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GROUND-WATER LEVEL, MOISTURE SUPPLY, AND VEGETATION IN THE NETHERLANDS

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Abstract: The goal of this study was to establish quantitative relationships among vegetation, soil, and ground water that can be used in ecological modeling and engineering. To investigate these relationships, we used data from nature conservation areas in the Netherlands where phreatic ground-water levels had been measured in piezometers for at least five years. The species composition and soil composition of sites near these piezometers were described in detail. The data were used to investigate the relationship between the occurrence of hydrophytes and xerophytes versus average ground-water levels and moisture supply. We found that the distinction between sites dominated by hydrophytes and sites dominated by mesophytes coincides with a mean spring ground-water level of 20–30 cm below surface. Dry sites, dominated by xerophytes, can be defined as sites where under grassland cover moisture deficits will be more than 10 mm in an average year.

Key Words: vegetation, ground-water level, moisture supply, hydrophytes, mesophytes, xerophytes

INTRODUCTION

Plant-Water Relationships

Plant species are adapted in different ways to the hydrologic conditions of their habitats. Special adaptations are needed for surviving in wet places that are fully saturated with water for at least part of the year. Permanently or periodically waterlogged sites are characterized by anaerobic conditions in the root zone. The low redox potential results in the formation of potentially toxic substances such as Fe^{2+}, Mn^{2+}, and H_2S. Species growing in wet sites are characterized by air-space tissues to transport oxygen to their roots or have a very shallow root system that hardly penetrates the soil (Landolt 1973). The deep rooting species often have the ability to oxygenate the soil around their roots so that potentially toxic reduced substances are oxidized and thus rendered harmless (Etherington 1982).

In dry places, where periods with moisture deficits occur, other adaptations are needed. Some perennial species are able to store water (succulents), while most species have an extensive root system. A sclerophyllic anatomy helps to prevent structural deformation due to wilting (Etherington 1982). Annual species avoid water stress by germinating and growing in periods with sufficient moisture supply.

Since the beginning of this century, many attempts have been made to classify plant species according to their response to hydrologic conditions. Schimper (1898) first classified species into hydrophytes (water plants), hygrophytes (species of wet sites), mesophytes (species of moist sites), and xerophytes (species of dry

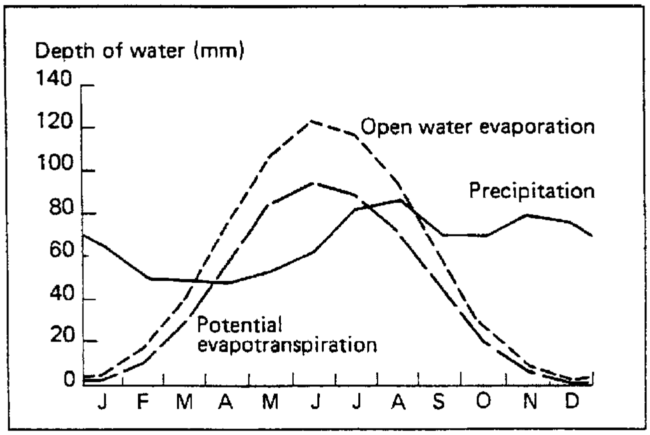

Figure 1. Mean monthly precipitation and potential evaporation over the year (spatial averages; Colenbrander et al. 1989).

Table 1. Adapted Braun-Blanquet scale used to describe the abundance and cover of species in the relevés. In the calculation of the cover of species groups, use has been made of the average cover in the last column.

Code	Description: No. of Species	Description: Cover (%)	Average Cover Used in Calculations
1	<5	<5	.1
2	<2/m^2	<5	.3
3	2–10/m^2	<5	1
4	>10/m^2	<5	3
5	—	5–12	8.5
6	—	13–25	18.5
7	—	26–50	37.5
8	—	51–75	62.5
9	—	75–100	87.5

sites). More recent examples are Londo (1991), who classified species according to their source of water supply (phreatophytes and aphreatophytes), and Ellenberg (1992) and Reed (1988), who give a classification of species according to the moisture regime of the sites on which they normally grow. Most classifications are based on expert judgment, and the relationships with the hydrology are described in a qualitative way.

Plants species are often used as indicators for hydrologic conditions. For example, in the USA, extensive use is made of the Hydrophyte List of Reed to identify wetlands (National Research Council 1995). However, the delineation of wetlands on the basis of vegetation does not always coincide with a delineation on the basis of hydrology (Davis et al. 1996), mainly due to the fact that our knowledge of the relations between hydrology and vegetation is incomplete.

Aim of the Study

For a proper understanding of wetland functioning, and for environmental impact assessment and ecological engineering, more explicit and quantitative relationships between vegetation, soil, and hydrology are needed. In agro-hydrologic literature there is much quantitative information about the relationship between soil, ground water, and plant growth. However, this information is not always directly useful in ecology, since crop production forms the main output parameter. In environmental impact assessment and ecological engineering, we are not so much interested in changes in production but in changes in species composition. These are mostly indirectly related to the physiological reponse of plant species, that is, through the competion between species.

To investigate the relationships between species composition, soil, and hydrology, we used data corresponding to existing classifications that were collected in nature reserves in the Netherlands. The main aim of this study was to find an ecologically meaningful delineation of wet, moist, and dry sites in terms of soil texture, ground-water depth, and moisture supply.

METHODS

Meteorological Conditions

In a small and flat country like the Netherlands, local differences in mean precipitation and evaporation are relatively small. The mean annual precipitation deviates by no more than 20% from the nationwide mean of 775 mm. Figure 1 shows the variation in precipitation and evaporation over the year. The mean annual evaporation for the whole of the Netherlands is around 500 mm. Although the geographical variation in mean annual evaporation is small, the evaporation rate varies considerably over the year, with a maximum of 4 to 5 mm/day in mid-summer to almost zero in winter. Ground-water tables are very shallow in the Netherlands; in 90% of the country, the water table is less than 1 m below surface in winter and less than 2.5 m below surface in summer (Colenbrander et al. 1989). However, in some higher lying sandy areas, ground-water tables in summer can fall so deep that the capillary flux to the root zone becomes insufficient for evaporation at the potential rate. In agriculture, this situation of drought results in lower crop production. In nature, dry conditions result in the establishment of species adapted to periods of drought.

Data Collection

Data were collected in nature reserves in different parts of the Netherlands, comprising dune areas, heath-

Table 2. Characteristics and classes used in the classification of terrestrial ecosystems in the Netherlands. Source: Runhaar and Udo de Haes (1994).

Characteristics	Classes
Moisture regime	wet, moist, dry
Nutrient availability	low, moderate, high
Acidity	acid, weakly acid to neutral, alkaline
Salinity	fresh, brackish, saline
Dynamics	sand drift, perturbation
Vegetation structure	pioneer, grassland, tall herbaceous, dwarf shrub, shrub, forest

lands, bogs, and fens. Ground-water levels were recorded by the responsible nature conservation agency (Staatsbosbeheer), with measuring intervals of 14 days. We selected 123 piezometers, which had been measured in the period 1982–1987. This period is characterized by rather average meteorological conditions, without exceptionally dry or wet periods. About 200 relevés were made of sites near the piezometers in summer 1987, describing the occurrence of higher plants and bryophytes with an adapted Braun-Blanquet scale for cover-abundance (Table 1).

A description was made of the soil profile of the sites, using an augur. Soil layers were described in terms of texture and organic matter content. Ground-water levels in the boreholes were measured after an appropriate time (depending on soil texture, varying from an hour to a day), to check for possible perched water tables. Piezometers and sites were chosen in such a way as to obtain a large variety in different types of terrestrial vegetation and a fair distribution over wet, moist, and dry sites. Only sites where hydrologic conditions had been stable over the previous ten years were selected. The average size of the relevés was 30 m^2, and they were situated in such a manner as to be homogeneous in height, soil composition, and vegetation structure.

Interpretation of Vegetation Data in Terms of Species Groups

Species were classified according to their moisture indication using the ecological species groups of Runhaar et al. (1987) for higher plants and Dirkse and Kruysen (1993) for bryophytes. The ecological groups indicate which species can be expected in certain ecosystem types, which are defined on the basis of vegetation structure and site factors (Table 2). The assignment of species is based on, amongst others, the work of Klapp (1965), Londo (1988) and Ellenberg (1991), and the resulting species groups have been extensively tested on their internal consistency using relevés from all over the Netherlands (Runhaar and Udo de Haes 1994). The species groups are used to determine the distribution and species richness of ecosystem types in the Netherlands (Witte and Van der Meijden 1995) and to predict the effects of water management measures on wet and moist ecosystems (Witte et al. 1992, Witte et al. 1993).

Since we were not interested in the relationship with other factors, species groups with the same preference for hydrologic conditions were lumped, resulting in 6 moisture groups:

1 species characteristic of wet sites, including water plants (hydrophytes)
2 species occurring on both wet and moist sites
3 species characteristic of moist sites (mesophytes)
4 species occurring on both moist and dry sites
5 species characteristic of dry sites (xerophytes)
6 species with no clear preference for wet, moist, or dry sites.

Because the study focuses on terrestrial sites, water plants are not distinguished as a separate group. Table 3 gives the relationship with the classifications of Ellenberg, Klapp, and Londo, which were used in the classification of species according to moisture regime (Runhaar and Udo de Haes 1994), and with some other commonly used classifications. In this paper, species characteristic of wet sites, permanently or periodically

Table 3. Comparison of the moisture groups used in this study with other classifications.

	Classification According to Moisture Regime in This Study:		
	Wet	Moist	Dry
Klapp (1965)	7–10	4–6	1–3
Ellenberg (1991)	7–9	4–6	1–4
Londo (1988)	obligate phreatophytes (W, F)	facultative phreatophytes (V, K, P, D)	—
Iversen (1936)	polyhygroob	oligohygroob	xeroob
Schimper (1909)	hygrophyte	mesophyte	xerophyte
Reed (1988)	obligate wetland	facultative	upland

saturated with water, will be indicated as *hydrophytes,* in accordance with the use of this term in the US. Note that this term is used differently in older European literature, where it is used exclusively for water plants (Tiner 1991). Species characteristic of dry sites where periodic moisture deficits occur will be indicated as *xerophytes.* The appendix indicates the moisture groups to which the plant species found in this study belong.

At each site, we calculated the relative number and cover of hydrophytes and xerophytes as follows:

Relative number of hydrophytes was calculated as the number of hydrophytes (moisture group 1) relative to the number of species characteristic of both wet and moist to dry sites (moisture groups 1, 3, 4, and 5). Sites where the number of facultative species (species occurring on both wet and moist sites, moisture groups 2 and 6) was more than 80% were discarded.

Relative cover of hydrophytes was calculated as the cover of hydrophytes (moisture group 1) relative to the cover of species characteristic of both wet and moist to dry sites (moisture groups 1, 3, 4, and 5). Sites where the cover of facultative species (moisture groups 2 and 6) was more than 80% were discarded.

Relative number of xerophytes was calculated as the number of xerophytes (moisture group 5) relative to the number of species characteristic of both dry and wet to moist sites (moisture groups 1, 2, 3, and 5). Sites where the number of facultative species (species occurring on both dry and moist sites, moisture groups 4 and 6) was more than 80% were discarded.

Relative cover of xerophytes was calculated as the cover of xerophytes (moisture group 5) relative to the cover of species characteristic of both dry and wet to moist sites (moisture groups 1, 2, 3, and 5). Sites where the cover of facultative species (moisture groups 4 and 6) was more than 80% were discarded.

Total cover and cover per moisture group were calculated on the basis of the average cover per Braun-Blanquet scale (Table 1). In the calculation of the relative abundance of xerophytes, *Molinia coerulea* (L.) Moench, now classified as characteristic of wet and moist sites, is also considered as a less-indicative species. Although in natural situations it may have a preference for wet and moist sites, it is now so common in places that have been affected by ground-water lowering and a high atmospheric input of nitrogen that it can hardly be considered as indicative for wet and moist sites (Runhaar et al. 1996).

In the calculation of the relative abundance of hydrophytes and xerophytes, a correction is made for the abundance of facultative species. For example, in calculating the relative number of hydrophytes, the number of hydrophytes (1) is compared to that of species characteristic of wet and of moist to dry sites (1,3,4,5), thereby excluding species occurring on both wet and moist sites (2,6). By excluding these species from the calculation, we obtain a measure that is easier to interpret. For example, a relative abundance of hydrophytes of 50% corresponds with the point where the abundance of species indicating wet conditions is in equilibrium with the abundance of species indicating moist to dry conditions (Figure 2). This 50% point coincides with the limit between wetland and upland according to Cowardin et al. (1979), which is defined as the boundary between land with predominantly hydrophytic cover and land with predominantly mesophytic and xerophytic cover. An additional reason is that the abundance of facultative species is often influenced by the dynamics of the system. In sites with large ground-water fluctuations or otherwise dynamic habitats, species with a broad ecological tolerance, often without a clear preference for certain hydrologic situations, tend to dominate. By excluding the less-indicative facultative species, we get a measure that is less dependent upon the dynamics of the systems. This is reflected in higher correlations (an increase in the explained variance in the range of 0 to 40% of the total variance, depending upon the relationship investigated).

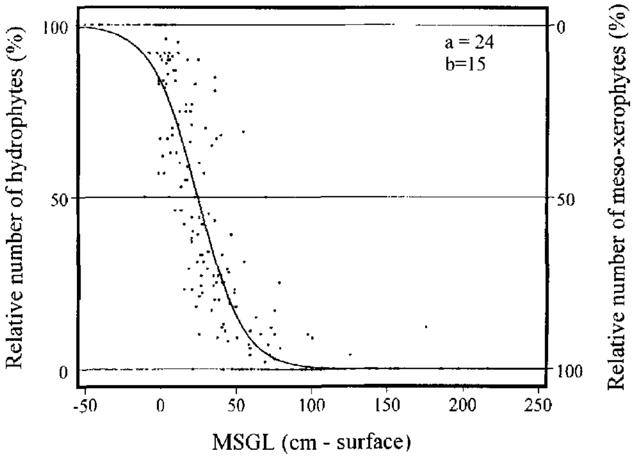

Figure 2. Relative number of hydrophytes in relation to the mean spring ground-water level and plotted sigmoid function: $y = 100/(1+\exp((MSGL-a)/b))$. a = midpoint of the curve, b = measure of the steepness of the slope.

Calculation of Average Ground-water Levels

We used the ground-water data to calculate the mean highest and lowest ground-water level and the mean spring ground-water level. These measures are used in land evaluation and classification to describe the seasonal fluctuations of water tables (Van der Sluijs and De Gruijter 1985) and are commonly used in agrohydrological and ecohydrological modelling.

The *mean highest ground-water level* (MHGL) was calculated as the average of the three highest ground-water levels in the period August–August. The highest ground-water levels usually occur in the period November–March. The calculation was based on a period of 7 years (August 1980–August 1987).

The *mean spring ground-water level* (MSGL) was calculated as the average ground-water level in the period March–April. The calculation was based on a period of 8 years (spring 1980 to spring 1987).

The *mean lowest ground-water level* (MLGL) was calculated as the average of the three lowest ground-water levels in the period February–February. The lowest ground-water levels are normally reached in the period July–September. The calculation was based on a period of 7 years (February 1980–February 1987).

The ground-water data were checked for completeness and for outliers. In many series, there were measurement gaps. Some gaps could be filled by linear regression with data of nearby piezometers. Corrections were made for remaining measurement gaps. For example, when there were fewer observations in the winter period, the MHGL was based not on the three, but on the two highest values, or only on the highest value, depending on the number of missing values (Runhaar 1989). Nine sites were disregarded because of too many gaps in the measurements, resulting in an expected standard error of more than 20 cm.

Calculation of Moisture Deficits

On soils with little available moisture and a low capillary rise, periods with a moisture deficit may occur. This means that the actual evaporation rate E is lower than the potential evaporation rate Ep (i.e., the rate when the vegetation would be optimally supplied with fresh water). The soil moisture deficit is calculated as Ep−E, when Ep>E. The yearly cumulative soil moisture deficit YMD (mm) of 39 moist and dry sites was simulated by Verburg (1995) with a non-stationary model for the unsaturated zone, SWATRE (Belmans et al. 1983). Computations were carried out on a daily basis in the following three steps. First, the actual vegetation with the measured vegetation cover was simulated using the observed ground-water level as a lower boundary condition. Evaporation characteristics of the vegetation, such as rooting depth and wilting point, were estimated from literature. This resulted in a computed drainage flux (i.e., the vertical flux from the site to its surroundings). Second, the computed drainage flux was plotted against the observed ground-water level, resulting in a drainage function for each site. Finally, the drainage functions thus obtained were used as a lower boundary condition for the simulation of the YMD of a standard crop (defined as a grassland with a rooting depth of 20 cm, a soil cover of 90%, and a Penman evaporation factor of 0.7). The YMD obtained in this way is a measure that depends only on the soil and the drainage characteristics of the site and not on the actual vegetation. Because vegetation of dry sites often has a lower potential evaporation, actual moisture deficits may be smaller than calculated deficits. We computed the mean YMD for the period 1980–1986 and the moisture deficit for 1983 (MD83), a year with a rather dry growing season (a 17% dry year). Values for YMD varied from 0 to 54 mm, with a mean of 13.6 mm. Values for MD83 varied from 0 to 120 mm, with a mean of 22.3 mm.

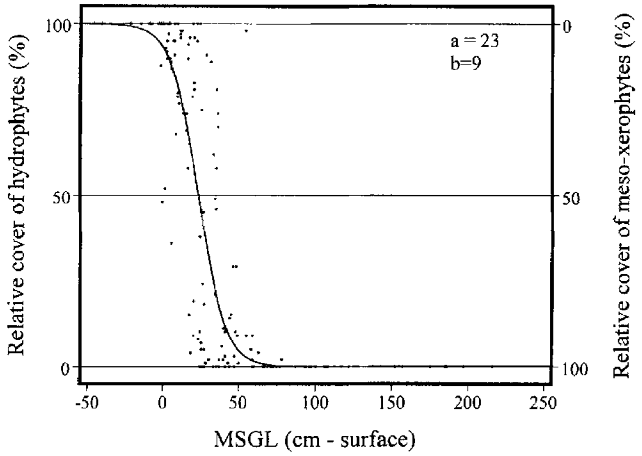

Figure 3. Relative cover of hydrophytes in relation to the mean spring ground-water level and plotted sigmoid function $y = 100/(1+\exp((MSGL-a)/b))$. a = midpoint of the curve, b = measure of the steepness of the slope.

RESULTS

Relationship Between Hydrophytes and Ground-water Levels

Because the relation between the occurrence of hydrophytes and ground-water level is clearly non-linear (Figures 2 and 3), we used a non-parametric method to determine the correlation coefficients. Table 4 gives the rank correlation coefficients according to Spearman for, respectively, the relative number and cover of hydrophytes, related to the average ground-water levels.

The results show there is a strong relationship between the occurrence of hydrophytes and ground-water level. The number and cover of hydrophytes can best be explained by the mean spring ground-water level (MSGL).

Figures 2 and 3 show the relationships between the

Table 4. Spearman rank correlation (R) between relative number and cover of hydrophytes and mean ground-water levels. In all cases, p is less than 0.0001.

	Number of Sites	R MHGL	 MSGL	 MLGL
Relative number of hydrophytes	188	−0.85	−0.89	−0.84
Relative cover of hydrophytes	168	−0.84	−0.87	−0.79

Table 5. Relationship between number/cover of hydrophytes and MSGL per soil type. The relationship is described by a fitted curve using the equation: y = 100/(1 + EXP((MSGL − a)/b)). The table gives the parameter values *a* (midpoint) and *b* (steepness), the percentage of variance explained (R^2), and the Root Mean Square (RMS) of the difference between the observations and the values computed according to equation (1).

Dependent Variable	Soil Type	n	*a*	*b*	R^2	RMS
Relative number of hydrophytes	total	188	24	15	0.77	17.2
	sand	108	23	16	0.76	17.6
	clay	62	24	14	0.68	16.9
	peat	18	20	8	0.81	14.6
Relative cover of hydrophytes	total	168	23	9.4	0.74	22.6
	sand	93	23.4	11.6	0.73	22.4
	clay	61	23.4	7.5	0.65	24.2
	peat	(14)	—	—	—	—

relative number and cover of hydrophytes and the MSGL. At spring ground-water levels above the surface, the vegetation is dominated by hydrophytes. The relative number of hydrophytes decreases greatly as spring ground-water levels drop below the surface. At levels of more than 100 cm below the surface hydrophytes are almost completely absent.

The relationship between the abundance of hydrophytes and the ground-water level can be described by a sigmoid function:

$$y = \frac{100}{1 + e^{(x-a)/b}} \tag{1}$$

where *a* gives the midpoint of the sigmoid (with a relative number or cover of 50%) and *b* is a measure of the steepness of the slope. Using non-linear regression according to Marquardt (1963), we fitted the curve that best describes the relationship between the occurrence of hydrophytes/xerophytes as a dependent variable and ground-water level as an independent variable (Figures 2 and 3). With the fitted functions, more than 70% of the variance can be explained (Table 5).

The midpoint of the curve, where there are as many species indicative of wet sites as species indicative of moist and dry sites, is at a mean spring ground-water level of about 23 to 24 cm below the surface (Table 5). The cover of hydrophytes responds most strongly to the spring ground-water level, as can be seen by the steeper curve. At spring ground-water levels of more than 70 cm below surface, there are still some hydrophytes present, but their cover has been reduced to almost zero (compare Figures 2 and 3).

The relationship between the relative number of hydrophytes and the MSGL differs between peat soils and other soil types ($p < 0.05$). However, the differences are small, the most important difference being that on peat the curve is steeper (Table 5). For relative cover, the number of points on peat is too small (14), and the points are too clustered for curve-fitting. Differences between sand and clay are very small.

Relationship Between Xerophytes and Ground-water Levels

Table 6 gives the rank correlation coefficients according to Spearman for, respectively, the relative number and cover of xerophytes, related to the average ground-water levels. Only sites on sand have been selected. On other soils, there are too few sites with low ground-water levels; 90% of the sites on these soils have a mean spring ground-water level of less than 50 cm below surface. Apart from sites on sand, xerophytes were found only on irreversibly desiccated oligotrophic peat soils with a mean spring ground-water level of more than 20 cm below the surface. The correlations are lower than those for hydrophytes but still highly significant ($p < 0.0001$). The differences between correlations with MHGL, MSGL, and MLGL are small.

The relationship between the relative abundance of xerophytes and ground-water level can be described with a sigmoid function according to Formula 1. In non-loamy, moderately fine sands, the curve that describes the relationship with the MSGL is very steep,

Table 6. Spearman rank correlation (R) between relative number and cover of xerophytes and mean ground-water levels on sand. In all cases, p is less than 0.0001.

	Number of Sites	MHGL R	MSGL R	MLGL R
Relative number of xerophytes	105	0.73	0.74	0.74
Relative cover of xerophytes	84	0.64	0.62	0.60

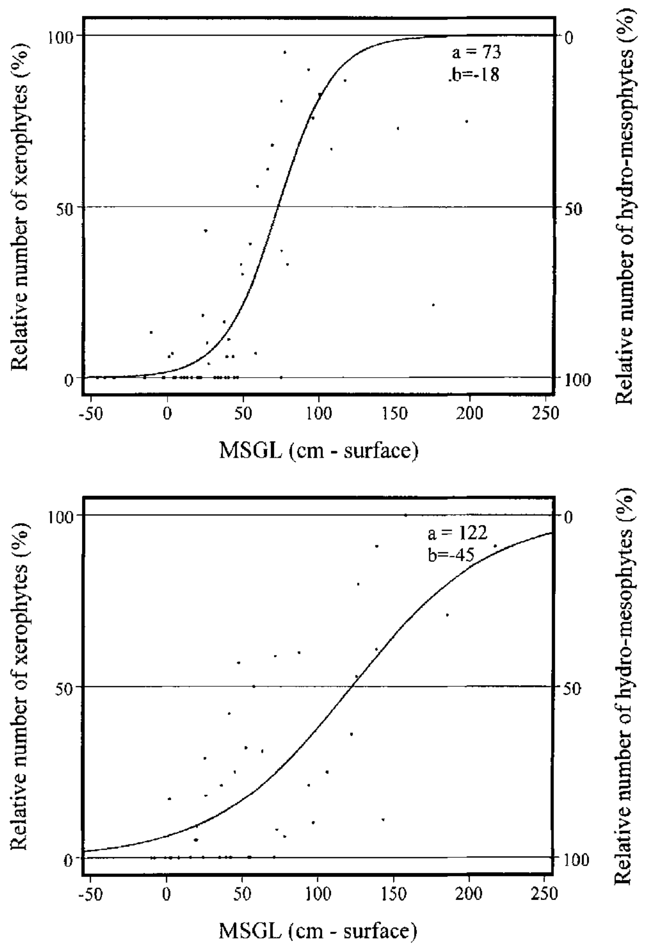

Figure 4. Relative number of xerophytes in relation to the mean spring ground-water level on sandy soils and plotted sigmoid function: y = 100/(1+exp((MSGL-a)/b)). a = midpoint of the curve, b = measure of the steepness of the slope. Top: on moderately fine sand. Bottom: on fine and/or loamy sand.

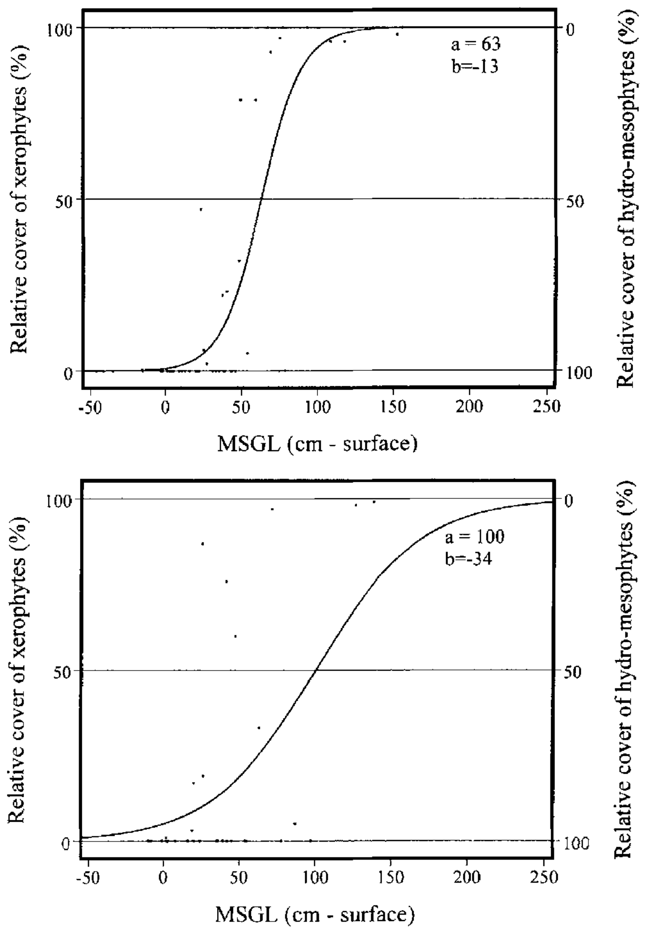

Figure 5. Relative cover of xerophytes in relation to the mean spring ground-water level on sandy soils and plotted sigmoid function: y = 100/(1+exp((MSGL-a)/b)). a = midpoint of the curve, b = measure of the steepness of the slope. Top: on moderately fine sand. Bottom: on fine and/or loamy sand.

with a midpoint at 60–70 cm below the surface (Figures 4a, 5a, and Table 7). In fine sands/loamy sands, the relationship is less clear, but the data suggest that the midpoint of the curve lies at higher values for the MSGL (ca 100–120 cm: see Figures 4b and 5b and Table 7), as would be expected from the fact that in fine-textured soils, the capillary rise of ground water reaches much higher than in coarse-textured soils.

Relationship Between Xerophytes and Moisture Supply

Table 8 gives the rank correlation coefficient according to Spearman for, respectively, the relative number and cover of xerophytes, related to the average yearly soil moisture deficit (YMD) and the soil moisture deficit in the dry year 1983 (MD83). Although highly significant, the correlations are rather low. They become much higher when 5 sites on heavy clay soil are left out of the calculation; on these sites, no xerophytes occur despite the fact that considerable moisture deficits are calculated (average mean yearly deficit on heavy clay soils is 10 mm for a standard grassland vegetation). The yearly mean moisture deficit is the best predictor for the abundance of xerophytes.

Figures 6 and 7 show the relationship between the relative number and cover of xerophytes and the YMD when the heavy clay soils are left out of the analysis. The relationship between the relative number of xerophytes and the YMD can be described by a saturation curve with the formula:

$$y = \frac{100 \cdot x}{x + a} \qquad (2)$$

where a gives the midpoint of the saturation curve (with a relative abundance of 50%). The midpoint is

Table 7. Relationship between number/cover of xerophytes and MSGL per soil type. The relationship is described by a fitted curve using the function: y = 100/(1 + EXP((a − MHGL)/b). The table gives the parameter values *a* (midpoint) and *b* (steepness), the percentage of variance explained (R^2), and the Root Mean Square (RMS) of the difference between the observations and the computed values according to equation (1).

Dependent Variable	Soil Type	n	*a* (cm)	*b* (cm)	R^2	RMS
Relative number of xerophytes	all sandy soils	105	103	−40	0.54	20.7
	non-loamy moderately fine sand	60	73	−18	0.64	18.7
	fine sand/loamy sand	45	122	−45	0.57	19.5
Relative cover xerophytes (corrected for Molinia)	all sandy soils	84	76	−23	0.52	26.2
	non-loamy moderately fine sand	52	63	−13	0.70	22.1
	fine sand/loamy sand	32	100	−34	0.30	28.7

reached at a YMD of 9 mm (Table 9). The relationship between the relative cover and the YMD is so steep that it is hardly possible to fit a saturation curve through these points. However, it is clear that at very small moisture deficits in an average year, the abundance of xerophytes already increases sharply. At moisture deficits of more than 10 mm, xerophytes completely dominate the vegetation.

DISCUSSION

The results indicate that spring ground-water levels are most discriminating between sites that, on the basis of the species composition, are characterized as wet and moist, respectively. This is not surprising. Spring is the period in which most species sprout or germinate, and the aeration of the soil then forms a decisive factor for the establishment and survival of species. Later in the year, the ground-water levels are usually lower and therefore less critical. Josselyn et al. (1990) found that in a seasonal freshwater marsh, hydrophytes dominated the vegetation despite a six-month dry spell in the period May–November. They attributed this to the inability of many facultative species (mesophytes) to germinate under water. Kemmers (1979) also found that in the hay meadows he studied, prolonged periods of high ground-water levels in the spring are more decisive for the occurrence of hydrophytes than ground-water levels later in the year.

To describe the differences between sites classified on the basis of species composition as moist and dry, we can use both ground-water levels and moisture deficits. The use of ground-water levels to describe differences between moist and dry sites has the advantage that ground-water levels are easy to measure. However, the relationship between the abundance of xerophytes and ground-water level is very much dependent on the soil texture. In non-loamy, moderately fine sands, the relationship between ground-water level and the occurrence of xerophytes is rather clear. However, in fine sand and loamy sands, the relationship is less clear, probably because of small differences in loam content and grain size.

The soil moisture deficit is a more generally applicable discriminating factor but has the disadvantage that the calculation is rather complex, requiring many parameter values, such as root depths, wilting points, and evaporation factors. Because the calculation of moisture deficits is mostly restricted to agro-hydrologic systems, many parameter values have to be estimated on the basis of the few data available for natural ecosystems.

On heavy clay soils, there is a discrepancy between the calculated moisture deficits and the moisture clas-

Table 8. Spearman rank correlation between relative number/cover of xerophytes and moisture deficits. The table gives the correlation coefficient R and the significance level (p).

		Number of Sites	Yearly Mean Deficit		Deficit 1983	
			R	p	R	p
Relative number of xerophytes	all sites	39	0.69	0.000	0.67	0.000
	without heavy clay	34	0.82	0.000	0.72	0.000
Relative cover of xerophytes	all sites	30	0.49	0.008	0.57	0.002
	without heavy clay	26	0.66	0.002	0.62	0.002

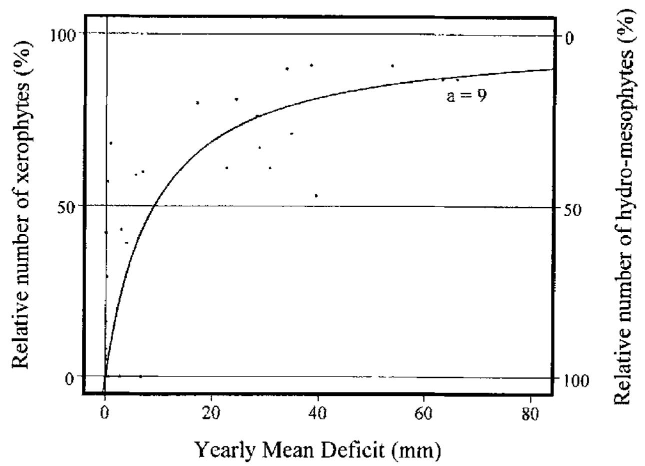

Figure 6. Relative number of xerophytes in relation to the yearly mean moisture deficit and plotted sigmoid function: y = 100.x/(YMD-a). a = midpoint of the curve.

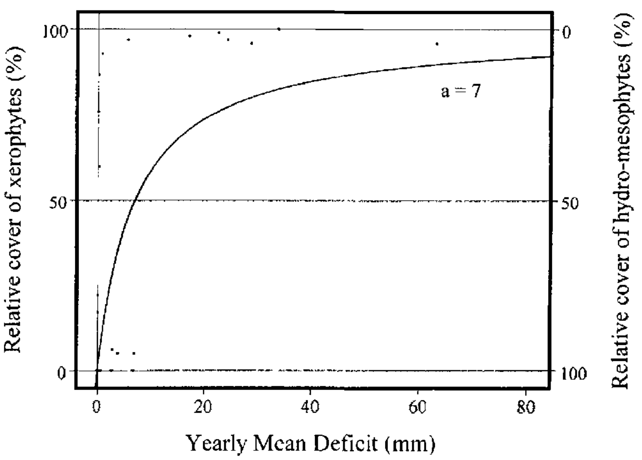

Figure 7. Relative cover of xerophytes in relation to the yearly mean moisture deficit and plotted sigmoid function: y = 100.x/(YMD-a). a = midpoint of the curve.

sification of the plants occurring there. In agriculture, heavy clay soils are considered as drought-susceptible soils. The water is so tightly bound to the very fine capillaries that the amount of soil moisture available for plant growth is restricted. This seems to be in disaccordance with the fact that the vegetation is completely dominated by meso- and hydrophytes. A possible explanation is that, in clay soils, the average rooting depth is much greater than in other soils, resulting in a sufficient supply of water despite the unfavorable soil moisture characteristics. By assuming a fixed root depth of 20 cm, we may have underestimated the moisture supply in these soils. Another explanation might be that many plant species are able to extract water at a very low suction, that is at pF values of more than 4.2, which is the assumed wilting point in agrohydrologic modeling.

The results of our study can be used to quantify the relationships among vegetation, soil texture, and ground water. In our climate, wet sites dominated by hydrophytes can be defined as sites with mean spring ground-water levels of 25 cm or less. This seems to correspond well with the hydrologic wetland threshold value in the 1987 Corps Manual of a seasonal high water table of less than 30 cm (Environmental Laboratory 1987). In our study, soil texture does not seem to influence the relation between the occurrence of hydrophytes and ground-water levels very much. This raises the question of whether a differentiation of the threshold value according to soil type, as in later manuals, is necessary (Tiner 1993a,b, Watts 1993).

Dry sites dominated by xerophytes can be defined as sites with moisture deficits under grassland cover of more than 10 mm in an average year. In moderately fine, non-loamy sands, this corresponds with a MSGL of more than 60–70 cm below the surface. Although the outcome of our research is rather clear, we must make some remarks regarding the general applicability of the relations found.

Influence of Climate

The relationship with soil texture and ground-water levels depends upon the climatic conditions. Therefore, the results of our study cannot be directly transposed to other climatic zones. The relation between hydrophytes and spring ground-water level is probably more or less the same for all climates with a pronounced seasonality, where the vegetation is dormant for part of the year. The relationship between the occurrence of xerophytes and ground-water levels depends strongly on the climate. In areas with much precipitation, no xerophytes will occur, not even on sandy soils with low ground-water levels. However, in drier climates, xerophytes will occur on soil types such as loam and clay soils that in our climate harbor lush vegetations dominated by mesophytes. The calculated

Table 9. Relationship between number/cover of xerophytes and moisture deficits. The relationship is described by a fitted saturation curve according to equation (2). The table gives the midpoint of the curve (a) and the percentage of variation explained (R-squared). Sites on heavy clay soils are excluded.

	Number of Sites	Yearly mean deficit		Deficit 1983	
		a (cm)	R^2	a (cm)	R^2
Number of xerophytes	34	9	0.63	22	0.53
Cover of xerophytes	26	7	0.30	19	0.23

moisture deficit under grassland cover probably forms a more generally applicable measure.

Interrelationship Between Hydrology and Factors Other Than Moisture Regime

The fact that spring ground-water levels are most predictive for the occurrence of hydrophytes does not mean that summer ground-water levels have no influence on the vegetation. For example, in peat soils, the summer ground-water level strongly influences the mineralization of organic matter. Although at high spring ground-water levels the vegetation is dominated by hydrophytes, it may be different species in sites with large and with small ground-water fluctuations. To distinguish between the influence of average ground-water levels and ground-water fluctuations we need experimental studies. An example of this type of research is the study by Hald and Petersen (1992), who experimentally lowered the summer ground-water level in an alder forest plot in Denmark while maintaining the winter ground-water table at the same level. However, experiments with complete ecosystems are difficult to manage and are time-consuming.

Interrelationship Between Root Depth and Moisture Supply

The interrelationship between rooting depth and moisture supply means that the moisture supply of a site cannot be considered as an independent variable. By calculating the moisture deficits for a hypothetical 'standard' vegetation, we tried to construct a measure independent of the actual vegetation. However, in this manner, we neglected the interdependency between root depth and soil type. On sites with conditions favorable for deep rooting, such as nutrient-rich sites with a fine texture, the moisture supply may be much greater than calculated for a hypothetical, shallow-rooting grassland vegetation, while on nutrient-poor sites with a coarse texture, the moisture supply may be much lower. In further studies, we will give more attention to the relation between rooting depth and other factors such as soil texture and nutrient supply.

Simplifications in Our Study

In our study, we related the abundance of species groups to the average moisture supply of a site. However, as Walter (1926) comments, plants growing on the same site do not necessarily share the same hydrologic conditions. For deep-rooting species, the moisture supply can still be sufficient in situations where shallow-rooting species face serious moisture deficits. Therefore, the moisture deficit calculated is only an average, which is not equally relevant for all plant species growing on a site.

Furthermore, the classification of species into moisture groups introduces a subjective element. From a scientific viewpoint, one might therefore argue that it is better to work with species rather than with species groups. However, it would take a large amount of data to establish plant-water relationships for all species. Not only are there many species, but if we study the response of individual species, we also have to take into account that species react to more factors than moisture regime alone. One should be certain that a preference found for wet sites is really based on a preference for certain hydrologic conditions and not on a preference for other site factors that are correlated with hydrology. Furthermore, our aim was not to study the autecology of species but to find an ecologically relevant classification of sites according to moisture regime. Although we realize that reality is far more complex, we think that our simple model is sufficient for this limited purpose.

Comparison with Other Results

Although the period in which the ground-water levels were measured (1980–1987) is a rather average period with respect to meteorological conditions, it cannot be ruled out that the depth of the critical ground-water levels are influenced by the research period. Therefore, it would be useful to compare our results with the outcomes of other studies. However, there is little quantitative material available for comparison. There are many studies in which the correlation between the occurrence of vegetation types and ground-water levels has been studied (e.g., Tüxen 1954, Zarzycki 1956, Balátová-Tuláčková 1968), but in these studies, no distinction is made between direct relationships between plant growth and moisture regime (i.e., via aeration and moisture supply) and indirect relationships (via the correlation between hydrology and other factors, such as acidity, nutrient availability, and soil texture). Therefore, the results of these studies cannot be compared with ours. However, there are a few more quantitative studies. Spoor et al. (1992) investigated the relationship between Ellenberg moisture groups and height above ditch level in southern England. On the basis of the relationship with calculated ground-water levels, they estimated that hydrophytes (species with Ellenberg moisture values of 7–10) dominate on sites with a mean depth to the water table of 20 cm or less in winter. This corresponds well with our results. Gremmen (1987) studied the relations between xerophytes (species with Ellenberg moisture values of 1–4) and the moisture supply. He found that dry sites dominated by xerophytes are characterized by a moisture deficit of 100 mm in a 10% dry year, which is much greater than in our study. However, the author does not specify how the deficits were calculated, which makes it difficult to compare these values.

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