their ecological restoration. We will also identify remaining gaps in scientific knowledge and understanding that need to be addressed to optimize biodiversity conservation and restoration of wetlands across the globe.

1.2 Functioning of Plants and Animals in Wetlands

Plant species inhabiting wetlands possess physiological and morphological adaptations that support long-term survival of flooding, even sometimes with remarkably high plant productivity (e.g. Mitsch and Gosselink 2000; Larcher 2003). The most widespread physiological adaptation to tolerate short-term anoxia is the ability to switch to fermentation as the main pathway for extracting energy. This takes place in combination with energy conservation measures derived from a complex down-regulation of non-essential energy-consuming processes. Furthermore, wetland species may have developed mechanisms to tolerate the toxic end-products of fermentation, especially by diversification of end-products or production of less toxic compounds (malate). The most important strategy of wetland plants against anoxic conditions is, however, the presence of air spaces (aerenchyma) in roots and stems, allowing oxygen diffusion from the aerial plant parts to the roots. In non-wetland species root porosity is rather low (2–7 %), whereas wetland species have much higher root porosities (on average 20–50 %). This internal pathway may sustain internal aerobic conditions across the root, even reaching the root tips. Well aerated roots of many wetland species may even release oxygen to the surrounding soil, forming an oxidized rhizosphere. This is an important mechanism to detoxify harmful soluble reduced ions such as manganese and sulfide. Red-brown deposits (Fe^{3+} oxides) around roots of wetland species are a clear indication of this phenomenon. Another morphological adaptation to waterlogged conditions is the formation of adventitious roots just above the anoxic zone of the soil, thus functioning in a more or less aerobic situation. This is especially triggered by increased ethylene concentrations after inundation in both wetland and terrestrial species.

Escape-mediated plant survival in wet environments is described by Jackson (Chapter 2). It is shown that the shoots of several plant species possess a means of escaping submergence through prompt, gravity-directed upward extension growth. The growth is usually O_2-dependent and mostly entrapped ethylene is the triggering signal. This gas initiates and sustains an abnormally fast rate of shoot elongation underwater. A rapid decrease in the growth-inhibiting hormone abscisic acid, mediated by ethylene, is often a pre-requisite for the escape to start. Thus, there is an increased probability of shoots regaining contact with the atmosphere before reserves become exhausted. This mechanism may especially be of importance for survival in ecosystems with unpredictable periods of complete submergence of the vegetation. In this situation, the ability to have some underwater photosynthesis may be of importance for the survival of normally non-aquatic plant species. In addition, it has been found that the shoots of certain species that over-winter as dormant tubers, rhizomes or turions are stimulated to elongate very rapidly, even under the complete absence of O_2. In contrast, some species have evolved suppression of this fast shoot extension, resulting in an underwater quiescence that may confer an advantage for survival where the prevailing water depth is too great for escape.

The crucial role of macrophytes in regulating trophic interactions in shallow lakes is clearly demonstrated by Burks et al. (Chapter 3). They define shallow lakes as permanently flooded wetlands that may be surrounded by emergent vegetation (i.e. marshy habitat). Water depth is typically less than 3 m. Studies on the role of trophic interactions with submerged plants in shallow lakes are not novel, but the study of other growth forms of macrophytes (i.e. floating-leaved, emergent, freely-floating) is an expanding field of research. Four key issues can be identified in this context. Firstly, zooplankton (and planktivorous fish) depend on macrophytes as habitat refuge, although the role of emergent vegetation is still unclear. Second, biochemical interactions ("allelopathy") between macrophytes and competing primary producers can be of major importance for the structure of the plant community; and the deterrent chemical nature of some aquatic plants may even strongly influence the biological community. Furthermore, macrophytes form a substrate for epiphyton. In eutrophic to hypertrophic lakes, a negative relationship exists between macrophyte biomass and epiphyton growth. However, the density of epiphyton, in turn, depends on the amount of grazing macroinvertebrates (e.g. snails), but not on nutrients. These grazers may help maintain littoral communities by continuously removing unwanted algae or sediments. Finally, the interaction between macrophytes and fish can be of major importance for the functioning of shallow lakes, but the complexity of these interactions is large and, in many situations, not known. It is suggested that the presence of aquatic macrophytes is a driving force for interactions within the rest of the food web, and thus determines which trophic interactions play a role in shifts between alternative shallow lake states.

The structure and functioning of wetlands can be (strongly) influenced by vertebrate herbivory, as recently reviewed by Van den Wyngaert and Bobbink (2006). The most important large herbivores of wetland ecosystems are several species of rodents and waterfowl, though the latter are mostly restricted to wetlands where open water is also present. The effects of wetland herbivores, which use above-ground plant parts, are in general more or less comparable with those found in terrestrial ecosystems. Two typical differences are distinguished between the effects of vertebrate herbivory in wetlands compared with those in terrestrial systems.

First, herbivory of leaves and shoots does not severely restrict annual above-ground plant production in wetland ecosystems, as long as there is oxygen transport to the below-ground storage organs. Damage to the shoots of emergent macrophytes below water level by foraging herbivores is in most cases lethal and strongly reduces above-ground plant production. In this way, the structure of the plant community can be strongly affected despite the removal of only a small part of the biomass. Second, the consequences of grubbing and consumption of below-ground storage organs by natural herbivores in wetlands with their wet and soft soils can be obvious. Grubbing for below-ground storage organs can severely disturb the vegetation; and, when the regeneration time is long, grubbed vegetation is much more sensitive to increasing grazing pressure. Increased grubbing may lead to denudation rather than replacement of the plant species by a less palatable one (Fig. 1.1). The affected wetland ecosystems may evolve to a "low steady state" or, if grazing pressure is above carrying capacity, can become completely deteriorated. It is clear that the effects of herbivores can be of major importance to the structure and dynamics of various wetlands, although their nutrient cycling is considered to be detritus-based. In contrast, herbivory of aquatic macrophytes is, in general, of minor importance in shallow lake ecosystems, although large invertebrate grazers (especially crayfish) affect the macrophyte cover in a few cases (Chapter 3).

Interest in biological invasions has rapidly increased in recent decades and today they are a major concern in ecology and conservation. Particularly dramatic consequences of invasions have been observed on island ecosystems where endemic species suffered severely, but wetlands (marshes,

Fig. 1.1 Grubbing of Canadian subarctic salt marsh by lesser snow geese (*Anser caerulescens caerulescens*) has created bare soil, where an increase in salinity inhibits revegetation (photo kindly made available by Peter Kotanen)

lakes, rivers) and estuaries are also among the most affected systems. The nature and impacts of invasions in these ecosystems are described in detail by Van der Velde et al. in Chapter 4. Human-mediated dispersal of transport of species is nowadays clearly much higher than natural dispersal in historical periods. The number of introduced species is related to the number of introduction events and to the number of individuals per event. Freshwater, estuarine and coastal wetlands are amongst the most invaded systems worldwide, because of the numerous introduction vectors and activities that facilitate invasions in these environments. Impacts of invasions may occur at all levels of ecological organization and are especially severe when the introduced species function as an ecosystem engineer (e.g. Crooks 2002). In addition, Van der Velde et al. give an overview of approaches that are used to understand and predict biological invasions. They clearly show that the relational key-lock approach is most promising, because it integrates the importance of ecosystem characteristics for the success of the invader, who in turn must possess the "right" characteristics to invade a particular ecosystem. Recent studies on propagule pressure generally met with success in explaining vulnerability of ecosystems to invasion, but in reality it is very likely that more than one mechanism simultaneously affects invasion success. Therefore, predictions by the different models are still quite inaccurate and have an observational nature. It is concluded that more experimentation is needed to verify the predictions of theoretical models with respect to (wetland) invasions and that we should not forget to learn from all historical "experiments".

1.3 Biodiversity Conservation and Wetlands

Biodiversity of wetland and freshwater ecosystems is currently under high risk, with a very high proportion of species threatened with extinction (Millennium Ecosystem Assessment 2005). Thus, wetland management and conservation is a huge challenge in the near future. Pittock et al. (Chapter 8) examine large-scale mechanisms for wetlands conservation based on: ecoregion prioritization and vision setting, integrated river basin management, poverty reduction, multilateral treaties, regional collaboration between countries and target-driven work by a non-government organization. These methods show some promise but also highlight the complexity of this task and long-term investments required to establish sustainable conservation initiatives. Integration of the expertise of hydrologists and that of biologists is needed; and starting at the catchment scale is clearly better than starting at small "hotspots". This conclusion is also drawn by Maltby in Chapter 5, in his extensive description of the "ecosystem approach" for the conservation and management of wetlands. Both chapters also highlight the need to build partnerships and capacities to meet the social and economic needs of local communities to sustain wetlands conservation, and thus to come to a "wise use" of these systems. In general, the conservation of biodiversity is not the primary motivation for most governments or stakeholders in managing wetlands, especially where local people live in poverty, as shown for the Yangtze river polders in China by Pittock et al. and for the restoration of Mesopotamian marshes by Maltby. Futhermore, it is obvious that conservation of ecological processes at the river basin scale or catchment scale are needed to protect wetland biodiversity and thus large-scale planning and strategic interventions are needed at the national and regional scale. One of the greatest challenges in the near future is to reach out and engage the many sectors of our society that have to be part of these large-scale solutions and help them choose for wetland biodiversity conservation. Not only the adequate use of scientific knowledge and integrative management is necessary to reach these objectives, but also the concept of "social learning" can be used to reach these objectives in wetland development, as discussed by Van Slobbe et al. (Chapter 12) using wetland management projects in the Netherlands, Belgium and Sri Lanka.

Conservation of biodiversity is thus one of the main objectives for the management of wetland ecosystems. This implies an urgent search in conservation policy for the identification of simple ecosystem-wide indicators for biodiversity in these systems. De Meester et al. (Chapter 7) have studied simultaneously the relationships between biodiversity among organism groups at different trophic levels and several environmental variables in shallow lakes across Europe (from Denmark to Spain). The patterns of association observed for biodiversity strongly indicate that biodiversity tends to be rather unrelated between different organism groups and trophic levels, although clear-water lakes are generally more species-rich for several groups (macrophytes, zooplankton, macro-invertebrates, amphibians, birds) than turbid lakes. This implies that the search for one simple index reflecting overall ecosystem diversity has little relevance. Rather, useful indicators may only be found for one or a restricted subset of organism groups that tend to be associated with a similar gradient. To assess richness at the ecosystem level, several of these indicators have to be combined and weighed according to the final aim of the assessment. Therefore, lake managers first have to define priorities, including, for instance, groups deserving special attention, the importance of rarity, etc. Second, given the low association in diversity between groups, future biodiversity studies would gain from the inclusion of taxonomic or functional groups that are often ignored in wetland science, such as microbial communities and periphyton. Finally, the obvious multidimensionality of diversity also has important implications for the definition of management objectives: management measures that may increase the diversity in one organism group may be ineffective or even counter-productive for diversity in other groups. Probably no management technique exists that leads to an enhancement of diversity at all trophic levels and for all taxonomic groups. One implication is that a good biodiversity strategy should involve variation in the management of shallow lakes in a region, so as to increase regional diversity.

Barendregt et al. (Chapter 6) describe the biodiversity and ecological functioning of tidal freshwater wetlands in both Europe and the United States, a relatively little-studied system but under high anthropogenic pressure in the past as well as presently. Tidal freshwater wetlands occur in the upper part of estuaries and can have tides of up to several meters in amplitude twice a day. They occur at the interface between the brackish zone in the estuary and the river; and where brackish and fresh water mix there is an area of maximum suspended matter. The tidal freshwater zone within the estuary plays an important role in overall patterns of nutrient cycling for the whole estuary and the pattern appears to differ in the brackish and saline sections. Although tidal freshwater wetlands do not include many endemic or restricted species, they are characterized by high species and habitat diversity. There is distinct zonation in flora and fauna species responding to the relationship between surface elevation and tidal amplitude. The tidal freshwater wetlands in Europe and North America also have a common history of being highly influenced by human activities, resulting in altered hydrology, losses in wetland area and high levels of sediment and nutrient input. Recently, management activities have been initiated on both sides of the Atlantic to maintain or restore its characteristic biodiversity and other free ecological services to man.

In many parts of the world, coastal wetlands are under pressure from increasing human populations and from predicted sea level rise. These wetlands are dynamic ecosystems with a characteristic species composition and include the freshwater–intertidal interface. Because of this, they are complex systems and at present limited knowledge is available for the processes operating in these coastal wetlands, making appropriate management a real challenge. Dale et al. (Chapter 9) demonstrate that "adaptive management strategies" are needed for the conservation and management of these coastal wetlands. They provide case studies from Australia and the United States that show the role science can (and has to) play in informing the adaptive management process. Several common themes emerge from these studies with respect to wetland conservation management. Hydrology appears to be a driving variable in all cases and may be impacted by various forms of development. The projects highlight the importance of monitoring water table levels and water quality (including salinity). Because of the complexity of coastal wetlands, all projects have involved interdisciplinary teams, bringing together skills from a wide range of areas including pedology, geomorphology, palynology, hydrology, plant science, entomology, remote sensing and, for all of them, aspects of management. They conclude that the sustainable management of coastal wetlands relies on knowledge of ecosystem processes, so that the rates and direction of ecosystem change can be assessed, whether due to ongoing environmental changes or direct human impacts. The adaptive management approach is strongly recommended, to improve the use of both existing and new knowledge of ecosystem processes in order to inform wetland management actions.

1.4 Ecological Restoration of Wetlands

Human activities have long caused the loss of large areas of wetlands because they become degraded as a result of changing their structure or function. Overviews of their status and the threats to wetlands in a global perspective are provided by Brinson and Malvarez (2002) for temperate freshwater wetlands, by Moore (2002) for bogs and by Junk (2002) for tropical wetlands. It is obvious that, besides reduction in the rate of wetland loss, restoration of degraded wetlands or creation of new wetland habitats is urgently needed to improve wetland condition and area.

Contrasting approaches to the ecological restoration of diverse herbaceous wetlands are evaluated by Boers et al. (Chapter 10). These species-rich herbaceous wetlands can shift to species-poor wetlands by alternations in water supply and/or the nutrient regime in response to human activities within the watershed. Both external eutrophication (e.g. phosphorus loading by surface water or atmospheric nitrogen deposition) and internal eutrophication by inputs of water with a changed chemical composition (e.g. higher alkalinity or increased sulfate concentration) can drastically impact the nutrient status of a wetland system, leading to dominance of aggressive species and loss of biodiversity. In addition, invasive non-native species may establish and outcompete native species. By comparison of restoration efforts in degraded herbaceous wetlands in Winconsin (USA) and the Netherlands, the authors have come to some general principles of restoration. Many of the constraints on restoration are abiotic. Hydrologic conditions, water chemistry and nutrient status are primary examples, e.g. a decline in groundwater levels at a restoration site can limit the ability to restore vegetation that depends on a consistent subterranean water supply. Furthermore, changes in the biota can limit a site's potential to be restored, e.g. the seed bank found at a site will degrade over time. For example, former wetlands that have been converted to agriculture for many years will lack a rich seed bank, constraining the development of a typical wetland vegetation even under appropriate abiotic conditions. In addition, the dispersal of wetland species can be low, especially in modern fragmented landscapes.

As shown for conservation management (see also Section 1.3), managers become better equipped to prioritize sites for restoration as the science of restoration advances and tools become available to deal with abiotic and biotic constraints. When degradation is not reversible within a reasonable time-scale, another site might have a higher priority for restoring diversity. In landscapes with many former wetlands and limited resources for restoration, it is strategic to develop management priorities first, then prioritize the sites where each goal can best be achieved. It may not be possible to recover exactly what was lost; in such cases, recovery of a general wetland vegetation type and recovery of ecosystem functions might be more realistic goals. Project goals can be adjusted to suit the site's potential to be restored. Projects can be designed to allow learning as restoration proceeds. To date, our understanding of the underlying processes that influence ecosystem development is poor; and specific outcomes are not highly predictable. If restoration projects were implemented as experiments, alternative approaches could be tested and results monitored; then, approaches that best achieve the goals could be used in future projects (Chapter 10).

Ecohydrological knowledge is of increasing importance in wetland management and restoration. It includes the study of the origin, flow and quality of groundwater and surface water and their implications for wetland functioning. It also takes in account the functional interrelations between hydrology and biota at the catchment scale. Undisturbed reference wetland ecosystems are sometimes needed to reveal environmental conditions necessary for the restoration of these wetlands in highly stressed or changed landscapes, where these conditions disappeared before quantification. Wassen et al. (Chapter 13) summarize the ecohydrological research in the Polish Bierbrza valley as an undisturbed reference system for comparable floodplain and fen systems elsewhere in Europe. They conclude that the information from reference areas may be useful to demonstrate general potentials for recovery or rehabilitation, but has to be treated with care to avoid too high expectations by wetland managers. In addition, experimentation is needed in many situations to verify the correlative data from most reference studies.

Fens are peat-forming mires that are fed by ground water or surface water and are found in both North America and Europe. In general, the vegetation of fens is rich in vascular plant species and bryophytes. Nowadays, many fens in the United States or Europe are lost through habitat destruction or are heavily degraded in structure or function. A prerequisite for successful restoration of degraded fens is the creation of suitable habitat conditions (nutrient status, hydrology), as shown in Chapter 11 by Middleton et al. There will be no adequate fen restoration without proper assessment of the hydrological functioning of the system. It is important that stagnation of surface water in the summer is prevented in restoration projects dealing with desiccated fens, in particular when the groundwater or surface water is rich in sulfate. The best option, which is not always available, is to stimulate the discharge of unpolluted (sulfate- and nitrate-poor) groundwater in such a way that this groundwater can flow through the fen system, leaving iron behind to bind phosphates in the top soil. Restoration measures are also needed to counterbalance, for instance, the increased atmospheric nitrogen deposition in northwestern European fens (Bobbink et al. 1998). Annual cutting of the vegetation, with removal of the hay can be necessary in this nitrogen-enriched situation, but sometimes has induced a shift to phosphorus limitation, which also may change biodiversity. Recently, it became obvious that the impact of reduced forms of nitrogen (ammonium and ammonia) on fen bryophytes is much more severe than the effects of oxidized nitrogen (Paulissen et al. 2004). In addition, Middleton et al. conclude that both soil seed persistence and seed dispersal capacity is rather underestimated, although the data in Chapter 10 are partly in contrast to this conclusion. Both types of seed sources can be influenced by restoration projects. For successful restoration, both temporal (time since alteration of the habitat) and spatial (degree of fragmentation/isolation) aspects have clearly to be taken into account.

Large areas on low-lying peaty soils in large parts of Europe and North America can no longer be maintained as intensely used agricultural areas. This offers good opportunities for the (re)creation of wetlands. However, in most cases the development of eutrophic wetlands is likely, as found in the Hungarian wetland restoration project described in Middleton et al. (Chapter

11). The reflooding of former agricultural areas usually results in very nutrient-rich soil conditions and in a persistent, highly-productive marsh vegetation, suitable to maintain waterfowl, but remarkable poor in other plant and animal species. Recreation of the peat-forming function is still unlikely in this situation, although it is a highly wanted target by managers in respect to carbon sequestration in natural systems. Full recovery of all fen qualities and functions is certainly not to be expected in cases where restoration of the hydrological system is not possible. Furthermore, the phosphorus status of the sediment or soil is highly increased. Setting clear targets, which can meet the opportunities that are being presented, combined with a realistic strategy for future possibilities may prevent much disappointment. A well explained modest result sometimes does more good for the public support than a scientifically sound project that lacks community or administrative support.

1.5 Synthesis

As shown by the examples in Section 1.3, the biodiversity conservation and management of wetlands requires clear insight into the ecosystem processes that maintain wetland functions. As we gain more knowledge about wetland functions, we also increase our understanding of the complex interactions between wetland biota and human activities. The results of the Utrecht symposia that are summarized in this book are yet another step in the directon of understanding how wetlands function. The syntheses also clearly demonstrate that effective management, restoration and conservation of wetland biodiversity will require the development of management tools that can be applied at a variety of scales. In some instances, ecological principles need to be integrated into assessment and management tools that can effectively result in the conservation of wetlands that have not been degraded to the point that they no longer provide high-quality ecological functions. Similarly, challenges continue to exist that require the applications of more effective tools to restored and create wetland as global attempts are made to reverse the long-standing trend of wetland loss. Now that the citizens of the world are increasingly asking for effect-driven management of wetland resources, the lessons learned and summarized in these chapters will hopefully move us closer to more successful application of knowledge about wetland ecology in the pursuit of a world in which human needs and natural wetland functions and biodiversity can coexist.

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