Eco-hydrology: Groundwater flow and site factors in plant ecology

Frans Klijn · **Jan-Philip M. Witte**

Abstract In plant ecology, site is a central concept. A site is the place where a plant species or plant community grows, and the site provides the set of conditions in which it lives. Within an initially homogeneous parent material, gravity-driven groundwater flow influences the site conditions through the spatial distribution of nutrients and other relevant chemical agents. Especially upward seepage may produce and maintain site conditions that are essential for various relatively rare plant species and communities. Increased attention to upward seepage among ecologists has resulted in cooperation with hydrologists and the emergence of a discipline of its own – eco-hydrology – on the boundary of two scientific fields, linked by the site concept.

In the Netherlands, a simple classification of water types, based on the groundwater's subsurface history, was applied for compiling a nationwide geographical database on ecologically relevant upward seepage. Correspondence analyses of this database with data on plant-species occurrence demonstrate that in poor Pleistocene sandy soils upward seepage explains the occurrence of some species and communities quite well, whereas in fluvial plains and polder areas with richer clay soils the influence of seepage is blurred by the importance of soil characteristics. It is concluded, therefore, that plant species may be used as seepage indicators in rapid assessments and surveys, but that constant awareness of the limitations is required.

Résumé En écologie végétale, le site est un concept central. Un site, c'est l'endroit où une espèce végétale ou une communauté de plantes se développe; le site assure un ensemble de conditions dans lesquelles elles vivent. Dans un matériau homogène à l'origine, l'écoulement gravitaire d'une nappe influence les conditions du site par l'intermédiaire de la distribution spatiale des nutriments et d'autres composés chimiques associés. Les remontées d'eau peuvent tout spécialement produire et maintenir les conditions du site essentielles pour différentes espèces et communautés de plantes relativement rares. Les écologues ont porté une attention accrue à ces remontées d'eau, en sorte qu'une coopération avec les hydrologues en a résulté, avec l'émergence d'une discipline propre, l'éco-hydrologie, à la limite des deux domaines scientifiques et liée au concept de site. Aux Pays-Bas, une classification des types d'eau, basée sur l'histoire de l'eau souterraine à proximité de la surface, a été mise en oeuvre pour constituer une base nationale de données géographiques sur les remontées d'eau d'intérêt écologique. Des analyses des correspondances des données de cette base, portant sur l'existence de certaines espèces de plantes, montrent que dans les sols sableux pauvres du Pléistocène la remontée d'eau explique très bien la présence de certaines espèces et communautés, alors que, dans les plaines fluviales et les régions de polders à sols argileux riches, l'influence de la remontée d'eau est masquée par l'importance des caractéristiques des sols. En conclusion donc, certaines espèces de plantes peuvent être utilisées comme des indicateurs de la remontée d'eau dans des diagnostiques et des levés de terrain rapides, mais à condition de prendre en permanence des précautions sur les limites de l'approche.

Resumen En ecología botánica un concepto de gran importancia es el de emplazamiento, definido como el lugar que proporciona unas condiciones de vida adecuadas que permiten el crecimiento de una especie o una comunidad botánica. En un material inicialmente homogéneo, el flujo subterráneo gravífico influencia las condiciones del emplazamiento variando la distribución espacial de los nutrientes y de otros agentes químicos relevantes. En especial, el flujo ascendente puede producir y mantener una serie de condiciones que son esenciales para algunas especies y comunidades de plantas relativamente raras. La especial atención hacia este fenómeno ha dado lugar a una cooperación entre ecologistas e hidrogeólogos y a la aparición de una

---

Received, July 1998
Revised, September 1998
Accepted, October 1998

Frans Klijn (✉)
WL Delft Hydraulics, P.O. Box 177
NL-2600MH Delft, The Netherlands
Fax: +31-15-2858582
e-mail: frans.klijn@wldelft.nl

Jan-Philip M. Witte
Department of Water Resources
Wageningen Agricultural University, Nieuwe Kanaal 11
NL-6709 PA Wageningen, The Netherlands

Hydrogeology Journal (1999) 7:65–77

nueva disciplina – eco-hidrología –, en la frontera de los dos campos científicos. En Holanda, se ha usado una clasificación sencilla de tipos de agua para crear una base de datos, a nivel nacional, de lugares donde la presencia de flujos ascendentes pueda ser de interés ecológico. El análisis de correspondencias entre esta base de datos y los tipos de plantas existentes muestra que en los suelos arenosos pobres del Pleistoceno los flujos ascendentes explican la presencia de algunas especies y comunidades de plantas. Por el contrario, en las llanuras fluviales y pólders, con suelos más arcillosos, la influencia de estos flujos es despreciable frente a la relativa a las propias características de los suelos. Se concluye que las especies botánicas se pueden usar como indicadores de la presencia de flujo ascendente sólo en campañas preliminares, pero que el método presenta grandes limitaciones para su extensión a casos generales.

Key words eco-hydrology · site · seepage indicators · groundwater management · the Netherlands

Introduction: What Ecologists Are Interested In

Ecologists wish to understand why certain species or communities occur where they do. They want to understand this in order to be able to explain present occurrence and to predict future occurrence under the influence of environmental changes, be it natural or man-induced. Especially in applied ecology, e.g., in the context of environmental impact assessment or physical (land-use) planning, the need to be able to forecast ecological changes is strongly felt.

In the search for explanations of species or community occurrence, especially in plant ecology, theories are converging. Usually, three major processes are taken into account that determine the possibility for a species to grow in a certain place (cf. Van der Maarel 1976). First, the environmental conditions are of foremost importance. Second, the history and context of a place are relevant: are any diaspores available from a seedbank or can they reach the place by active dispersal from nearby populations? Third, interactions among the species may play a role, such as competition for resources, parasitism, symbiosis, or killing each other (by means of allelopathic chemicals), all acting in a continuous process of succession: a community changing all the time under changing conditions and by its very self (self-organization). This paper focuses on the first of the three groups of processes: the plant's or the community's environment, or in other words, the *site*.

The Site Concept

In plant ecology, site is a central concept. A site is the place where a plant species or plant community grows, and the site provides the set of conditions in which it lives. The whole of a particular plant community with its site is called an ecotope (Tansley 1939; Troll 1968, 1970; Runhaar and Udo de Haes 1994): an ecosystem of a particular type at a certain place.

Highlighting plants and vegetation in terrestrial ecosystems, one may ask which site factors are ecologically the most important. Probably, the most basic site factors are rooting space, moisture, and nutrients. These factors, however, can be subdivided and/or related to other site factors of more indirect importance, such as pH (affecting both nutrient availability and moisture exchange between plant and soil), salinity (affecting moisture exchange), temperature, aeration, etc. Following the causal relationships even further back, factors such as soil texture, soil structure, organic-matter content, groundwater levels, or even geomorphological position, composition of parent material, and elevation are relevant.

In fact, a vegetation's site may be determined merely by rooting space, water, and nutrients on the one hand; and a wealth of climatic factors (radiation, light, temperature, frost, precipitation, etc.), parent material (degree of consolidation, chemical composition, content of weatherable minerals, etc.), physiographic factors (exposition, altitude, erosion, etc.), groundwater, surface water, and soil factors on the other hand. Fortunately, most of these factors are somehow related. By unraveling the relations, a practical handful of factors can be selected for a relevant spatial scale level (cf. Klijn 1997).

In search of the most relevant factors for explaining ecotope or plant community occurrence, it helps to distinguish between physiologically operative, conditioning, and topological site factors (cf. Jenny 1941; Van Wirdum 1979; Kemmers 1993). Because the distinction between these categories is not always easy, the distinction is primarily made between *relatively conditioning* and *relatively operative* factors, as shown in *Figure 1*, as advocated by Van Leeuwen and Van Wirdum (cf. Van Wirdum 1979 and Zonneveld 1995, p. 61); these two categories closely correspond, respectively, with Hills' (1953) 'potential features' and 'available features'. The operative site factors have a relatively direct and unambiguous impact on plant growth, e.g., moisture availability, whereas the conditioning factors interact in determining the operative site factors. An example of the latter is the interaction between groundwater depth and soil texture, which together largely determine the soil-moisture conditions within a given climatic context. Topological site factors are related to the physiographical position, such as elevation, slope, and others, which influence gravity-driven groundwater flow.

In the Netherlands, according to Stevers et al. (1987), four operative site factors provide the best explanation for the country's diversity in plant communities (see also Runhaar and Udo de Haes 1994), as is the case for many other areas in the world, perhaps with the exception of those with extreme climates (cf.

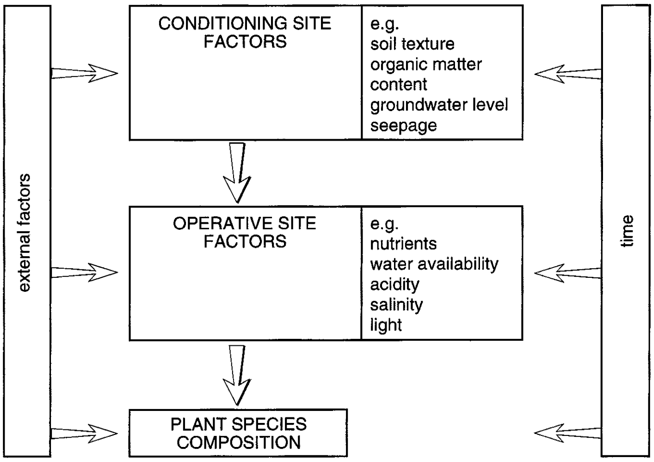


Figure 1 The difference and relationship between conditioning site factors and operative site factors, which successively affect the plant-species composition of vegetation

Arnborg 1964; Bannink et al, 1973; Ellenberg 1979; Klijn 1997). The following *abiotic* site factors are the most important:

1. Salinity
2. Moisture regime
3. Nutrient availability
4. Acidity

Unfortunately, operative site factors are often difficult to establish. Firstly, no maps are available on operative factors, thus prohibiting spatial analyses. Secondly, operative site factors may change very rapidly as a result of human influence, implying that the present state does not necessarily correspond with the pristine or potential state. Species may even exist in environments that are no longer suitable for their regeneration. In fact, for a full understanding of plant–site relationships, it is also necessary to take into account conditioning site factors.

Such an approach is increasingly being followed in the context of applied ecological studies, among others by the present authors. In this context, many analyses of the relationships between the above-mentioned operative site factors and conditioning factors have been carried out (Klijn 1988, 1997; De Waal 1992). These analyses generally consider parameters that are related to two main components of the environment that are of prime importance, viz. soil and groundwater.

Groundwater as Conditioning Factor

The role of groundwater in determining site conditions is manifold, both on the short term and on the long term, and both for its quantitative and qualitative aspects. On the short term, groundwater determines not only the availability of water, the main constituent of living tissue, but also the availability of oxygen in the rooting zone. High groundwater levels prohibit aeration and allow only species adapted to such circumstances to grow, i.e., hydrophytes. Therefore, the groundwater level is the first ecologically important aspect of groundwater. This fact is well known, and groundwater levels have therefore attracted much attention from ecologists for a long time. However, the precise influence of the groundwater level on soil moisture and aeration can only be established in connection with the role of soil texture and organic-matter content in the soil, because these determine the infiltration capacity, the rate of capillary rise, and the water-retention capacity.

Groundwater levels are also important in the long term, because they co-determine the environment in which soil formation takes place. In humid areas, a leaching soil-water regime predominates on elevated terrain. This condition causes the leaching of cations and nutrients from the topsoil, which often forms the rooting zone. Only by recycling nutrients can the vegetation sustain a certain nutrient availability of the topsoil for some time, but the overall process is directed toward depletion and often acidification. The latter is especially important in sandy and other permeable and initially poor sediments. Consequently, areas where groundwater recharge, or infiltration, predominates, are characterized by specific soil types, among which are Podzols, Luvisols, or in more extreme climates, Planosols. Many tropical soils are related to intensive leaching, which explains the susceptibility of many tropical ecosystems (rainforest) to disturbance. The nutrient recycling can be disturbed very easily.

In contrast, areas with groundwater discharge, or upward seepage, are enriched with the same cations that are leached from higher grounds. This condition means that in discharge areas the nutrient availability is often higher than in the surroundings, and acidification is counteracted by the absence of depletion, and, even more importantly, by the constant supply of buffering agents with the upward seepage. Thus, the higher grounds sustain the lower discharge areas, where nutrients and other ecologically important ions are delivered. Consequently, seepage areas and other terrains with shallow groundwater levels have their own specific soil types. Organic matter often accumulates in such areas, when climate allows, eventually culminating in the formation of peaty soils or even peat (Histosols) under climatic conditions that do not appear very favourable, such as in the tropics or the temperate zones. For example, the Netherlands comprise one of the largest lowland peat areas of Europe, mainly due to the Holocene impoundments behind an extensive beach barrier system with shallow groundwater levels.

Within these typical 'wet soil types', the types that are influenced by upward seepage of groundwater are somewhat special. The constant supply of nutrients and other elements influences the plant-species composition, which in the long term affects the soil type. This development primarily relates to the type of organic matter, which is partly determined by the plant litter; sedges and reeds produce poorly degradeable tissues that differ from those originating from Alder forest, whereas *Sphagnum* produces a very special kind of acid organic matter. Thus, the relationship between groundwater level, seepage, vegetation, and soil formation is a very intricate one.

All these observations, especially those on the importance of discharge for the chemistry of the rooting zone, generated an increasing interest in groundwater flows among ecologists, especially in the Netherlands, where unconsolidated sediments underlie more than 90% of the surface area. In fact, when ecologists realized that some plant species and even entire plant communities largely depend on the conditions sustained by discharge, and that discharge depends on recharge elsewhere, they took an interest in geo-hydrological cycles and began working together with hydrologists. In the Netherlands, this development resulted in the emergence of a discipline of its own, on the boundary of two scientific fields: eco-hydrology (Pedroli 1987; Van Wirdum 1979, 1991), which is gaining interest abroad as well (IHP 1998).

Groundwater Types

Although eco-hydrologists are interested in many aspects of the relationship between hydrology and ecology, most attention is given to groundwater discharge, or upward seepage. The reason for this is the ecological importance of upward seepage for plant growth, because it largely determines site conditions and may be altered easily by (mis-)management. The ecological importance of upward seepage relates to:

1. Temperature
2. Salinity
3. $CaCO_3$
4. pH (acidity)
5. Iron (hydr)oxides
6. Oxygen content
7. Other (cat)ions

This is a list of primarily chemical parameters, with only temperature as an exception, which explains the attempts to define discharge areas not only by the flux but also by the type of groundwater that reaches the rooting zone on the basis of its chemical composition.

In this respect, the separate chemical parameters could be defined individually. Or, any of the many diagrams could be used that illustrate overall water chemistry, such as Piper diagrams, Stiff diagrams (Stiff 1951; Pedroli et al. 1992), Collins' diagrams, or Maucha diagrams, to gain insight in the various chemical groundwater types. A detailed classification on the basis of groundwater chemistry is proposed by Stuyfzand (1986). Van Wirdum (1980, 1991) presents a commonly used ordination scheme that shows the similarity of water samples to reference water types in the hydrological cycle. In its simplest form, this ordination can be based on only two composite variables, as shown in *Figure 2*, viz. Electrical Conductivity (EC) and Ionic Ratio (defined as $[Ca^{2+}]/([Ca^{2+}]+[Cl^{-}])$, where concentrations are in meq/L). By plotting the result of measurements in groundwater samples in this graph, one may establish the similarity with any of three reference water types (*Figure 2*), indicated as atmotrophic (precipitation), lithotrophic (calcareous groundwater), and thalassotrophic (seawater). Most surface-water samples from large, slightly polluted rivers, such as the Rhine River or the Mississippi River, plot somewhere in the middle of the bent triangle formed by these three reference water types (M = RH: Rhine). This part of the diagram thus represents 'mixed-water'.

The Subsurface History of Groundwater as a Quality Conditioner

The classification of Van Wirdum relates to the origin and travel distance of the (ground)water. Precipitation that has barely touched the ground or that remains in a chemically almost inert soil environment is atmotrophic. In alluvial sediments, in contrast, a chemical equilibrium is soon established between the water and

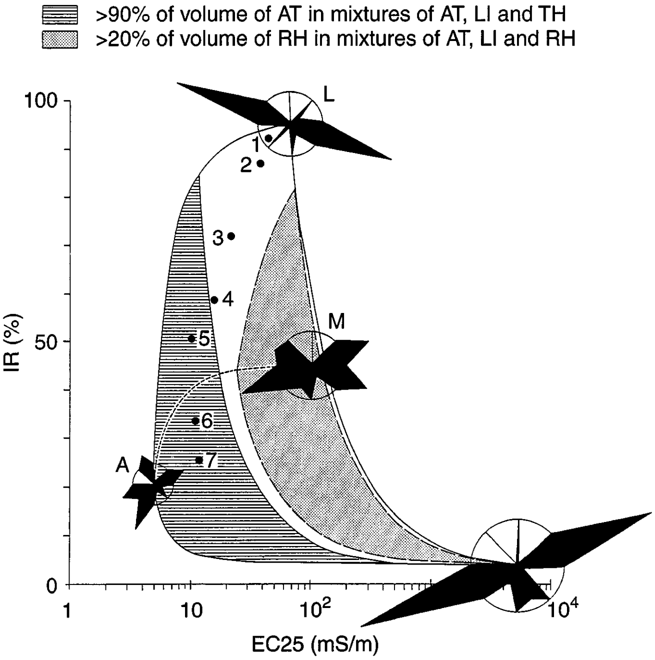


Figure 2 EC–IR diagram, showing the relative positions of reference water samples for precipitation (*A* = AT: atmotrophic), calcareous groundwater (*L* = LI: lithotrophic) and seawater (*T* = TH: thalassotrophic). Also shown is polluted water from the Rhine River (*M* = RH: mixed/Rhine River). *EC25* is the Electrical Conductivity at 25 °C, *IR* is $[Ca^{2+}]/([Ca^{2+}]+[Cl^{-}])$, with concentrations in meq/L. The reference samples are chemically characterized by Maucha diagrams. The numbers refer to a typical series, from groundwater-fed fen *(1)* to rainwater-fed bog *(7)*. (After Van Wirdum et al. 1992)

the sediment particles. Especially in clay and loamy soils, enrichment with cations occurs after only a short travel distance. Thus, even groundwater flow along short routes, e.g., within an agricultural field, may significantly alter the groundwater chemistry. In Pleistocene sandy soils, however, which in the Netherlands are very poor, much longer travel distances are required to cause substantial enrichment with cations. Consequently, in such areas especially, groundwater flows over longer distances are ecologically important. Moreover, only in relatively poor soils is the influence of upward seepage pronounced, i.e., has visible effects on the spatial heterogeneity of the vegetation. In rich clay soils, a high nutrient availability and sufficient buffering is already guaranteed within the unaltered alluvial soils. Thus, in the Netherlands, upward seepage has received the most attention as a conditioning site factor in Pleistocene sandy areas, the coastal dunes, and relatively poor peaty areas, especially lowland peats.

Because the Netherlands consists partly of land conquered from the sea, has a long coastline, and lies partly below sea level, the influence of saline and brackish groundwater and groundwater flow from the sea and estuaries toward low-lying polders also attracts attention, not only from agriculturists, but also from ecologists. Brackish and saline sites sustain very special vegetation types, which are highly valued by nature conservationists. Here again, the origin and history of the groundwater may be an important clue, though perhaps the cultural history of the impoldering determines the chemistry of the local groundwater at depth rather than the groundwater flow itself. Still, the direction and flux rate of the groundwater are important factors to understand, both from a scientific and an applied point of view.

After having ascertained that a close relationship exists between the chemical composition of groundwater and its subsurface history, it is no surprise that this relationship is fully exploited in two directions. Ecologists, who are familiar with doing chemical analyses of water, use the composition of groundwater at various depths as an indicator of groundwater flow. In contrast, hydrologists tend to use the history of the groundwater, which they derive from hydrogeological system analysis and groundwater modeling, to forecast the chemical composition of upward seepage. Thus, the disciplines support each other, learn from each other, and progress in understanding hydro-ecological relationships. Below, some progress in this respect is described, using nationwide geographical data.

Mapping Ecologically Relevant Upward Seepage: An Example

The subsurface history of groundwater can be used to forecast the chemical composition of upward seepage. In this respect, the travel time and travel length of groundwater are important, which is where the concept of nested systems (Tóth 1963) applies. In this context, one should, however, realize that ecologists are interested in the conditions in the rooting zone only, which explains the use of the term "upward seepage" instead of "discharge," which is more appropriate in relation to aquifers.

In permeable sediments, various groundwater systems are recognized, as shown in *Figures 3*, *4*, *5*, and *6*. Often, these are nested within each other, and they relate to a certain spatial scale. In the Netherlands, for example, a general large-scale groundwater flow occurs from the elevated Pleistocene sediments in the south and west, as well as in all directions away from ice-pushed ridges in the centre of the country. Nested within this large-scale system, with recharge in the Pleistocene sands and discharge in the Holocene fluvial and marine areas, flows on regional and local scales occur (1) toward shallow brook valleys in the undulating Pleistocene terrain (*Figure 3*); or (2) into low-lying drained lakes and polders (reclaimed land) from more elevated surroundings (*Figure 4*); or (3) from diked rivers (*Figure 5*) and estuaries.

Especially for agricultural areas, groundwater flow on a sub-local level must also be recognized. The many ditches and/or subsurface drains that are installed to regulate the groundwater level in low-lying areas, such as drained lakes, polders (reclaimed land) and peat plains, attract all upward seepage. This prevents the upward seepage from an aquifer from reaching the surface, and sometimes even from reaching the rooting zone in the soil. From an ecological point of view, this means that very small-scale groundwater flow within the local or regional pattern is indeed relevant. As

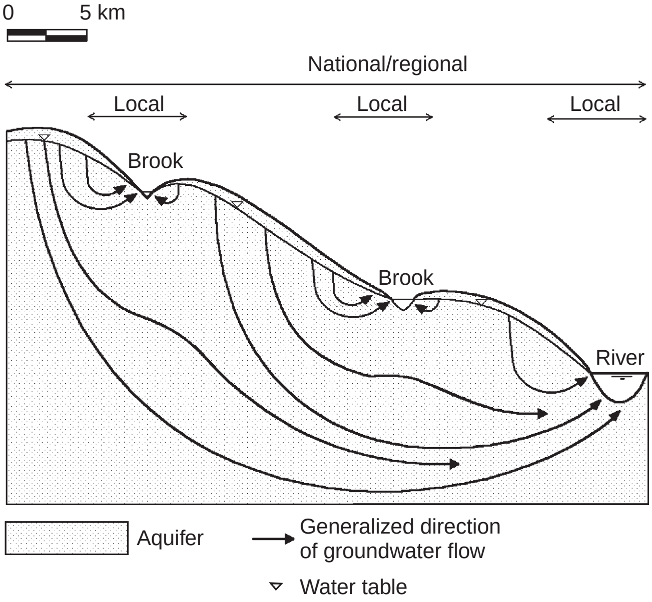


Figure 3 Typical groundwater flow systems in undulating to hilly Pleistocene areas. Local groundwater systems discharge into brooks, nested within a larger system that discharges toward a river

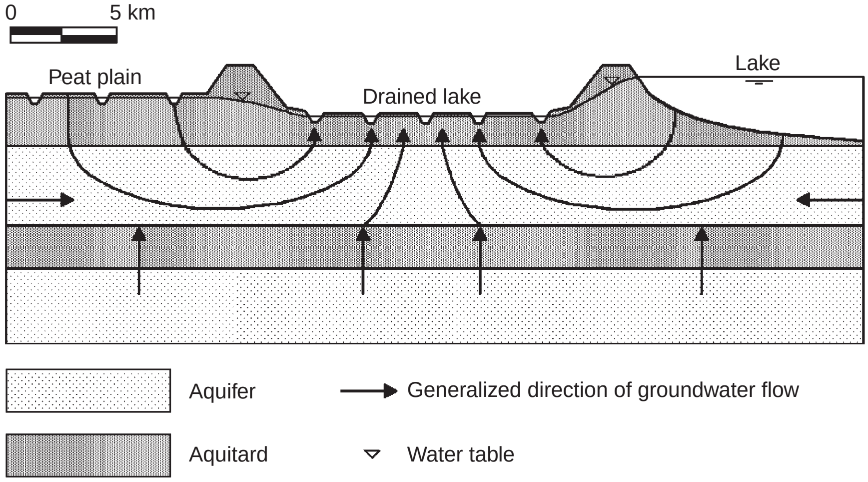


Figure 4 Typical groundwater flow from peat plains that were not cut over *(left)* and adjoining lakes that have not been drained *(right)* toward drained lakes, reclaimed after peat excavation

shown in *Figure 6*, the patterns of these sub-local systems may vary considerably between the seasons, because the surface-water levels in the ditches are usually adapted to the requirements of agricultural practice in relation to the season's precipitation surplus or deficit.

Combining knowledge on the general character of such nested groundwater systems with sufficiently detailed field survey data (maps) and geo-hydrological model results at various scales allows identification of areas where ecologically relevant upward seepage occurs. Such an approach was followed by Klijn (1989) in the context of the Landscape Ecological Mapping of the Netherlands (Canters et al. 1991; Harms and Klijn 1996). In this project, all ecologically relevant data were compiled in one nationwide database for about 36,000 grid cells of 1 km^2.

In this project, the questions of vegetation ecologists concerning the level (fluctuations) and chemistry of soil water were combined with the theory and practice of nested groundwater systems. This effort resulted in the recognition of the following four relevant scales of groundwater flow systems in the Netherlands:

1. Supra-regional groundwater flow systems through deep, generally confined aquifers. In the Netherlands, these systems are generally oriented from southeast to northwest. The water is 'fossil', i.e., thousands of years old, and completely chemically conditioned. Mapping scales are usually <1:1,000,000.
2. Regional systems at the scale of larger physiographic units, such as ice-pushed ridges, dune complexes, polders, etc. (*Figure 3*). The groundwater flow may be through either confined or phreatic aquifers, with smaller flow systems overlying or within. The residence time generally ranges from several decades to many centuries, implying the establishment of a complete chemical equilibrium with the aquifer. Mapping scales are between 1:250,000 and 1:2,000,000 (see, for example, Engelen et al. 1988).

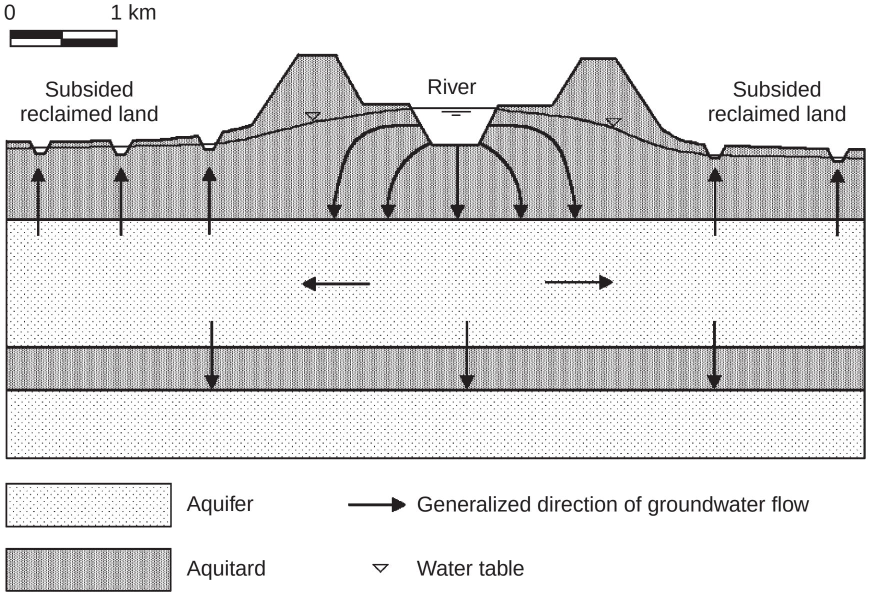
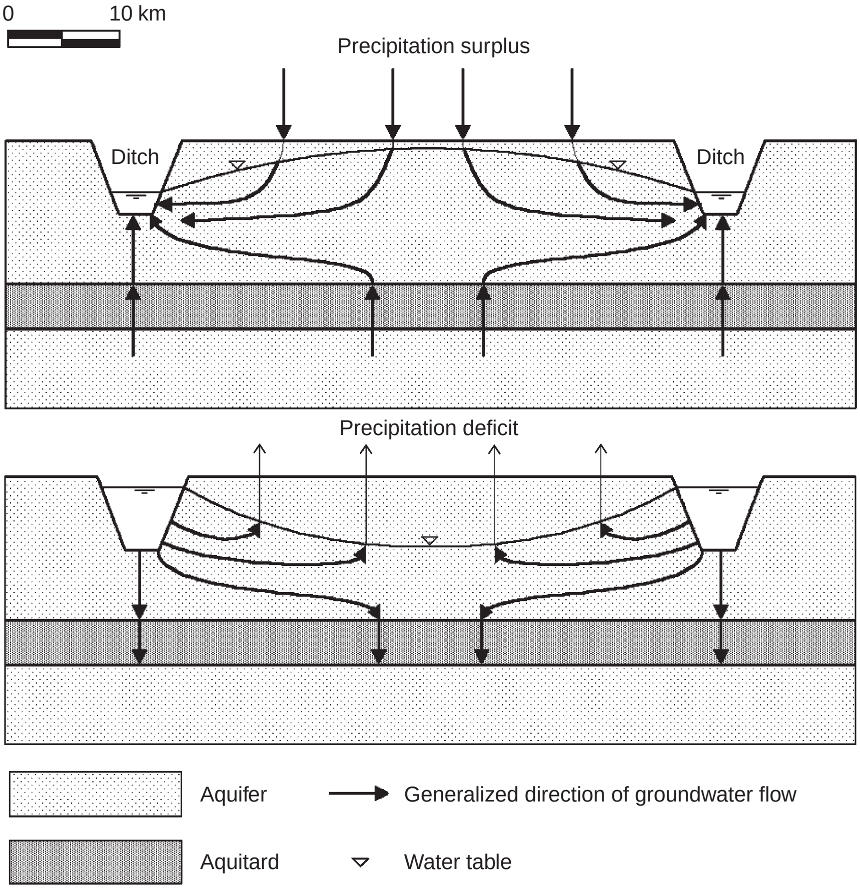


Figure 5 Typical groundwater flow from a large river and floodplains toward reclaimed land that has subsided

Figure 6 Groundwater flows beneath an agricultural field between ditches with regulated water levels, a very common situation in the Holocene fluvial and marine sediments of the western and northern parts of the Netherlands. The surface-water level is controlled to ensure optimal agricultural use, and this control influences the seasonal direction of the groundwater flow. *Top*: early spring; *bottom*: late summer



3. Local and subregional systems, generally within unconfined aquifers, with recharge and discharge areas bordering (*Figures 3*, *4*, and *5*). Such systems comprise, for example, lowland brook valleys and divides in the Pleistocene sandy region, dunes and dune slacks, fluvial levees and floodplains, etc. Residence time usually ranges from one to many decades. Mapping scales range from 1:10,000 to 1:100,000.
4. Sublocal/field-scale systems. Usually very shallow flows between agricultural fields and ditches (*Figure 6*). Seasonal fluctuations cause very large temporal variability. Residence time is generally less than 10 yr. Mapping scales are generally >1:5000.

The question of ecological relevance of these scales in relation to the practical requirement of compiling a nationwide map of ecologically relevant seepage resulted in an emphasis on levels 2 and 3. The field level was considered too variable in time and space and too susceptible to interventions on behalf of agriculture (e.g., drainage works). In contrast, the supra-regional level was considered insufficiently relevant for the rooting zone, whereas it was estimated that upward seepage from systems at this level amounts to much less than 5% of the surface area. This scale was considered by combining level 1 with level 2.

Because of the intended ecological applications, emphasis was put on upward seepage and its chemical composition, using the Van Wirdum types as reference. Thus, four seepage classes are distinguished, as well as the class 'irrelevant'. The latter was especially applied to infiltration areas (i.e., recharge areas) and areas where no ecologically significant vertical exchange occurs, because groundwater systems at the field scale dominate and either overlie or drain other, potentially relevant systems. This is the case in many agricultural areas with massive peat or clay cover and little difference in hydraulic head between the phreatic groundwater and the first aquifer. Another differentiating characteristic is the seepage rate.

In the case of the Landscape Ecological Mapping of the Netherlands, the fact that the geographical database uses 1 km^2 grid cells as a basis required special attention. Ecologists are not interested in the mean situation in such cells, but rather in all interesting features within these cells: a small spot with intense seepage may sustain a patch of vegetation with large nature value within a 'desert' of more elevated agricultural fields; it may also feed a small stream with highly valued riparian vegetation. This situation required attention to the presence of seepage as much as to the abundance. Or, in other words, some tribute had to be paid to the internal heterogeneity of the grid cells. This problem was addressed by emphasizing the occurrence of seepage of any relevant type, even when 'local' in its extent, and by distinguishing three abundance classes.

The compilation of the geographical database was based on existing data, as well as on local and regional model results available at that time. No sufficiently detailed and reliable model results were available for the national scale at that time, and even with the rapid progress in this respect, one should be very careful with such model results (cf. Klijn and Pastoors 1995), because the reliability and detail commonly do not match the requirements of ecological applications.

The overview map that was derived from the geographical database is shown in *Figure 7*. In the southern and eastern parts of the country, groundwater discharge is primarily through brooks and small rivers (see *Figure 3*), reflected by the dendritic and parallel patterns of locally lithotrophic seepage amidst infiltration areas. In the middle of the country, infiltration dominates in a large complex of ice-pushed ridges with coarse sand and gravel, surrounded by large areas with lithotrophic seepage. Along the branches of the Rhine River that trend east–west, seepage of mixed-water type occurs, originating from the more elevated floodplains (see *Figure 5*). In the southwestern estuarine area, brackish and saline seepages are abundant, especially in polders that lie below sea level. Brackish seepage also occurs in the very deep drained lakes (as much as 5 m below sea level) in the western and northern parts (see *Figure 4*), where the groundwater discharge rate results in saline groundwater moving from great depths.

Plant Species as Seepage Indicators

The preceding discussion concentrates on what hydrology may do for ecologists. In contrast, ecologists with much field experience can help hydrologists as well. Plant ecologists are very aware of differences in the vegetation's composition and of site-factor indications by individual plant species.

Plant species and species composition are regarded as response parameters. They respond to spatial or temporal changes in site conditions. Therefore, they are regarded as 'excellent' indicators, either of spatial heterogeneity or of changes in the environment. For the Netherlands, the Marsh marigold (*Caltha palustris*) and Water-violet (*Hottonia palustris*) are generally regarded as good indicators of upward seepage from regional systems.

When reliable data on species occurrence became available for the whole country of the Netherlands, various correspondence analyses were carried out using the database on the Netherlands' flora (Groen et al. 1994) and the above-mentioned database on ecologically relevant seepage. Thus, Van Moorsel and Barendregt (1993) established that *Hottonia* is indeed a good seepage indicator in most of the country, but for *Caltha* they found no significant correspondence between its occurrence and upward seepage of lithotrophic water. They therefore rejected its use as a seepage indicator entirely.

However, a comparison of the maps of the distribution of *Caltha*, shown in *Figure 8*, and the map of upward seepage (*Figure* 7), indicates some correspondence, but additional knowledge is needed. The correspondence in the southern and eastern parts of the country is quite significant, but the abundance of this species in the western and northern lowland peats negatively affects the overall correspondence. Therefore, the correpondence analysis of Van Moorsel and Barendregt (1993) was repeated, not only with more recent data but also with the sample split into two subsets, one of only the Pleistocene uplands and another of only the Holocene lowlands. Moreover, the analysis was extended to all species, with the exception of the very rare ones.

Table 1 shows the results for *Caltha* and *Hottonia* and for those species that have the largest correspondence with lithotrophic seepage in the Pleistocene uplands and/or the Holocene lowlands. The table shows that indeed both *Caltha* (53%) and *Hottonia* (49%) far exceed the expected 35% of occurrence in cells with lithotrophic seepage in the Pleistocene region, whereas for the Holocene region only *Hottonia* (14%) significantly exceeds the 8% expected. The table also reveals, however, that some less common species are much better indicators for lithotrophic seepage. Most of these are species from aquatic or very wet sites, which perform very well in the Pleistocene region. Only some are good indicators in the Holocene clays and peats as well, but when interpreting the percentage occurrence, their relative rareness in this region should also be taken into account.

The results of this analysis lead to consideration of the often misunderstood conception of site indication and the difference between operative and conditioning site factors. A plant species can only reliably indicate *operative* site conditions, because these are the only ones that matter ecologically. *Caltha* is reported to indicate high oxygen availability (Van Moorsel and Barendregt 1993) and conditions that are slightly acid to alkaline and moderately nutrient rich. These conditions may result from seepage, as they do in areas with poor Pleistocene cover sands. But in the lowland peat areas, such conditions also result from distributing water from the Rhine River throughout the dense network of ditches and canals. In other words, *Caltha* does not indicate upward seepage, but rather site conditions that may result from upward seepage in a certain geological setting: so the context is decisive for its usefulness as seepage indicator.

In contrast, *Hottonia*, whose distribution is shown in *Figure 9*, is a good indicator of upward lithotrophic seepage not only in the sandy Pleistocene areas, but in the whole country, as already established by Van Moorsel and Barendregt (1993). This can be explained by examining more closely the operative physiological factors behind it. *Hottonia* requires high carbon-dioxide

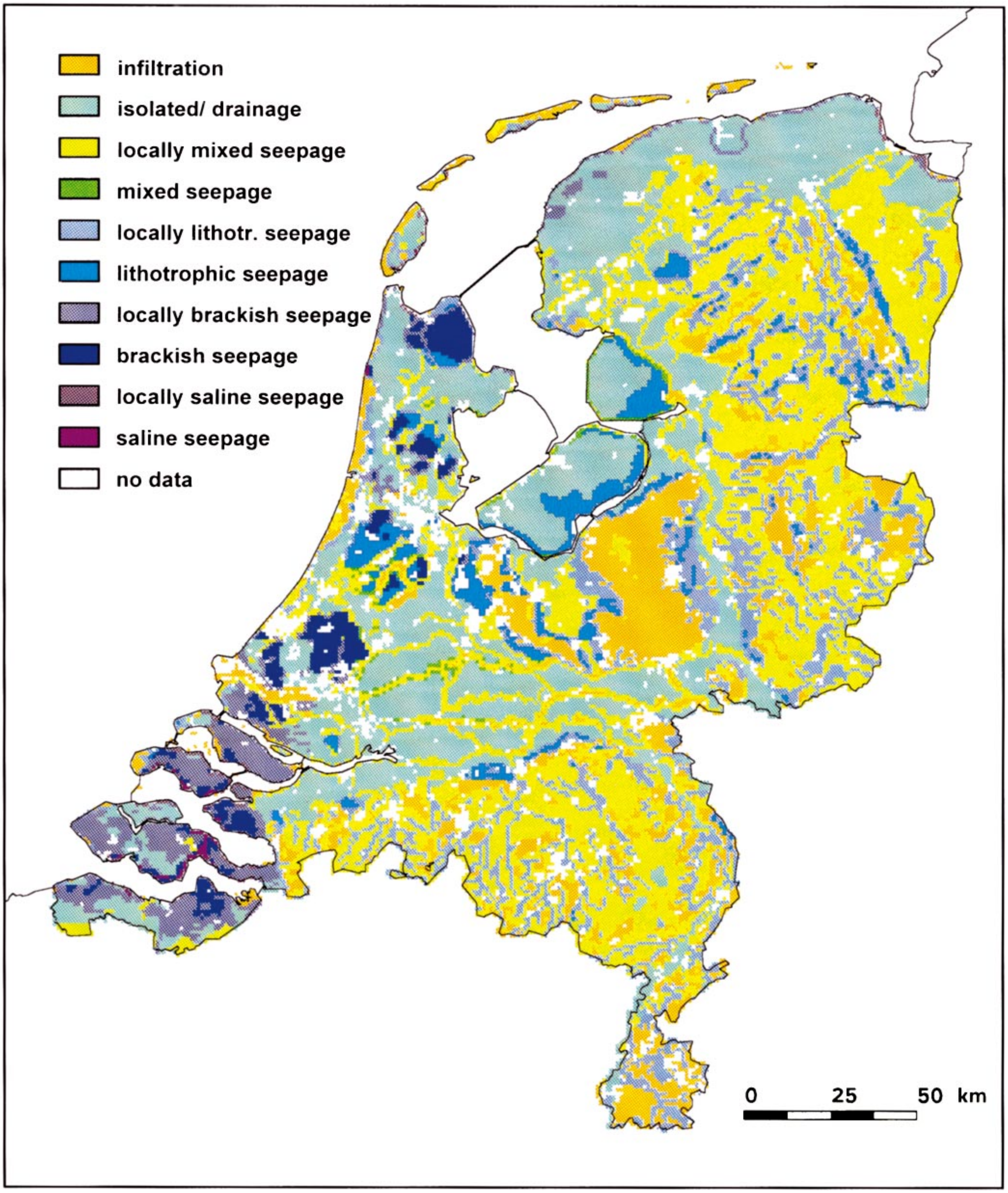


Figure 7 Distribution of ecologically relevant upward seepage in the Netherlands. (Klijn 1989)

levels for its growth (De Lyon and Roelofs 1986), and it is able to outcompete other species because of its survival strategy of remaining green in winter. This strategy enables it to get an early start in spring, before its competitors. This behaviour may explain its related-

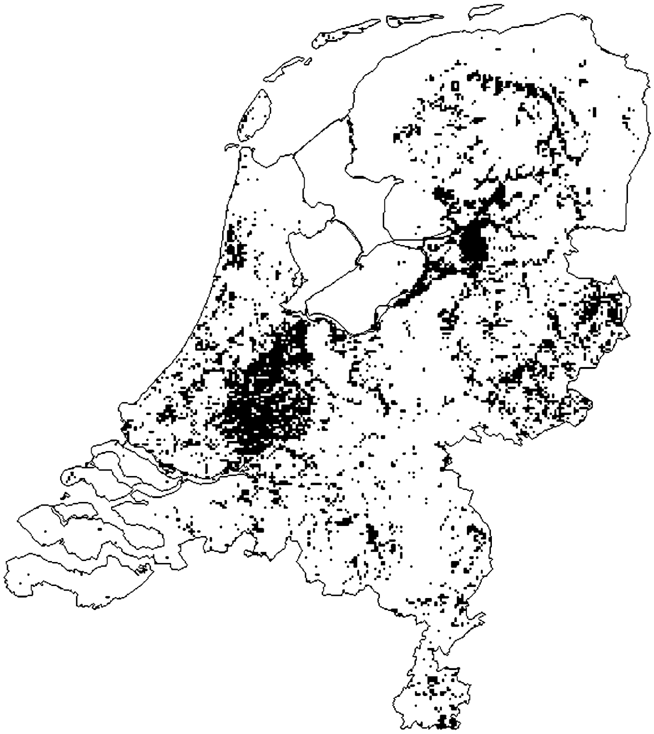


Figure 8 Distribution of Marsh Marigold (*Caltha palustris*) in 1-km^2 grid cells in the Netherlands. (After FLORBASE-2C, courtesy of Stichting FLORON)

ness to seepage, because seepage not only ensures the right chemical environment but also allows an early start because of the water's constant temperature.

The above analysis is based on nationwide data. Regional and local studies previously had obtained similar results on the indicative value of biota, but these studies did not prevent a too-easy application of plant species as indicators for upward seepage. In the 1970s, Van Wirdum (cf. Van Wirdum 1991) showed that a nature reserve, which had long been regarded as being dependent on upward seepage, in fact depends on surface water flowing freely beneath a quagmire, i.e., a floating fen. From a geohydrological point of view, the area would even be classified as an infiltration area, with no upward seepage whatsoever. More recently, Hoogeveen and Vermulst (1997) questioned the applicability of plant species as seepage indicators and emphasized the importance of taking into account other conditioning site factors, especially soil characteristics and/or the geological setting. Although the analysis presented herein provides a list of fairly reliable seepage indicators for (parts of) the Netherlands (*Table 1*), it is emphasized that the whole abiotic environmental context should be taken into account.

Applications of Eco-Hydrological Maps and Models

Although ecologists are interested in groundwater as a possible explanation for site factors, explanations are only a first step in the formulation of a theory, one that not only allows explanations afterwards, but also permits assessment and forecasting. The development of predictive models is becoming more important with the increasing interest in the relationship between man and the biosphere in general, and in the preservation of biotic diversity in particular. Predictive models are needed to assess possible ecological effects of human interference, comprising physical interventions and management, i.e., for sound planning and policy-making. In the Netherlands, policy-making for integrated water management takes into account nature conservation goals as well as safety, health, and economic aspects. Policy-making for integrated water

Table 1 Absolute occurrence of seepage indicators (expressed as number of 1-km^2 grid cells) and their relationship to upward seepage of lithotrophic (calcareous) groundwater (expressed in percentages for two geologically different regions: Pleistocene sands and Holocene clays and lowland peat). When the percentage occurrence of a plant species significantly exceeds the expected occurrence (the percentage of cells with lithotrophic seepage; see the top row), the species is considered to be a good indicator

	Number of cells		% with lithotrophic seepage	
	Pleistocene	Holocene	Pleistocene	Holocene
Well-searched cells	6741	7126	35	8
Caltha palustris	1933	2248	53	9
Hottonia palustris	1791	1116	49	14
Carex appropinquata	53	3	58	0
Carex aquatilis	251	83	67	6
Chrysosplenium alternifolium	70	4	66	50
Crepis paludosa	72	30	67	10
Juncus filiformis	67	19	76	16
Pedicularis palustris	56	143	63	13
Potamogeton alpinus	159	87	72	25
Groenlandia densa	77	237	70	19
Ranunculus hederaceus	133	11	68	45
Bromus racemosus	76	112	64	4

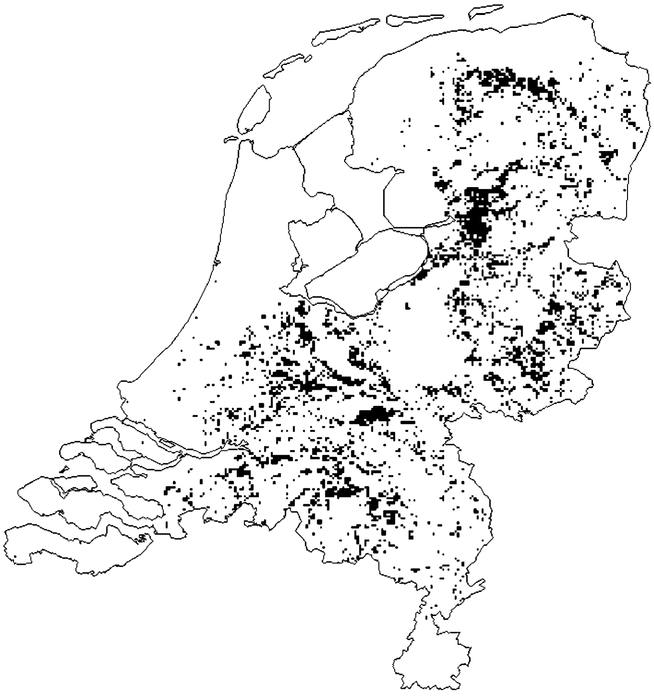


Figure 9 Distribution of Water Violet (*Hottonia palustris*) in 1 km^2 grid cells in the Netherlands. (After FLORBASE-2C, courtesy of Stichting FLORON)

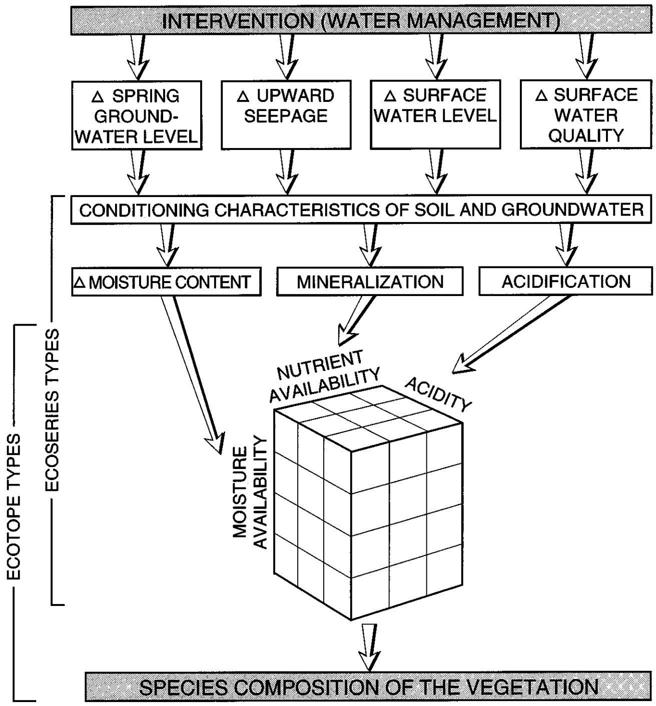


Figure 10 Scheme of the hydro-ecological effect model DEMNAT (Witte 1998), which links geohydrological models and biotic response models through the central site concept (Klijn 1997)

management requires a sound scientific underpinning in the form of policy analyses and environmental impact assessments (EIA). Recent examples include the policy analysis on behalf of the national water-management policy (Claessen et al. 1994, 1996) and the EIA for the national policy document on public water supply (Beugelink et al. 1992; Claessen and Beugelink 1995).

In this context, two types of analysis are frequently applied, viz. potential-site mapping and ecological-effect forecasting. For both, knowledge of groundwater flows and changes in these flows is essential, because of the ecological significance and because they are easily affected by human interference. Potential-site mapping is especially useful for identifying promising areas for nature conservation or restoration (Klijn et al. 1996), which sometimes requires adaptations of surface-water management or relocation of groundwater extractions. In the Netherlands, the usual approach of using soil maps as the basis for potential-site mapping has recently been upgraded by also including data on upward seepage (cf. Klijn et al. 1997).

Effect forecasting is a more important analysis than the rather static potential-site mapping; the general scheme is represented in *Figure 10*. To this end, nation-wide hydro-ecological models are being developed (cf. Witte et al. 1992, 1993; Witte 1998) and linked to geohydrological models. The linked models are used to forecast the changes in nature values of various ecosystem types, classified by site conditions and vegetation structure and described by means of characteristic species composition. *Figure 10* shows the causal processes and site factors taken into account. Changes in hydrological variables resulting from water-management measures are translated into abiotic processes and responses of site factors and the species composition of the vegetation. Through ecoseries types, conditioning soil and groundwater characteristics are linked to operative site factors, which are correlated with the vegetation's species composition through ecotope types.

For a sound linkage of geohydrological models with ecological response models, traditional geohydrological modeling (e.g., Pastoors 1992a, 1992b; De Lange 1991, 1996) had to be adapted and upgraded in order to achieve the required input for the ecological response model. Ecologists need input for their modeling of operative site conditions other than what geohydrologists are used to delivering. New elements comprise the change of focus toward spring groundwater levels, an increase in spatial resolution (cf. Klijn and Pastoors 1995; Hoogeveen and Vermulst 1997), linkages with models for the unsaturated zone (Hoogeveen and Vermulst 1997), and linking seepage intensity and groundwater chemistry. In part because of the cooperation between ecologists and hydrologists, rapid progress was made in hydrological modeling, not only at the national scale but also at regional and local scales.

Reflection

The increased interest of ecologists in upward seepage as an important site factor has enhanced cooperation with geohydrologists. Benefits are a better understanding of each other's language, way of thinking, and problems, and additional progress in geohydrological modeling. One of the largest problems in linking the two scientific fields relates to spatial and temporal scales. A large gap exists between the size and rate of change of an individual plant or plant community and the scale of geohydrological processes. However, two important concepts help to bridge this gap. One is the concept of nested systems, which enables one to deal with different time and space frames within geohydrology. Secondly, and most importantly, the site approach may prove to be the real interlock between conditioning factors such as groundwater flows on the one hand, and plants and vegetation on the other hand. Recognition of the causal chain of conditioning factors, operative site factors, and biota provides the ideal unifying concept for eco-hydrology and eco-pedology, because it combines elegant simplicity with providing links between geohydrology and plant ecology in a meaningful and purposeful way.

Acknowledgments Thanks are due to Dr. Geert van Wirdum of the Institute for Forest and Nature Research, Wageningen, to Prof. Dr. J. Tóth, and to an anonymous reviewer for their comments on the draft of this contribution.

References

Arnborg T (1964). Det Nordsvenska skogstypschemat (The North-Swedish forest type scheme) 7th edn. Svenska Skogsvårdsfóreningen, Stockholm (in Swedish)

Bannink JF, Leijs HN, Zonneveld IS (1973) Vegetatie, groeiplaats en boniteit in Nederlandse naaldhoutbossen (Vegetation, site and site quality in Dutch coniferous forests). Bodemkundige Studies 9, Stiboka, Wageningen (in Dutch)

Beugelink GP, Claessen FAM, Mühlschlegel JHC (1992) Effecten op natuur van grondwaterwinning t.v.b.v. Beleidsplan Drink- en Industriewatervoorziening en MER (Effects of groundwater extraction on nature; on behalf of Policy Document on Public and Industrial Water Supply). RIVM/RIZA, Bilthoven/ Lelystad (in Dutch)

Canters KJ, den Herder CP, de Veer AA, Veelenturf PWM, de Waal RW (1991) Landscape–ecological mapping of the Netherlands. Landscape Ecology 53:145–162

Claessen FAM, Klijn F, Witte JPM, Nienhuis JG (1994) Ecosystem classification and hydro-ecological modelling for national water management. In: Klijn F (ed) (1994) Ecosystem classification for environmental management. Kluwer Academic Publishers, Dordrecht Boston London, pp 199–222

Claessen FAM, Beugelink GP (1995) National groundwater supply policy in the Netherlands and the terrestrial ecological values. In: Belland DGB, Emig C (eds) Functioning and dynamics of perturbated ecosystems. Lavoisier Publ., Paris, pp 759–771

Claessen FAM, Beugelink GP, Witte JPM, Klijn F (1996) Predicting species loss and gain caused by alterations in Dutch national water management. European Water Pollution Control, 6:36–42

De Lange WJ (1991) A groundwater model of the Netherlands (Basisrapport 3^{e} Nota Waterhuishouding). RIZA nota 90.066, Lelystad

De Lange WJ (1996) Groundwater modelling of large domains with analytic elements. PhD Thesis, Delft University of Technology

De Lyon MJH, Roelofs JGM (1986) Waterplanten in relatie tot waterkwaliteit en bodemgesteldheid. Technical report, Catholic University, Nijmegen (in Dutch)

De Waal RW (1992) Landschapsecologische Kartering van Nederland: Boden en groundwater-trappen. SC-DLO report 132, Wageningen (in Dutch)

Ellenberg H (1979) Zeigerwerte der Gefaesspflanzen Mitteleuropas. Scripta Geobotanica 9

Engelen GB, Gieske JMJ, Los SO (1988) Grondwaterstromingsstelsels in Nederland (Groundwater flow systems in the Netherlands). Staatsbosbeheer, Utrecht (in Dutch)

Groen CLG, van der Meijden R, Runhaar J (1994) The use of floristic data to establish the occurrence and quality of ecosystems. In: Klijn F (ed) (1994) Ecosystem classification for environmental management. Kluwer Academic Publishers, Dordrecht Boston London, pp 275–290

Harms HB, Klijn F (1996) Nederland in hokjes: de Landschapsecologische Kartering van Nederland (English summary: The Netherlands in grids: Landscape Ecological Mapping of the Netherlands). Landschap 13:257–272 (in Dutch)

Hills GA (1953) The use of site in forest management. For Chron 29:128–136

Hoogeveen J, Vermulst JAPH (1997) Kwelmodellering op nationale schaal (English summary: Modelling of seepage on a national scale). Landschap 14:5–17 (in Dutch)

IHP (UNESCO-IHP) (1998) Workshop on Ecohydrology. Lodz, Poland

Jenny H (1941) Factors of soil formation. MacGraw-Hill, New York London

Kemmers RH (1993) Staalkaarten voor een ecologische landevaluatie. Landschap 10:5–22 (in Dutch)

Klijn F (1988) Ecoseries. Aanzet tot een standplaatstypologie. CML-report 45, Leiden/DBW-RIZA working document no 8.084 X, Lelystad (in Dutch)

Klijn F (1989) Landschapsecologische Kartering Nederland: Grondwaterrelaties. CML report 51, Leiden/Stiboka report no. 2107, Wageningen (in Dutch)

Klijn F (1997) A hierarchical approach to ecosystems and its implications for ecological land classification; with examples of ecoregions, ecodistricts and ecoseries of the Netherlands. PhD Thesis, Leiden University, 186 pp

Klijn F, Pastoors MJH (1995) Een landsdekkend overzicht van kwel: definitie-en schaalproblemen in de ecohydrologie (A nationwide overview of upward seepage: definition and scale problems in eco-hydrology). Stromingen (1)1995:29–44 (in Dutch)

Klijn F, Groen CLG, Witte JPM (1996) Ecoseries for potential site mapping, an example from the Netherlands. Landscape and Urban Planning 35:53–70

Klijn F, Runhaar J, van't Zelfde M (1997) Ecoseries 2.1; verbetering en operationalisatie van een classificatie van ecoseries voor DEMNAT 2.1. CML report, Leiden (in Dutch)

Pastoors MJH (1992a) Landelijk Grondwater Model; conceptuele modelbeschrijving. RIVM-rapport 714305004 (in Dutch)

Pastoors MJH (1992b) Landelijk Grondwater Model; berekeningsresultaten. RIVM-rapport 714305005 (in Dutch)

Pedroli GBM (1987) Ecohydrologie, een overzicht. Landschap 4:320–330 (in Dutch)

Pedroli GBM, Meuleman AFM, JansenAJM (1992) Over de weergave van de watersamenstelling door Stiff-diagrammen. H_2O 25:144–146 (in Dutch)

Runhaar J, Udo de Haes HA (1994) The use of site factors as ecosystem classification characteristics. In: Klijn F (ed) Ecosystem classification for environmental management. Kluwer Academic Publishers, Dordrecht Boston London, pp 139–172

Stevers RAM, Runhaar J, Udo de Haes HA, Groen CLG (1987) Het CML-ecotopensysteem, een landelijke ecosysteemtypologie toegespitst op de vegetatie. Landschap 4:135–150 (in Dutch)

Stiff HA Jr (1951) The interpretation of chemical water analysis by means of patterns. J Pet Technol 3:10

Stuyfzand PJ (1986) Een nieuwe hydrochemische classificatie van watertypen, met Nederlandse voorbeelden van toepassing. H_2O 19:562–568 (in Dutch)

Tansley AG (1939) The British isles and their vegetation. Cambridge University Press

Tóth J (1963) A theoretical analysis of groundwater flow in small drainage basins. J Geophys Res 68:4795–4812

Troll C (1968) Landschaftsökologie. In: Tüxen R (ed) Pflanzensoziologie und Landschaftsökologie. Junk, the Hague

Troll C (1970) Landschaftsökologie (geoecology) und Biocoenologie. Eine terminologische Studie. Rev Roum Géol Géophys et Géogr: Série de Géographie 14:9–18

Van der Maarel E (1976) On the establishment of plant community boundaries. Ber Deutsch Bot Ges 89:415–443

Van Moorsel RCMJ, Barendregt HE (1993) Dotterbloem en Waterviolier in Nederland (English summary: *Caltha palustris* and *Hottonia palustris* in the Netherlands). Gorteria 19:33–44

Van Wirdum G (1979) Dynamic aspects of trophic gradients in a mire complex. In: Proceedings and Information no. 25, TNO-Committee on Hydrological Research, The Hague, pp 66–82

Van Wirdum G (1980) Eenvoudige beschrijving van de waterkwaliteitsverandering gedurende de hydrologische kringloop ten behoeve van natuurbescherming. CHO/TNO rapport 5:118–143 (in Dutch)

Van Wirdum G (1991) Vegetation and hydrology of floating richfens. PhD Thesis, University of Amsterdam, 310 pp

Van Wirdum G, Den Held AJ, Schmitz M (1992) Terrestrializing vegetation in former turbaries in the Netherlands. In: Verhoeven TTA (ed.) Tens and logs in the Netherlands; history, nutrient dynamics and conservation. Kluwer, Dordrecht. pp. 323–360

Witte JPM, Klijn F, Claessen FAM, Groen CLG, van der Meijden R (1992) A model to predict and assess the impacts of hydrological changes on terrestrial ecosystems, and its use on a climate scenario. Wetland Ecol Manage 2:69–83

Witte JPM, Groen CLG, van der Meijden R, Nienhuis JG (1993) DEMNAT: a national model for the effects of water management on the vegetation. In: Hooghart JC Posthumus CWS (1993) The use of hydro-ecological models in the Netherlands. Proceedings and Information TNO Committee on Hydrological Research no 47

Witte JPM (1998) National water management and the value of nature. PhD Thesis, Wageningen Agricultural University, 223 pp

Zonneveld IS (1995) Land ecology. SPB Academic Publishing, Amsterdam