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REVIEW

Ecohydrology in The Netherlands: principles of an application-driven interdiscipline[§]

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INTRODUCTION

Ecohydrology was introduced in The Netherlands as 'the science of the hydrological aspects of ecology; the overlap between hydrology and ecology, studied in view of ecological problems'. The pith of it is the hypothesis that hydrology controls the

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Nomenclature: Van der Meijden *et al.* (1990) for vascular plants; Westhoff & Den Held (1969) and Schaminée *et al.* (1995) for plant communities.

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composition of vegetation of a site through the water and solute budgets and through the conditions imposed upon the local nutrient cycling. Social impulses in the early 1970s shaped a niche for ecohydrology in studies for integrated water resources management, because agro-hydrological models fell short for nature conservation. Mires and river valleys were favourite objects of landscape-scale ecohydrological pattern analyses. Other substantial work was done on the occurrence of species with environmental factors, in search of suitable botanical indicators of complex hydrological conditions.

In this contribution, we discuss how non-aquatic ecohydrology developed into a landscape-ecological discipline, with firm roots in various branches of vegetation science in particular. Approaches and concepts were developed in order to understand the influence of water management on the observed decline of endangered plant species, even in seemingly undisturbed nature reserves. The more recent ecohydrological investigations for the restoration of damaged ecosystems benefited considerably from a further integration with geohydrological and soil-chemical studies.

This review refers to publications in English or German only, or with sufficiently detailed English summaries.

INTEGRATED WATER RESOURCES MANAGEMENT, A BREEDING POND OF ECOHYDROLOGY

The Netherlands is densely populated and intensive water management takes place in almost every part of the country. Most of its soils are very transmissive to water flow, so changes in the water management usually have wide impacts. The post-war development of The Netherlands called for an intensification of the water management in the early 1950s: drainage for agriculture, redistribution of surface water from the rivers Rhine and Meuse for navigation, salt and drought abatement, and groundwater abstraction for urban and industrial use. As a result, drought and eutrophication damages were reported for semi-natural wet plant communities (Westhoff 1979a). In the early 1970s, politicians acknowledged that both water pollution and public demands for recreation and conservation needed more attention in water management plans. Hence, water management was redefined in view of all relevant interests.

Studies appeared in which the relations between surface water and groundwater, between water quantity and water quality, and the great variety of functions of water, were considered in a hierarchical systems' approach of 'integrated water resources management' (Colenbrander 1976; Van de Nes 1976). Such studies soon showed that ecologists should obtain a much better understanding of the relationship between hydrology and vegetation in established nature reserves. They had to explain why in wetlands drastic changes in species composition occurred after only minor changes in the local hydrology (Van Wirdum 1979, 1982; Grootjans 1980; Smeets *et al.* 1980). In a test case an ecological analysis showed that the changing species composition of a degenerating wetland reflected large changes in ecological conditions while agricultural simulation models indicated that water shortage could not be a problem for normal plant growth (Van Wirdum 1981). This urged ecologists to look for other eco-hydrological relations between a changed water management and vegetational responses. As ecologists working on conservation effects of groundwater abstraction and drainage started to discuss their findings with hydrologists and other colleagues, with very different backgrounds, a new interdiscipline emerged: eco-hydrology.

SCIENTIFIC ROOTS OF ECOHYDROLOGY

Ecologists working for nature conservation supposed that the steady decline of many endangered plant species in wetlands was caused by changes in the hydrological cycle, sometimes originating at great distances from the damaged nature reserves. They realized that nature conservation could hope for a more favourable water management only if the relevant hypotheses could be substantiated with convincing scientific results.

Ecohydrological research in The Netherlands is rooted in three lines of scientific research: (i) phytosociological research of grassland communities, with an emphasis on land evaluation, (ii) agro-hydrological modelling of site conditions, and (iii) research on hydrologically determined vegetation gradients in mires. These three lines of research were associated with different scientific disciplines: vegetation science (i), soil science (ii) and groundwater chemistry (iii), respectively.

(i) Phytosociological research of grassland communities

The use of botanical indicators for the evaluation of grassland quality has a strong basis in The Netherlands. De Vries (1953) and Kruijne *et al.* (1967) used quantitative sampling and processing techniques to establish statistical associations between species and between species and site factors. Unlike De Vries, most vegetation ecologists following the Central-European tradition (Braun-Blanquet) used to pool their analyses according to pre-conceived vegetation types. With monthly measured groundwater tables Tüxen (1954), Niemann (1963, 1973) and Kleinke (1968) established characteristic relations between such vegetation types and groundwater regimes. They characterized the water regimes by the cumulative frequency distribution of the observed groundwater table depths (Dauerlinien). Although the relation was treated as a black box, the regimes were considered indicative of important ecological processes, such as soil aeration and the mineralization of organic matter, which could not be easily measured. Adopted by Grootjans & Ten Klooster (1980), this synecological usage of Dauerlinien became a key tool in ecohydrology. It was a step forward from the mere application of the groundwater regime classes given on Dutch soil maps. In that time there was a great need for baseline data concerning little disturbed semi-natural ecosystems and the above-mentioned approach provided such information. Similar techniques were used by Zonneveld (1960) with regard to the freshwater–tidal influence on the vegetation patterns in De Biesbosch, and by Klötzli and co-workers working on mesotrophic *Molinietum* communities in Switzerland (Klötzli 1969; Yerly 1970). The relations between fen vegetation and site conditions were studied quantitatively in the former Czechoslovakia (Balátová-Tuláckovà 1968, 1976; Rybníček 1974). These and other publications about site-to-vegetation correlations (reviews and bibliographies: Krause & Balátová-Tuláckovà 1977; Tüxen & Grootjans 1978a,b; Schipper & Grootjans 1986) inspired Dutch ecohydrologists studying the possible effects of land drainage (Grootjans & Ten Klooster 1980; Kemmers 1980).

A drawback of working with water tables in relation to vegetation composition is that the results obtained are only applicable within narrow environmental and time ranges (Niemann 1973; Everts & De Vries 1991). The differentiation within related plant communities could be assessed accurately on a local (Sykora 1983) or regional (Everts

& De Vries 1991) scale, but the results could not always be applied elsewhere. They appeared to depend on other factors as well, such as soil type, the position in the wider land system and the local climate. Very different plant communities were sometimes found with similar hydrological regimes. In short, these limitations stem from the black-box approach: available environmental factors were usually grouped according to phytosociological associations. This correlative approach left the ecologist with little quantitative understanding of the interactions between a plant community and the local hydrological system. A similar approach is used in agricultural ecology, where means of factors are related to crops. However, as most crops are single-species communities on homogenized soils, rather than multispecies spontaneous associations on heterogeneous soils, the problems are less severe in the agricultural applications.

Ellenberg (1952, 1963, 1974) and Londo (1975) followed a more qualitative approach, culminating in several lists of indicators of environmental factors, which were meant for application in land evaluation projects. Apart from relatively few reference studies where environmental factors were actually measured, these lists were derived from association analysis: the co-occurrence of plant species was used to arrange the species according to an environmental axis.

(ii) Agro-ecological modelling of site conditions

Agro-hydrological research aims at the specification of optimal site conditions for crop production. The modelling is based on process control in single-species ecosystems without nutritive constraints. According to such models, water availability for plant growth is controlled by a whole hydrological regime, rather than by incidental water table depths. The hydrological regime is influenced by geological, meteorological, soil-physical and crop properties, and it may be managed by drainage and water supply. Hence, the models can be made specific for particular sites. This is commonly done by linking them with models of the regional water flow (Kemmers 1986a), which provide the necessary context. The models can then be used to simulate crop production in relation to water availability for various scenarios of the regional water management, inclusive of groundwater abstractions (De Laat *et al.* 1981; Van Bakel 1988; Querner 1989). They are also very valuable tools to check for possible physiological drought problems in nature reserves. In critical applications, however, they gave no evidence of any reduced production in response to a small lowering of the water table which had been shown to cause dramatic changes in the species composition of the spontaneous vegetation (Boedeltje & Bakker 1980; Grootjans & Ten Klooster 1980; Van Wirdum 1981). It was suggested that the observed changes might result from mineralization, or even simply from changes in the water chemistry. A small lowering of the drainage base could facilitate the expanse of a body of rainwater, sufficient to cover the water demands of the vegetation throughout the year, but gradually rendering the root zone permanently base poor and starting a succession towards other types of vegetation (Grootjans 1980; Kemmers 1980; Van Wirdum 1981).

So far, no deterministic approach could successfully replace such empirical relations established on the basis of, for example, Dauerlinien or indicator lists.

(iii) Research on vegetational gradients in mires

Vegetation ecologists have long been curious about the causes of the enormous diversity and variability observed in mires. Simultaneously, an applied interest was raised in the potential use of mires for agriculture. The main factors studied in this respect were fertility (Balátová-Tuláckova 1976; Succow 1988), base state (Sjörs 1950; Gorham 1956; Malmer 1961), and hydrological regimes (Kulczynski 1949; Gosselink & Turner 1978; Ivanov 1981; Succow 1982, 1988). Several authors stressed the importance of interactions between these factors, and various classifications have been developed (see for reviews: Moore & Bellamy 1973; Gore 1983; Moore 1984).

Several Dutch authors (references in Van Wirdum 1991a and Segal 1966) studied gradients in floating fens in The Netherlands, where a clear vegetational zonation was present in abandoned and overgrown, rectangular turbaries. The most species-rich fen vegetation with species as *Dactylorhiza incarnata, Carex diandra* and many moss species as *Scorpidium scorpioides* and *Campylium stellatum* were found in base-rich sites, supposedly fed by artesian wells. Van Wirdum (1979, 1982, 1991a) studied these sites and found that no wells existed in some key sites, but that a strong downward leakage of mire water towards the underlying aquifer made room for a lateral seepage of surface water from ditches into the fen peat. The interaction between the local peat and solute concentrations in the surface water produced and supported gradients in base state and fertility reflected by the vegetation.

Although the peculiarities of the water–soil–plant system remained largely unknown, the hydrology was studied in detail. The use of a 2-m-long field probe to map the electrical conductivity in sections of water-saturated peat found wide application. Such studies were often complemented by a more precise analysis of groundwater samples. Peat temperatures measured with such probes were used to apply models for heat flow resulting from the annual atmospheric temperature wave. The models were based on theories developed by Suzuki (1960), De Vries (1963) and Stallman (1965), and result in an estimation of vertical water movement through the local water-saturated peat profile (Van Wirdum 1983). Electrical conductivity and calcium and chloride concentrations in water samples were suggested to arrange analytical results according to a framework of three extreme types in the water cycle (groundwater, rain, sea). It was used to interpolate between dates and locations for which more complete analyses were available. This method, which was precedented by methods proposed by Gibbs (1970) for global use, was used as a substitute for more demanding ones from groundwater chemistry (Schoeller 1962; Hem 1972). The work of Van Wirdum focused ecohydrology in The Netherlands on the calcidity of the mire water as an intermediate between the wider hydrological system and the local fertility and flora.

A HIERARCHICAL SYSTEMS APPROACH

The three lines of research emphasized were combined in a hierarchical way (Van Wirdum 1979, 1981, 1986; Kemmers 1980, 1986a) according to a theoretical framework proposed by Van Leeuwen (1981). It was considered that (i) fertility and vegetation (ii) are conditioned by soil water relations within the site, and (iii) externally controlled by hydrological gradients. The ecological definition of the hierarchy between (i), (ii) and (iii) was partially based on Jenny's (1946, 1958) distinction between dependent and independent factors and on Spomer's (1973) description of the operational environment of organisms. According to Jenny, the state of any local ecosystem is finally controlled by the independent state factors climate, topography, biogenetic potential ('species pool'), initial state, and time passed since any serious disturbance ('initialization'), whereas Spomer warns that individual organisms rather respond to such operational variables as fluxes of water and heat between them and the environment. Van Wirdum

(1979) pointed out that indirect factors could be modifying (conditional) or driving a process (positional, referring to the ecological field describing the spatial variance of driving forces). A conceptual model of the ecohydrological relationships is shown in Fig. 1. Positional, conditional and operational relations are depicted in a hierarchical way. Positional relationships, measured as water levels and water composition, are controlled by geomorphological processes. Differences in altitude generate water flow to the vegetation site. These groundwater flows influence site conditions, such as soil moisture and soil temperature in the rooting zone, where processes take place that control the fluxes of nutrients and toxins to the operational environment of the plants. In the view of Van Wirdum the main task of ecohydrology is to apply knowledge of the physical functioning of ecosystems in order to protecting distinct qualities of nature reserves against autonomous processes in human society (agriculture, recreation, public water supply). Nature reserves would be successful when they protected distinct ecological qualities. In this respect they could be regarded as a kind of ecological devices: ecodevices (Van Wirdum 1979).

The study of positional and conditional factors became the central themes of ecohydrology in The Netherlands. Much attention was given to the functioning of the local and regional water cycles. Water chemistry is modified during groundwater flow depending on the mineral composition of parent material. The discharging, often calcareous, groundwater creates a distinct differentiation in base state of the soil throughout the landscape. The direct relation between soils' base state and nutrient turnover (see, for a review, Verhoeven *et al.* 1994) implies that in The Netherlands the distribution of the natural soil fertility, soil types and macro-ecological patterns mirror the relief in the landscape. In time, the control of the water cycle produces typical series of soil and vegetation types according to the regional relief. Van Leeuwen (1966) traced the occurrence of many rare and endangered plant species to particularly species-rich gradients in such series. This dynamic interpretation of the species-rich gradient zones stimulated research on water chemical aspects of such gradient zones in relation to the calcidity of the sites in particular (Grootjans 1985; Beltman & Grootjans 1986; Wassen *et al.* 1989, 1990b).

Different lines of applied research developed which were more or less based on this hierarchical approach to wet ecosystems: (i) the use of distribution patterns of indicative plant species in order to define functionally different landscape zones, or land units, in view of their hydrological characteristics; (ii) the 'prediction' of possible ecological consequences of different scenarios for the water management; (iii) the analysis of water chemistry as a key factor coupling the ecological field to single nature reserves.

DEVELOPMENTS IN APPLIED ECOHYDROLOGY

Species distribution as a guideline in ecohydrological surveying

Planning for integrated water resources management in The Netherlands typically has a spatial resolution of 10–100 ha, 10 000 times less detailed than vegetation ecologists are used to in their field work. Hence, it was not easy for ecologists to estimate possible vegetational responses to groundwater abstractions reliably on the basis of maps showing simulated hydrological impacts. Ecologists from the University of Groningen then developed an ecohydrological vegetation survey method that combined knowledge on indicator species from traditional phytosociological and mire research with

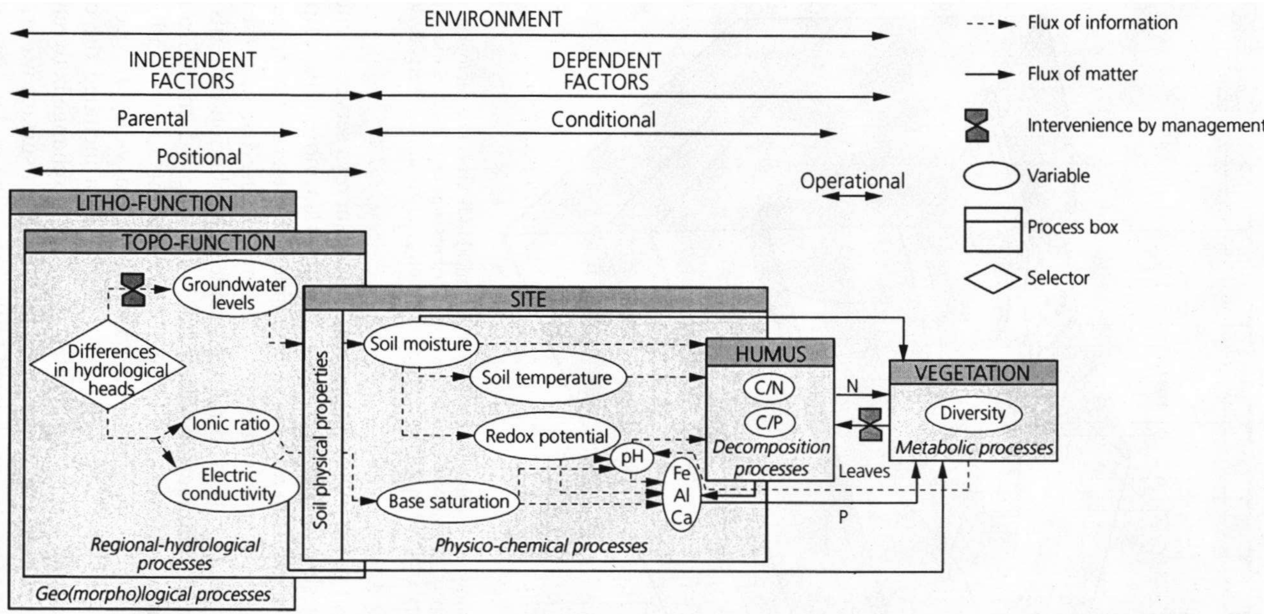

Fig. 1. Conceptual model of the eco-hydrological approach, showing the hierarchy of relationships. Positional relationships are studied in a hydrological field where geomorphological processes control water flow to the vegetation site. Both groundwater levels and hydrochemical composition influence conditions in the rooting zone, where processes take place that control the fluxes to the operational environment of the plants (changed after Kemmers 1986a).

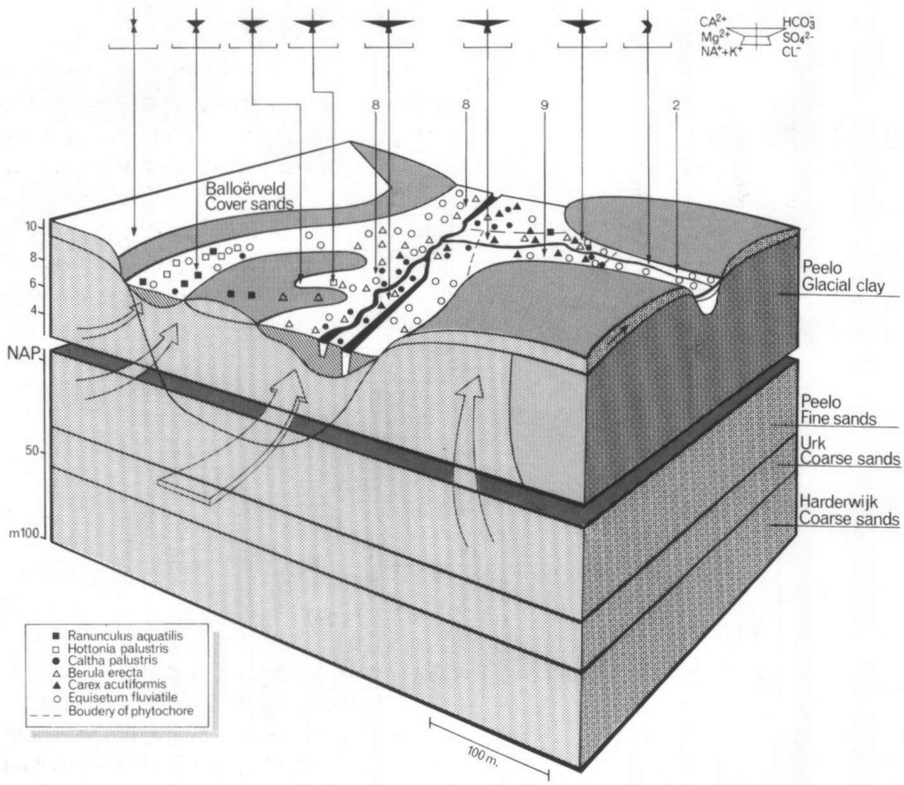

Fig. 2. Landscape model showing distribution patterns of botanical indicators in a geological setting. Arrows indicate interpreted pattern of groundwater discharge from various aquifers. The relationships were tested with groundwater chemistry sampled in transects across the ecological zonation (Everts & de Vries 1991).

hydrological relationships on a landscape level. These surveys served to indicate where hydrological research should focus in order to support a more reliable prediction of responses of wetland vegetation and possibly enable an assessment of the opportunities for regeneration of wetland ecosystems in agricultural areas. The method was inspired by the work of Haeupler (1974), who related gridded distribution patterns of phanerogams to climatic and edaphic factors with a resolution of 5×5 km^2. Grootjans (1985) related the occurrences of over 100 phreatophytic plant species and of 17 plant communities in the catchment area of the Drentsche Aa valley to geohydrological information in 1×1 km^2 grid cells. The hydrological data included the calcidity and salinity of the groundwater in the deep aquifer, the rate of exchange between this aquifer and the phreatic aquifer, and the incidence of flooding with surface water. They found that the occurrences of many species related to the upwelling of deep groundwater, and that the calcidity of the deep groundwater was expressed by the distribution of plant species and communities. The number of rare phreatophytic species and species richness were positively correlated with upwelling and with hard groundwater. The approach led to the mapping of complex hydrological gradients on the basis of the distribution of combinations of marsh plants (Everts *et al.* 1988; Everts & De Vries 1991), considered to be indicative of the groundwater composition (Grootjans *et al.* 1993). The final landscape model (Fig. 2), displays the observed ecological zonation in relation to geological information and a suggested pattern of discharge from different bodies of groundwater. The relationships were tested with groundwater composition along transects across the ecological zonation. This approach of ecohydrological problems is cheap, not restricted to nature reserves, and hence widely applied in land evaluation in The Netherlands (Vegter *et al.* 1993), wherever the lithofactor (Jenny 1958) may be neglected. In some cases, however, local deposits of calcareous substrates are present in the subsoil, leading to a high calcidity of groundwater of very local origin (Hoogendoorn 1983; Van Wirdum 1991a; Everts & De Vries 1991; Schot 1991). The indicator value of plant species may thus vary between landscapes (Niemann 1973; Walter 1977; Hulbusch 1986; examples in Grootjans *et al.* 1993; Wheeler & Shaw 1995a,b). Furthermore, species indicating very different hydrological conditions may co-occur at the same site in case of stratification of water types and retarded vegetation response (examples in Kulczynski 1949; Everts *et al.* 1988). The method, therefore, is sensitive to misinterpretations.

The use of indicator species increased the demand for good indicator values. Several projects have been carried out to relate the occurrence of species with measurements of the water table and analysis of the water composition and on this basis construct reliable response curves (Barendregt *et al.* 1986; Van Diggelen *et al.* 1991a, 1995b; Wierda *et al.* 1996). The drawback, however, is that immense amounts of data are required to achieve reliable results.

Use of water chemistry to interpret hydrological systems

Many studies were initiated in the 1980s that used differences in groundwater composition in the soil profile to indicate drainage-associated acidification of the topsoil (Kemmers 1980, 1986b; Van Wirdum 1981; Kemmers & Jansen 1988; Grootjans *et al.* 1988a; Wassen *et al.* 1988; Beltman & Verhoeven 1988). In most cases differentiation in groundwater composition was reflected in the species composition of mires and meadows, but in fen woodland, where floating mats were often connected to the soil causing increased water table dynamics, differences in groundwater composition did not match vegetation composition (Wiegers 1985).

All these local studies carried out in various parts of The Netherlands in various ecosystems soon generated much debate on groundwater typologies and on the indicative value of groundwater parameters and plant species for hydrological conditions (Beltman & Verhoeven 1988; Pedroli 1989, 1990a,b) and soon geohydrologists joined the debate (Hoogendoorn 1983; Stuyfzand 1986, 1990a,b; Schot 1991; Schot & Van der Wal 1992).

The interpretation of groundwater flow patterns from the ionic composition of groundwater was not only done by ecologists who were eager to understand ecohydrological relationships in a landscape, but also by geohydrologists. In fact, many ecologists were inspired by the work of Engelen (Engelen 1981; Engelen & Jones 1986; Van Elburg *et al*, 1987), who developed a hydrological systems analysis, stressing the coherence within and between water systems (Tóth 1962). The analysis focused on the characterization and deliniation of infiltration and exfiltration areas connected by water flow. The interpretation of changes in groundwater composition along flow lines was an important facet of the hydrological systems analysis (see Appelo 1988). Natural isotopes in the groundwater, such as tritium ^{3}H and ^{18}O were used to assess the age and origin of groundwater (Mook 1984). Schot (1991) showed that in many situations the calcium content of the groundwater was a bad tracer for the origin of groundwater (Schot *et al.*

1988; Schot & Molenaar 1992; Schot & Wassen 1993; Stuyfzand 1993). The groundwater composition often reflects past hydrological conditions and the results of stream flow modelling should therefore be verified by the presence of chemical tracers in the groundwater.

Ecohydrological modelling

The first attempt to use computer models to predict changes in species composition after groundwater abstraction or drainage was presented by Reynen & Wiertz (1984). On the basis of agricultural models that predict changes in moisture content, soil aeration and soil nitrogen availability, the disappearance of species from the local flora was predicted, using the indicator values of Ellenberg as an intermediate (see also Gremmen *et al.* 1990). The first relatively simple local models on nitrogen and phosphorus behaviour in soils with spontaneous vegetation appeared (Kemmers 1986). More sophisticated models were developed later, including all relevant processes controlling site factors, but always using best professional judgement with respect to the ecological requirements of plant species (see, for overviews, Van Wirdum 1986; Wassen & Schot 1992). Although knowledge increased considerably with model evaluations the result was often a crisis concerning data input. Finally more simple and practical models, partly knowledge-based, became dominant. Such models, generating rough predictions, are generally used for evaluating the impacts of national water management scenarios (Witte *et al.* 1992; Latour *et al.* 1993). Ecohydrological models using measured field data on water tables, water composition and soil nutrient status are generally more accurate, but require large datasets, both for the hydrological and ecological subroutines (Ertsen *et al.* 1995; Wierda *et al.* 1996). A disadvantage is that such models can only be used for prediction within a specific region. Examples are discussed by Barendregt *et al.* (1986, 1991, 1992, 1993), Noest (1991), Barendregt (1993), Van Diggelen *et al.* (1991a, 1995b) and Spieksma *et al.* (1995). Nowadays the situation exists that practically every institute working on ecohydrological problems has its own model. Several symposia have been organized to discuss which model is best for which problem, and how more elaborate models can be made. This has prompted more fundamental discussions about the use of elaborate models. Some stress the need to integrate various types of models, combining expert systems, statistical models and mechanistic models (Wassen & Schot 1992; Vermeer & Joosten 1992; Latour *et al.* 1995). Others question this approach and state that elaborate simulation models generally are a bad option for good ecological prediction. Their complexity prevents insight being obtained into mechanisms that underlie the prediction (Scheffer & Beets 1995). For nature management most models are not suitable because they are too expensive and predict vegetation changes without analysing the local vegetation. Most ecohydrological modelling in The Netherlands is presently carried out on behalf of the planning of national or regional water management. A very challenging task is to model whole catchment areas while coupling hydrological and ecological process knowledge in a Geographical Information System (GIS).

ASSESSING RESTORATION PROSPECTS OF DAMAGED ECOSYSTEMS

The rapid developments in the field of hydrology between 1980 and 1985 had much impact on ecologists working in the field of ecohydrology. At the national level, the demands for physical planning and the movement towards integrated water resources management further improved cooperation between hydrologists and ecologists (Van Buuren & Kerkstra 1993). The cooperation with geochemists and soil chemists increased the interest in processes involved in nutrient dynamics in wetlands, which were already known from agricultural research in, for instance, rice paddies (Ponnamperuma 1972; Patrick & Khalid 1974) and from research on the use of wetlands for purification of waste water (Klopatek 1978; Richardson *et al.* 1978; Duel *et al.* 1993). Most of the research on nutrient availabilty in wetlands in The Netherlands had been carried out by aquatic ecologists of the University of Nijmegen, who were also engaged in studies on the effect of acid precipitation on aquatic ecosystems. Later these aproaches were also applied by other universities to terrestrial ecosystems (Roelofs 1983, 1986, 1991; Roelofs *et al.* 1984; Verhoeven *et al.* 1983, 1988, 1991, 1993, 1994; Verhoeven 1986; Verhoeven & Schmitz 1991; Koerselman & Verhoeven 1995).

Ecohydrological approaches became more complex in the early 1990s (Pedroli 1992). In order to assess the restoration prospects of damaged ecosystems studies were published that dealt with many aspects of the ecosystem: hydrological systems analysis, influence of water management, palynological history and nutrient dynamics (Koerselman & Beltman 1988; Wassen 1990; Beltman & Rouwenhorst 1991; Van Wirdum *et al.* 1992; Van Diggelen *et al.* 1991a,b). Rich fens and fen meadows especially attracted much attention of ecohydrologists. Not only are these ecosystems rich in endangered species (Westhoff 1979a), but they often occur in a complex landscape setting as well. They are found almost exclusively in low-lying areas and are typically fed by discharging groundwater which makes them sensitive to practically every hydrological change in the valley itself and in the surrounding areas. Dune slacks and acid systems such as heathlands and bogs were considered less complex and, consequently, received less attention from ecohydrologists. Recently, however, this picture has begun to change. The results obtained until now will be summarized per ecosystem in the next sections.

Rich fen systems

Rich fens have become one of the most threatened ecosystems of The Netherlands and were investigated intensively in an attempt to formulate restoration strategies (Van Wirdum 1979, 1986; Wassen *et al.* 1988, 1989, 1990a; Koerselman 1989a,b; Beltman *et al.* 1991; Schot 1991; Van Wirdum 1991a,b, 1993; Wassen & Barendregt 1992; Barendregt 1993; Van Diggelen *et al.* 1994). Although the present vegetation composition shows a large similarity to old descriptions (De Leeuw 1929) or to the situation in sparsely populated areas (Dierßen 1982) these fens appeared to be highly affected by human activities. They are situated in river plains where large hydrological gradients have been split up into numerous short ones (Wassen 1990; Wassen *et al.* 1990a, 1996; Van Wirdum 1991a) resulting in large hydrochemical differences even within a single small fen (Fig. 3). Authors from the University of Antwerp described rich fens in the northern part of Belgium which were even more artificial. They not only withstood human activities but even had a completely anthropogenic origin (Boeye 1992; Boeye *et al.* 1994; Boeye & Verheyen 1994).

To assess the restoration perspectives of disturbed rich fens it was felt that the relationship of vegetation–abiotic conditions should be better understood, especially under more natural conditions. This goal was pursued by studying less damaged

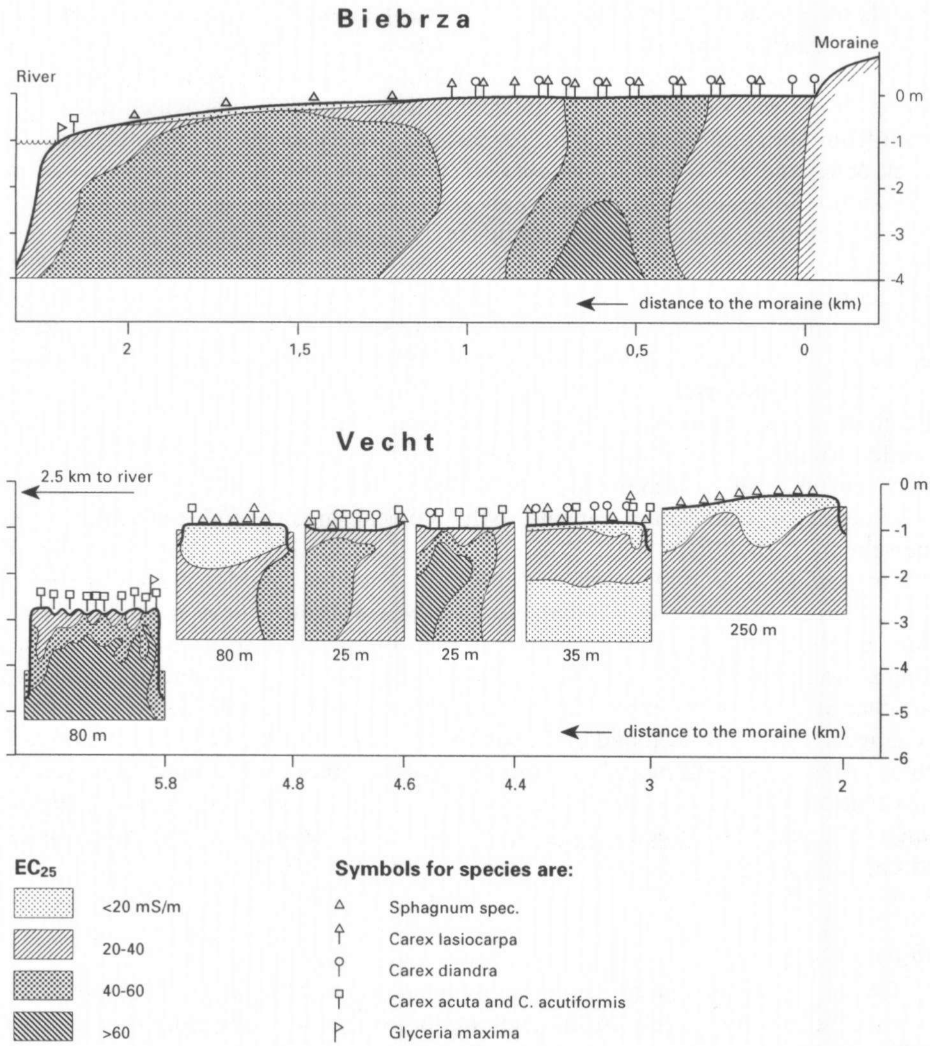

Fig. 3. Schematic representation of ecohydrological relationships in two very different landscapes (Biebrza valley in Poland and Vecht river plain in The Netherlands). Both transects show the spatial position of some characteristic fen plant species in relation to the mineral-richness of groundwater (measured as EC). The transect in the Biebrza catchment shows hydrochemical and vegetational gradients which are very smooth over large distances, due to the absence of drainage works. Human interventions in the Vecht area have split up the large hydrological gradients into numerous short ones resulting in large hydrochemical differences over small distances (changed after Wassen 1990).

'reference' ecosystems, particularly in eastern Europe (Wassen 1990; Van Diggelen *et al.* 1991b; Van Leerdam & Wassen 1994; Wolejko *et al.* 1994) or by palaeoecological methods (Van Diggelen *et al.* 1991a,b; Grootjans *et al.* 1992).

Ecohydrological research in fens in the Biebrza catchment in eastern Poland showed that the hydrochemical and associated trophic gradients were very smooth over large distances (Wassen *et al.* 1990b, 1992; Wassen & Joosten 1996). This spatial uniformity was related to the absence of drainage works resulting in an almost stagnant water body in the mire that keeps it saturated with mineral rich water. Schot & Molenaar (1992) showed that in the Vecht river plain in The Netherlands a very similar situation had probably existed before human hydrological intervention started in the 14th century. Van Diggelen *et al.* (1991c) studied former hydrological conditions in the Hunze area in the northern part of The Netherlands by palaeoecological methods (Casparie 1972; Casparie & Streefkerk 1992; Succow 1988) and got similar results. Reconstructions of the vegetation zonation during peat formation pointed to a once extensive rheophilous mire (*sensu* Kulczynski 1949) bordered by bogs and flood plain mires.

The search for natural undisturbed reference systems, however, was not always successful. Detailed studies of fen systems in eastern Germany (Van Diggelen *et al.* 1991b; Grootjans *et al.* 1991, 1992) and western Poland (Wolejko *et al.* 1994) showed that many fens were not undisturbed at all, but instead were degenerating very slowly. Conversely, some other previously considered undisturbed mires were shown to be in fact regenerating, albeit still affected by human interferences with the hydrology (Van Diggelen *et al.* 1995b; Van Diggelen & Wierda 1994). The mire they studied was partly covered by forests but it could be shown that these had only developed after the abandonment of fen meadows during the first half of the century. Groundwater-fed meadows changed into *Betula* and *Alnus* woods while flooded meadows close to the river turned into eutrophic *Phragmites* reeds. The effects of drained polder areas and of groundwater abstraction by many small pumping stations were clearly expressed in the present vegetation (Van Diggelen *et al.* 1995b).

Despite large differences in hydrological systems, site conditions in rich fens were found to be rather similar in both artificial and more natural landscape settings. The groundwater table never dropped more than a few cm below surface and the water in the root zone was rich in base cations, especially Ca^{2+} and Fe^{2+} (Wassen 1990, Wassen & Joosten 1996; Wassen *et al.* 1996). However, these fens appeared to be rather unstable in the Dutch situation and low-productive vegetation was often replaced by high-productive and species-poor vegetation. At first this was associated with an influx of eutrophicated surface water into the fens but nutrient budget studies showed that differences between high-productive and low-productive fens could not be explained by differences in the nutrient balances (Koerselman 1989a; Koerselman *et al.* 1989, 1990). Instead, these changes were associated with accelerated intra-system nutrient availability, called *internal eutrophication* (Verhoeven *et al.* 1993). This led to research on nutrient limitation for plant growth in both pristine and hydrologically disturbed mire systems (see, for an overview, Verhoeven *et al.* 1994; Wassen *et al.* 1995). From a series of fertilization experiments in the field it was concluded that nitrogen is often the primary limiting nutrient, while harvesting results in eventually phosphorus limitation (Verhoeven *et al.* 1994). The exact mechanism of low P-availability was and is still somewhat obscure (see Wassen *et al.* 1996). Experimental research had shown that Ca can limit P-availability in extreme rich fens (Boyer & Wheeler 1989) but in less calcareous rich fens Fe and Al seem to play a more important role (Boeye & Verheyen 1994; Wassen *et al.* 1995; De Mars 1996). Several authors (Caraco *et al.* 1889; Koerselman & Verhoeven 1995; Smolders 1995) pointed to the devastating effects of high sulphate levels in the surface water, causing depletion of iron and subsequent release of phosphorus which may lead to an increase in productivity and in extreme cases to a total collapse of low productive vegetation types.

While substantial knowledge was gathered about the functioning of rich fen ecosystems very few restoration attempts of degraded fens have actually been reported. Instead, this knowledge was mainly used for impact studies or to evaluate water management options for regeneration scenarios (Van Diggelen *et al.* 1991c, 1994, 1995b; Barendregt & Nieuwenhuis 1991; Nieuwenhuis *et al.* 1991; Barendregt *et al.* 1992, 1993; Grootjans & Van Diggelen 1995; Van Wirdum 1995). At present the recommendations from such studies are being implemented and the first results are emerging. Beltman *et al.* (1995, 1996) reported attempts to regenerate rich fen vegetation by sod-cutting to remove existing vegetation or digging of shallow ditches to remove the acid precipitation surplus. They showed that rich fen vegetation survived after 2 years only in the areas where both measures had been applied and even then this was only successful in areas with upward groundwater movement (B. Beltman, personal communication). Results of a reintroduction of *Scorpidium scorpioides* in a rich fen spring site were reported by Kooijman (1992, 1993).

Brook valleys and fen meadows

Species-rich meadows in groundwater-fed brook valley reserves appear to be very sensitive to changes in the hydrology of the catchment area as well. Even small changes in fluctuation patterns of the groundwater cause changes in the groundwater composition in the rooting zone (Kemmers 1986a,b; Grootjans *et al.* 1988a). This affects the availability of nutrients, even when the changes in the water table regime are very small (Vermeer 1985; Grootjans *et al.* 1986; Vermeer 1986a,b). Regional measures of groundwater management such as abstraction of groundwater for the public water supply from deep aquifers may cause relatively small changes in the water table, but will extend over large areas (Baaijens & De Molenaar 1980; Grootjans *et al.* 1993; Van Diggelen *et al.* 1994, 1995b). Local measures such as intensive drainage generate effects that are evident and trigger a rapid and drastic change in species composition. A lowering of *c.* 60 cm in a *Calthion palustris* meadow on eutrophic fen peat may increase the annual net N-mineralization from *c.* 50 kg N. $ha^{-1}.yr^{-1}$ to *c.* 400–450 kg N. $ha^{-1}.yr^{-1}$ (Janiesch 1978; Grootjans *et al.* 1985). A rapid expansion of nitrophilous herbs occurs within 2 years. If the intensity of drainage is low the response of the vegetation is slow. Changes of less than 10 cm lead to dinstinct changes in the species composition only after 10–15 years (Grootjans *et al.* 1996a).

Short-term fluctuations in weather conditions and the ability of adult plants to survive unfavourable conditions may mask distinct directional changes in species composition as a response to low drainage intensities. A regular mowing regime, which is a prerequisite for species rich meadow conservation, leads to multiple nutrient deficiencies when fertilization is stopped (Pegtel *et al.* 1996). Potassium and phosphorus often emerged as limiting nutrients in drained fen peats (De Mars *et al.* 1996; Grootjans & Van Duren 1995). The continuation of the mowing regime adds considerably to the nutrient stress in severely drained peat soils (De Mars 1996) and eventually leads to low productive species-poor swards of grass species.

Pollution of infiltration water on the valley flanks by agricultural practices is a serious threat to, in particular, low-productive fen meadows of the *Cirsio-Molinietum* community, but if the discharge of base-rich groundwater is strong enough, the influence of polluted groundwater from local infiltration areas is restricted to the valley margins (Grootjans & Van Duren 1996). Drainage of peat soils not only promotes desiccation and associated acidification (Ter Braak & Wiertz 1994), but may also stimulate the inflow of polluted base-poor groundwater from local infiltration areas (Bakker & Grootjans 1991; Van Diggelen *et al.* 1995a). The long-term effects of drainage in organic soils, such as the partly irreversible changes in physical and chemical properties of the peat (see De Mars 1996 for an overview), impose severe restrictions on the restoration prospects of species-rich meadows. Many relics of the *Cirsio-Molinietum* have persisted under relatively acid conditions (Pegtel 1983), but most of them lost their characteristic basiphilous species, such as *Parnassia palustris* and *Carex hostiana* (Grootjans & Ten Klooster 1980; De Mars 1996). In such cases very local hydrological systems, which are often purely man-made, only retard a further decline by preventing intensive infiltration. This may prevent the rapid loss of dissolved minerals but it does not, for instance, restore the originally higher base saturation of the exchange complex (Oomes & Kemmers 1995).

Conservation of species-rich wet meadow reserves in brook valleys urges the protection of infiltration areas in the catchment area.

Dune slacks

Although reports on the effects of groundwater abstraction on dune(slack) vegetation exist that have been published already in 1924 (Goedhart and co-workers), the thesis of De Vries (1961) on the relation between dune slack species, decalcification and groundwater composition on the Wadden Island of Vlieland can be regarded as one of the first serious attempts to unravel ecohydrological relationships in the Dutch coastal area. Van der Laan (1979) studied the relationship between groundwater tables and species composition in wet dune slacks in the Voorne dunes. Van Dijk and co-workers investigated the effects of artificial infiltration of polluted surface water from the rivers Rhine and Meuse into large parts of the Dutch dune area (Van Dijk 1984; Meltzer & Van Dijk 1986). The inlet of surface water was necessary to compensate for the enormous amounts of groundwater which were abstracted on behalf of the public drinking water supply. The infiltration of polluted water led to phosphate saturation of the dune sand, resulting in high phosphate and other nutrients in both ground- and surface water. This led to an enormous increase of nitrophilous herbs, such as *Urtica dioica* and *Epilobium hirsutum*. Van Dijk showed that the differentiation of nutrient status of the soil was related to the nutrient load of the groundwater, flowing through the slacks with relatively high flow velocities (Van Dijk *et al.* 1985; Van Dijk & de Groot 1987; Van Dijk & Grootjans 1993). Since then the knowledge on the hydrology of the dune area has increased considerably (Bakker 1990; Bakker & Stuyfzand 1993), in particular by the work of Stuyfzand. He developed new approaches, based on geochemical processes in the groundwater, to map groundwater bodies with comparable origin (hydrosomes: Stuyfzand 1990b, 1993). Stuyfzand & Moberts (1987) showed that artificial seepage ponds, used in the production of drinking water were basically 'flow-through lakes', with groundwater discharge in one part of the slack and infiltration of surface water in another. This hydrological mechanism also functioned in natural dune slacks that were flooded in the wet season (Lammerts *et al.* 1995). Hydrological modelling and the interpretation of groundwater composition and natural isotopes revealed how the decline of many basiphilous dune slack species during the last decades (Grootjans *et al.* 1988b, 1991) was related to changes in the local hydrological conditions (Grootjans *et al.* 1996b; Sival & Grootjans 1996). Based on chronosequences Lammerts *et al.* (1995) suggested that the life span of basiphilous pioneer stages with many endangered (Red List) species was longer in seepage slacks than in infiltration slacks, due to constraints on the accumulation of organic matter in seepage slacks.

Pioneer stages in calcareous dune slacks are very susceptible to the increased deposition of NO_x during the last decades. Both the pioneer stages and the later successional stages are N-limited (Olff *et al.* 1993; Koerselman 1992; Koerselman & Verhoeven 1992, 1995; Lammerts & Grootjans 1997). The acid precipitation itself appears not to be a major threat to basiphilous pioneer species, because the (temporary) discharge of calcareous groundwater can compensate for this input, but the increased availability of nitrogen compounds accelerates the build-up of organic matter in the topsoil (Sival 1996). In later successional stages the discharge of calcareous groundwater is not large enough in many dune slacks to compensate for the influence of acidifying processes in the organic layer. A rapid development to acid grassy heathland vegetation or forest then follows. On the Wadden Sea Islands this occurs usually within 10–20 years (Grootjans *et al.* 1988b; Van Beckhoven 1995; Ernst *et al.* 1996).

Heathlands and bogs

Much research was carried out on nutrient cycling in heathland ecosystems, which have experienced a major shift from *Calluna vulgaris* and *Erica tetralix*-dominated stands to monotonous fields of grass species (*Deschampsia flexuosa* and *Molinia caerulea*). Since most of the research is aimed at restoration prospects of dry heathlands we will discuss these ecosystems only briefly and further refer to reviews on this topic (De Smidt 1977; Westhoff 1979b; Aerts & Heil 1993). The currently high atmospheric N-deposition levels in The Netherlands (*c.* 50 kg N. $ha^{-1}.yr^{-1}$) are only partly responsible for this change in species composition (Aerts & Berendse 1988; Berendse *et al.* 1989; Aerts 1989; Berendse 1990; Bobbink *et al.* 1992). High N-deposition has an indirect effect and causes a chain of effects in the ecosystem: increased biomass production: increased litter production: increased accumulation of organic matter in the top soil: increased N-mineralization: replacement of heathland species. The decline of many endangered species in nutrient poor heathlands affected by drainage and a high ammonium deposition, was associated with ammonium and/or aluminium toxicity (Pegtel 1987; Houdijk *et al.* 1993; De Graaf 1994; Roelofs *et al.*, this issue).

At the moment all the bog remnants in The Netherlands are in a high degenerated state (Vermeer & Joosten 1992). We refer to Casparie & Streefkerk (1992) and Casparie (1993) for an extensive discussion of the origin and development of the original bog complexes, in particular that of the former Bourtanger Moor along the Dutch–German border. Nature management today aims (and has aimed for some decades), to restore several large bog remnants, but at present it is not yet possible to conclude whether large scale rewetting of the reserves will have the desired effect (Vermeer & Joosten 1992; Schouwenaars 1993; Joosten 1993). Palaeoecological studies, however, show that bog regeneration has occurred after minor natural and anthropogenic disturbances (see, for an overview, Joosten 1995). The best examples of bog vegetation are found nowadays in small heathland pools. For a review on these ecosystems and related eco-hydrological research we refer to Barkman & Baaijens (1992).

FROM ECOHYDROLOGY TO RESTORATION ECOLOGY

At present alternatives for intensive arable and grassland farming are being sought in The Netherlands. As a response to these new possibilities for nature development, ecohydrological research has become less defensive. At present the same techniques and approaches are increasingly aimed at understanding successes and failures of restoration measures in damaged wetlands. Before 1990 such studies were rare in literature (examples: Van Leeuwen 1964; Klötzli 1987; Zeeman 1986; Schouwenaars 1988; Bakker

1989). The contribution of Dutch authors to restoration ecology is rapidly growing, on fens (Grootjans *et al.* 1992; Beltman *et al.* 1995; Van Wirdum 1995), on fen meadows (Bakker & Grootjans 1990; Bakker & Olff 1995; Oomes & Kemmers 1995; Grootjans & Van Duren 1995; Jansen & Roelofs 1996; Jansen *et al.* 1996; De Mars 1996), on riverine grasslands (Van Oorschot 1996), on dune slacks (Van Beckhoven 1995; Sival 1996; Koerselman & Verhoeven 1992, 1995) on heathlands (Jansen & Maas 1993; Roelofs *et al.* 1996, this issue) and on bogs (Vermeer & Joosten 1992). Restoration ecology requires new approaches because restoration of damaged ecosystems reveals new problems. For instance, seed banks of required species may have been depleted (Bakker *et al.* 1996, this issue) which makes the introduction of species necessary. Soil formation during the degeneration period often causes new problems when the soil is rewetted. Since we know little about such hysteresis effects, a better understanding of persistent and easily decomposable humic substances is required (Hassink 1995; Kemmers 1996). The role of feedback mechanisms initiated by growth characteristics of the plants themselves have to be investigated in more detail to enable reliable predictions. Some authors hold the opinion that the course of regeneration processes is highly individualistic and that predictions on species replacement will always be unreliable (Klötzli 1991; Pfadenhauer & Klötzli 1996). They stress that a development concept for each wetland to be restored should be elaborated before any measures are taken. Such a study will force restoration ecologists to consider ecohydrological conditions in the entire wetland as well as the conditions of the surroundings. We could not agree more.

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