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VEGETATIONAL SUCCESSION, MANAGEMENT AND HYDROLOGY IN A BROOKLAND (THE NETHERLANDS)

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SUMMARY

The relation is discussed between management, hydrology and the resulting vegetational succession during the period between 1975 and 1980 in a characteristic lower course of a Drenthian brook. The hay-making without fertilizer application could eventually lead to a gradient from *Caricion-curto nigrae* at the valley flank to *Magnocaricion* adjacent to the brook. These communities are related to mesotrophic mineral-rich groundwater seeping from a deep aquifer, groundwater with a short residence time in the soil with rainwater characteristics, and an intermediate groundwater type. The actual vegetational succession reveals an increase of the nutrient-rich communities of *Glyceria maxima* and *Carex acuta/Carex aquatilis typicum* and of the nutrient-poor community of *Carex nigra*, whereas mesotrophic *Magnocaricion* communities decreased. This is probably caused by a deep land consolidation ditch adjacent to the nature reserve diverting the base flow. Mineral-rich groundwater, therefore, is replaced by mineral-poor rainwater on the one hand and by nutrient-rich flood water on the other hand. Management practices inside a nature reserve can thus be seriously countered by qualitative hydrological changes outside a reserve even with slightly higher groundwater tables.

1. INTRODUCTION

Large areas of grassland with marginal agricultural value are being taken out of agricultural use in the Netherlands. Continuation of agricultural practices is usually too labour intensive to be economically feasible in view of the low yield or low forage quality e.g. in wet areas. Such land is often acquired by the State or by private organizations for landscape or nature conservation purposes. This is also the case with the 'Stroomdallandschap Drentsche A' containing c. 3000 ha of heathland and grassland, including wet meadows along brook systems. Research is being carried out in order to maintain or restore species-rich plant communities.

Reducing the residual effects of earlier fertilizer applications in order to increase species diversity has been a major objective (RESEARCH INSTITUTE FOR NATURE MANAGEMENT 1979). In Dutch nature reserves hay-making, without the application of fertilizers, is often adopted as a management practice aimed at the removal of nutrients (VAN DUUREN et al., 1981; OOMES & MOOI 1981; WILLEMS 1983). This internal management practice can, however, be countered by changes in groundwater regimes initiated outside reserves e.g. land consolidation programmes. The result can be a lowering of the groundwater table within the reserve with subsequent N-mineralization in wet meadows (GROOTJANS et al., 1985). Another possibility is that a change in the composition of groundwater types takes place with subsequent changes in levels of macro-nutrients and other minerals despite high groundwater tables (GROOTJANS et al., 1986).

The hydrology of the brook system is governed by three main sources (GROOTJANS 1980): (i) the brook itself including flooding with nutrient-rich water, (ii) a base flow discharging nutrient-poor but mineral-rich (Calcium) seepage water, and (iii) a subsurface flow discharging mineral-poor rainwater. The balance in such a hydrological system can be influenced by man-made changes in agricultural areas and by natural fluctuations including dry and wet years.

In a previous paper (BOEDELTJE & BAKKER 1980) the relationship was described between vegetation, soil types, groundwater tables and management in brookland communities. Little relationship was found between plant communities and soil types. It was pointed out that the groundwater table appeared to determine the plant communities in the wettest areas. The somewhat drier communities seemed to be determined by (i) earlier application of fertilizers, (ii) recent nature management practices, and (iii) possible draining towards agricultural areas outside the nature reserve.

In this paper we will investigate the vegetational succession from 1975–1980 as affected by hay-making without fertilizer application. Since this management practice aims at nutrient removal from the soil, its effect has to be measured. This is done by using the indicator values of plant species on soil fertility. The succession will be discussed in relation to groundwater tables and their effects were measured using the indicator values of plant species on wetness. Finally the succession will be related to groundwater quality as affected by adjacent agricultural areas.

2. MATERIALS AND METHODS

2.1. The study area

The study area 'Kappersbult' is located south of Groningen (53°08′NL, 6°37′EL) along the Drentsche A, a catchment area draining 30.000 ha of a Pleistocene landscape. It represents a lower course situation (cf. GROOTJANS 1980) featuring Holocene peat accumulation up to a few metres in a brook valley incised in older glacial deposits. *Magnocaricion* communities were predominantly found in this area. Some sandridges were built up by cover sands and reach 15–80 cm higher than the adjacent peat soils. They carry *Molinio-Arrhenatheretea* communities. These sand-ridges, therefore, influence groundwater regimes locally by discharging a subsurface flow with mineral-poor rainwater which had infiltrated and had a short residence time in the soil. This process results in *Caricion curto-nigrae* communities. The main hydrological system of the study area included nutrient-rich flood water from the brook during the winter months and a base flow originating from the plateau containing nutrient-poor but Calcium-rich seepage water.

The 'Kappersbult' was acquired as a nature reserve (27 ha) by the State Forestry Commission in 1966 and 1967. The preservation and restoration of species-rich wet meadows was pursued by hay-making in the period from the end of June to September without the application of fertilizers. The frequency of hay-making depended on the local wetness of the area and therefore varied from no hay-making at all to twice a year. The dry areas were cut at least once every year, the wet areas were not cut in wet years. The first half of the 1970's was relatively dry, whereas the last years of that decade were rather wet. Moreover, land consolidation programmes resulted in drainage early in the spring and subsequent agricultural drought problems during the summer months. To counter this problem the brook was kept on a higher level during the last few years by the authorities in charge of the management.

The study area was separated from the adjacent intensively farmed agricultural area by a dam in the middle of the 1960's (BOEDELTJE & BAKKER 1980). The dam prevents the agricultural areas from winter flooding in the nature reserve. In order to lower the groundwater table in the agricultural areas, they were drained by a two metres deep ditch outside the study area. Affecting the groundwater regime inside the nature reserve was not precluded (GROOTJANS et al., 1979; STREEFKERK &VAN HOORN 1985; JANSEN & ZONNEVELD 1985).

2.2 Vegetation recording

In 1975, 101 relevés (2 × 2) m^2 were made according to the Braun-Blanquet approach (WESTHOFF & VAN DER MAAREL 1973) in order to characterize the different plant communities. The relevés were arranged in a synoptic table by hand sorting. In 1980 again 114 relevés were made at random and arranged in community types in the same way as in 1975. The person who carried out the mapping in 1975 verified the description of the communities in 1980.

In 1975 and 1980 vegetation maps (1:2000) were compared by overlaying. The extent of plant communities was worked out in a transition scheme by means of a dot grid with a dot spacing of 0.5 cm.

The nomenclature of the Phanerogams followed VAN DER MEIJDEN et al. (1983), that of the Bryophytes MARGADANT (1959) and LANDWEHR & BARKMAN (1974). The nomenclature of the syntaxa was derived from WESTHOFF & DEN HELD (1969).

2.3. Groundwater measurements

Groundwater tables were measured in a transcet perpendicular to the brook and thus covering most plant communities, from April to December 1975, from March 1980 to March 1981 and from July to September 1983. The thus obtained quantitative groundwater data have been supplied by some qualitative measurements. Groundwater samples were collected in the summer and autumn of 1983 from capped tubes, placed at 0.4, 0.8 and 1.2 m below the soil surface in four sites along the transect. One day before sampling, the tubes were emptied in order to allow refilling with fresh groundwater. The samples were stored at 4 °C in polyethylene bottles with no air enclosed. The following parameters were measured in the samples: electrical conductivity (EC_{25}), Ca^{2+} (Atomic Absorption Spectrophotometer) and Cl^- (chlorocounter using an Ag-electrode) in order to distinguish between different types of groundwater (VAN WIRDUM 1982, 1984; GROOTJANS et al. 1986). GROOTJANS et al. (1986) found a good correlation between types of groundwater distinguished from chemical analysis and electric conductivity.

The groundwater samples were classified into groups. The Ca^{2+}-content according to GROOTJANS et al. (1986) was used as a parameter. The groundwater types obtained in this way were defined:
type 1 – groundwater which greatly resembled precipitation water due to the very short residence time in the upper soil layers,
type 2 – groundwater with higher concentration of ions, but the concentration of ions was still low compared with the remaining water types. The resemblance to precipitation water was small,
type 3 – in between the types 2 and 4 due to the long residence time in deeper soil layers,
type 4 – groundwater with very high amounts of ions resembling the deep groundwater in the main aquifer.

The above mentioned data were completed with assessment in the literature concerning indicator values of the species occurring in the stands (see following sections). Indicator values on wetness and soil fertility have been considered. The latter could provide information not only on the balance of groundwater types but also on the process of nutrient removal by hay-making without fertilizer application.

2.4. Indicator values on soil fertility

KLAPP (1965) and ELLENBERG (1979) compiled a list of values for nitrogen and KRUIJNE et al. (1967) one for phosphate. All species occurring in the study area were subdivided into three groups indicating nutrient-poor soil conditions, intermediate- and nutrient-rich soil conditions ('poor', 'intermediate' and 'rich' species). Species with the nitrogen values of 1 to 4 according to ELLENBERG were grouped as 'poor' species, values of 7 to 9 as 'rich'. Species with nitrogen values of 1 and 2 according to KLAPP were grouped as 'poor' species and values of 4 and 5 as 'rich'. The phosphate values according to KRUIJNE et al. range from −100 to 100 but only some salt marsh species show values over 50. Species with phosphate values of −100 of −50 were therefore grouped as 'poor' species and values of 1 to 50 as 'rich'. If one author disagreed with the other two one group about the soil fertility, the two in agreement tipped the balance, if the authors disagreed two groups the species was categorized unknown. The same was the case if only two authors classified a species and disagreed. If only one author classified a species his classification was simply used.

If no 'rich' species were found the 'poor'/'rich' quotient becomes infinite making a ranking impossible. The quotient number of 'poor' and total number of species was, therefore, taken as a measure of the nutrient status of the soil. The 'poor'/'total' quotient was calculated for each relevé in a community. Eventually the mean and standard error was calculated for each community. The plant communities were classified as follows:

rich in nutrients	$0 \leqslant$ poor/total < 0.1
moderate rich in nutrients	$0.1 \leqslant$ poor/total < 0.2
moderate poor in nutrients	$0.2 \leqslant$ poor/total < 0.3
poor in nutrients	$0.3 \leqslant$ poor/total < 0.4

2.5. Indicator values on wetness

KRUIJNE et al. (1967), LONDO (1975) and ELLENBERG (1979) compiled a list of indicator values on wetness. All the species which occurred were classified into three groups indicating dry, intermediate and wet conditions. ('dry', 'intermediate' and 'wet' species).

Aphreatophytic species by LONDO were considered as 'dry' species, hydrophytes and waterplants as 'wet'. Species with moisture figures of 1 to 4 according to ELLENBERG were considered as 'dry' species and figures of 9 to 12 as 'wet'. The moisture values according to KRUIJNE et al. range from –100 to 100, but only include hayfield species and many marsh species are not listed. Species with moisture values of –100 of –15 were therefore considered as 'dry' species and values of 76 to 100 as 'wet'.

The same procedure was used in comparing the three afore mentioned authors' assessments as was the case with the soil fertility. Since only 'wet' or 'dry' species occurred in many relevés, the 'wet'/'dry' quotient was often zero or infinite making a ranking impossible. Hence the number of 'wet' species was related to the total number of species in each relevé in the 'wet'/'total' quotient. Finally the plant communities were classified as follows:

moderate moist	$0 \leqslant$ wet/total < 0.125
moist	$0.125 \leqslant$ wet/total < 0.250
very moist	$0.250 \leqslant$ wet/total < 0.375
wet	$0.375 \leqslant$ wet/total < 0.500
very wet	$0.500 \leqslant$ wet/total < 0.625
extremely wet	$0.625 \leqslant$ wet/total

Special attention was paid to species indicating flooded soils in accordance with ELLENBERG (1979), resulting in a 'flooded'/'total' quotient analogous to the 'wet'/'total' quotient.

3. RESULTS

3.1. The vegetation

Nearly all the communities present in 1975 were still found in 1980. The synoptic table of the communities referred to in this article was published by BOEDELTJE & BAKKER (1980). The communities and their wet/total quotient (indicating the wetness) and flooded/total quotient (indicating the flooding influence) are listed in *table 1*. These quotients are positively correlated ($r = 0.857$, $P < 0.01$). Moreover, the groundwater type is given for most communities (see 3.3) as well as a list of the poor/total quotient (indicating the soil fertility).

The groundwater tables in the period from March to December in five plant

Table 1. Plant communities, their groundwater type, wet/total, flooded/total, and poor/total quotient with standard error (1975–1980 combined).

Community of	Wet/ Total	Flooded/ Total	Poor/ Total	Ground-water type
Glyceria maxima	0.85 ± 0.06	0.24 ± 0.05	0.03 ± 0.02	3/4
Carex elata typicum	0.84 ± 0.05	0.35 ± 0.04	0.04 ± 0.01	
Carex elata comaretosum	0.52 ± 0.08	0.30 ± 0.01	0.19 ± 0.02	
Carex acuta or C. aquatilis typicum	0.67 ± 0.03	0.37 ± 0.02	0.06 ± 0.01	3
Carex acuta or C. aquatilis comaretosum	0.60 ± 0.03	0.33 ± 0.02	0.20 ± 0.02	3
Carex acuta or C. aquatilis/Holcus lanatus	0.36 ± 0.02	0.20 ± 0.02	0.10 ± 0.02	3
Carex disticha typicum	0.69 ± 0.08	0.43 ± 0.04	0.06 ± 0.03	4
Carex disticha comaretosum	0.53 ± 0.02	0.31 ± 0.04	0.19 ± 0.02	4
Carex disticha/Holcus lanatus	0.37	0.26	0.11	
Carex disticha/Agrostis stolonifera	0.44 ± 0.04	0.31 ± 0.02	0.07 ± 0.01	
Phalaris arundinacea and Calamagrostis canescens typicum	0.51 ± 0.02	0.26 ± 0.02	0.03 ± 0.02	
Phalaris arundinacea and Calamagrostis canescens/ Holcus lanatus	0.30 ± 0.02	0.21 ± 0.03	0.10 ± 0.02	
Carex nigra	0.44 ± 0.03	0.21 ± 0.02	0.31 ± 0.02	1/2
Succisa pratensis and Carex panicea	0.17 ± 0.01	0.07 ± 0.01	0.34 ± 0.01	2/3
Holcus lanatus	0.08 ± 0.02	0.08 ± 0.01	0.06 ± 0.01	
Festuca rubra and Agrostis capillaris	0.02 ± 0.01	0.02 ± 0.01	0.15 ± 0.04	
Agrostis stolonifera/Agrostis canina	0.26 ± 0.02	0.12 ± 0.02	0.34 ± 0.03	1
Agrostis stolonifera/Ranunculus repens	0.17 ± 0.04	0.12 ± 0.02	0.09 ± 0.02	

communities of transect A-B are shown in *fig. 1 A-E* for 1975 and 1980, respectively. The 1983 data are not depicted, since these were very similar to the 1980 data (cf. JANSEN & ZONNEVELD 1985). It is obvious that, except for the spring period, the groundwater tables in the study areas were higher in 1980 (and 1983) than in 1975.

Some main types (columns 1, 2, 3 and columns 5 and 6 in *table 2*) were subdivided into different subtypes revealing marked differences with respect to the poor/total, wet/total and flooded/total quotient.

1. The community of *Carex acuta* or *C. aquatilis typicum* (column 1) was relatively species-poor, and indicated soils rich in nutrients. It was found adjacent to the brook and was flooded during long periods (*fig. 1F*) and indicated very wet soils.
2. The community of *Carex acuta* or *C. aquatilis comaretosum* (column 2) was relatively species-rich, featured an abundancy of many *Parvocaricetea* species and indicated soils which were moderately rich in nutrients. It was found in the central part of the study area east of the ditch in the transect A–B (*fig. 2*). The flooding period was short (*fig. 1F*) and the groundwater table was permanently high due to mesotrophic deep seepage water (*fig. 2*).

The two above mentioned subtypes were also found in the main community of *Carex elata* (*table 1*).

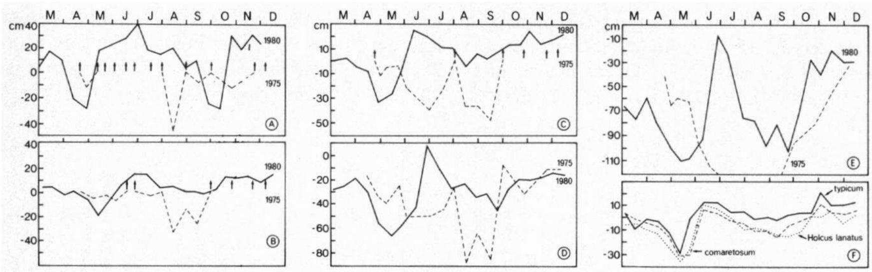

Fig. 1. Groundwater fluctuations in 1975 and 1980 under different plant communities in a lower course situation of the Drentsche A.
A: Community of *Glyceria maxima.*
B: Communities of *Carex elata, Carex acuta* or *C. aquatilis, Carex disticha, Carex nigra.*
C: Community of *Phalaris arundinacea* and *Calamagrostis canescens.*
D: Communities of *Holcus lanatus* and of *Succisa pratensis* and *Carex panicea.*
E: Community of *Festuca rubra* and *Agrostis capillaris.*
F: Groundwater fluctuations in 1980 under three subtypes of the community of *Carex acuta* or *C. aquatilis.*

3. The community of *Carex acuta* or *C. aquatilis* with *Holcus lanatus* (column 3) was relatively species-rich, including many *Calthion palustris* and *Filipendulion* species, and indicated soils rich to moderate rich in nutrients. It was found in the central part of the study area west of the ditch in the transect A–B (*fig. 2*) and more to the valley flank. The flooding period was similar to the *comaretosum* subtype, but the groundwater table was somewhat lower during the spring period.

The three above mentioned subtypes were also found in the main community of *Carex disticha* (*table 1*) which, however, contained a fourth subtype.

4. The community of *Carex disticha* with *Agrostis stolonifera* (column 4) was found in the northern part of the study area. It was species-poor including many *Lolio-Potentillion anserinae* species and indicated soils rich in nutrients. It was wetter than the *Holcus lanatus* subtype.
5. The community of *Phalaris arundinacea* and *Calamagrostis canescens typicum* (column 5) was relatively species-poor. It was sometimes co-dominated by *Glyceria maxima* or *Carex aquatilis.* It indicated soils rich in nutrients and was very wet, although the groundwater tables fluctuated.
6. The community of *Phalaris arundinacea* and *Calamagrostis canescens* (column 6) with *Holcus lanatus* was species-rich including many *Molinio-Arrhenatheretea* and *Lolio-Potentillion anserinae* species. It indicated soils rich to moderate rich in nutrients and was less wet than the previous subtype.
7. The community of *Agrostis stolonifera* with *Agrostis canina* (column 7) was related to the community of *Carex nigra* (the latter was described by Boedeltje & Bakker 1980). It contained many species of the *Caricion curto-nigrae* and *Lolio-Potentillion anserinae.* It indicated soils poor to moderate poor in nutrients, whereas the *Ranunculus repens* subtype indicated soils rich

Table 2. Synoptic table of some subtypes of plant communities in 1980: Pe: Phragmitetea, Ma: Magnocaricion, P: Parvocaricetalia, M: Molinio-Arrhenatheretea, C: Calthion palustris, F: Filipendulion, J: Juncion-acutiflori, A: Arrhenatheretea elatioris, Fe: Festuco-Cynosuretum, L: Lolio-Potentillion anserina. R: Remaining species. Presence: I 1–20%, II 21–40%, III 41–60%, IV 61–80%, V 81–100%. *Main cover over 25%.

		Community of Carex acuta or Carex aquatilis typicum	Community of Carex acuta or Carex aquatilis comaretosum	Community of Carex acuta or C. aquatilis/ Holcus lanatus	Community of Carex disticha/ Agrostis stolonifera	Community of Phalaris arundinacea and Calamagrostis canescens	Community of Phalaris arundinacea and Calamagrostis canescens/ Holcus lanatus	Community of Agrostis stolonifera/ Agrostis canina
	Mean cover herb layer (%)	55	55	50	45	65	65	70
	Mean cover bryophytes (%)	12	26	11	–	5	2	14
	Mean number of species	14	18	19	17	11	16	22
	Number of relevés	11	7	8	5	14	6	7
Pe	Glyceria maxima	V	V	IV	II	V	.	.
	Equisetum fluviatile	II	I	III	III	I	.	.
	Rorippa amphibia	.	.	.	I	I	I	.
	Myosotis palustris	II	II	V	V	IV	II	.
Ma	Carex acuta	III	III	III	II	I	.	.
	Carex aquatilis	V*	V*	V*	III	IV	II	II
	Carex elata	I	I	I	.	I	.	.
	Carex disticha	II	.	.	V*	.	I	.
	Galium palustre	V	V	IV	IV	III	II	II
	Poa palustris	II	III	II	I	I	I	.
P	Potentilla palustris	.	IV	.	.	.	.	IV
	Pedicularis palustris	I	III	I	.	.	.	.
	Stellaria palustris	II	IV	IV	I	II	.	I
	Calliergon cordifolium	III	IV	II	.	IV	I	II
	Carex curta	.	.	.	.	.	.	III
	Carex nigra	.	II	II	.	I	II	V
	Ranunculus flammula	II	III	III	III	IV	I	V
	Viola palustris	.	.	I	.	.	.	I
	Menyanthes trifoliata	.	III	.	.	.	.	.
	Agrostis canina	.	I	II	.	.	II	V*
M	Holcus lanatus	II	II	V	III	I	V	III
	Cardamine pratensis	V	V	V	II	III	V	V
	Rumex acetosa	I	I	IV	IV	I	V	V
	Cerastium fontanum	.	.	II	.	.	.	.
	Rhytidiadelphus squarrosus	.	.	I	.	.	.	.
	Achillea ptarmica	.	.	.	.	.	I	.
C	Lychnis flos-cuculi	.	I	IV	.	.	.	.
	Caltha palustris	V	III	III	IV	II	I	III
	Senecio aquaticus	.	.	II	.	.	I	.

		Community of Carex acuta or Carex aquatilis typicum	Community of Carex acuta or Carex aquatilis comaretosum	Community of Carex acuta or C. aquatilis/ Holcus lanatus	Community of Carex disticha/ Agrostis stolonifera	Community of Phalaris arundinacea and Calamagrostis canescens	Community of Phalaris arundinacea and Calamagrostis canescens/ Holcus lanatus	Community of Agrostis stolonifera/ Agrostis canina
	Mean cover herb layer (%)	55	55	50	45	65	65	70
	Mean cover bryophytes (%)	12	26	11	–	5	2	14
	Mean number of species	14	18	19	17	11	16	22
	Number of relevés	11	7	8	5	14	6	7
F	Filipendula ulmaria	.	.	III	II	I	.	I
	Lythrum salicaria	.	II	II	.	.	I	.
J	Carex panicea	.	.	.	.	.	.	III
A	Festuca pratensis	.	III	I	.	.	III	III
	Alopecurus pratensis	.	.	.	II	.	.	.
	Ranunculus acris	.	I	I	II	.	I	III
Fe	Festuca rubra	.	.	II	.	.	.	I
	Agrostis capillaris	.	.	.	.	I	.	.
L	Agrostis stolonifera	II	V	IV	V	IV	V	V
	Ranunculus repens	III	III	V	IV	IV	V	IV
	Leontodon autumnalis	.	.	.	.	.	.	III
	Eleocharis palustris ssp. uniglumis	I	I	.	.	.	.	II
	Juncus effusus	.	II	II	I	.	.	V
	Alopecurus geniculatus	.	.	.	III	.	I	.
	Glyceria fluitans	.	I	.	V	II	III	III
	Poa trivialis	IV	III	V	V	IV	V	.
	Poa pratensis	.	.	II	II	I	III	.
R	Phalaris arundinacea	V	V	V	IV	V*	V*	.
	Calamagrostis canescens	V	IV	IV	III	V	IV	.
	Leptodictyum riparium	IV	IV	II	.	II	I	.
	Calliergon cuspidata	II	III	III	.	II	II	.
	Carex rostrata	.	II	.	.	.	.	.
	Mentha aquatica	.	III	II	.	.	.	.
	Lysimachia nummularia	.	II	.	.	.	.	.
	Stellaria uliginosa	.	I	.	.	I	.	.
	Cirsium palustre	.	.	I	.	.	.	.
	Anthoxanthum odoratum	.	.	III	.	.	II	V
	Urtica dioica	.	.	.	.	.	I	.
	Taraxacum spec.	.	.	.	.	.	II	.
	Plantago lanceolata	.	.	.	.	.	.	I
	Eriophorum angustifolium	.	.	.	.	.	.	III
	Juncus articulus	.	.	.	.	.	.	II

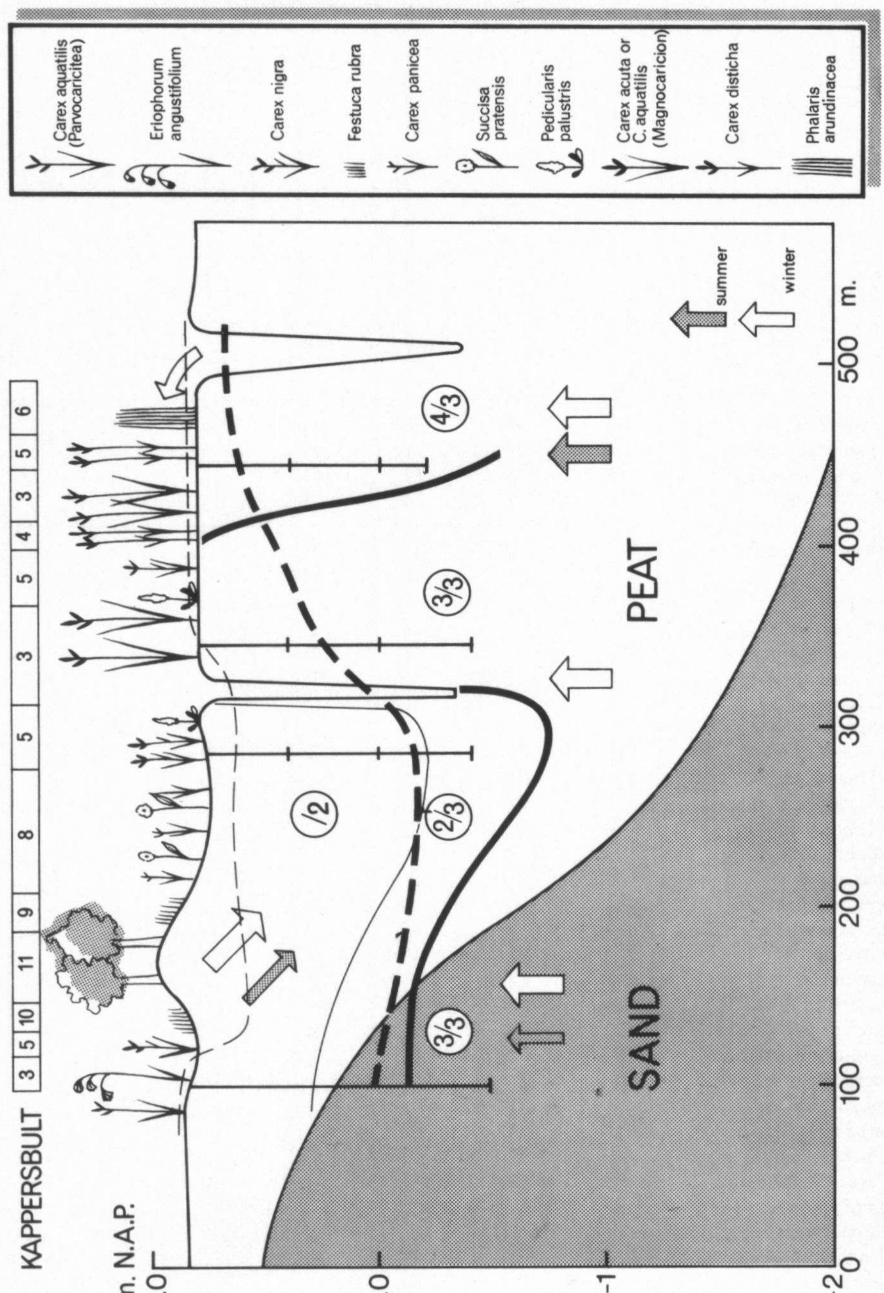

Fig. 2. Transect A–B (cf. *fig. 4*) indicating the distribution of groundwater types under the occurring plant communities during the summer period (thick solid line) and winter period (thin solid line). Thick broken line indicates the groundwater table in the summer, thin broken line in the winter. Figures in rectangles indicate plant communities as in *fig. 4*. Figures in circles indicates groundwater types in summer and winter, respectively. The thickness of the arrows indicates the estimated influence of (ground)water types.

in nutrients. The groundwater table fluctuated more than in the community of *Carex nigra.*

The distribution of the main vegetational types is shown in *fig. 3* and *4* for 1975 and 1980, respectively.

3.2. Vegetation dynamics

The number of points resulting from the vegetation map comparison under each plant community in 1975 and in 1980 is shown in *table 3*. Fifty-five percent of the points were found under the same plant community in both years. The communities of *Glyceria maxima, Carex acuta* or *C. aquatilis typicum, C. acuta* or *C. aquatilis* with *Holcus lanatus, Carex disticha* with *Agrostis stolonifera, Carex nigra,* and *Agrostis stolonifera* with *Ranunculus repens* increased, whereas the communities of *Carex acuta* or *C. aquatilis comaretosum, Phalaris arundinacea* and *Calamagrostis canescens typicum* and with *Holcus lanatus* decreased.

Despite the fact that several communities occupied almost the same surface area in 1975 and 1980, the location of those communities changed considerably. Each community mapped in 1975 may have changed into several other communities by 1980. On the other hand, each community mapped in 1980 may have originated from several other communities than those in 1975. All the changes

Table 3. Number of points resulting from a grid with dot spacing of 0.5 cm under the plant communities in 1975 and 1980, respectively, and the number of unchanged points (100 points equals 1 ha).

Community of	1975	1980	Not changed
Glyceria maxima	167	279	155
Carex elata typicum	15	0	–
Carex elata comaretosum	10	13	7
Carex acuta or C. aquatilis typicum	183	242	66
Carex acuta or C. aquatilis comaretosum	140	83	62
Carex acuta or C. aquatilis/Holcus lanatus	75	139	47
Carex disticha typicum	11	14	7
Carex disticha comaretosum	22	33	15
Carex disticha/Holcus lanatus	7	0	–
Carex disticha/Agrostis stolonifera	6	39	5
Phalaris arundinacea and Calamagrostis canescens typicum	318	266	128
Phalaris arundinacea and Calamagrostis canescens/Holcus lanatus	329	95	49
Carex nigra	109	177	58
Succisa pratensis/Carex panicea	90	52	40
Holcus lanatus	173	142	101
Festuca rubra and Agrostis capillaris	29	14	11
Agrostis stolonifera/Agrostis canina	24	53	12
Agrostis stolonifera/Ranunculus repens	24	85	5
Total	1726	1726	958

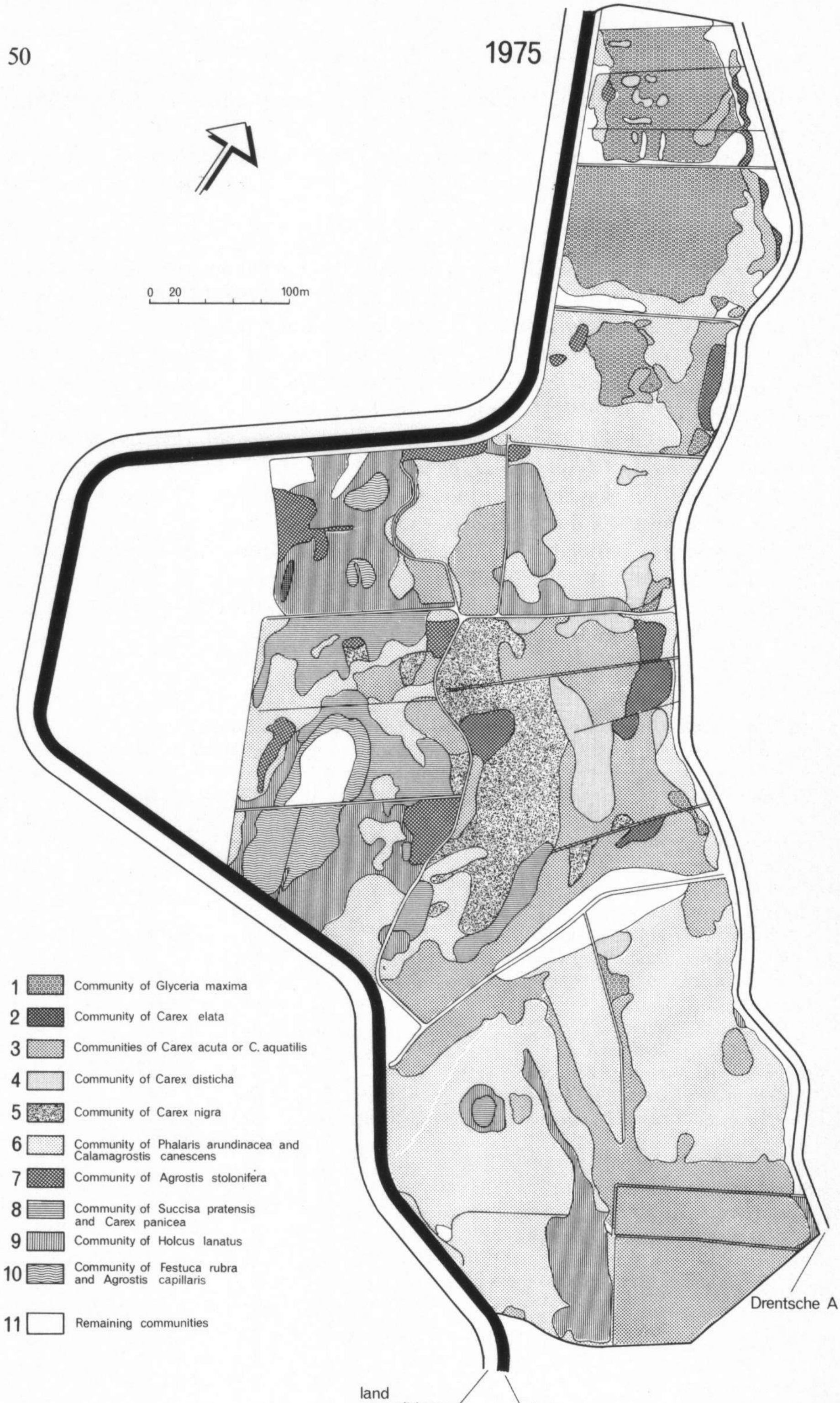

Fig. 3. Vegetation map of a lower course situation of the Drentsche A in 1975.

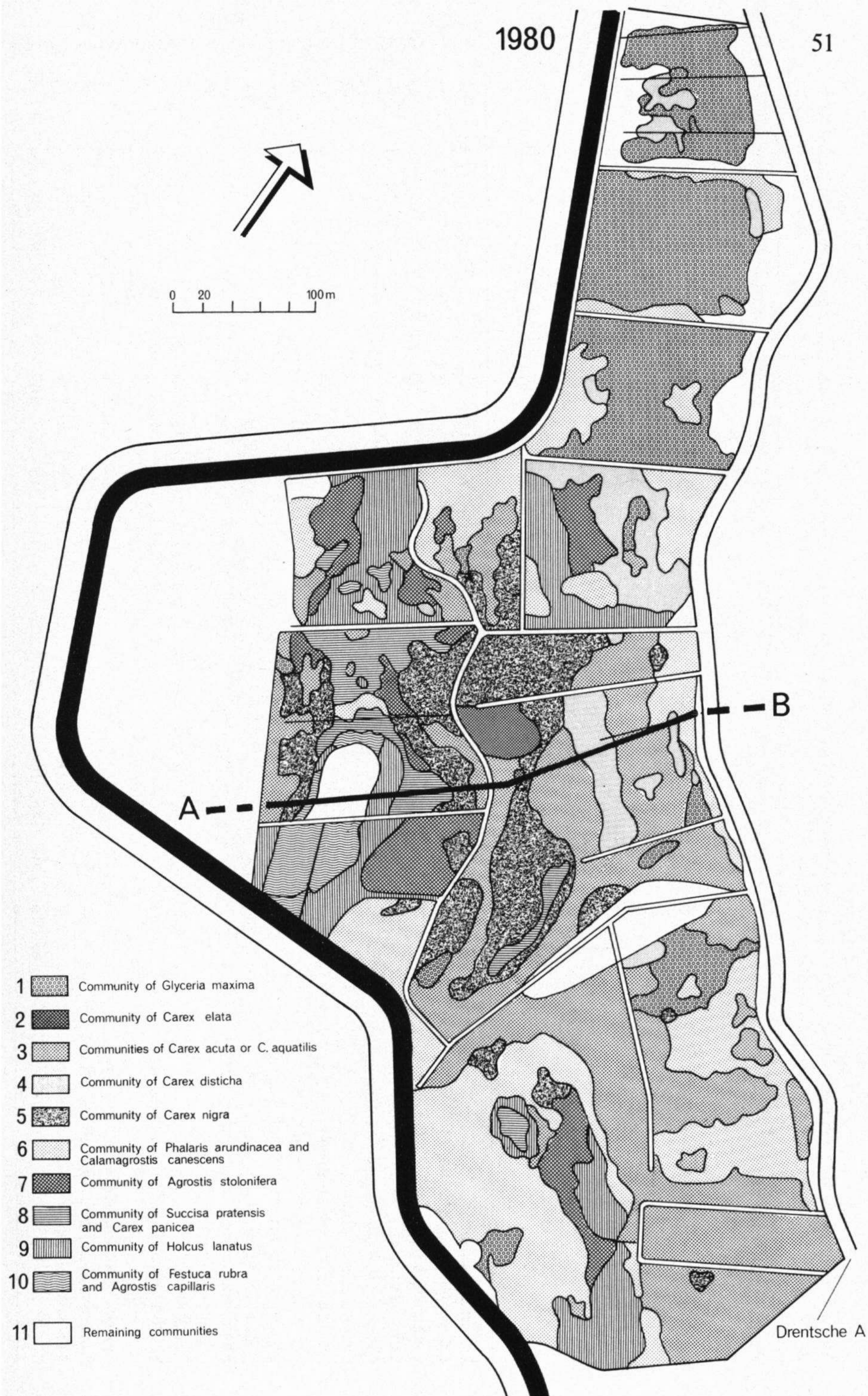

Fig. 4. Vegetation map of a lower course situation of the Drentsche A in 1980 and the position of transect A–B depicted in *fig. 2*.

Table 4. Transitions between plant communities during the period 1975 to 1980. The points result from a grid with dot spacing of 0.5 cm. Italicized figures indicate the numbers of unchanged points in each community.

Plant communities 1980 \ Plant communities 1975	Glyceria maxima	Carex elata typicum	Carex elata comaretosum	Carex acuta or C. aquatilis typicum	Carex acuta or C. aquatilis comaretosum	Carex acuta or C. aquatilis/Holcus lanatus	Carex disticha typicum	Carex disticha comaretosum	Carex disticha/Holcus lanatus	Carex disticha/Agrostis stolonifera	Phalaris arundinacea and Calamagrostis canescens typicum	Phalaris arundinacea and Calamagrostis canescens/Holcus lanatus	Carex nigra	Succisa pratensis and Carex panicea	Holcus lanatus	Festuca rubra and Agrostis capillaris	Agrostis stolonifera/Agrostis canina	Agrostis stolonifera/Ranunculus repens	n
Glyceria maxima	*155*	–	–	23	–	–	2	–	–	1	84	11	–	–	–	–	–	3	297
Carex elata comaretosum	–	–	*7*	–	–	–	–	–	–	–	–	–	5	1	–	–	–	–	13
Carex acuta or C. aquatilis typicum	4	2	2	*66*	36	10	2	6	–	–	60	23	30	–	–	–	–	1	242
Carex acuta or C. aquatilis comaretosum	–	–	–	–	*62*	–	–	–	–	–	9	4	5	–	–	–	2	1	83
Carex acuta or C. aquatilis/Holcus lanatus	–	–	–	66	2	*47*	–	–	4	–	9	5	–	1	5	–	–	–	139
Carex disticha typicum	7	–	–	–	–	–	*7*	–	–	–	–	–	–	–	–	–	–	–	14
Carex disticha comaretosum	–	–	–	6	–	2	–	*15*	–	–	4	–	3	–	1	–	–	2	33
Carex disticha/Agrostis stolonifera	–	–	–	–	–	–	–	1	–	*5*	3	30	–	–	–	–	–	–	39
Phalaris arundinacea and Calamagrostis canescens typicum	–	13	–	9	3	2	–	–	–	–	*128*	110	–	–	–	–	–	1	266
Phalaris arundinacea and Calamagrostis canescens/Holcus lanatus	1	–	–	2	–	–	–	–	–	–	16	*49*	–	3	18	–	–	6	95
Carex nigra	–	–	1	6	22	13	–	–	3	–	2	33	*58*	26	4	–	9	–	177
Succisa pratensis and Carex panicea	–	–	–	–	–	1	–	–	–	–	–	4	1	*40*	3	2	1	–	52
Holcus lanatus	–	–	–	1	–	–	–	–	–	–	1	15	–	6	*101*	15	–	3	142
Festuca rubra and Agrostis capillaris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	*11*	–	2	14
Agrostis stolonifera/Agrostis canina	–	–	–	–	–	–	–	–	–	–	–	7	–	12	22	–	*12*	–	53
Agrostis stolonifera/Ranunculus repens	–	–	–	4	15	–	–	–	–	–	2	38	1	1	18	1	–	*5*	85
	167	15	10	183	140	75	11	22	7	6	318	329	103	90	173	29	24	24	1726

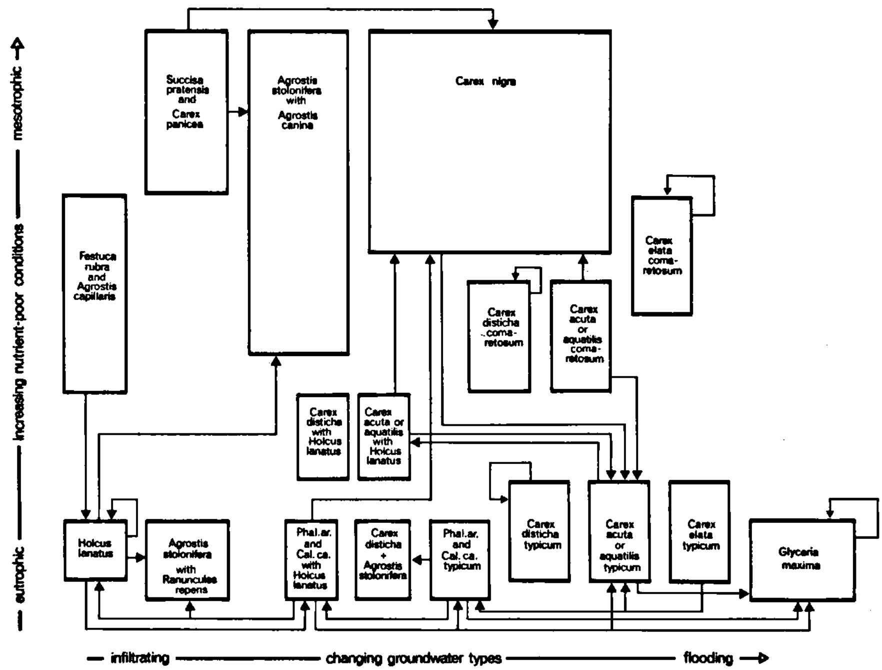

Fig. 5. Transition scheme of plant communities in the period 1975 to 1980. Only transitions involving over 10% of the 1975 area of each community are shown. The ranking and spreading along the axes of soil fertility and groundwater types were derived from data in *table 2* and do not represent the area of communities concerned.

have been quantified in the matrix of *table 4*. The changes concerning over 10% of the 1975 area of each community are shown in the transition scheme of *fig. 5*. The ranking of the communities along axes of soil fertility and groundwater types was derived from data in *table 1*.

The *Carex nigra* community spread at the cost of several other communities and lost to the community of *Carex acuta* or *C. aquatilis typicum*. The latter community also spread at the cost of other communities and only lost to the subtype of *Holcus lanatus*. The *Glyceria maxima* community only spread at the cost of other communities. The community of *Phalaris arundinacea* and *Calamagrostis canescens typicum* diminished in favour of the communities of *Glyceria maxima* and *Carex acuta* or *C. aquatilis typicum*. It had increased at the cost of the *Holcus lanatus* subtype of the same community.

The complex transitions between the communities have been summarized with respect to an indication for soil fertility (*table 5*). It is remarkable that the areas of both the groups nutrient-rich and nutrient-poor groups increased from 897 to 1067 and from 217 to 282 points, respectiviely, between 1975 and 1980. The areas of moderate nutrient-rich and moderate nutrient-poor groups decreased from 472 to 294 and from 140 to 83 points, respectively, between 1975 and 1980.

Table 5. Transitions between soil fertility groups during the period 1975 to 1980. The points result from a grid with dot spacing of 0.5 cm.

	Nutrient-rich	Moderate nutrient-rich	Moderate nutrient-poor	Nutrient-poor	Total 1980
Nutrient-rich	711	264	54	38	1067
Moderate nutrient-rich	139	140	2	13	294
Moderate nutrient-poor	10	4	62	7	83
Nutrient-poor	37	64	22	159	282
Total 1975	897	472	140	217	1726

Table 6. Transitions between wetness groups during the period 1975 to 1980. The points result from a grid with dot spacing of 0.5 cm.

	Extremely wet	Very wet	Wet	Very moist	Moist	Moderate moist	Total
Extremely wet	268	188	31	44	4	0	535
Very wet	28	288	13	120	5	1	395
Wet	6	21	63	95	27	4	216
Very moist	69	35	0	117	21	45	287
Moist	4	17	2	44	46	24	137
Moderate moist	1	1	0	15	11	128	156
Total 1975	376	490	109	435	114	202	1726

Table 7. Ionic composition of groundwater types according to GROOTJANS et al. 1986. For each parameter the first column indicates the summer value and the second column the autumn/winter value. Sample number 1 is taken far from the brook, sample number 4 close to the brook (see *fig. 2*). Rainwater figures are the mean values from the meteorological station Witteveen (1978–1982).

Sample number and depth	Groundwater type		EC_{25} $\mu S\ cm^{-1}$		Ca^{2+} meq l^{-1}		Cl^{-} meq^{-1}	
1 120 cm	2	3	303	363	1.97	2.24	0.60	0.86
2 40 cm	–	2	–	210	–	1.43	–	0.28
2 80 cm	–	2	–	165	–	0.75	–	0.63
2 120 cm	2	3	261	187	1.04	2.23	0.50	0.57
3 40 cm	–	3	–	295	–	1.58	–	1.08
3 80 cm	3	3	282	230	2.09	1.56	0.72	1.06
3 120 cm	3	3	464	297	3.03	1.58	1.04	1.18
4 40 cm	4	–	564	–	3.86	–	1.20	–
4 80 cm	4	–	680	–	4.03	–	2.25	–
4 120 cm	4	–	547	–	3.64	–	0.82	–
Rainwater			62		0.05		0.09	
Brook surface water	–	3	–	346	–	1.90	–	1.08

Transitions between the communities with respect to indication for wetness are summarized in *table 6*. A general trend can be seen, namely that the area of nearly all groups increased at the cost of drier groups and decreased in favour of wetter ones. This phenomenon resulted in an increase in the three wettest groups from 975 points in 1975 to 1146 points in 1980.

3.3. Distribution of water types

The chemical analysis of groundwater samples revealed the occurrence of four groundwater types (*table 7*). The classification of water types was derived from GROOTJANS et al. (1986). The water type 2 shows little resemblance to precipitation water due to its residence in the soil, but the concentration of ions was still low in comparison with the next two types. Watertype 4 showed a high resemblance to groundwater from a deep aquifer containing much Ca^{2+}. This type of water reached the surface in the valley as seepage water. Watertype 3 was in between the types 2 and 4.

Groundwater table measurements and EC-field measurements along the transect A–B in *fig. 4* revealed the watertype distribution shown in *fig. 2*. It appeared that watertype 4 was only found in the centre of the valley near the brook. Watertype 2 occurred below and around the coversand ridge and at the valley flank. The intermediate watertype 3 was found in deep layers along the valley flank and reached the valley surface between the other watertypes. The flood water from the brook was classified as watertype 3.

4. DISCUSSION

We have seen that the area of the nutrient poor communities increased. This was mainly due to the increase in the communities of *Carex nigra* and *Agrostis stolonifera* with *A. canina*. These transitions also implied an increasing wetness (cf. *fig. 5*). This increasing wetness was, in fact, found throughout the study area. Although the area covered by nutrient-rich communities was already large in 1975, it still increased somewhat particularly due to the communities of *Glyceria maxima* and *Carex acuta* or *C. aquatilis typicum*. The increasing wetness of the study area occurred with the spreading of both nutrient-poor and nutrient-rich communties.

The above mentioned phenomena were clearly illustrated by the decreased area of the community of *Carex acuta* or *C. aquatilis comeratosum* in favour of the subtype *typicum* west of the central ditch, and of the community of *Carex nigra* east of the central ditch along the transect A–B in *fig. 4*. The vegetational changes mentioned can be related to mainly man-made changes in the hydrology. The groundwater tables east of the central ditch became very low during the summer period, probably because the land consolidation ditch diverted the mesotrophic groundwater type 3. The shortage was replenished naturally with recently infiltrated nutrient and mineral-poor rainwater (watertype 2) during the autumn and winter periods. Locally, the influence of the land consolidation ditch went beyond the central ditch. There, closer to the brook, the shortage was replenished by flood water from the brook which was rich in nutrients, thus favouring *Glyceria maxima* (KOVACS 1968). The community of *Phalaris arundinacea* and *Calamagrostis canescens* depended on fluctuating groundwater tables or oxygen-rich water. These communities succeeded into communities of *Glyceria maxima* and *Carex acuta* or *C. aquatilis* (BALÁTOVÁ-TULÁČKOVÁ 1966) as a consequence of longlasting flooding periods with subsequent anaerobic conditions. Moreover, during the dry spring and summer periods the brook level was kept high which was necessary for agricultural purposes after the land consolidation works. The spreading of wet, very nutrient-rich communities was, therefore, related to the increased influence of flood water from the brook. The spreading of wet, nutrient-poor communities was related to the replacement of the mesotrophic groundwater type 3 by mineral-poor precipitation water. GROOTJANS et al. (1986) anticipated problems for vegetation if the base flow is prevented from reaching the surface for a long period by overlying infiltration water. They suggested that species prefering areas with little seasonal change in the prevailing alkaline conditions, have great difficulty in dealing with such enormous changes in water quality. The decrease of *Pedicularis palustris* in this study area supports this idea (JANSEN & ZONNEVELD 1985).

Vegetational changes were slight in the higher and drier parts of the study area. The existing community of *Festuca rubra* and *Agrostis capillaris* might represent the final stage when hay-making without fertilizer application (EVERS et al. 1984). This management practice was expected to enhance the development of the communities of *Holcus lanatus* and of *Phalaris arundinacea* and *Calamagrostis canescens* with *Holcus lanatus* into *Calthion palustris* communities in wetter areas (EVERTS et al. 1984). Character species of the *Calthion palustris*, however, prefer soils influenced by mineral-rich (type 4) or intermediate (type 3) groundwater, and avoid peat soil influenced by mineral-poor (type 1/2) groundwater (GROOTJANS et al. 1986). The replacement of groundwater by rainwater, therefore, prevents the development of *Calthion palustris* communities.

The increasing wetness of the major part of the reserve not only had a hydrological impact, but it also changed the management practices, since hay-making was no longer possible every year. The failure to practice hay-making might enhance the increase of *Glyceria maxima* in the community of *Phalaris arundinacea* and *Calamagrostis canescens*. This community often changed into the community of *Carex acuta* or *C. aquatilis typicum* with regular hay-making. The change of the community of *Carex acuta* or *C. aquatilis typicum* to the *Holcus lanatus* subtype particularly took place in areas with irregular hay-making. If hay-making is omitted litter accumulates resulting in locally drier areas, and facilitating the establishment of grassland species analogous to the establishment of grassland species on *Calliergon cordifolium* carpets within *Magnocaricion* communities mentioned by NEUMANN (1957).

The desired nutrient removal from the soil by hay-making without fertilizer application can be measured indirectly by using the indicator values of plant species. The process of nutrient removal is, however, affected by changing groundwater levels and groundwater types which influence the nutrient status of the soil. However, in wet circumstances this process is influenced by stopping hay-making. In the latter case not only the nutrient status of the soil becomes affected, but also the mechanical process of litter accumulation hampers the performance of many species.

Our conclusion is that with hay-making without a fertilizer application a gradient would eventually develop from *Caricion curto-nigrae* at the valley flank to *Magnocaricion* adjacent to the brook in the 'Kappersbult' area provided there was an undisturbed hydrology (Grootjans 1980). However, the man-made diminished base flow and high brook levels resulted on the one hand in the replacement of groundwater by brook water and the subsequent spreading of nutrient-rich *Glyceria maxima* communities at the cost of mesotrophic *Carex aquatilis* communities. On the other hand groundwater was replaced naturally by rainwater with the subsequent spreading of more oligotrophic *Caricion curto-nigrae* communities at the cost of mesotrophic *Magnocaricion* communities. Management practices inside a nature reserve can, therefore, be seriously countered by man-made hydrological changes outside a reserve.

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