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Eco-hydrology and biodiversity

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Abstract

One of the branches of eco-hydrological research deals with relationships of hydrology and biodiversity, especially the relation between hydrology and the occurrence of individual plant species and plant communities.

Every plant has specific demands on its environment, such as temperature, light and the availability of water, oxygen and nutrients. These demands are called the 'environmental site conditions' of species. Because of differences in site conditions between plant species, species have an indicator value for the state of the environment.

Indicator values can be used to assess which species are to be expected on certain soil types and under which hydrological conditions, but also which species will appear or disappear after certain measures have been taken at a site. They are, therefore, often used in environmental-impact studies and ecological engineering projects.

In this chapter we will discus the problems encountered by researchers who study the demands that plant species make on their environment. We shall argue why eco-hydrologists often use indicator values of plant species for site factors related to water management (e.g. moisture regime, nutrient richness, acidity) and demonstrate how these indicator values can be applied successfully to the eco-hydrological modeling of biodiversity. We will introduce a novel model that predicts the occurrence probabilities of vegetation types with the aid of indicator values.

Introduction

What is Eco-hydrology about?

Throughout the world eco-hydrology has lately been discovered as a scientific discipline. Several authors have stressed its importance to the progress of hydrology and ecology (Eagleson 2002; Grootjans et al. 1996; Nuttle 2002; Rodriguez-Iturbe 2000) but there appears to be a wide range of ideas on the topics eco-hydrology is supposed to include.

Zalewski, Janauer and Jolankai (1997) define eco-hydrology as "the study of the functional interrelations between hydrology and biota at catchment scale" and "a new approach to achieve sustainable management of water". The main contributions to the International Hydrological Program under Zalewski's supervision deal with rivers and

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lakes, i.e. with fishery and aquatic ecology (see the journal *Ecohydrology & Hydrobiology*, first issued in 2001).

Baird and Wilby (1999) define eco-hydrology as the study of plant–water relations and the hydrologic processes related to plant growth. Their definition includes evapotranspiration studies and research into the hydraulic resistance of water plants. According to this definition, Penman, Monteith and Manning were eco-hydrologists, even before the term eco-hydrology was introduced (presumably by Van Wirdum, in 1982)Van Wirdum in 1982).

Inspired by Rodriguez-Iturbe (2000) and Rodriguez-Iturbe et al. (2001), Nuttle (2002) defines eco-hydrology as "the sub-discipline shared by the ecological and hydrologic sciences that concerns with the effects of hydrological processes on the distribution, structure and functioning of ecosystems, and on the effects of biotic processes on elements of the water cycle". This definition is also very broad and leaves room for meteorologists studying crop transpiration, vegetation scientists studying wetlands, agro-hydrologists, aquatic ecologists, etc.

In our opinion, eco-hydrology implies that this science is about relationships of organisms and the hydrological component of their environment. A study should concentrate on ecology and hydrology as well as the interaction between both to deserve the adjective 'eco-hydrologic'. We distinguish two major branches of 'real' eco-hydrology: one that deals with vegetation structure and one that deals with biodiversity. The first branch tries to explain spatial patterns and the dynamics in vegetation structure from hydrological processes *vice versa* (e.g. Rietkerk et al. 2002; Rodriguez-Iturbe 2000; Rodriguez-Iturbe et al. 2001; Van Breemen 1995; Van der Schaaf and Streefkerk 2002; Wainwright, Mulligan and Thornes 1999). Keywords are 'spatial self-organization', 'feed-back mechanisms', 'climate change' and 'cellular automata'. To keep things relatively simple, research is usually performed in extreme ecosystems such as drylands (lack of water) and rain-fed bogs (anoxic soil conditions caused by too much water). An example is given in the Appendix. The second branch of eco-hydrology is probably older than the first one. It deals with relationships of hydrology and biodiversity, especially the relation between hydrology and the occurrence of individual plant species and plant communities. Studies are mostly carried out in nature reserves, usually wetlands, often with the final aim of protecting them from hydrological threats, such as a lowering of the groundwater table or the inlet of polluted surface water. One of the goals of this type of research was the establishment of ecological-impact assessment models that explain and predict biodiversity as a result of water management measures.

Scope of this chapter: explaining and predicting biodiversity

The aim of this chapter is to provide hydrologists with an insight into the type of problems encountered by eco-hydrologists who want to explain and predict biodiversity. We shall describe the use of indicator values of plant species devised for weighting habitat factors related to water management (e.g. acidity, nutrient availability, moisture regime) and discuss why these indicator values are frequently used by eco-hydrologists. We shall focus on the habitat factor 'moisture regime' and show that indicator values based on expert judgment are pretty good, provided the underlying causal relationships are taken into account. Much of what is put forward in this chapter also holds for other habitat factors, such as 'nutrient availability' and 'acidity'.

Study of the relationship of water and vegetation: a lions' den

The environmental site conditions of plant species and vegetation types

Every plant has specific demands on its environment, such as temperature, light and the availability of water, oxygen and nutrients. These demands are called the 'environmental site conditions' of the species involved. For example, the site conditions of the Stinging nettle (*Urtica dioica*) are characterized by nitrogen-rich soils, whereas that of the Cross-leaved heath (*Erica tetralix*) is nutrient-poor, acid and wet to moist. Because of this difference in site conditions between plant species, plant species can be used as indicators for the state of the environment. For example, if one sees Cross-leaved heath, one knows the soil is nutrient-poor, acid and wet to moist. The same knowledge of the environmental site conditions of plants can be used to predict which plant species are to be expected at a certain location, e.g. after this location has become wetter or has been ecologically restored.

The demands of plants on their environment have been studied for decades now (Grootjans et al. 1996). In this, many problems have been encountered; the four most important of these are (1) limited possibilities for experimental research, (2) delayed reaction by plants on changes in site conditions, (3) rareness of species, causing problems with statistical inference, and (4) heterogeneity of sites. They are briefly discussed below.

(1) Limited possibilities for experimental research

Extensive experimental research has been carried out in agriculture, e.g. into the relationship between groundwater level and crop yield of monocultures. In such research, factors that are expected to affect crop yield are varied experimentally, while the other factors are kept at a constant level, often for optimum growth, e.g. by administering nutrients and pesticides. Thus, a relationship can be determined between, for example, groundwater level and potato yield. However, such an approach is often difficult to apply on wild plant species. Firstly, the conditions under which such species occur in nature are usually not those under which they show optimal growth. In a monoculture, for instance, Wavy Hair-grass (*Deschampsia flexuosa*) grows optimally at a soil pH of 5, whereas in a forest it does so at a pH of 4 (Müller-Dombois and Ellenberg 1974). This is because in addition to site conditions, competition with other species plays a significant role. Hence, the seeming preference of some species for wet or dry sites might sometimes be determined by competition rather than an intrinsic preference for wet or dry sites. Therefore, to infer relationships between wild plant species and site factors experimentally, we need to include effects of competition.

Another reason why it is hard to infer such relationships is that site factors may strongly affect each other. For example, the groundwater level not only affects water supply but also acidity and availability of oxygen and nutrients (Figure 1).

Finally, a complicating factor is that ecologists are interested mainly in rare and threatened species and ecosystems, especially when doing research for the purpose of nature conservation. Carrying out experiments with such species and ecosystems may harm them, and this of course should be avoided by all means.

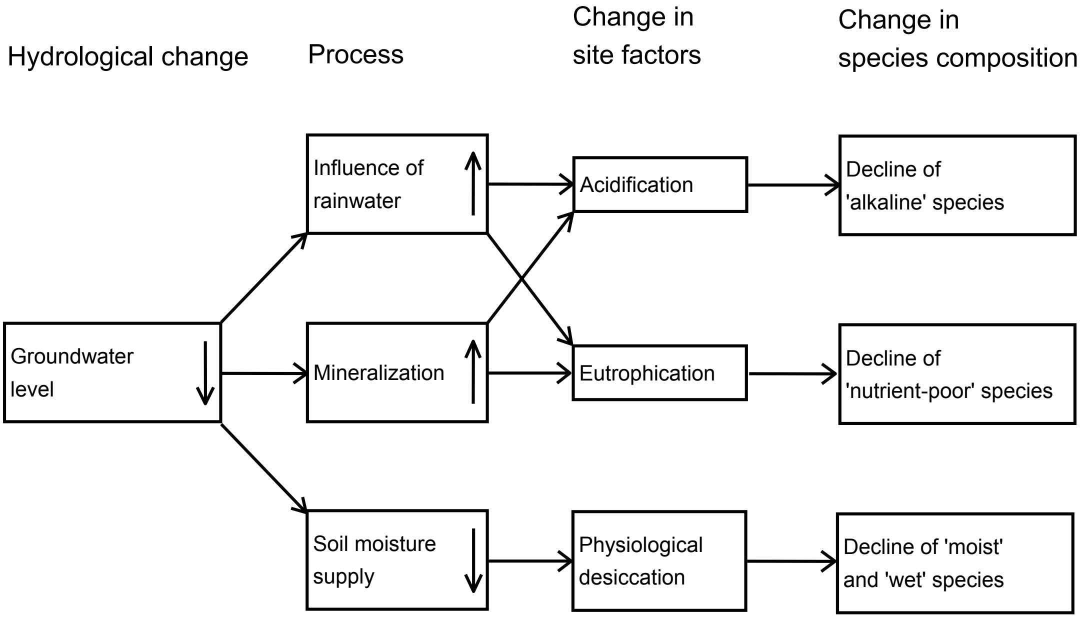

Figure 1. Main negative effects of a groundwater fall on important operational factors of wet and moist sites. Direction of change indicated by arrows: upward = increase, downward = decrease.

Lowering the groundwater level may result in a lack of water in the root zone, so that plants are no longer to transpire at a maximum rate and, as a result, to a physiological desiccation of the vegetation: species that are adapted to wet and moist environments will disappear. Because as a result more oxygen will penetrate into the soil, organic matter is mineralized. During the mineralization process, nutrients are released, making the soil eutrophic. Hence, species characteristic for nutrient-poor sites will disappear. Moreover, protons are released in this process, so that the pH decreases (i.e. the soil acidifies), causing species of neutral and alkaline sites to vanish. Acidification may also occur because the soil is more under the influence of rainwater and its pH is no longer buffered by base-rich upward seepage water.

(2) Plants may lag behind

It may take years before changes in the site of an individual plant become visible in the species composition of the vegetation. This phenomenon is known as ‘retarded response’. For instance, the effect of one dry summer may be visible in the composition of species in the vegetation for many years and completely overshadow the effects of measures that make the site moister. Species with rhizomes and radical tubers generally remain on the same location for a long time. In order to relate the presence of a plant species reliably to measured environmental values, one has to be sure that the plant is at equilibrium with its site and not a relict of former conditions.

(3) Species are too rare to allow proper statistical research

Some researchers attempt to derive site requirements of species statistically from field data (e.g. Bakkenes et al. 2002; Barendregt 1993; Ertsen et al. 1995). At a number of field plots, they collect data on the flora present and the local environmental site conditions. These data are then statistically processed to form probability functions, which describe the occurrence probability P of a species being present as a function of one or more environmental factors (Figure 2). However, P is deduced from a database with plant species and environmental factors, and strictly speaking it thus merely reflects the *occurrence probability in the database* instead of in the field. This remark may seem trivial and superfluous, but we have experienced that it is necessary to repeat it again and again. We estimate that the plant species we usually see in our landscape comprise less than 20% of the total national flora of a country (Witte and Torfs 2003). In The Netherlands, examples are very common species as Perennial Rye-grass (*Lolium perenne*), Yellow Iris (*Iris pseudacorus*) and Lady's Smock (*Cardamine pratensis*), but also less common species such as wild Marsh Marigold (*Caltha palustris*), Ragged Robin (*Lychnis flos-cuculi*) and the orchid Broad-leaved Helleborine (*Epipactis helleborine*). The other 80% of the species are so rare that the average person will never encounter them. So the majority of species is rare in a statistical sense, and therefore these species are easily missed with the random-sampling procedure that is required for statistical analyses. What makes the sampling problem all the worse is the fact that conservationists have a special interest in *very* rare species, since they particularly attribute to the value of an area for nature protection (Dony and Denholm 1985; Margules and Usher 1981; Witte 1998). The only practical way to gather information about such rare species is to forget about statistical requirements, to search for them and sample non-randomly. In this way, a good statistical tool like logistic regression is abused.

The sampling method employed may affect not only the height but also the optimum and shape of a probability function.

	[Cl] classes (mg/l)						
	0-15	15-30	30-45	45-60	60-75	75-90	90-105
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# all sampling sites	10	20	17	18	21	15	8

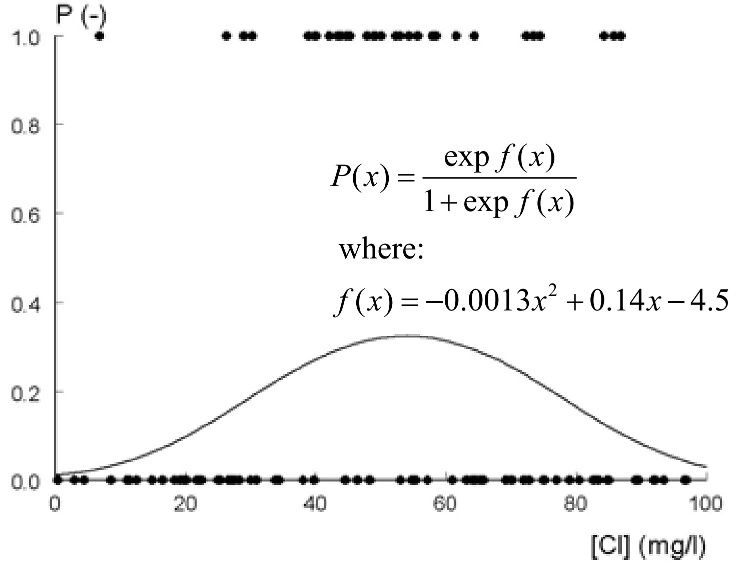

Figure 2. Imaginary example of how an occurrence-probability function for a species is obtained. Out in the field, many plots are visited where the chloride concentration [Cl] is measured and the occurrence of different plant species is recorded. After collecting these field data logistic regression is applied to fit an occurrence-probability function P([Cl]) through the observations for each species *s*

(4) Sites are usually heterogeneous

Contrary to homogeneous agricultural fields, the abiotic conditions in natural ecosystems may vary strongly over short distances. Some species grow predominantly at locations with highly heterogeneous environmental factors. For example, quagfens and wet mesotrophic meadows characterized by Meadow Thistle (*Cirsium dissectum*), Purple Moor-grass (*Molinia caerulea*), small Sedges (*Carex spp.*) and several rare Orchids, are known for their heterogeneous soil environments, which explain their species richness (e.g. Van Wirdum 1990). In wet situations, such heterogeneity is often caused by the supply of alkaline seepage or surface water. Seepage or inlet, combined with precipitation excess, may lead to steep vertical gradients in water quality across the upper part of the soil. For instance, at the soil surface the water may be nutrient-poor and acid (a pH < 4 is very common), and at a depth of a few dm it is neutral to alkaline (e.g. pH > 7) and possibly also nutrient-rich and brackish (depending on the quality of the water supplied). As a result of differences in rooting depth, species of completely different sites grow next to and interwoven with each other. For example, the Round-leaved Sundew (*Drosera rotundifolia*) has shallow roots only in the upper, nutrient-poor soil. In its immediate vicinity one may find Common Reed (*Phragmites australis*), which profits from the deeper, nutrient-rich water. Because of small differences in soil level, there is also a horizontal heterogeneity. It is evident that the method of sampling employed in such heterogeneous environments strongly affects one's conclusion about the relationship between a plant species and its abiotic environment (Figure 3).

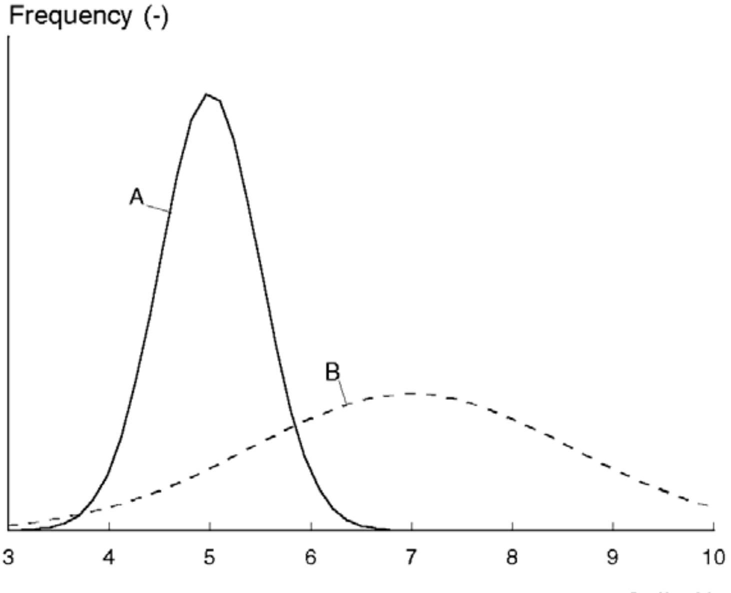

Figure 3. The effect of the sampling method applied on the calculated 'behavior' of a species. The figure shows two frequency distributions describing the presence of a certain plant species in relation to soil pH. Researcher A was scrupulous and carried out pH measurements only very close to the plants, whereas researcher B was less careful; he was satisfied as long as pH measurements were carried out somewhere in the vicinity of a plant

Indicator values

Introduction

To avoid the problems discussed, eco-hydrologists often resort to indicator values. Based on knowledge gained in the field, measurements and literature, several experts have compiled lists showing their estimate of the indicator value of plant species in relation to site factors on an ordinal scale. Such lists are useful in that they facilitate corrections to compensate for the afore-mentioned selective sampling, apparent correlations and differences resulting from differences between measuring methods. From a scientific viewpoint, however, it is of course unsatisfactory that such lists are based on expert judgment.

The indicator values established for the site factor 'moisture regime' are expanded upon below.

Adaptations of plant species to water

The site factors' indicator values are related to, are often complex. For instance the factor 'moisture regime' implies various factors, all having to do with availability of water. This becomes clear if we look at the different ways in which plants can be adapted to the presence or lack of water (Figure 4; see Color pages elsewhere in this book). Water plants (hydrophytes) occur at sites that are permanently or almost permanently submerged. Such plants are adapted to living in water: they often lack supporting tissues, have floating leaves and often take up nutrients directly from the surrounding water rather than from the soil via roots (Figure 4A). Whether or not such plants occur at a site depends mainly on factors as stream velocity and how long the site is submerged each year.

Species from locations that are very wet in winter and spring, are adapted to growing on anoxic soils, because they either have open spaces in stems and roots that transport air (e.g. Reed, *Phragmites sp.*, and different Rushes, *Juncus spp.*, Figure 4B). These species have the ability to transport oxygen into the root zone, which results in the oxidation of toxic reduced substances (e.g. Fe^{++}, Mn^{++}, H_2S), thus making them harmless (Etherington 1982). Other species avoid anoxic conditions by growing late and rooting only superficially (Sundew, *Drosera sp.*) or they lack root-like organs (Peat Moss, *Sphagnum sp.*). Species adapted to growing on wet, anoxic soils are called hygrophytes.

On sandy soils with low groundwater levels, the supply of water rather than of oxygen is a growth-limiting factor. Species occurring on such soils are adapted to dry conditions, either by limiting their transpiration rate or by surviving the dry summer period in the form of seeds. Such species are called xerophytes. Xeromorphous characteristics include a low ratio between leaf surface and leaf volume, i.e. a succulent structure (e.g. Biting Stonecrop, *Sedum acre*, Figure 4D), the presence of hairs on the leaves (e.g. Mouse-ear Hawkweed, *Hieracium pilosella*), and stomata submerged in leaf grooves (e.g. Marram Grass, *Ammophila arenaria*).

Finally, there are species called mesophytes, which cannot adapt to anaerobic conditions or a moisture deficit, and therefore occur only at moist sites (Figure 4C). Most of our agricultural crops are in this category.

So, moisture regime is not a separate factor but refers to a complex of factors related to the extent to which water is present, i.e., how long a site is submerged each year, the degree of aeration and to what extent water is supplied.

Moisture-regime indicators

Very well known is the list of indicator values compiled by Ellenberg (1992). This list describes the ecological optimum of species on a 9- to 12-piece ordinal scale for, among other things, the following site factors that can be affected hydrologically (see, for example, Figure 1): 'salinity' (ranging from S0 = salt-intolerant, to S9 = highly saline), 'nitrogen richness' (ranging from N1 = very poor, to N9 = abundantly rich), 'acidity' (ranging from R1 = strongly acid, to R9 = strongly alkaline/calcareous), and 'moisture regime' (ranging from F1 = extremely dry, to F12 = permanently submerged; see Table 1). These factors have a rather direct, causal relationship with the functioning of plant species. Ellenberg's list can, for example, be used to qualitatively establish spatial or temporal changes in site factors (Figure 5). To this end, the indicator values of a vegetation relevé[1] are usually averaged (Käfer and Witte in press).

In addition to Ellenberg's list – which was developed for the western part of Central Europe – there is a subdivision into indicator values that corresponds to a classification into ecosystem types made for The Netherlands (Runhaar and Udo de Haes 1994; Witte 2002). This subdivision into indicator values is based on similar operational site factors as those used by Ellenberg, namely salinity, moisture regime, nutrient richness (not 'nitrogen richness', as used by Ellenberg) and acidity. Each of these characteristics is subdivided into coded classes (Table 2). For example, the characteristic 'moisture regime' is subdivided into the classes water (1), wet (2), moist (4) and dry (6). Site types are combinations of these classes, e.g. site type 22: wet (2), nutrient-poor and weakly acid (2) (Table 2). Certain theoretically possible combinations of classes have been omitted, because they do not occur in The Netherlands (e.g. 'saline' and 'dry') or are ecologically irrelevant. For example, under saline conditions the salt content dominates the vegetation composition to such an extent that differences in nutrient richness have become unimportant.

All species of the Dutch flora have been classified by ecosystem type (Runhaar et al. 1987). In this, the 'ecological amplitude' (i.e. the degree to which a species has a preference for a specific environment) was taken into account, with some species belonging to more than one type. For instance, a choosy species like the White-beaked Sedge (*Rhynchospora alba*) was assigned only to site type 21 (wet, nutrient-poor, acid), whereas the generalist Common Reed (*Phragmites australis*) was assigned to nine site types, varying from b10 (brackish water) to 48 (moist and highly nutrient-rich).

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[1] A vegetation relevé is the result of a sampling carried out in a plant cover. At a chosen location an area of a prescribed size is marked out (in grassland often approximately 10 m^2). Next, it is noted, amongst other relevant information, which species occur within the area and to what extent each species covers it.

Table 1. Moisture figures F, taken from Ellenberg (1992)

F	Description
1	Indicator of extreme dryness, restricted to soils which often dry out for some time
2	Between 1 and 3
3	Dry-site indicator, more often found on dry ground than on moist places, never on damp soil
4	Between 3 and 5
5	Moist-site indicator, mainly on fresh soils of average dampness, absent form both wet and dry ground
6	Between 5 and 7
7	Dampness indicator, mainly on constantly moist or damp, but not on wet soils
8	Between 7 and 9
9	Wet-site indicator, often on water-saturated, badly aerated soils
10	Indicator of sites occasionally flooded, but free from flooding for long periods
11	Plant rooting under water, but at least for a time exposed above, or plant floating on the surface
12	Submerged plant, permanently or almost constantly under water

Table 2. Classification of site types according to the ecotope system. Site types are defined by a combination of classes (indicated by means of fat codes). E.g.: 'b40' is a brackish, moist site

		Fresh					Brackish	Saline
		Nutrient-Poor			Moderately nutrient-rich	Very nutrient-rich		
		Acid	Neutral	Alkaline				
		1	**2**	**3**	**7**	**8**	**b**	**z**
Water	**1**	*11*	*12*	*13*	*17*	*18*	*b10*	
Wet	**2**	*21*	*22*	*23*	*27*	*28*	*b20*	*z20*
Moist	**4**	*41*	*42*	*43*	*47*	*48*	*b40*	
Dry	**6**	*61*	*62*	*63*	*67*	*68*	*b60*	

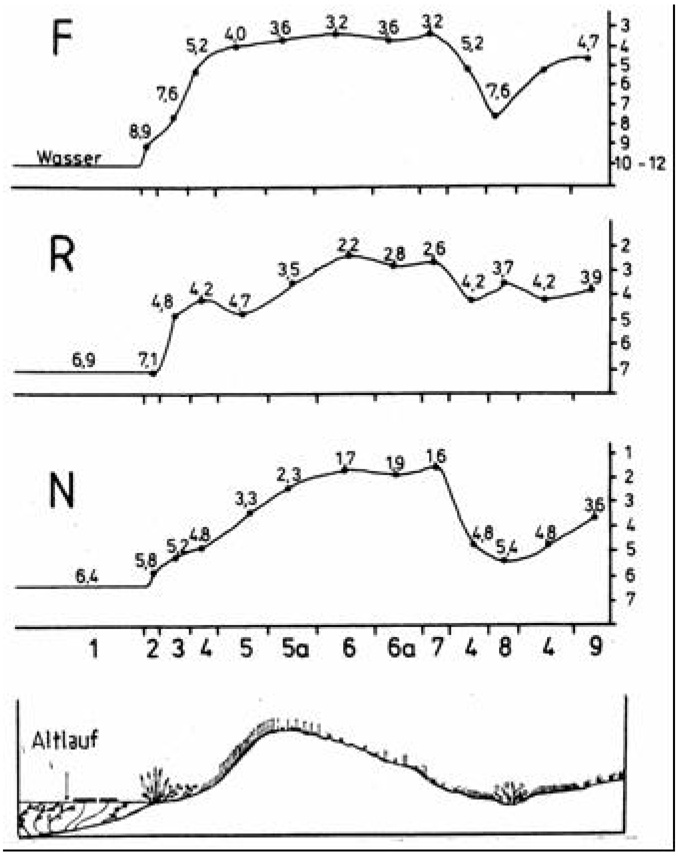

Figure 5. Averages of Ellenberg's moisture indicator F, acidity indicator R and nitrogen indicator N in a cross-section of a river dune. They have been calculated from indicator values of species at 9 relevés, and show that higher parts of the river dune are dryer (lower F), more acid (lower R) and nutrient-poorer (lower N) than lower ones. Source: Ellenberg (1992)

An important difference between this list and Ellenberg's list is that indicator values have been combined in advance to form site types and ecosystem types in order to exclude absurd combinations. Also, the ecological amplitude of species has been included in the system, while Ellenberg only gives the optimum.

Ellenberg's list and the ecotope system are widely applicable because they are based on rather direct (i.e. operational) factors. Because of its causal nature, Ellenberg's list is applied in many countries.

Calibration of the indicator value 'moisture regime' against physical quantities

Indicator values can be used to assess which species are to be expected on certain soil types and under which hydrological conditions, but also which species will appear or disappear after certain measures have been taken at a site. They are, therefore, often used in environmental-impact studies and ecological engineering projects. For example, in The Netherlands they are used in most eco-hydrological models that predict the effect of water management on biodiversity (Gremmen et al. 1990; Latour, Reiling and Slooff 1994; Koerselman, De Haan and Meuleman 1999; Van Ek et al. 2000; Wamelink, Ter Braak and Van Dobben 2003; Witte 1998). For both the assessment of the environmental conditions from vegetation relevés and for the prediction of the vegetation from known or simulated values, indicator values must be translated to abiotic parameters, or *vice versa*. For example, only if indicator values are calibrated against physical quantities the effect on the vegetation of a drop in groundwater level can be predicted. In recent years various attempts have been made to calibrate indicator values against measured abiotic variables (e.g. Bakkenes et al. 2002; Ertsen et al. 1995; Runhaar, Witte and Verburg 1997; Wamelink et al. 2002; Witte and Von Asmuth 2003). Calibration has an additional advantage in that it provides an insight into the reliability of indicator values. Some examples are given below, again focused on the site factor 'moisture regime'.

In Figure 6 (Ellenberg 1992), the average indicator value for 'moisture regime' of 10 relevés in a forest at Göttingen (Germany) are plotted against the number of days per year during which a certain soil-suction value was exceeded. The figure shows that the higher the number of dry days, the lower the average indicator value. Although the outcome is statistically significant ($P < 0.05$), the relationship is not very convincing, partly because the indicator values do not greatly differ and the number of relevés is small. Ellenberg used soil suction rather than groundwater level as an expression of moisture regime, because it accounts for the effects of both soil texture and groundwater level.

In the climate of The Netherlands, the groundwater level in spring is assumed to be decisive for the species composition of the vegetation. Therefore, Alkemade, Wiertz and Latour (1996) calibrated Ellenberg's indicator value against the average spring groundwater level. In Figure 7, for example, average spring groundwater levels at relevés on sandy soils are plotted against average indicator values for moisture, F_m. Alkemade, Wiertz and Latour (1996) derived relationships for the texture classes 'sand', 'loam/clay' and 'peat' because the moisture regime of a site depends not only on the spring groundwater level but also on the soil texture. However, the significant scatter around the regression line in Figure 7 demonstrates that these three texture classes are rather coarse. The figure clearly illustrates that low spring groundwater levels are poor predictors for F_m: at such levels there is a wide scatter in Ellenberg's indicator values.

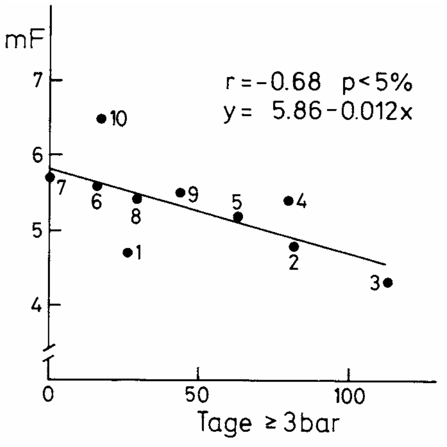

Figure 6. Relationship between the number of days per year during which the soil suction is at least 3 bar (pF~3.5) and the average Ellenberg indicator value for moisture (mF). Source: Ellenberg (1992)

Because Ellenberg's indicator values are of an ordinal nature, strictly speaking one should not average the species indicator values of a relevé, as was done for Figure 5, Figure 6 and Figure 7. Another objection to averaging indicator values is that it results in a narrower range of such values.

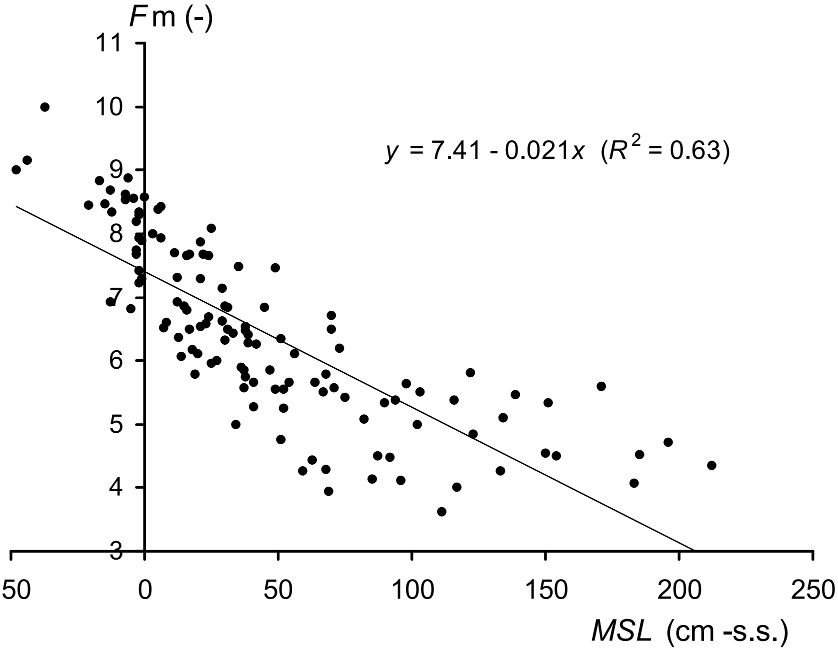

Figure 7. Relationship between Ellenberg's mean value for moisture F_m and the average spring groundwater level *MSL* (1980-1986) on sandy soils. Modified after Alkemade, Wiertz and Latour (1996); data taken from Runhaar (1989)

These objections have been dealt with in Figure 8, because here the percentage of hygrophytes or 'wet' species ('wet' according to the ecotope system) in the relevé is plotted against the spring groundwater level. This figure is based on the same data as those in Figure 7 but also includes relevés on peat and clay soils. It shows that the percentage of hygrophytes in the vegetation sharply decreases within a few decimeters of groundwater depth. The sigmoid line drawn through the points shows that at a spring groundwater level of 24 cm below soil surface, half of the species are hygrophytes. In the subdivision into ecosystem types, the boundary between wet and moist ecosystems has therefore been drawn at a spring groundwater level of 2.5 dm – soil surface.

In Figure 8, the relationship between groundwater level and vegetation is clearer than in Figure 7. This is probably because Figure 8 shows the percentage of hygrophytes on the y-axis, as the number of hygrophytes is assumed to be closely related to the groundwater level. This relationship was found to be completely independent of soil texture (Runhaar, Witte and Verburg 1997).

In order to investigate how 'dry' species (xerophytes) are related to the soil moisture regime, Witte and Runhaar (2000) selected from Runhaar (1989) the relevés without species typical of wet soils. In Figure 9A, the percentage of xerophytes is plotted against the spring groundwater level at these relevés. As expected, the figure shows no relationship between the spring groundwater level and the percentage of xerophytes in the vegetation.

A better measure for characterizing the moisture regime at dry sites is the average annual moisture deficit (Figure 9B). Witte (2002) defined it as the absolute difference between the potential and actual evapotranspiration of a short grass cover covering 90% of the soil with a root depth of 20 cm (Runhaar, Witte and Verburg 1997) in an average year. The moisture deficit was calculated using the SWAP model (Van Dam et al. 1997). A standard crop was used, because Witte and Runhaar needed a measure that depends only on soil and is independent of the vegetation present.

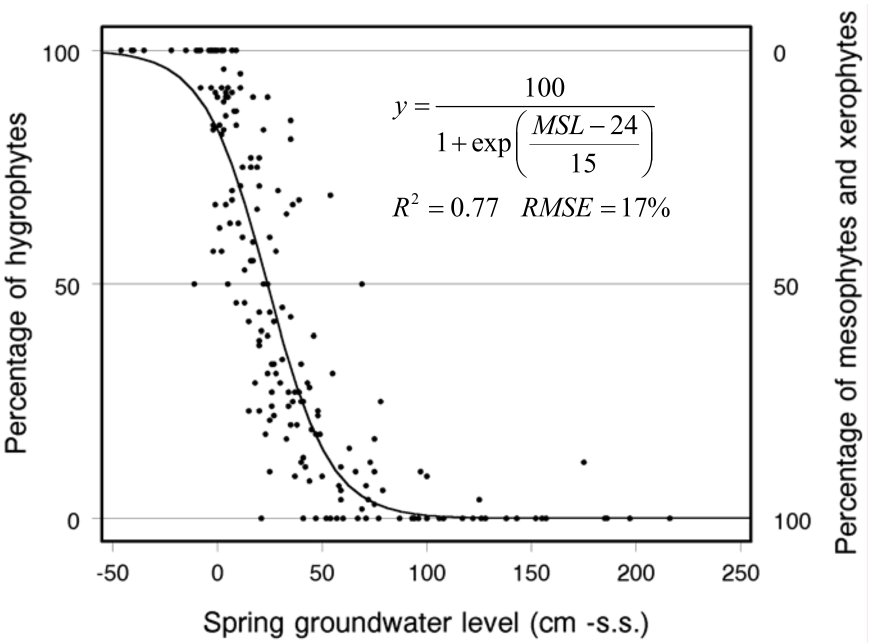

Figure 8. Relationship between the average spring groundwater level *MSL* (1980-1986) and the percentage of hygrophytes in the vegetation. Based on 188 relevés; taken from Runhaar (1989)

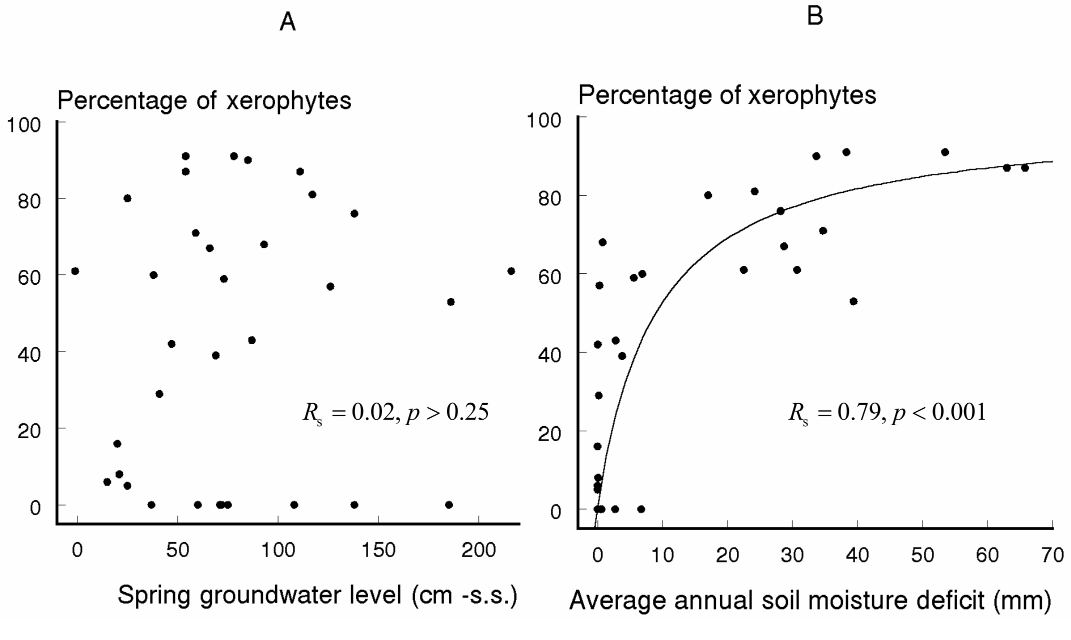

Figure 9. Percentage of xerophytes in the vegetation versus: A - the measured average spring groundwater level; B - the computed annual moisture deficit. Based on 33 relevés

Although the points in Figure 9B are rather scattered, the result is quite good, especially since the moisture deficit calculated by SWAP involves several assumptions. It can be concluded from the figure that as soon as even the slightest moisture deficit occurs, xerophytes will dominate the vegetation. Based on this, we can draw the boundary between 'moist' and 'dry' ecosystems at a moisture deficit of 0 mm per year.

A novel method to predict vegetation types using indicator values

Introduction

In this section we will demonstrate how indicator values can be applied successfully to the eco-hydrological modeling of biodiversity. We shall do so on the basis of a model we are currently developing.

All eco-hydrological models for biodiversity are part of a chain of models, the output of a model being the input of the following model (Figure 10). The chain starts with a groundwater model that is used to compute a spatial picture of the depth of the groundwater table as well as the intensity of upward and downward seepage (e.g. MODFLOW, Hill 2003). This may, of course, be done for various hydrological situations, i.e. the current situation, a situation with a new groundwater extraction, or a situation with a climate that has changed due to global warming. The second model is one-dimensional and calculates water flow in the unsaturated zone, such as SWAP (Van Dam et al. 1997). It computes, for instance on a daily basis, the depth of the groundwater table and the soil moisture deficit, factors that are relevant to the species composition of the vegetation and which we shall therefore call ‘site variables’. Output of this model is used as an input to a one-dimensional soil chemical model, such as ANIMO (Kroes and Roelsma 1998), NICHE (Koerselman, De Haan and Meuleman 1999) or SMART (Kros, Reinds and De Vries 1995), which computes other variables that are important for the vegetation, such as soil pH and N-mineralization. The effect of the computed site variables on the vegetation may then be computed in a direct manner, e.g. with probability functions of the occurrence of plant species or with the aid of groundwater duration lines of vegetation types. However, such direct relationships are usually rather weak because of the usual poor availability of soil chemical and soil physical field data from which they have been derived.

Moreover, to avoid statistical nonsense, we feel that correlative relations between site and vegetation should be based as much as possible on ecological knowledge. In practice, this means two things. Firstly, one should use those site variables that are known to have a strong influence on the species composition of the vegetation via water management. In The Netherlands, such variables are for instance chlorine content (as a measure for the site factor ‘salinity’), spring groundwater level and soil moisture deficit (for ‘moisture regime’), N-mineralization (‘nutrient availability’) and soil pH (‘acidity’). Secondly, one should correlate these variables with parameters of the vegetation that are supposed to have a causal relationship with these site factors. Such a parameter is for instance the average indicator value for acidity to be correlated with the soil pH-H_2O (as a measure of ‘acidity’). Other examples, relating to the site factor of ‘moisture regime’ are given in Figure 6, Figure 7, Figure 8 and Figure 9. Most eco-hydrological models use calibration curves established from well-investigated relevés to translate computed site variables into indicator values (e.g. Gremmen et al. 1990; Latour, Reiling and Slooff 1994; Koerselman, De Haan and Meuleman 1999; Van Ek et al. 2000; Wamelink, Ter Braak and Van Dobben 2003; Witte 1998).

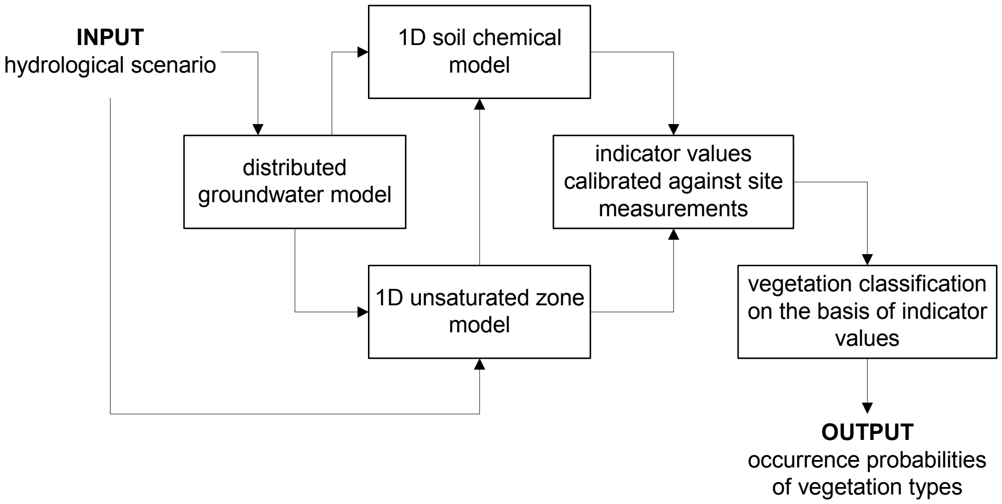

Figure 10. General process chain of our eco-hydrological model for biodiversity

Classification of vegetation types on the basis of indicator values

In our proposed model, we add a last link to the model chain (Figure 10): we use indicator values established in the previous step to compute the occurrence probabilities of vegetation types. To do so, we describe each vegetation type as a function of indicator values with the aid of Kernel fitting (i.e. using probability densities that are constructed by weighted sum of Gaussians) (Wand and Jones 1995). Data for the statistical functions come from a database with relevés. The functions are made in the following three steps:

- Each relevé in the database is assigned to a vegetation type on the basis of its species composition;
- On the basis of its species composition average indicator values are computed for each relevé;
- Each relevé is a point in an *n*-dimensional space that is formed by *n* indicator-value axes. Species of the same vegetation type form a cluster in this space. This cluster is described by Kernel functions. It may be interpreted as the *ecological niche* of the vegetation type.

As an example, Figure 11 shows the three-dimensional space of indicator values for moisture regime, nutrient richness and acidity (see Color pages elsewhere in this book). A relevé is depicted as a ball and a vegetation type is indicated by a color. The position of vegetation types in this space is described by Kernel functions, using the statistical program PARDENS (Torfs et al. 2002; Wójcik and Torfs 2003).

It should be noted that in The Netherlands more than 400,000 relevés are available (www.synbiosys.alterra.nl) that can be used to build Kernel functions of vegetation types. The geographical position of most of these relevés is well known. This enables us to derive regional functions for specific landscapes, such as dunes or brook valleys. Moreover, our method does not depend on a particular division of vegetation into types: any division can be used, provided, of course, that the division makes ecological sense. Each Kernel function attributes relevés to vegetation types on the basis of habitat factors and not, as regular vegetation classification systems do, on the basis of their species composition. This feature makes our method especially suitable to be applied in environmental impact-assessment studies.

By way of example Figure 12 shows the predicted occurrence probability of a vegetation type in the province of Gelderland, The Netherlands (see Color pages elsewhere in this book). Distribution maps of different vegetation types can be combined into one map, showing vegetation types with the highest occurrence probabilities. This is demonstrated in Figure 13 for a small region in Gelderland (see Color pages elsewhere in this book). It shows the potential distribution of vegetation types of woods that are most likely to occur before (Figure 13A1) and after (Figure 13B1) a groundwater level fall of 25 cm. The corresponding occurrence probability of these predictions is given in Figure 13A2 and Figure 13B2, respectively.

Model testing

The reliability of the vegetation model was investigated by performing a cross-validation in which we compared ‘observed’ vegetation types with expected vegetation types assigned to relevés. For the classification of the vegetation we took the standard work of Schaminée, Stortelder and Westhoff (1995), which describes a national division of the Dutch vegetation into vegetation types on a number of hierarchical levels, i.e. ‘orders’, ‘alliances’, ‘associations’ and ‘sub-associations’. The fundamental level is the ‘association’. The division into associations is rather detailed, because more than 200 vegetation types are described for this hierarchical level. We used a database with 35,000 relevés that already had been classified by expert judgment or an automatic procedure (e.g. Van Tongeren 2000) into associations according to their species composition. For each relevé we computed average indicator values for ‘salinity’, ‘moisture regime’, ‘nutrient availability’ and ‘acidity’. We took the ecotope system (Runhaar et al. 1987, Table 2) for this purpose and simply assigned integer values in sequence to each class within each of these four characteristics (e.g. for the characteristic ‘nutrient availability’ we used: 1 = nutrient-poor, 2 = moderately nutrient-rich, 3 = very nutrient-rich). To take account of the fact that in the ecotope system species can be assigned to more than one class, we computed weighted average indicator values with weights inversely proportional to the number of classes assigned. One half of the database was used to calibrate Kernel functions, the other half to validate them. In the validation, each relevé was assigned to the association for which the highest occurrence probability was computed.

Part of the result of the cross-validation is presented in Table 3. This table contains ecologically very closely related grassland associations that occur in the Pleistocene cover-sand landscape in the eastern part of the Netherlands. The indicator value for salinity was not considered for this table, because in this part of the country shallow saline or brackish groundwater does not occur. It appears that 86% of the relevés in Table 3 are classified correctly on the basis of three indicator values only. In the remaining 14%, relevés are paired with ecologically closely related associations. This result implies that the indicator values we employed must have been quite good, as well as that the division of the vegetation into associations makes ecological sense. Note that the division into associations, which is entirely based on species composition, is essentially a subjective matter (see for instance Kershaw and Looney 1985).

Table 3. Efficiency table showing the relationship of the numbers of classified relevés with 'observed' (rows) and expected (columns) associations. Expected associations based on Kernel functions that were derived from an independent data set. Meaning of the codes: 08BC01 = *Caricetum ripariae*, 08BC02 = *Caricetum gracilis*, 09AA03 = *Carici curtae-Agrostietum caninae*, 11AA02 = *Ericetum tetralicis*, 16AA01= *Cirsio dissecti-Molinietum*, 16AB01 = *Crepido-Juncetum acutiflori*, 16AB04 = *Ranunculo-Senecionetum aquatici*, 16BC01 = *Lolio-Cynosuretum*, 19AA02 = *Gentiano pneumonanthes-Nardetum*, 20AA01 = *Genisto anglicae-Callunetum*

	Predicted										
Expected	**08BC01**	**08BC02**	**09AA03**	**11AA02**	**16AA01**	**16AB01**	**16AB04**	**16BC01**	**19AA02**	**20AA01**	**Total number**
08BC01	**19**	15	1			1	3				39
08BC02	12	**26**	1				2				41
09AA03		1	**64**		3	2					70
11AA02			1	**160**	1				19	7	188
16AA01			6		**110**	12	1	1	9		139
16AB01			1		3	**19**	2	1			26
16AB04	1	1				9	**20**	7			38
16BC01	1						6	**185**			192
19AA02				3	6				**40**	1	50
20AA01				10					8	**308**	326

We also performed a sensitivity analysis. Vegetation scientists are especially interested in associations containing rare and threatened species, and these associations therefore show an over-representation in the database of the vegetation relevés employed. It may be expected that our method will attribute an association with relatively few relevés in the database to an over-represented association from a similar ecological niche, for this association will have a higher Kernel density function. To find out whether this is really the case, we plotted for all of the Dutch associations the percentage of correctly classified relevés against the number of relevés per association, see Figure 14. This figure shows there is no relationship at all between the percentage of correctly classified relevés and the number of relevés per association, used to build the Kernel function. Thus, our method appears to be insensitive to over- and under-representation of associations in the database. This suggests that each association has its own particular ecological niche. Of course a poor vegetation division would not yield such a good result: it would contain an overlap of the ecological niches and therefore such a division would be sensitive to the number of relevés per vegetation type.

Figure 14 also shows that most relevés are correctly classified with our method, in spite of various succession stages having been considered (water, pioneer vegetation, grassland, wood etc.) and that we classified on the basis of four indicator values only (i.e. for salinity, moisture regime, nutrient richness and acidity).

In the near future, we intend to compare spatial distribution patterns of predicted vegetation types with vegetation types that have actually been attributed to geographically localized relevés.

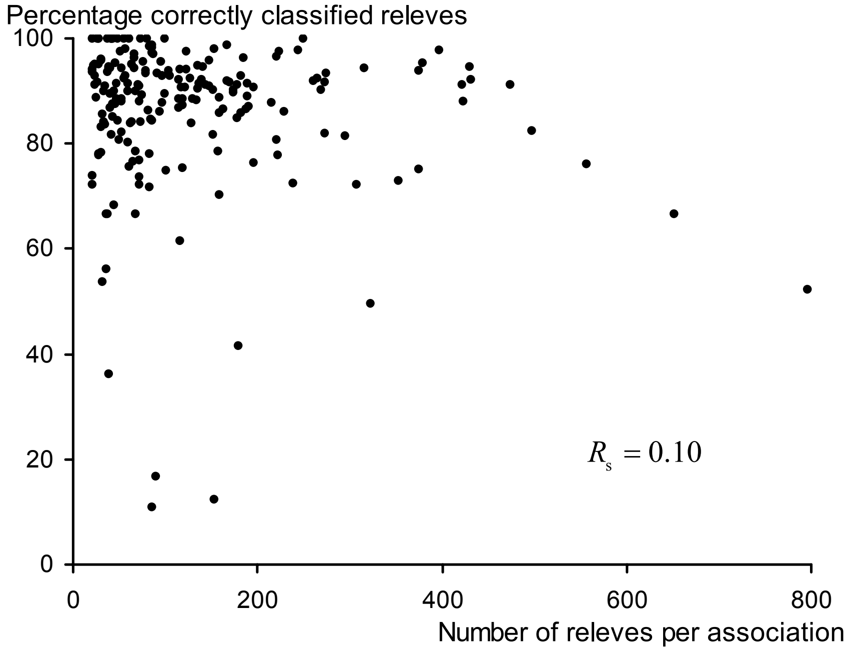

Figure 14. Percentage of relevés that is correctly classified with the aid of a Kernel function versus the number of relevés per association used to build this function. Kernel functions are based on indicator values for salinity, moisture regime, nutrient richness and acidity. All Dutch associations with more than 25 relevés are considered, including for instance those of waters, grasslands and woods. R_S = Spearman correlation coefficient

Discussion

Indicator values and the relation environmental site conditions and vegetation

Figure 9 and Figure 10B show that indicator values are quite reliable, provided some common sense is applied when they are used. The significance of these figures to eco-hydrology is comparable to the significance of groundwater-level – crop-yield functions to agro-hydrology: they are simple empirical relationships of a high practical value. From these figures, we derived the following rules of thumb: (1) ‘wet’ vegetations dominated by hygrophytes occur on soils with a spring groundwater level shallower than approx. 2.5 dm below soil surface (Figure 8); (2) ‘dry’ vegetations dominated by xerophytes occur on soils with a moisture deficit in an average year (Figure 9B); (3) ‘moist’ vegetations dominated by mesophytes occur on soils without a moisture deficit and with a spring groundwater level below approx. 2.5 dm below soil surface.

In predictive eco-hydrological models, such figures can be used to calculate how the percentages of hygrophytes, mesophytes and xerophytes in the vegetation change as a result of a given hydrological measure. However, as illustrated in Figure 1, hydrological measures affect not only the factor ‘moisture regime’ but also other important site factors, e.g. ‘nutrient richness’ and ‘acidity’. Vegetation is therefore also affected by measures aimed at affecting such site factors. To account for this, functions similar to those given in Figure 8 and Figure 9B can be applied. For example, the percentages of ‘acid’, ‘weakly acid’ and ‘alkaline’ species in a vegetation have been estimated based on the soil pH, and the percentages of ‘nutrient-poor', 'moderately nutrient-rich' and 'very nutrient-rich' species have been estimated based on the degree of N-mineralization (Runhaar 1999).

Research into vegetation-site relationships should make as much use as possible of abiotic factors known to be of operational importance to the vegetation, and – *vice versa* – of vegetation characteristics known to be closely related to such abiotic factors. We do not trust statistical correlation of plant species with a large number of measuring variables, which are not clearly ecologically important. Due to apparent correlations and coincidences, such correlative models always yield poor results when they are applied to another region than the region on which the probability functions are based (see e.g. Ertsen et al. 1998). Broodbakker (1990) describes an example of a wrong prediction founded on apparent correlations. Using a logistic regression model he predicted a decrease in the species richness and conservation value of the aquatic vegetation in the shallow lake 'Naardermeer' after the inlet of lake 'IJsselmeer' water from which phosphate was removed but which still contained high concentrations of Cl^- and SO_4^{2-}. In reality however, the lower P level resulted in a higher transparency of the water and the restoration of a species-rich vegetation with *Characaeae* and *Najas marina* (Bouman 1992). Because of the removal of phosphate, the negative correlations between plant species and high chloride and sulphate contents no longer applied.

Apparent correlations can be avoided by exclusively considering those site factors that are most important for the species composition of the vegetation. Logically, these factors influence the vegetation in a direct (operational) way. There is an overwhelming number of publications (e.g. Etherington 1982; Koerselman and Meuleman 1996; Runhaar and Udo de Haes 1994; Runhaar 1999; Schlesinger 1997; Stevenson and Cole 1999) showing that the most important operational factors for the vegetation are 'light', 'salinity', 'moisture regime', 'nutrient availability' and 'acidity'. No surprise, nearly all eco-hydrological models solely use these factors.

How could the relationships between the moist indicator and hydrological variables be improved further? In the first place we could, of course, include more field data in the research and establish data more accurately (e.g. by deriving average groundwater levels from observations made over a period longer than the period 1980-1987 used in Figure 9, or – see for instance Von Asmuth, Bierkens and Maas (2002) – by computing averages from a relatively short time series of groundwater levels with the aid of an impulse-response model).

We may also search for better variables than the average spring groundwater level to characterize the availability of oxygen in wet and moist soils at the start of the growing season, especially because of global warming. Empirical relations between mean spring groundwater level and vegetation cannot be applied under changed climatic conditions as, from an ecological point of view, spring in The Netherlands may start in February instead of in April. So we need to correlate vegetation to climate-related variables, for instance to the groundwater level that corresponds to a certain heat sum (compare for instance with Feddes (1971), who studied combined effects of soil temperature and soil moisture on germination and seedling emergence of various crops).

We may also improve our empirical relationships by taking into account the response time of the vegetation. Plant species can be grouped into plant functional types, like annuals and geophytes, according to the presumed rate at which they respond to environmental changes. We can determine the response time of each plant functional type with the aid of existing databanks on time series of vegetation samples and habitat measurements. This will allow us to compute time-weighted average habitat variables for each plant functional type, thus correcting for time-lag effects.

As a result of the above research, our empirical relationships will become better, but at a certain moment further attempts to improve them would be rather pointless, because the indicator values established on the basis of expert judgment would show too much noise. Based on the newly acquired insights, indicator values could then be adjusted, if such seems justified. Next, the adjusted indicator values would have to be tested for their validity against new field data. This approach would result in a method called ‘successive approximation’ by Poore (1962): the relationships between site characteristics and the occurrence of plant species can gradually be better described by: (1) first defining site conditions more accurately, (2) then classifying them into their relevance to species, and finally (3) adjusting the division of species into ecological groups on the basis of measured site conditions. This will be a difficult task, but we see it as the most appropriate way to gain more knowledge about the relationship between wild plant species and their habitats, since this relationship can hardly be studied by means of statistical methods or pot experiments.

Closing the gap between the two approaches in eco-hydrology

Current eco-hydrological models for biodiversity are based on the assumption that vegetation is in equilibrium with its site: a clear-cut, new species composition corresponds with the predicted site conditions. Succession from the old to the new equilibrium is not modeled, nor is the interaction between plants of different species incorporated in the prediction. Such a simplification of reality is necessary for practical applications. It arises from a lack of both ecological knowledge and data. For long-term predictions however, for instance in the face of global warming, we have to model the succession of soil and vegetation. Due to succession, be it by nature or influenced by human activities, habitat factors gradually change in the course of time, and, as a result, species composition gradually changes as well. To account for this we have to include feedback processes between soil, water and vegetation in our model. This comes down to closing the gap between the two approaches in eco-hydrology, described in the introduction of this chapter.

A good example of an existing dynamic and mechanistic biodiversity model for the soil–water–vegetation system is NUCOM (Van Oene and Berendse 2001; Van Oene, Berendse and De Kovel 1999). This model simulates the competition of species, or groups of species, for water, light and nutrients. The roots, stems and leaves of each species produce a particular amount of litter, each with a certain rate of decomposition. In the course of time, the amount of soil organic matter generally increases and, with that, the availability of nutrients to plants. The effect of this feedback is species-dependent. Species that are able to grow faster will out-compete other species through light availability.

The modeling approach of NUCOM, however, has several shortcomings. For instance, we believe it is questionable whether this model will ever become generally applicable, because it is not feasible to model the competition between all species of the flora considered (for The Netherlands this would require, given the number of about 1400 Dutch vascular plant species, about one million relationships to be described (*i.e.* $\frac{1}{2} n(n-1)$)). Another shortcoming is that it does not account for changes in soil physical characteristics that determine the water regime of the soil. Soil organic-matter content affects the water availability in the root zone, as well as the amount of capillary flow from the groundwater table into the root zone. Finally, this model does not give an estimate of the uncertainty of the output. The latest version of

NUCOM uses 30 equations with a total of 95 parameters (Van Oene and Berendse 2001). In a research setting these large numbers may not be a problem; the NUCOM model has proven to be useful as a research tool. However, for a general application with an inherent lower data availability, the model output should be accompanied by uncertainty analysis.

To model spatial and temporal changes of the soil–water–vegetation system in a general and successful manner, we have to compromise between a mechanistic approach and a limited availability of data. For practical applications we propagate a *semi-mechanistic* approach, in which site factors are modeled in a mechanistic way as far as possible. This is then followed by the prediction of the vegetation in a more or less correlative way using indicator values.

We may incorporate succession of soil physical characteristics in a model for the vadose zone as these may change as a result of changes in soil organic-matter content. This can be done by applying published functions between organic-matter content and soil physical characteristics (Wösten, Pachepsky and Rawls 2001). Suitable variables of soil nutrient availability should be selected on a time scale of years, like total soil C, soil N and NaOH-extractable P. Since soil pH is too variable to be applied directly, this variable may be derived from groundwater-depth information in combination with soil characteristics obtained from the soil map, like texture and mineralogy.

We propose to account for species composition *in an implicit way* by modeling gradual changes in the occurrence probabilities of *vegetation types* as a function of indicator values for the habitat factors 'moisture regime', 'nutrient availability' and 'acidity'.

The combined development of the various ecosystem components may be determined dynamically in three steps (Figure 15):

1. The effect of all site variables is predicted in terms of indicator values. Using Kernel statistics, indicator values will be calibrated against soil physical and soil chemical variables. Thus, we will be able to compute the probability distribution of indicator values for any habitat variable.
2. The occurrence probabilities of vegetation types may be determined on the basis of the probability distribution of indicator values established in the previous step. To this end, classified vegetation samples are used – note that 400,000 vegetation samples are available in The Netherlands – to describe each vegetation type as a Kernel function of indicator values (Figure 11).
3. Plant properties, like litter production and litter pH are strongly linked to plant functional types (Cornelissen et al. 2003). Calculation of the contribution of each plant functional type to a vegetation type allows us to predict these plant properties, which feed back to the habitat variables.

Note that the output of our model would not be just one vegetation type, but the occurrence probabilities of different vegetation types.

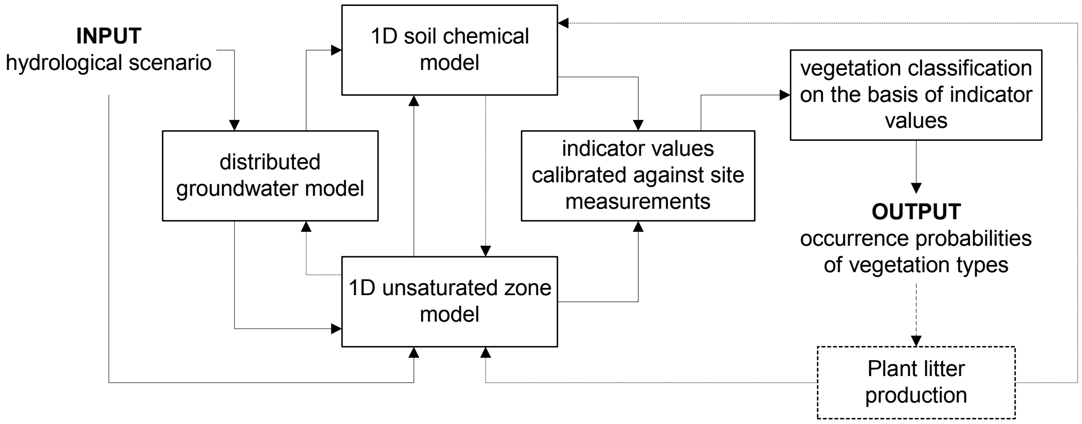

Figure 15. General process chain of a dynamic eco-hydrological model for biodiversity. Dotted lines represent extensions of the model in Figure 10, needed to take account of feedback mechanisms

Analysis of Strengths and Weaknesses, Opportunities and Threats (SWOT)

S: In the past few decades eco-hydrological research has produced an enormous amount of knowledge on relationships between water regime and vegetation biodiversity. This knowledge seems sufficient for the prediction of biodiversity in equilibrium conditions and on a rather course spatial scale (e.g. 1:50,000).

W: The knowledge about water and biodiversity is to a large extent based on field experience (expert judgment) as well as on correlative research with field data that have not been collected in a standardized and randomized manner. Processes underlying correlations are to a large extent only partly known or unknown. This limits the understanding of causality in ecological processes.

O: To gain a more accurate and reliable insight into the relation between water and biodiversity we have to:

a. collect field data in a standardized manner in the root environment of plants and at a large number of sites;
b. take account of the fact that species lag behind environmental changes, such as changes in weather conditions and in groundwater-table depth;
c. search for abiotic factors that influence vegetation composition in a more operational manner;
d. focus on autecology of species to obtain a better understanding of their presence under specified abiotic conditions.

T: We shall never be able to know exactly what plant species desire from their natural environment because:

a. it is practically impossible to collect enough reliable soil samples very close to the roots of plants;
b. in addition, soil, water and vegetation should be considered as a dynamic, continuously developing ecosystem. Even plant species themselves are no invariant entities: they adapt genetically to environmental changes, for instance as a result of global warming;
c. the response of a plant species to its environment depends to a large extent on the competition with other species and there are simply too many possible assemblages of species to investigate.

Because of these problems, our knowledge about the habitat requirements of plant species will always have, to some extent, a correlative character. This implies that empirical relationships between vegetation and habitat may lose their validity in a world that changes rapidly, for example as a result of global warming. It also means that modeling of ecosystem succession, including feedbacks, might be a bridge too far in a number of complex cases.

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Appendix

Eco-hydrological feedback mechanisms in ecosystems: the example of raised bogs

Most ecosystems are largely controlled by one or more feedback loops. Both positive and negative feedback loops exist. Negative feedback loops generally cause stable systems, positive feedback may cause instability and is therefore uncommon in long-existing ecosystems, unless it is compensated by negative feedback.

Generally, raised bogs are looked upon as stable systems, although strictly speaking the continuing accumulation of organic matter in undisturbed raised bog systems implies a long-term instability. Discharge in such systems occurs almost entirely via the acrotelm, the permeable top layer of a few dm deep, which is the one and only aquifer of a raised bog. Because the hydraulic gradient is almost equal to the surface slope, it is approximately constant in time. Hence the discharge is regulated via acrotelm transmissivity T_a, which in turn is determined by the phreatic level H (Ivanov 1965). This leads to the feedback loop shown in Figure 16.

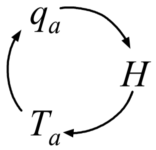

Figure 16. Feedback loop of phreatic level H, acrotelm transmissivity T_a and flux q_a in the acrotelm (Van der Schaaf 2002)

T_a is also the result of processes of production and decay of organic matter in the acrotelm. The decay process in particular depends strongly on the mean and the fluctuation of *H*, which regulates the aeration of the layer of freshly formed dead plant material. Under aerated conditions the decay rate of remains of *Sphagnum*, the main peat-forming genus in raised bogs, is relatively rapid (approximately 0.15 a^{-1}) whereas under fully anaerobic conditions it is in the order of magnitude of 10^{-4} a^{-1} (Clymo 1992). This means that Figure 16, which holds for any time scale, can be completed with a long-term component, which represents the production ecology of the system as controlled by the fluctuation and mean of *H* (Figure 17). Controlling quantities are surface slope and precipitation and evapotranspiration (Van der Schaaf 2002).

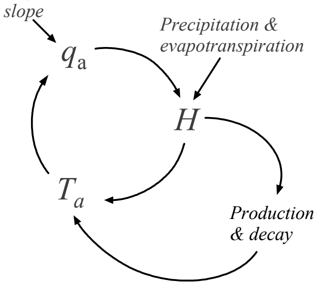

Figure 17. Integrated feedback loops of phreatic level H, acrotelm transmissivity T_a and flux q_a (short and long term) and production and decay (long term) with surface slope and precipitation and evapotranspiration as controlling quantities (Van der Schaaf 2002).

However, inside raised bogs and some other types of mires, a distinct internal patterning exists. Such patterns are usually referred to as microtopes. Common elements in raised bog microtopes are pools, hollows, hummocks, ridges and lawns.

Pools are depressions in the bog surface, which permanently or almost permanently contain surface water, whereas hollows contain surface water depending on seasonal conditions. Hummocks are mounds on the bog surface between a few cm to over a meter in height (Kelly and Schouten 2002). Ridges are elongated higher parts of the bog surface, generally more or less perpendicular to the main direction of flow, and lawns are more or less flat areas, usually dominated by a single *Sphagnum* species. Examples of microtopes are hummock-hollow, pool-ridge, ridge-hollow microtopes, etc. For a long time, the question has been asked what mechanism or mechanisms may cause such a differentiation. Patterning suggests the presence of feedback mechanisms at a spatial scale of about the size of a microtope.

During the last decades it has gradually become clear that the underlying mechanism of hummock formation is a somewhat higher net productivity of typical hummock-forming *Sphagnum* species such as *S. rubellum*, *S. imbricatum* or *S. fuscum*, compared to typical hollow species such as *S. cuspidatum* (Ilomets 1982; Masing 1997). This explains the positive feedback mechanism suggested by the existence of microtopography. On a relatively dry spot in a bog, hummock-forming *Sphagnum* species, which require drier conditions than typical hollow species, will thus build their hummocks, at the same time creating hollows in between, where the typical hollow species find their place. Hence the formation of hollows is a passive process, whilst hummocks are the result of an active process. Thus internal biodiversity is created by a natural process, which ensures a stable distribution of different hydrological conditions over short distances.

The next question is, which negative feedback process overrules this positive feedback system and prevents hummocks from forever growing faster than the surrounding hollows. This is decreasing upward capillary flow as the hummock grows. *Sphagnum* species have no active vertical transport system for water. Hence, upward water transport in a *Sphagnum* hummock to compensate for evapotranspiration losses is by capillary rise. Depending on the pore-size distribution inside the hummock, which is to a large extent related to the constituting species, the maximum hummock level in continental raised bogs is up to nearly 40 cm above the average level of the water table in the hollows (Ivanov 1981). In Atlantic raised bogs, often much higher old hummocks are sometimes found. Their existence may be attributed to the more even distribution of rainfall over the year, compared to continental conditions and thus to shorter continuous periods of excess evapotranspiration. As a result of the negative feedback by reduction of capillary rise, the growth rate of hummocks will eventually become equal to the growth rate of the hollows, once a hummock-hollow pattern has formed. The process of forming such structures could take in the order of 300 years as reported by Karofeld (1999) for hollows in raised bogs in Estonia.

To some extent, hummocks form a barrier to flow, partly because of their height, partly because their internal material may be more decayed as a result of aeration than material in pools or lawns and thus may have a lower hydraulic conductivity (Swanson and Grigal 1988). Generally, drier conditions are more suitable for hummock formation, wetter conditions for the formation of hollows, where water can flow more easily (Joosten 1993). The mechanism is the same as shown in Figure 17. Hence flat parts of bogs with a large upstream catchment area have to develop a sufficiently large acrotelm transmissivity for the discharge of water coming from upstream at a small hydraulic gradient. Such a part of a bog will adapt itself by creating a large proportion of hollows and a small proportion of hummocks, whilst steeper parts will develop a larger proportion of hummocks.

The described processes do not explain why in many bogs and also in patterned fens, microtopes of elongated ridges, hollows and/or pools occur, approximately perpendicular to the direction of flow. Because ridge-pool and ridge-hollow systems occur around the globe in temperate and boreal climates, they probably have a process in common that eventually produces these patterns. In such microtopes, the average surface slope is relatively large. Ivanov (1981) mentioned values of 1 to more than 3 m km^{-1}. Some authors have suggested creep as the basic process (Pearsall 1966; Lappalainen 1996). Others have suggested that the concentration of the flow in the hollows between the less permeable hummocks creates a larger availability of nutrients – a condition often referred to as rheotrophy – and hence a tendency of lateral expansion of hummocks (Ivanov 1965; , cited by Swanson and Grigal 1988). This explanation seems a little odd, since hummock-forming species as *S. fuscum* thrive under extremely ombrotrophic conditions.

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