

ON THE VEGETATION OF FORMER RIVER BEDS IN THE NETHERLANDS

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I. INTRODUCTION

A considerable part of the Netherlands consists of the deltas formed by the great rivers Meuse and Rhine and by some smaller ones. These rivers played an important part in the geological evolution of the country. During the whole of the Quaternary period oxbow lakes and other types of former river beds came into existence. Originally they resulted from spontaneous diversions of the streams, later on mainly from artificial cut-offs.

In this paper every expanse of water which once formed part of the summer bed of a river, but which now, at least in summer, no longer functions as such, is considered to be a "former river bed".

Up till 1954 little attention has been given to the scientific investigation of these former river beds. Of course, their presence is mentioned in handbooks of geology, geography and soil science (e.g. FABER, 1947/48; SCHUILING *c.s.*, 1934; EDELMAN, 1950 a and b), but only a few papers enter into details (BOISSEVAIN, 1941; PANNEKOEK VAN RHEDEN, 1942; HOEKSEMA, 1947).

The flora and the vegetation of the former river beds in the Netherlands have never been systematically investigated. More attention than to other aspects has been given to hydrobiological problems. Very valuable is an investigation of the planctonic organisms by LEENTVAAR (1954, 1955, 1957). BOER (1942) is the only author who gives some information with regard to the communities formed by the higher plants.

There is very little literature on the vegetation that is found in former river beds occurring outside the Netherlands, but comparable with ours. VON MITTIS (1939) classifies and denominates, on purely geographical grounds, the "Altwässer" (former beds) of the river Danube. For the rest here too hydrobiological papers dominate (e.g. VON MITTIS, 1940; GROHS, 1943). Some information with regard to the communities of higher plants can be found in papers by LAUTERBORN (1916-1918, Rhine in Switzerland and Germany), OBERDORFER (1957, Rhine in S. Germany), ALLORGE (1922, Seine in France) and KOCH (1926, Linth in Switzerland).

This publication deals with the plant communities of the former river beds and their habitats, except the carrs, i.e. the humid woods consisting of small trees such as willows and alders. Ir. L. G. KOP (1961) wrote a paper on the carrs and as the latter are here left out of consideration, it may be regarded as supplementary to this one. W. A. E. VAN DONSELAAR-TEN BOKKEL HUININK (1961) gave special attention to the ecology of some communities in a restricted number of former river beds, and published her results separately. VAN DER VOO published descriptions of some of the former river beds (1956 a and b, 1957). Other papers are concerned with the ecology of some plant species (VAN DER VOO and WESTHOFF, 1961), with the importance of the work from the point of view of nature preservation, and with the geological and geographical aspects of the former river beds (VAN DONSELAAR, 1956, 1957 a).

II. THE FORMER RIVER BEDS AS HABITATS FOR PLANTS (See Fig. 1)

Origin and development of former river beds have been described comprehensively by VAN DONSELAAR (1957 a). Here it will be sufficient to mention the main lines. More attention will be given to those properties of the former river beds which may influence plant life now.

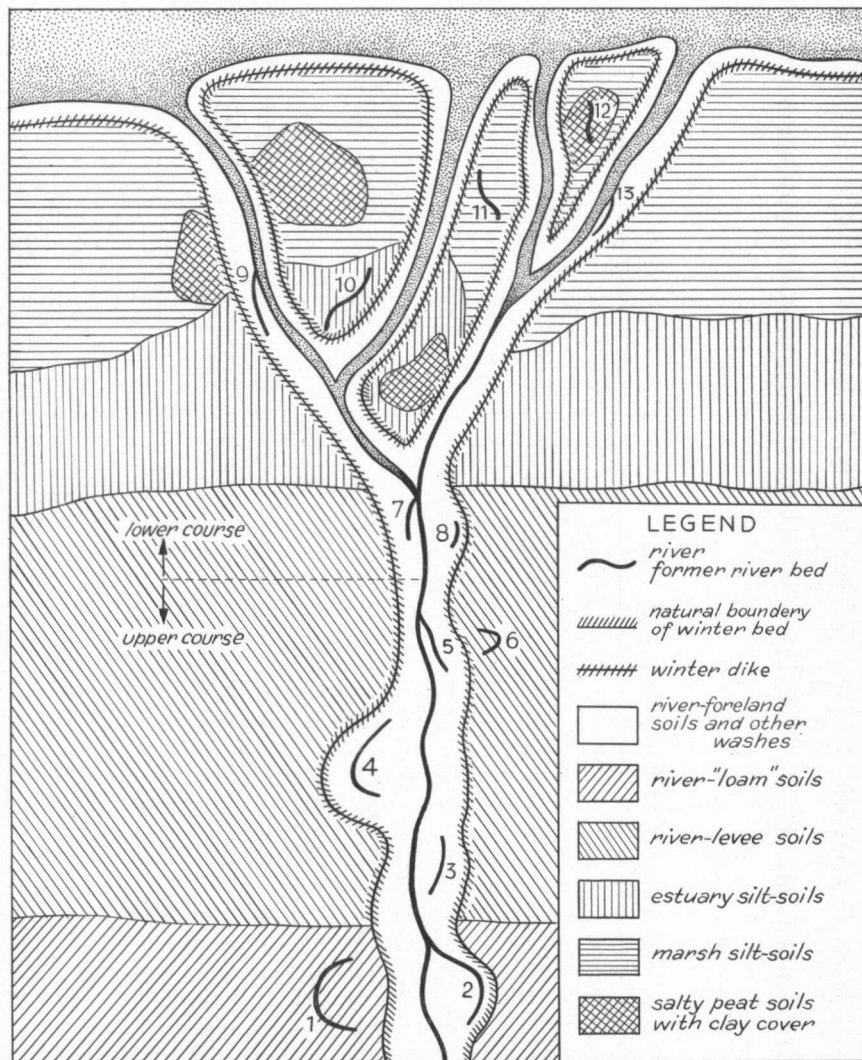


Fig. 1. Schema of a great river in the Netherlands with its former river beds and adjoining deposits.

1. SOME IMPORTANT ASPECTS OF THE LARGER RIVERS

1.1. WATER HOUSEHOLD

The larger rivers have a summer bed and a winter bed. During the greater part of the year the water is carried off by the summer bed. As a rule, it is bordered by small summer dikes. The winter bed comprises the summer bed and the low grounds (forelands) on both sides of it. Along the Meuse in the province of Limburg, and along some minor parts of the Rhine and the IJssel the boundaries of the winter bed are formed by the edge of higher grounds; for the rest the winter bed is enclosed by the heavy winter dikes.

Nearly every year, either late in winter or early in spring, floods inundate the forelands and thus bring the winter bed into function. Apart from local factors (e.g. the height of the summer dikes), the frequency of the inundation of the foreland areas increases with the distance from the mouth of the river. Near the Dutch frontier nearly every year inundation occurs, whereas at a certain distance from the mouth the forelands are never inundated as a consequence of the annual floods.¹⁾ There inundations result only infrequently and irregularly from the stowing of high water by storm (EDELMAAN, 1950). A special feature of the rivers in winter is the drift of ice.

This simple picture completely fits for the IJssel, which debouches in the tideless IJsselmeer. With the other rivers we must distinguish between an upper and a lower course. The upper course shows the phenomena just described. The lower or tidal course is influenced by the tide of the North Sea. Here it is better to speak of a low tide bed and a high tide bed instead of using the terms summer bed and winter bed. The amplitude of the tidal fluctuations in the river declines with the increase of the distance from the mouth. The same relation holds for the width of the foreland strip which is inundated during high tide. Here too at a certain distance from the mouth the amplitude becomes zero, and this point nearly coincides with the point where the influence of the annual floods ends. So the border line between the upper and the lower course is rather sharply marked by the effect of two different causes.

There are differences between the upper courses of the individual rivers, that is to say of the Meuse, the Rhine-Lek, the Waal and the IJssel. The other river branches, e.g. the Merwede, the Heusdense Maas and the Oude Maas, only form their lower courses. Since the comprehensive canalization of the Meuse (1927–1937) this river hardly ever inundates its forelands (PONS, 1949). If an inundation occurs, it lasts only for a very short period: by the opening of the sluices the surplus of water is immediately disposed of. The forelands of the IJssel lie relatively high and consequently they are less frequently inundated than the forelands of the Rhine-Lek and the Waal.

¹⁾ Ir. J. W. Tops (afd. Studiedienst van de Directie Bovenrivieren van de Rijkswaterstaat) kindly gave this and other valuable information about the water household.

1.2. ALLUVIAL AND MARINE DEPOSITS

(see EDELMAN 1950 a and b)

During the last part of the Pleistocene the alluvial deposits of the larger rivers consisted of river "loam" (rivierleem).¹⁾ Originally the properties of these soils will not have differed much from the younger river clay. In the greater part of the river area the "loams" have been covered by "clays", but along the Meuse in the province of Limburg outside the present winter bed the river "loam" is still found at the surface (SCHELLING, 1951; PONS, 1954 a). The soil type, however, has degenerated under the continuous influence of climatic factors. It is now, in contrast with the river clay soils, poor in mineral nutrients.

All rivers are, at least along their upper course, bordered by forelands, which consist of river-foreland clay (uiterwaardgronden). This clay is very fertile. The soils inside the dikes, which are no longer inundated, are called river-levee soils (stroomruggronden). In the Netherlands till now no degeneration of these soils has been observed. The river-foreland soils and the river-levee soils are calcareous, except those of the Meuse up to Heerwaarden (PONS, 1949). There is no satisfactory explanation for this fact.

During the Roman period the lower courses of the rivers crossed an extensive peat area. By later incursions of the sea the lowermost part of the rivers obtained the character of estuaries, and many islands were formed. Part of the peat landscape was completely destroyed, elsewhere the peat was covered with a layer of marine clay or silt. The peat became soaked with sea water, and ever after kept a high salt content. In places where the clay cover is thin, the soil is called "salty peat soil with clay cover" (poelgrond). Where the peat disappeared completely under the marine deposits, we must make a distinction between the inner and the outer part of the flooded area, viz. deeper inland in fresh water the estuary silt-soils (gorsgronden), and nearer to the coast in brackish or salt water the marsh silt-soils (schorggronden) were deposited. All areas consisting of these three soil types have been embanked long ago. Against the dikes the sea deposited new washes, which mostly were embanked later on, thus adding new parts of marsh silt soil to the existing land area.

The soils from which the lower courses of the rivers are for the greater part separated by their dikes belong to these three types. The forelands mainly consist of silty washes; those soils are not considered in the soil classification of EDELMAN.

The uppermost part of the lower courses, however, is bordered by soils of a different type. Here they are the continuation of those found along the upper courses: inside the dikes river-levee soils, outside the dikes river-foreland soils.

¹⁾ A soil map is added both to the Dutch and to the English edition of EDELMAN's handbook. Some of the English soil-type names on this map differ from those used in the English text. The names on the map are used here.

1. 3. CHLORINE CONTENT

In the upper course the water is fresh. In the lower courses the average chlorine content increases with the decrease of the distance from the mouth. There is a freshwater, a brackish and a saltish tidal zone (see VAN LEEUWEN, 1954).

For a more precise classification the following scale of REDEKE (1932) will be used.

fresh water		0- 100 mg Cl/l
brackish water	{ oligohalinic	100- 1.000 mg Cl/l
	{ mesohalinic	1.000-10.000 mg Cl/l
	{ polyhalinic	10.000-17.000 mg Cl/l
saltish water		> 17.000 mg Cl/l

2. DEVELOPMENT AND PROPERTIES OF THE FORMER RIVER BEDS

2. 1. UPPER COURSE

When under natural circumstances a river leaves a part of its bed, whatever the cause may be, the former river bed as a rule remains at one side in connection with the new summer bed (Fig. 1: 2 and 5; see also PANNEKOEK VAN RHEDEEN, 1942). In this stage the water of the former river bed has for this reason many properties in common with that in the river itself. Along the upper course this means that it is eutrophic and fresh with a P_H of 7 to 8, that it remains in motion during the greater part of the year, and that it will flood the banks with a certain frequency. In this stage the depth may be considerable. It depends on the frequency and the duration of the flooding and on the force of the current during that time, whether the former bed will remain open, or will be silted up gradually. Under natural conditions the high water of a lowland river floods a very extensive area and therefore the force of the current during the inundation period is only weak. If there is a narrow bed, naturally or as a result of dike building, the force of the current will be much greater, and consequently the silting up slower or even wholly lacking (VON MIRRIS, 1939). In the Netherlands, where the beds are relatively narrow, an important factor influencing the speed of the silting up is the position of the former river bed with regard to the edge of the present winter bed. In a former river bed which follows the bend of a dike during a period of inundation only a sluggish stream or none at all will be found (Fig. 1: 2), whereas in a similar one parallel to the stream a strong current may be present (Fig. 1: 5). In every instance, however, the possible deposit of plant remains is inconsiderable in comparison with the deposit of alluvium.

In the next stage the former river bed has totally lost contact with the summer bed (Fig. 1: 3 and 4). This means that there is during the greater part of the year no movement in the water. This may aid the silting up, but for the rest all properties remain the same.

Under natural conditions the frequency of inundation in a certain place decreases with the progress of the silting up of its surroundings. At last the high water does not reach the place any more, and the former river bed, if not completely silted up, becomes a pool with

permanently stagnant water (Fig. 1: 1; see VON MITIS, 1939). This, however, may also result from a sudden diversion of the stream. Anyhow the properties in this stage are quite different from those in the former two. Inundation and silting up have come to a stop. Now the bottom is raised only by the accumulation of plant remains. At first the whole environment (soil and water) remains eutrophic and slightly alkaline. In the long run, however, the properties change. The plants take up nutritive salts from their environment and when they die off part of these nutrients is deposited in the peat layer, so that it is no longer available. As long as a sufficient amount of new nutrients is supplied by the surrounding soil, the only important change is a decrease in depth of the pool. The surrounding soil, however, degenerates, and the peat layer grows continuously thicker, so that at last the vanished minerals can no longer be replaced. Consequently the habitat becomes mesotrophic or even oligotrophic, and the alkalinity changes into a slight acidity (see RUTTNER, 1952).

Indeed, in the Netherlands the former river beds in the river-“loam” soils along the Meuse are meso- to oligotrophic. They are, however, no longer in their natural condition, and that they still can be recognised in the landscape, is due to the fact that the peat has been dug out by former generations (SCHELLING, 1951).

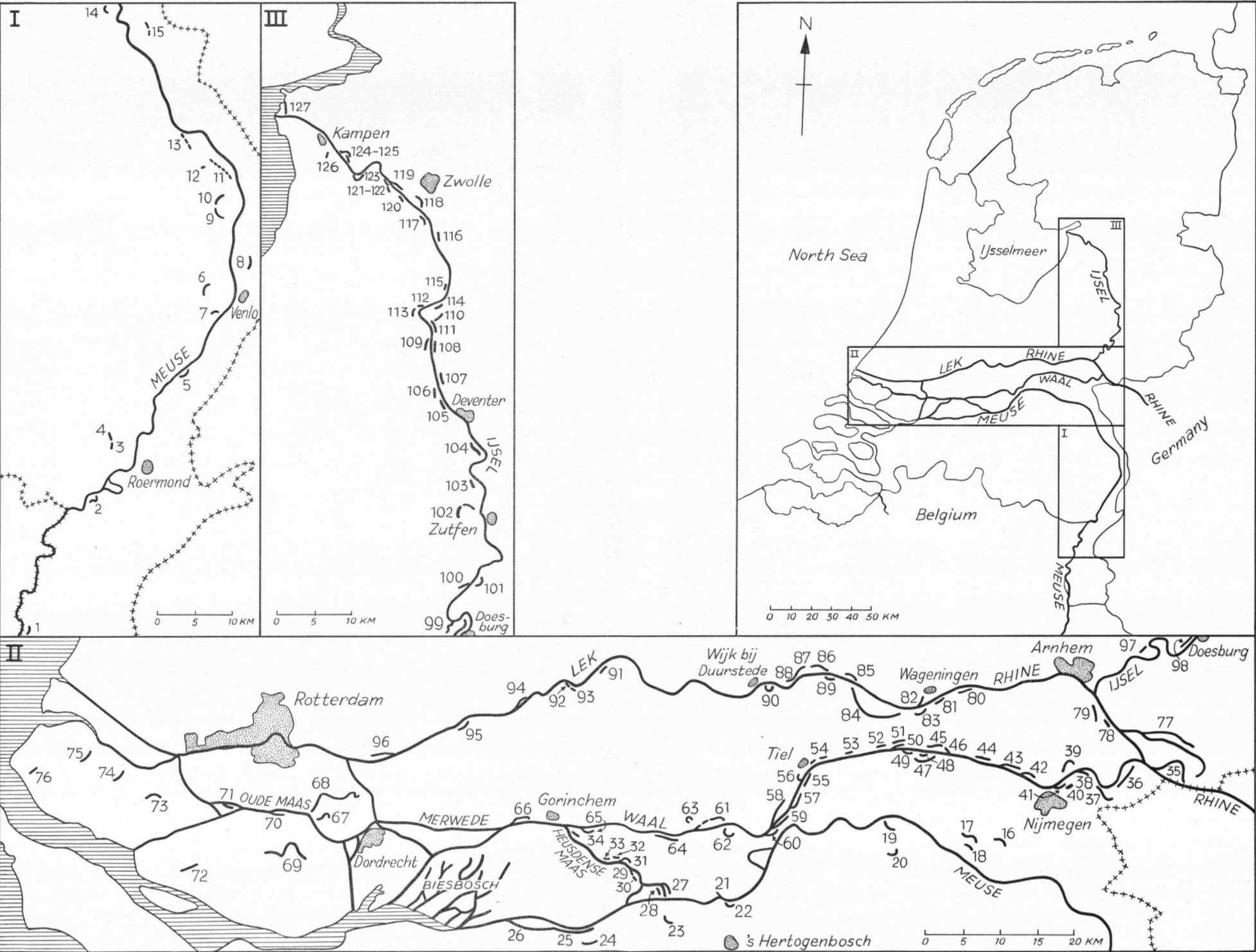
In the river-clay area too there is a number of isolated former river beds (Fig. 1: 6). The greater part of them came into existence as a result of dike building, and is much younger than the just discussed group (see DIBBITS, 1950). As a rule peat formation has not advanced very far, and the habitat is still eutrophic and slightly alkaline. This is caused by the properties of the surrounding river-levee soil (see under II. 1. 2).

A fluctuation of the water level parallel to that in the river itself was found in some former river beds of this type along the Danube (GROHS, 1943) and in a number of “wash-outs” (wielen) in the Netherlands (VAN HEUSDEN, 1945). It will certainly be present also in the isolated former river beds that are situated in the vicinity of the dikes.

2. 2. LOWER COURSE

Along the upper part of the lower course too the first two stages mentioned under 2. 2. 1 are present (Fig. 1: 7 and 8). However, compared with these stages along the upper course and mutually, their properties are rather different. In the first stage there is a permanent tidal movement. Though this has only a small amplitude, it is sufficient to keep the former river bed in connection with the river, and to prevent the development of peat. If it happens to pass into the next stage, the water becomes stagnant. In both stages the water is fresh or slightly oligohalinic (up to 110 mg Cl/l) and slightly alkaline.

Nearer to the mouth of the rivers former river beds still staying in the first stage are found in the washes (Fig. 1: 9 and 13). They consist of long, narrow stretches of water. With every high tide the whole high tide bed is flooded with slightly oligohalinic water (up to about 130 mg Cl/l).



Map showing all former river beds included in this study.

Since the great floods mentioned in II. 1. 2, many of the new islands have been united by dikes to bigger ones, and the latter have continually been enlarged by reclamation. In this way quite a number of isolated former river beds came into existence. They all have stagnant, eutrophic water and a peat layer of a certain thickness. There is some variety in the chlorine content of the water in accordance with the properties of the surrounding soil types: those in contact with the estuary silt soils have fresh water (Fig. 1: 10), those in contact with the marsh silt-soils (Fig. 1: 11) and the salty peat soils with clay cover (Fig. 1: 12) have oligo- to mesohalinic water (250 to 2000 mg Cl/l).

III. METHODS

The former river beds were visited in the months May up to and including August. The investigators worked individually or in groups of two or three. The examination of the greater part of the objects took one day.

1. SURVEY OF THE HABITAT

1. 1. AGE AND DEVELOPMENT

Data with regard to age and development of the individual objects were obtained mainly from the literature and from old maps. The most important sources were the publications of BEEKMAN (1913-1930) and TEIXEIRA DE MATTOS (1952), the map collections of the Topographical Service at Delft and of the "Maarten van Rossumhuis" at Zaltbommel.

1. 2. WATER HOUSEHOLD

At the day of our visit the actual water depth was measured, wherever necessary and possible, with a stone on a rope, with an oar or with a similar device. Data about low and high (tidal) water level were obtained mostly from indirect observations (e.g. drift line), from the literature or by information from inhabitants of the region. The position of the former river bed with regard to the boundaries of the winter bed and the relations to the summer bed were observed directly in the field and studied on maps.

1. 3. CHEMICAL FACTORS

The degree of acidity, expressed as P_H , was measured with strips of indicator paper (from MERCK). The results of this rough method should not be compared with those obtained by means of more accurate methods of investigation. They only have a relative value within the scope of the present investigation.

The chlorine content was measured with a simple, but reliable field method. A solution of silver nitrate was used for titration, with potassium bichromate as indicator.

In order to obtain a general idea of the content of nutritive salts

only indirect observations have been used. As a rule the food supply was deduced from other environmental factors (e.g. soil type and relation to the river). In some cases the data of LEENTVAAR (1954) could be used.

1. 4. SOIL TYPE

In the field only casual observations were made with regard to the soil. Most information was obtained from the literature and from maps. The main sources were the maps of the Geological Service, the soil map in the handbook of EDELMAN (1950 a and b) and several publications of the Soil Survey Service (Stichting voor Bodemkartering), e.g. EDELMAN c.s. (1950), SCHELLING (1951), VAN DIEPEN (1954) and PONS (1948, 1949, 1954 a and b).

2. SURVEY OF THE VEGETATION

In principle the vegetation was investigated according to the concepts and methods of the Braun-Blanquet school (BRAUN-BLANQUET, 1932, 1951; BECKING, 1957). In recent years this system of classification has been the subject of many critical discussions among its followers (see DOING KRAFT, 1955). It became evident that a number of new ideas had to be incorporated as necessary supplements. Some of the new views, generally practised in the Netherlands and in this investigation in particular, will briefly be mentioned.

In the first place it must be stated that our starting-point was the idea that it must be possible to distinguish vegetational units as abstractions on the ground of a certain discontinuity in the vegetation itself, which would already be recognisable at the level of the association. This conception has its most convinced opponents among the U.S. investigators, especially J. T. CURTIS and his collaborators (see e.g. CURTIS and McINTOSH, 1951). In the Netherlands this matter was discussed in 1951 (see MEIJER and WESTHOFF, 1957) and in 1957 (MEIJER, ZONNEVELD, VAN DONSELAAR). Our working-method was based on the view that vegetational classification should be "typifying", not "dividing" (see also TÜXEN, 1955; DOING KRAFT, 1956).

So far the classification of the communities has most often been based on the presence of characteristic species (i.e. "faithful" taxa). These, however, are now considered to be a special case of the more generally useful differential species. Differential species often were used to discriminate between vegetational units, and also to indicate a certain differentiation within the limits of a definite unit. In the latter case variants may be distinguished. Another special case of differential species are the "characteristic species within the formation". (See ELLENBERG, 1954; SCHWICKERATH, 1942; DOING KRAFT, 1956.)

There were a number of units, poor in species, which could not be described as associations, but better as sociations in the sense of the Scandinavian investigators (DU RIETZ, 1930). It is possible to incorporate these communities in the existing classifications, e.g. by uniting a number of associations and sociations in an alliance (see ELLENBERG, 1954; WESTHOFF, 1949; ZONNEVELD, 1960).

In conformity with the generally accepted practice in the Braun-Blanquet school no highly specialised statistical methods were applied. This point will not be discussed here.

3. DETERMINATION OF THE RELATIONS BETWEEN PLANT COMMUNITIES AND HABITATS

First the vegetational units were determined. Then a correlation of such a unit with a definite constitution of the environmental factors, that is to say with a certain habitat, was established. As e.g. WESTHOFF (1951 b) and TÜXEN (1954) pointed out, this does not permit us to draw definite conclusions with regard to the causal relations between the communities and their habitat. The composition of a community does not only depend on the habitat, but also on historical and other factors, which are not included in this investigation. In particular the interrelations between the plant species (e.g. their power of competition) must be mentioned (see also HEYBROEK, 1955).

4. CLASSIFICATION OF THE FORMER RIVER BEDS

As a rule in every former river bed the communities were found to be situated concentrically. Within the scope of this investigation it was not possible to determine the succession experimentally or by the use of permanent quadrats. Nevertheless, in many instances, succession could be established. Sometimes by comparing our data with the results of the quadrat method (see Vlieger and van Zinderen Bakker, 1941), sometimes by the use of a new method (see van Donselaar-Ten Bokkel Huinink, 1961). In other instances it was only possible to speak of "zonation". (In considering the succession Tansley's terms "autogenic" and "allogenic succession" proved to be very useful.)

Anyhow, it was evident that former river beds with the same or nearly the same set of communities also possessed quantitatively similar environmental factors. Thus types could be established, characterized by special sets of communities and by correlated abiotical properties.

IV. THE PLANT COMMUNITIES

Though the communities were determined without any preconceived notion, a great part of the results proves to be in accordance with the "Synopsis of Plant Communities" generally used in the Netherlands (Westhoff c.s., 1946). To simplify the description of the results, this Synopsis will be used as our starting-point. In cases where our results are in accordance with it, this will generally not be mentioned separately.

1. Class LITTORELLETEA Braun-Blanquet et Tüxen 1943

1. 1. ORDER LITTORELLETALIA Koch 1926

1. 1. 1. Alliance Littorellion Koch 1926

1. 1. 1. 1. *Eleocharetum multicaulis* Allorge 1922 (Table 1)

A few records were made of the *Eleocharetum multicaulis*. The vegetation was everywhere rather fragmentary, consisting mainly of a few characteristic species of the association and of the alliance. In other places than those of the records *Scirpus fluitans* (ch. of the association) and *Luronium natans* (ch. of the alliance) were observed too.

TABLE 1 ¹⁾*Eleocharetum multicaulis*

nr. of record	1	2
nr. of former river bed	24	24
river	M	M
water depth (cm)	25	25-75
area (sq.m)	10	10
cover (%)	80	100
Ch. Ass. <i>Hypericum elodes</i> L.	1.2	4.3
Ch. All. <i>Potamogeton polygonifolius</i> Pourr.	4.5	.
<i>Juncus bulbosus</i> L.	2.3
Acc. <i>Phragmites communis</i> Trin.	+1	+1
<i>Hydrocharis morsus-ranae</i> L.	+2	.
<i>Sphagnum palustre</i> L.	1.2

1. D 56-1132, 15-9-1956

2. D 56-1128, 15-9-1956

¹⁾ See explanation on p. 85.

The community was found in a part of the former river beds along the Meuse, viz. in those with stagnant, oligo- to mesotrophic, fresh water and a P_H of 5,9 to 6,1. The soil on the bottom consisted of loose peaty material resting on firmer peat and river "loam". The community formed narrow zones between vegetations belonging to the *Potamion* and to the *Caricion fuscae*.

2. Class POTAMETEA (Narayanayga 1928) Tüxen 1942

2. 1. ORDER POTAMETALIA Koch 1926

2. 1. 1. Alliance Potamion eurosibiricum Koch 1926

In the former river beds quite a number of communities occurred belonging to the *Potamion*. Some of these are generally accepted associations; some other ones will be introduced here. In this connection we wish to draw attention to the fact that *Polygonum amphibium* fo. *natans* must be eliminated as characteristic species of the alliance (see under IV. 2. 1. 1. 3). In accordance with WESTHOFF (1949) the same will have to be done with *Utricularia vulgaris* (see under IV. 2. 1. 1. 4).

2. 1. 1. 1. *Potametnm lucentis* Hueck 1931 (Table 2)

This association is not mentioned in the Synopsis, but it is nevertheless widespread in the Netherlands. In older literature it is generally called *Potametum perfoliati potametosum lucentis* (e.g. SCHWICKERATH,

TABLE 2

<i>Potametum lucentis</i>				
nr. of record	1	2	3	P in 9 records
nr. of former river bed	45	39	123	
river	W	W	IJ	
water depth (cm)	250	250	100	
area (sq.m)	16	6	9	
cover (%), total	80	90	95	
floating layer	—	<5	50	
submersed layer	80	90	60	
Ch. Ass. <i>Potamogeton lucens</i> L.	4.4	5.5	4.4	V
Ch. All. <i>Nuphar luteum</i> (L.) Sm.	.	+2	3.2	IV
<i>Lemna minor</i> L.	.	.	+2	III
<i>Lemna trisulca</i> L.	.	+2	.	II
<i>Nymphaea alba</i> L.	.	.	+2	II
<i>Nymphoides peltata</i> (Gmel.) O. Kuntze	.	+2	.	I
Ch. Cl. <i>Ceratophyllum demersum</i> L.	.	1.2	.	II
Acc. filiformous algae	+3	+3	.	II
<i>Equisetum fluviatile</i> L.	.	.	+1	I

Supplement to the table. Ch. All.: *Potamogeton natans* L. I, *Elodea canadensis* Michx. I, *Spirodela polyrhiza* (L.) Schleiden I, *Hydrocharis morsus-ranae* L. I; Ch. Cl.: *Potamogeton pectinatus* L. I; Acc.: *Phragmites communis* Trin. I, *Scirpus lacustris* L. ssp. *lacustris* I.

1. D 55-1056, 12-8-1955

2. D 55-1008, 14-7-1955

3. V 56-68, 12-7-1956

1933; Vlieger, 1937; Van Zinderen Bakker, 1942, 1947). Under this name the community is, according to Koch (1926) and a former edition of the Synopsis (1942), considered to be a subassociation of the *Potameto perfoliati-Ranunculetum fluitantis*. Later on the community has been identified with the *Potametum lucentis* of Hueck, first in Germany (see Tüxen, 1955), and recently also in the Netherlands (Van Dijk and Westhoff, 1955).

In the Dutch "broads", large sheets of water which in the Netherlands have been formed by the removal of peat,¹⁾ the association consists mainly of submersed *Potamogeta*, especially *Potamogeton lucens* and *P. perfoliatus*, but the former is the only one which evidently has its optimum in it. It always occurs on a more or less peaty soil in deep, stagnant, eutrophic, fresh water, and is occasionally preceded by a vegetation of *Characeae*.

The association was found in those former river beds which are

¹⁾ On account of their slight depths they are best comparable to the broads of East Anglia and for this reason in this paper they will be called by the same name.

situated in the forelands without tidal influence, generally on mineral soil. It forms a narrow zone on the outer side of the other *Potamion* communities (*Myriophylleto-Nupharetum* and *Polygoneto-Nymphoidetum*), and is therefore the vegetation occurring on the deepest spots (1 to 3 m). This river foreland variant is poorer in species than the variant found in the broads; especially the absence of *Potamogeton perfoliatus* must be mentioned. The scarcity of the other submersed species may be ascribed to the density of the stratum formed by *Potamogeton lucens*. It is true that this species is itself submersed, but it produces the greater part of its leaves just below the surface, and in consequence catches most of the light. This, however, does not explain the nearly total absence of *Potamogeton perfoliatus*, for this species grows in the same way.

2. 1. 1. 2. *Myriophylleto-Nupharetum* Koch 1926 (Table 3)

This association is very common in the Netherlands. It has its optimum development in those fens in which the water is deeper than 1 m and which are sheltered from the wind (see e.g. CLASON, 1928; VLEIGER, 1937; VAN ZINDEREN BAKKER, 1942, 1947; BENNEMA, 1943; MEIJER, 1955; VAN DIJK and WESTHOFF, 1955; WESTHOFF c.s., 1946). It consists mainly of species with floating leaves, viz. *Nymphaea alba* (ch), *Nuphar luteum* and *Potamogeton natans*, but *Potamogeton lucens* and

TABLE 3

<i>Myriophylleto-Nupharetum</i>	A	B						A	B
nr. of record	1	2	3	4	5	6			
nr. of former river bed	12	112	62	54b	79b	119			
river	M	IJ	W	W	R	IJ			
water depth (cm)	>75	>220	170	125-200	150-250	150			
P _H open water	6,7	7,5	7,5	7,3	7,3	6,9			
area (sq. m)	4	24	25	25	25	9			
cover (%), total	60	55	70	80	80	60			
floating layer	60	50	70	80	80	60			
submersed layer	—	10	—	<5	<5				
							P in 3 records		P in 6 records
Ch. Ass. <i>Nymphaea alba</i> L.	4.5	2.2	2.2	5.5	5.5	4.2	3		V
D. B. Ch. All. <i>Lemna trisulca</i> L.	+2	+2	.			III
<i>Lemna minor</i> L.	+2			II
<i>Spirodela polyrrhiza</i> (L.) Schleiden	+2	.			II
<i>Nuphar luteum</i> (L.) Sm.	2.2	2.2	.	.	.			II
<i>Potamogeton lucens</i> L.	+2	.	.	+2	.			II
<i>Nymphoides peltata</i> (Gmel.) O. Kuntze	+2			I
Ch. Cl. <i>Ceratophyllum demersum</i> L.	1.2	.	+2	+2	.			IV
Acc. filiformous algae	+3			II
1. D 56-1092, 22-6-1956	4. D-DBH-MB 55-1119, 1-9-1955								
2. K 56071, 8-8-1956	5. D 55-1069, 17-8-1955								
3. D-DBH 55-20, 31-5-1955	6. V 56-95, 13-7-1956								

Myriophyllum spicatum are also frequently present. In the Synopsis the last two are mentioned as characteristic species. However, if we include the *Potamogeton lucentis* in the list of *Potamion*-communities occurring in the Netherlands, *Potamogeton lucens* can no longer be regarded as a characteristic species of the *Myriophylleto-Nupharetum*.

In the former river beds the association shows a certain variability corresponding to variations in the habitat. In isolated fen waters the association answers the general description. In the river forelands it occurs only on a muddy soil in those former river bed which have no connection with the summer bed and are situated in parts that are not often inundated, or that, if they are inundated, are not exposed to a strong current during inundation time. Here the composition of the vegetation is rather poor (see rec. 2-6). Even *Nuphar luteum* does not occur very frequently. This species has in the former river beds found in the forelands its optimum in the *Polygoneto-Nymphoidetum*. There are, however, many transitions between the two associations. The eutraphentous variants of the association occur at a depth of 1 to 2 m. The vegetation may be preceded by the *Potamogeton lucentis*, and is bordered at the land side by the *Hydrochareto-Stratiotetum* or by a community belonging to the *Phragmition*.

A very poor variant of the association occurs in the oligo- to mesotrophic former river beds with a P_H of 6 to 7 at a depth of about 1 m. *Nymphaea alba* is usually the only species (rec. 1). This is mentioned also by MÖRZER BRUIJNS and WESTHOFF (1951). Perhaps this variant is similar to the *Association of Nymphaea alba-minor* Vollmar 1947. PASSARGE (1955 a) describes it as loose colonies of *Nymphaea alba* fo. *minor* and *Potamogeton natans* in water with a P_H of 6,2. Indeed, the colonies of *Nymphaea alba* (the forma was not determined) sometimes are accompanied by colonies of *Potamogeton natans*.

2. 1. 1. 3. *Polygoneto-Nymphoidetum* ass. nov. (Table 4, see p. 16)

A new association is established here: the *Polygoneto-Nymphoidetum*. Comparison of our results and of data from the literature leads to the establishment of the following characteristic species: *Nymphoides peltata*, *Polygonum amphibium* fo. *natans*, *Potamogeton pectinatus* fo. *vulgaris* and *P. perfoliatus*. The association occurs on mineral soils in eutrophic, slightly alkaline (P_H 7 to 8) fresh water with a depth ranging from 5 to 300 cm. Some water movement caused by wind, current or tide, is essential.

Two subassociations can be distinguished, viz. *P.-N. typicum* and *P.-N. potametosum pectinati*. These have differential species, partly identical with characteristic species, as is demonstrated in the table on p. 17.

Subass. *typicum*

The optimum habitat for the subass. *typicum* is formed by those former river beds occurring along the upper courses in the forelands, in permanent connection with the summer bed. The more the former river bed is exposed to the current in times of inundation, the greater

TABLE 4

<i>Polygono-Nymphoidetum typicum</i>													
	1	2	3	4	5	6	7	8	9	10	P in 19 records		
nr. of record	58	119	44a	77	41	45	39	36	55	59			
nr. of former river bed	W	IJ	W	R	W	W	W	W	W	W			
river	225-	150	>130	140	130	100-	120	100	20-	5-40			
water depth (cm)	300					225			75				
area (sq. m)	50	4	20	4	12	40	50		50	100			
cover (%), total	80	95	80		100	80	80		95	80			
floating layer	80	60	80	70	95	80	80	10					
submersed layer	40	80	8	50	15	20	10	<5		1			
Ch. Ass.	1.2	4.3	4.3	4	3.2	4.4	4.3	5	5.5	5.5			
(D. subass.)	4.3	+2	.	.	+2	1.2	3.3	.	1.2	1.2			
Nymphoides peltata (Gmel.) O. Kuntze	+2	+2			
Polygonum amphibium L. fo. natans Mnch.	+2	.	1.2	+	.	1.2	3.3	+	.	.			
Potamogeton pectinatus L. fo. vulgaris Cham.	3.3	5.5	.	1	2.2	1.3	.	1	.	.			
et Schlecht	.	.	.	2	.	+2	+2	1	1.2	.			
Nuphar luteum (L.) Sm.	.	.	.	2	+2	.	.	2	+2	.			
Potamogeton lucens L.	.	.	.	2			
Lemna trisulca L.	.	.	.	2			
Lemna minor L.	.	.	.	2			
Spirodela polychiza (L.) Schleiden			
Potamogeton natans L.	1.2	+2	.	.	.	+3			
Elodea canadensis Michx.	.	+2			
Ranunculus circinatus Sibth.			
Hydrocharis morsus - ranac L.	.	.	.	+	.	+2	+2	.	.	.			
Ch. Cl.	1.2	.	1.2	3	.	2.3	2.3	+	.	.			
Ceratophyllum demersum L.			
Acc.			
filiformous algae			

Supplement to the table. Ch. All.: Potamogeton crispus L. I, Potamogeton compressus L. I, Riccia fluitans L. I; Acc.: Potamogeton cf. trichoides Cham. et Schld. I (8: 1), Phalaris arundinacea L. I (9: +.1), Rorippa amphibia (L.) Besser I (10: +.1), Butomus umbellatus L. I (10: +.2), Alisma plantago-aquatica L. I, Oenanthe aquatica (L.) Poir. I.

1. D 55-1101, 25-8-1955	4. MB-QB-S-V 54-23, 29-7-1954	7. D 55-1007, 14-7-1955	10. D 55-1125, 5-9-1955
2. V 56-91, 13-7-1956	5. D 55-1033, 21-7-1955	8. QB-S-V 54-59, 3-8-1954	
3. D 55-1092, 24-8-1955	6. D 55-1057, 12-8-1955	9. D 55-1126, 5-9-1955	

Subassociation	typicum	potametosum pectinati
<i>Ch. and D. species</i>		
Ch. <i>Nymphoides peltata</i>	tot. est. 1 to 5	tot. est. + to 2
Ch. <i>Polygonum amphibium</i> fo. <i>natans</i>	x	.
Ch. <i>Potamogeton pectinatus</i> fo. <i>vulgaris</i>	x
Ch. <i>Potamogeton perfoliatus</i>	x
<i>Potamogeton crispus</i>	x
<i>Potamogeton pusillus</i>	x
<i>Elodea canadensis</i>	x

the chance that the soil remains purely mineral, and the better accordingly the community is developed. Only here, where the current during the floods and maybe the drifting ice floes prevent the development of a herb vegetation, the community occurs also in shallow water. It consists mainly of extensive and close vegetations in which as a rule *Nymphoides peltata* and sometimes *Polygonum amphibium* or *Nuphar luteum* dominate. It is remarkable that *Nuphar luteum* in the former river beds with which we are dealing here, has its optimum in the *Polygoneto-Nymphoidetum* and not in the *Myriophylleto-Nupharetum*.

On the deeper side the community is generally bordered by the *Potametum lucentis*, on the land side by the community of *Ranunculus circinatus* and *Elodea canadensis* or by the *Scirpeto-Phragmitetum oenanthetosum*.

In the Dutch literature there are some indications that this sub-association, or at least transitions of the latter to the *Myriophylleto-Nupharetum* are found also outside the river area. See VAN ZINDEREN BAKKER (1942) and KUIPER and SEGAL (1955).

Subass. potametosum pectinati

The subass. *potametosum pectinati* is identical with the *Limnanthemopotametum pectinati* Allorge 1922 in the (wrong) interpretation of the latter given in the Synopsis. It is the so-called "canal-side-community" of the Dutch literature and it does not occur in the former river beds. It arises from the subass. *typicum* on spots where either a too lively water movement or else cleaning during the vegetational period reduce the extent of the floating layer. *Polygonum amphibium* is probably more sensitive to this influence than *Nymphoides peltata*: the former vanishes totally, the latter remains with low total estimates. Consequently the light supply for the submersed species increases considerable, and causes the extension of e.g. the differential species of the subassociation. The optimal habitat of this community are the canal sides. These are periodically cleaned, and have now and then water movement caused by wind, boats or sluicing. The community also occurs in large, exposed broads (see VLEIGER, 1937; BENNEMA, 1943; WESTHOFF c.s., 1946; MÖRZER BRUIJNS and WESTHOFF 1951).

Occurrence of this and allied communities outside the Netherlands

In some papers dealing with the vegetation of Europe indications of the occurrence of the *Polygoneto-Nymphoidetum* are to be found. ALLORGE (1922) established for a part of the Seine valley the "*Association of Limnanthemum peltatum and Potamogeton pectinatus*". The description of this community shows elements of the *Polygoneto-Nymphoidetum*, of the *Myriophylleto-Nupharetum* and even of the *Hydrochareto-Stratiotetum*. ALLORGE mentions vegetations consisting mainly of *Nymphoides peltata* especially in the "active" former river beds. These probably belong to the subass. *typicum*.

LEBRUN c.s. (1949) mention under the name *Limnanthemum-Potametum pectinati* vegetations of *Nymphoides peltata* especially in former river beds which are influenced by high water.

In N.W. Germany the association has not been recorded; it has probably been considered to be a part of the *Myriophylleto-Nupharetum* (see TÜXEN, 1937, 1955).

LAUTERBORN (1917) certainly found the subass. *typicum* in a number of "active" former river beds situated along the Rhine between Bingen and Bonn in W. Germany: the only species in the floating layer were *Nymphoides peltata* and *Polygonum amphibium*. LAUTERBORN's data from the Rhine between Basel and Bingen are more difficult to translate in plant-sociological terms. Anyhow, it is obvious that in the communities of hydrophytes in the latter area the characteristic species of the *Polygoneto-Nymphoidetum* are present; but in addition *Trapa natans* occurs here.

In 1957 OBERDORFER proposed the *Trapo-Nymphoidetum*, and indicated *Nymphoides peltata* and *Trapa natans* as characteristic species. *Polygonum amphibium* fo. *natans*, considered to be a characteristic species of the alliance (the *Nympheion*, v. infra), does not occur in this community. The habitat of the community are the former river beds in the valley of the Rhine in S. Germany. The bottom must be humic and muddy.

OBERDORFER has divided the *Potamion* into two alliances, the *Eu-Potamion* and the *Nympheion*. To the latter belongs a.o. an association-group consisting of associations which are dominated by *Nymphoides peltata*. These associations resemble one another, but on the other hand they present floristic differences depending on geographical factors, and are called for this reason geographical vicariants. This principle is also explained by WESTHOFF (1950). According to OBERDORFER the *Trapo-Nymphoidetum*, the *Limnanthemum-Potametum pectinati* and a similar community occurring on the Balkan peninsula are geographical vicariants. On account of what we have said above on the *Limnanthemum-Potametum*, it will be clear that the *Trapo-Nymphoidetum* and the *Polygoneto-Nymphoidetum* are to be regarded as geographical vicariants. The border line between the areas in which they occur may lie somewhere in the vicinity of Bingen (see LAUTERBORN).

TABLE 5

<i>Hydrochareto-Stratiotetum</i>	A		B							A	B	tot.					
	stagnant water		river foreland														
			eutrophic														
	mesotrophic																
nr. of record	1	2	3	4	5	6	7	8	9	P in 6 records	P in 13 records	P in 19 records					
nr. of former river bed	24	3	10c	127	19	30	116d	45	93								
river	M	M	M	IJ	M	HM	IJ	W	L								
water depth (cm)	>75	>75	130	<100	130	>60	>85	75	100								
P _H open water	6.0	6.2	6.9	7.3	7.7	7.2	7.5	7.3	7.2								
area (sq. m)	1	25	4	25	15	4	16	6	9								
cover (%), total	100	75	50	50	<5	90	60	100	90								
floating layer	100	75	—	—	—	95	<5	25	<5								
submersed layer	—	—	—	—	—	25	80	—	80								
Ch. Ass. <i>Hydrocharis morsus-ranae</i> L.	5.5	2.2	3	1	1	4.3	2.2	5.5	1.2				V	V V V I	V IV I		
(D. B.) <i>Stratiotes aloides</i> L.	.	.	.	3.5	3.5	4.3	3.5	+1	.							V V V IV I	III II II I

Supplement to the table. Acc.: *Comarum palustre* L. 2: 1.2, *Equisetum nuviatile* L. 3: 1, *Sagittaria sagittifolia* L. 3: +, *Sium erectum* Huds. 4: +2, *Cicuta virosa* L. 4: 1.2, *Typha latifolia* L. 4: +2, *Glyceria maxima* (Hartm.) Holmb. 5: 1.2, *Mentha aquatica* L. 5: +1.1, *Cardamine pratensis* L. 5: +1.1, *Myosotis scorpioides* L. 5: +1.1, *Rorippa amphibia* (L.) Besser 7: +1.1, *Oenanthe aquatica* (L.) Poir. 8: +1.1, *Sium latifolium* L. 8: +2, *Lythrum salicaria* L. 8: +2, *Typha angustifolia* L. 8: 1.2, *Poa palustris* L. 8: +2.

1. D 56-1130, 15-9-1956
2. D 56-1049, 19-6-1956
3. QB-S-V 54-375, 8-9-1954
4. QB-S-V 54-354, 3-9-1954
5. QB-S-V 54-241, 13-8-1954
6. D-K-V 56-1034, 6-6-1956
7. QB-S-V 54-343, 2-9-1954
8. D 55-1058, 12-8-1955
9. V 56-107, 17-7-1956

2. 1. 1. 4. *Hydrochareto-Stratiotetum* (Van Langendock 1935) Kruseman et Vlieger 1937 (Table 5)

Vegetations belonging to the *Hydrochareto-Stratiotetum* mainly consist of the two characteristic species mentioned in the Synopsis, viz. *Hydrocharis morsus-ranae* and *Stratiotes aloides*. However, sometimes, *Utricularia vulgaris* becomes dominant, and, according to WESTHOFF (1949), this species too should be included among the characteristic species (see also VAN DIJK and WESTHOFF, 1955). In this connection it must be mentioned that OBERDORFER proposed in 1957 the *Hydrocharetum rhenanum*, an association with *Hydrocharis* and *Utricularia vulgaris*, but without *Stratiotes aloides*, and considered it to be a geographical vicariant of the *Hydrochareto-Stratiotetum*. In the Netherlands the community mostly occurs in stagnant, shallow, fresh water on sheltered spots, to which the plants possibly may have been blown by the wind. It is generally succeeded by a floating-mat vegetation. See e.g. VLIJGER (1937), VAN ZINDEREN BAKKER (1942, 1947), BENNEMA (1943), WESTHOFF c.s. (1946), MÖRZER BRUIJNS and WESTHOFF (1951), MEIJER (1955), KUIPER and SEGAL (1955).

In the Synopsis two subassociations are distinguished, though not named. The first is the most typical one, with closed vegetations of *Hydrocharis* and/or *Stratiotes*. The second presents more open vegetations, and comprises *Ranunculus circinatus* and *Potamogeton compressus* as differential species.

A variant of the association corresponding with the general description and without *Ranunculus circinatus* and *Potamogeton compressus* was found in the former river beds with eutrophic, fresh water either inside the winter dikes or in the forelands in a sheltered position and without contact with the summer bed (Table: B). It occurs, as a rule, at a depth of 75 to 100 cm; it is preceded by the *Myriophylleto-Nupharetum* and succeeded either by the *Scirpeto-Phragmitetum typicum* or by the the *Cicuteto-Caricetum pseudocyperus typicum*. On less sheltered spots it appears sometimes in the form of a long and narrow zone of *Hydrocharis*, with very few or without *Stratiotes*, just in front of the swamp vegetation (see rec. nr. 8).

In the oligo- to mesotrophic former river beds a special variant can be distinguished (Table: A). This community has no *Stratiotes* and no *Lemna trisulca*. In this habitat *Hydrocharis* is generally accompanied by *Potamogeton natans*, whereas in eutrophic water the latter shows preference for the *Myriophylleto-Nupharetum*. Thus it is a differential species which distinguishes the mesotraphentous variant of the *Hydrochareto-Stratiotetum* from the eutrappentous one. In the table *Nuphar luteum* seems to be in the same position. The literature, however, proves that this species may occur also in the eutrappentous variant (see e.g. BENNEMA, 1943).

This community may be preceded by the mesotraphentous variant of the *Myriophylleto-Nupharetum*; on the land side it is bordered either by the *Eleocharetum multicaulis*, the *Caricetum lasiocarpae*, the *Cicuteto-Caricetum pseudocyperus comaretosum* or the *Caricetum elatae comaretosum*.

2. 1. 1. 5. *Community of Ranunculus circinatus and Elodea canadensis*
(Table 6)

In 1943 BENNEMA and WESTHOFF proposed an association with the name *Ranunculeto-Potametum compressi* (BENNEMA, 1943). The characteristic species should be *Ranunculus circinatus* and *Potamogeton compressus*. The community was said to occur in ditches where the water was in contact with a mineral soil. Floristically it resembled the *Hydrochareto-Stratiotetum* but it differed from the latter ecologically; it required a habitat with more or less moving water.

The Synopsis drops the association, but divides the *Hydrochareto-Stratiotetum* into two subassociations for which no names are proposed. The one differs floristically from the other by two differential species, viz. *Ranunculus circinatus* and *Potamogeton compressus*. This subassociation obviously corresponds with the *Ranunculeto-Potametum compressi*.

TABLE 6

Community of Ranunculus circinatus and Elodea canadensis

nr. of record	1	2	3	4	5	P in 9 records
nr. of former river bed	95	39	104	92	101	
river	L	W	IJ	L	IJ	
water depth (cm)	80	100	75	50	100	
area (sq. m)	9	1	6	30	6	
cover (%), total	90	100	95	100	95	
floating layer			5	20	<1	
submersed layer			95	90	95	
Ch. All. <i>Ranunculus circinatus</i> Sibth.	2.2	3.3	2.2	.	2.2	IV
<i>Elodea canadensis</i> Michx.	2.2	3.3	1.2	5.5	.	IV
<i>Potamogeton natans</i> L.	2.2	.	+2	1.2	.	III
<i>Lemna trisulca</i> L.	3.2	.	+2	.	2.2	III
<i>Potamogeton lucens</i> L.	3.2	.	4.4	III
<i>Nuphar luteum</i> (L.) Sm.	3.2	.	.	+3	.	III
<i>Lemna minor</i> L.	+2	+2	.	+1	II
<i>Myriophyllum spicatum</i> L.	1.2	.	2.2	II
<i>Stratiotes aloides</i> L.	+2	.	.	+2	.	II
<i>Hydrocharis morsus-ranae</i> L.	+2	.	.	II
<i>Spirodela polyrhiza</i> (L.) Schleiden	+2	.	.	I
<i>Hottonia palustris</i> L.	+2	I
Ch. Ord. <i>Potamogeton pusillus</i> L.	4.3	.	.	I
Acc. filiformous algae	4.4	.	.	.	II
<i>Sagittaria sagittifolia</i> L.	1.2	.	+1	II
<i>Sparganium erectum</i> L.
ssp. <i>polyedrum</i> (A. et G.) Sch. et Th.	+2	+1	II

Supplement to the table. Ch. All.: *Nymphaea alba* L. I, *Polygonum amphibium* L. fo. *natans* Mnch. I, *Hippuris vulgaris* L. I; Acc.: *Rorippa amphibia* (L.) Besser II (3: +1), *Alisma plantago-aquatica* L. II (3: +1), *Phragmites communis* Trin. II (4: +2), *Glyceria maxima* (Hartm.) Holmb. II (4: +2), *Sparganium simplex* Huds. II, *Acorus calamus* L. I (4: +2), *Oenanthe aquatica* (L.) Poir. I, *Myosotis scorpioides* L. I.

1. V 56-46, 3-7-1956

4. V 56-102, 17-7-1956

2. D 55-1009, 14-7-1955

5. K 56047, 27-6-1956

3. K 56043, 21-6-1956

In the former river beds a community was found characterized by *Ranunculus circinatus* and high total estimates of *Elodea canadensis*. It has many features in common with the *Ranunculeto-Potametum compressi*, in which *Elodea* also may have high total estimates. The only striking difference is the absence of *Potamogeton compressus*. Though *Hydrocharis* and *Stratiotes* are present with low abundances, the community does not resemble the *Hydrochareto-Stratiotetum* very much. It was mainly found on mineral soils in slightly moving water, in one case even under some tidal influence (rec. nr. 4). The optimum habitat seems to be the former river beds in the forelands in contact with the summer bed and exposed to the current during the period of inundation. There, at a depth up to 1 m, *Ranunculus circinatus* is present in extensive but loose colonies, with *Elodea* and other submersed species in big patches under the surface. It must be mentioned that *Elodea* decreases in the presence of *Potamogeton lucens* (compare rec. nrs. 2 and 4 with nrs. 3 and 5). Probably the community takes the place of a swamp vegetation whose development was prevented in some way. Under these circumstances it is bordered on its deeper side by the *Polygoneto-Nymphoidetum* (often forming transitions with it) and is on the other side in contact with the edge of the meadows.

In accordance with advice received from Dr. V. WESTHOFF this community is not described as a new association. In view of the facts mentioned above its ecological position can not be regarded as sufficiently clear.

2. 1. 1. 6. *Vegetations in oligo- to mesohalinic water*

Our observations of the vegetation in the stagnant, oligo- to mesohalinic former river beds (250 to 2000 mg Cl/l) are not sufficient to justify any conclusion with regard to the communities to which they should be referred. Very few species are present, and the differences between the single vegetations are too considerable.

In the deepest spots *Chara* div. sp. and *Vaucheria* sp. may occur. In less deep water were found e.g. *Lemna trisulca*, *Lemna minor*, *Potamogeton pectinatus* (div. formae), *Enteromorpha intestinalis* and in one case *Zannichellia palustris*. The following record gives an example.

Fieldnr. V 56-122. Date 25-7-1956. Spui near Brielle (nr. 75). Water depth 90 cm, 250 mg Cl/l. Total cover 100 %, floating layer 85 %, submersed layer 90 %.

Ceratophyllum demersum L. 5. 5, *Enteromorpha intestinalis* Link. 5. 5., *Vaucheria* sp. 3. 2, *Myriophyllum spicatum* L. 1. 2, *Lemna minor* L. 1. 2, *Ranunculus circinatus* Sibth. +. 2.

3. Class PHRAGMITETEA Tüxen 1942

3. 1. ORDER PHRAGMITETALIA EUROSIBIRICA (Koch 1926) Tüxen 1942

The order has many characteristic species. Generally our results are in accordance with the Synopsis, but some differences must be mentioned.

Rumex hydrolapathum, in the Synopsis mentioned as a characteristic species of the *Phragmition*, occurs also in the *Magnocaricion*. In both alliances its frequency is about 30 %. In the *Caricetum acutiformo-paniculatae*, an association of the *Magnocaricion*, its frequency is even 42 %. This is in accordance with BOER (1942), who gives in this connection 41 %. The species is better considered to be characteristic for the order.

Equisetum fluviatile, according to the Synopsis a characteristic species of the order, does not deserve this position. It occurs frequently and with rather high abundances in the *Caricetum lasiocarpae* and allied associations. VANDEN BERGHE (1952 b) regards it even as a characteristic species of the *Caricetum lasiocarpae*.

Oenanthe fistulosa can in our opinion not be regarded as a species of the *Phragmitetalia*, though it is mentioned as such in the Synopsis. TÜXEN and PREISING (1951) call it a characteristic species of the *Caricetum vulpinae* (*Magnocaricion*). We doubt, however, whether the *Caricetum vulpinae* belongs to the *Magnocaricion* (see p. 48). *Oenanthe fistulosa* was frequently found in wet meadows along the former river beds.

3.1.1. Alliance Glycerieto-Sparganion Braun-Blanquet et Sissingh 1942

The Synopsis distinguishes two associations of the alliance *Glycerieto-Sparganion*, viz. the *Glycerieto-Sparganietum neglecti* Koch 1926 and the *Helosciadietum nodiflori* Braun-Blanquet 1930. Recently, however, difficulties arose with regard to the characteristic species. It appeared that in these communities not only *Glyceria fluitans*, but also *G. plicata* and *G. declinata* are present which may sometimes have been confused with the former one, and that apart from *Nasturtium officinale* also *N. microphyllum* is present. Moreover *Scrophularia alata* has been divided into *S. neesii* and *S. balbisii*. Another difficulty is that several Dutch investigators may have confused *Apium nodiflorum* and *Sium erectum*. As a result of this increase in our knowledge the subdivision of the alliance had to be changed. For the Netherlands a first step was taken by MAAS (1959). According to this author characteristic species of the alliance are: *Sium erectum*, *Sparganium erectum* ssp. *neglectum*, *Nasturtium officinale*, *N. microphyllum*, *Veronica beccabunga*, and *V. anagallis-aquatica*. In our opinion *Callitriche stagnalis* must be added to this list. (see p. 24). More or less in accordance with OBERDORFER (1957) MAAS distinguished the following associations: *Scrophulariето-Glycerietum plicatae*, *Sparganieto-Glycerietum fluitantis* and *Helosciadietum nodiflori*. A community of the alliance occurring in the tidal area (ZONNEVELD, 1960) is not comprised in this revision.

3.1.1.1. *Sparganieto-Glycerietum fluitantis* Oberdorfer 1957

MAAS mentions in his text as characteristic species *Glyceria fluitans*, *Agrostis stolonifera* var. *natans* and *Callitriche* sp. (mainly *C. hamulata* and *C. stagnalis*). In his table, however, it says that the *Callitriche* sp.

is mainly *C. hamulata*. In this respect it must be mentioned that the community of ZONNEVELD (1960), which is probably different from this association (see p. 26), comprises a species indicated as *Callitriche* cf. *stagnalis*. Therefore we think that for the moment it is better to consider *C. stagnalis* to be a characteristic species of the alliance.

According to MAAS, the association in the Netherlands is a community occurring in acid to neutral water, rather poor in minerals and lime. He distinguishes three subassociations, viz.:

1) *Subass. typicum*. The records given by MAAS of this subassociation are all made in and along springs and brooks, who accord with his description of the habitat. The subassociation, however, occurs also in ditches, as can be seen from the records in BOER (1942). Undoubtedly these ditches had alkaline water rich in plant nutrients.

2) *Subass. bidentosum*. Differential species: *Bidens tripartitus*, *B. cernuus*, *Polygonum hydropiper* and *Mimulus moschatus*. Habitat: small, shallow brooks; transition to *Bidenton*.

3) *Subass. ranunculetosum aquatilis*. Differential species: *Ranunculus aquatilis*, *Potamogeton natans*, *Elodea canadensis* and *Ceratophyllum demersum*; transition to *Potamion*.

In the river forelands a fourth subassociation can be distinguished (Table 7):

Subass. polygonetosum subass. nov.

Differential species: *Oenanthe aquatica*, *Rorippa amphibia*, *Polygonum amphibium* (both formae) and *Eleocharis palustris*. *Glyceria fluitans* is the only characteristic species present.

This subassociation was found in the former river beds occurring in the forelands, especially in those of the Rhine and the Waal. The mineral soil, clay as a rule, may be either solid or weak and muddy. These forelands are calciferous, except those of the Maas upstream from Heerwaarden (see p. 6). The water is fresh and eutrophic, and its depth varies from 80 to 0 cm. Maybe in many cases the water is polluted by grazing and paddling cattle. The former river beds in which this community was found, are not in communication with the summer bed. Therefore the greater part of the year the water is practically stagnant. Only during the short-lasting inundations in winter and spring the vegetation is more or less influenced by the current. This is in contrast with the habitat of the three other subassociations, where the water is moving either permanently (brooks) or at least now and then (ditches).

The community may be rich in species of the *Potamion*, especially in places where the deeper side of its habitat is in contact with that of a *Potamion*-community. Therefore it is no longer possible to use most of the *Potamion*-species as differential species of the subass. *ranunculetosum aquatilis*. *Ranunculus aquatilis*, however, can be maintained as this species does not occur in the river forelands.

In many cases this community was found bordering a vegetation

TABLE 7

Sparganieto-Glycerietum fluitantis polygonetosum

		1	2	3	4	5	6	P in 10 records
nr. of record		39	79	88	48b	80	81	
nr. of former river bed		W	R	R	W	R	R	
river		40-	15-	30-	5-	20-	0-	
water depth (cm)		80	70	60	70	60	20	
area (sq. m)		50	40	40	40	20	25	
cover (%), total		90	90	100	70	80	100	
herb layer		15	15	80	70	80	100	
floating layer		25	40	100	<5	<10	—	
submersed layer		80	50		<1	10	—	
Ch. Ass.	<i>Glyceria fluitans</i> (L.) R. Br.	2.2	1.2	4.3	4.4	3.2	3.3	V
Ch. All.	<i>Veronica anagallis-aquatica</i> L.	1.1	I
	<i>Callitriche stagnalis</i> Scop.	+3	I
Ch. Ord.								
(D. subass.)	<i>Oenanthe aquatica</i> (L.) Poir.	1.1	+2	+2	+1	+2	1.2	IV
(D. subass.)	<i>Rorippa amphibia</i> (L.) Besser	+1	1.2	+2	+2	+2	1.2	IV
	<i>Glyceria maxima</i> (Hartm.) Holmb.	3.3	.	+2	1.2	+2	1.2	IV
	<i>Alisma pantago-aquatica</i> L.	1.2	+2	+1	+2	+2	III
	<i>Phalaris arundinacea</i> L.	+2	.	+2	III
	<i>Sium latifolium</i> L.	+1	+2	II
	<i>Galium palustre</i> L.	+2	1.2	II
	<i>Typha latifolia</i> L.	+2	I
	<i>Scirpus lacustris</i> L. ssp. <i>lacustris</i>	1.2	I
Ch. Potamion	<i>Lemna minor</i> L.	+2	2.2	+2	+2	+2	.	III
	<i>Lemna trisulca</i> L.	+2	2.3	.	+2	1.2	.	III
	<i>Hydrocharis morsus-ranae</i> L.	1.2	1.2	+2	+2	.	.	II
	filiformous algae	1.3	1.3	+3	.	.	.	II
	<i>Elodea canadensis</i> Michx.	2.3	1.2	II
	<i>Potamogeton lucens</i> L.	1.3	.	+2	.	.	.	I
	<i>Ranunculus circinatus</i> Sibth.	+2	+2	I
	<i>Ceratophyllum demersum</i> L.	2.3	1.2	I
	<i>Spirodela polyrrhiza</i> (L.) Schleiden	+2	.	+2	.	.	I
Acc.								
(D. subass.)	<i>Polygonum amphibium</i> L.	+2	+2	+2	+1	1.2	1.2	V
	<i>Myosotis scorpioides</i> L.	+1	+2	+2	+2	+2	+2	IV
(D. subass.)	<i>Eleocharis palustris</i> (L.) R. et Sch.	+2	.	.	+2	1.2	2.3	III
	<i>Poa palustris</i> L.	1.2	+2	II
	<i>Mentha aquatica</i> L.	+2	.	.	+2	.	II

Supplement to the table. Acc.: *Potamogeton pectinatus* L. 1: 1.2, *Rumex maritimus* L. 1: +1, *Juncus articulatus* L. 1: +2, *Ranunculus sceleratus* L. 2: +2, *Mentha arvensis* L. 5: +2, *Rumex acetosa* L. 5: +2, *Rumex crispus* L. 6: +2, *Ranunculus repens* L. 6: +2.

1. D 55-1010, 14-7-1955

4. D 55-1050, 11-8-1955

2. D 55-1066, 16-8-1955

5. D 55-1081, 19-8-1955

3. D 55-1118, 31-8-1955

6. D 55-1085, 19-8-1955

belonging to the *Scirpeto-Phragmitetum oenanthetosum*. On the land side it is always bordered by foreland meadows.

3. 1. 1. 2. *Community in the tidal area* (Table 8)

In two former river beds of the freshwater tidal area records were made who certainly indicate a community belonging to the *Glycerieto-Sparganion*. On the slight slopes on which these vegetations were found, clay was deposited. At low tide the zone rose above the water.

Apium nodiflorum which occurs in one of the records, is generally considered to be a characteristic species of the *Helosciadietum nodiflori*. In the Netherlands the last mentioned association is found along rivulets in the province of Limburg and in some polder and fen areas (WESTHOFF, 1943; id. c.s., 1946). It does not seem to be correct to incorporate one or all of our records into this association, for there are several differences, both in floristic composition and in habitat.

ZONNEVELD (1960) describes a community of the freshwater tidal area which he does not know how to classify. It contains a.o. *Apium nodiflorum* and differs from all other communities of the alliance by the occurrence of *Scirpus lacustris* ssp. *lacustris*, *Lythrum salicaria*, *Bidens frondosa* and *Vaucheria* div. sp. Our records more or less resemble this

TABLE 8

Glycerieto-Sparganion community in the tidal area

nr. of record	1	2	3
nr. of former river bed	94	31	31
river	L	HM	HM
area (sq.m)	16	2	1,6
cover (%)	95	40	90
Ch. All. <i>Nasturtium officinale</i> R. Br.	+2	3.2	.
<i>Veronica beccabunga</i> L.	+2	.	.
<i>Veronica anagallis-aquatica</i> L.	.	+1	.
<i>Apium nodiflorum</i> (L.) Lag.	.	.	2.2
Ch. Ord. <i>Glyceria maxima</i> (Hartm.) Holmb.	5.5	2.1	3.5
<i>Phalaris arundinacea</i> L.	+2	2.1	+1
<i>Rorippa amphibia</i> (L.) Besser	4.2	.	+1
<i>Alisma plantago-aquatica</i> L.	+2	+1	.
<i>Carex acuta</i> L.	.	+2	+2
<i>Sium latifolium</i> L.	+2	.	.
<i>Acorus calamus</i> L.	.	.	3.5
Acc. <i>Caltha palustris</i> L.	+2	+2	+1
<i>Myosotis scorpioides</i> L.	+2	+1	.
<i>Mentha aquatica</i> L.	+2	.	1.2
<i>Lythrum salicaria</i> L.	1.2	.	.
<i>Agrostis stolonifera</i> L.	3.2	.	.
<i>Equisetum fluviatile</i> L.	.	1.1	.
<i>Polygonum mite</i> Schrank.	.	1.1	.
<i>Stachys palustris</i> L.	.	.	+1

1. V 56-113, 19-7-1956

2. V 55-121, 26-7-1955

3. V 55-120, 26-7-1955

community. Only after further investigations and after a total revision of the *Glycerieto-Sparganion* it will be possible to give these communities of the tidal area a place in this alliance.

3. 1. 2. Alliance *Phragmition eurosibiricum* (Koch 1926) Tüxen 1942 em. Braun-Blanquet et Sissingh 1942

The Synopsis mentions five characteristic species for the alliance *Phragmition*. In our opinion some alternations must be made.

Rumex hydrolapathum has to be transferred to the order. (see p. 23). In the Synopsis *Typha latifolia* is claimed as a characteristic species of the *Scirpeto-Phragmitetum*. Its abundance, however, may be equally high in the *Cicuteto-Caricetum*, especially in the subass. *comaretosum* (see p. 34). The presence in the two associations is, according to our results, resp. 8 % and 43 %, according to BOER (1942) 20 % and 27 %. In our opinion the species is characteristic for the alliance.

If we take the preceding remarks into account, we may say that in the Netherlands the *Phragmition* has the following characteristic species: *Scirpus lacustris* ssp. *lacustris*, *Butomus umbellatus*, *Typha angustifolia*, *T. latifolia* and *Ranunculus lingua*.

In the Netherlands the alliance includes three associations, viz. the *Scirpeto-Phragmitetum*, the *Cicuteto-Caricetum pseudocyperus* and the *Scirpetum triquetri et maritimi*. A number of associations which for one reason or another are not accepted here, will also be dealt with, viz. the *Glycerietum maximae*, the Association of *Oenanthe aquatica* and *Rorippa amphibia*, the *Calletum palustris* and the *Scirpetum maritimi*.

3. 1. 2. 1. *Scirpeto-Phragmitetum medio-europaeum* (Koch 1926) Tüxen 1941 (Table 9).

The Synopsis gives four characteristic species for the *Scirpeto-Phragmitetum*, viz. *Sparganium erectum* ssp. *polyedrum*, *Sagittaria sagittifolia*, *Acorus calamus* and *Typha latifolia*. The latter is better transferred to the alliance (v. supra).

The community is known from many European countries, and in the Netherlands it is very common. See e.g. HAVINGA (1919), KOCH (1926), CLASON (1928), SCHWICKERATH (1933), VAN LANGENDONCK (1935), VAN ZINDEREN BAKKER (1942, 1947), BOER (1942), VAN DIJK and WESTHOFF (1955), KUIPER and SEGAL (1955), VAN DONSELAAR-TEN BOKKEL HUININK (1961).

According to these descriptions, the association has its optimum development in eutrophic, stagnant, fresh water on a more or less peaty soil. Sometimes it is represented by a mixed vegetation rich in species, but more often by various facies which are rather poor in species. Pioneering facies (into vegetations of the *Potamion*) or at least facies in relatively deep water may consist of *Scirpus lacustris* ssp. *lacustris*, *Sparganium erectum* ssp. *polyedrum*, *Typha angustifolia* and *T. latifolia*. The two *Typha*-species prefer a more muddy soil than the other ones. Also on a muddy soil, but in more shallow water, a facies of *Glyceria maxima* may occur. *Phragmites communis* forms facies in shallow

<i>Scirpeto-Phragmitetum medio-europaeum</i>		typicum								
		stagnant water			river foreland,					
nr. of record		1	2	3	4	5	6	7	8	9
nr. of former river bed		17b	37	102	91	62	62	116a	32	40
river		M	W	IJ	L	W	W	IJ	HM	W
water depth (cm).		40	35	40	50		40	<40		75
area (sq. m)		6	16	4	12	25	9	9	2	100
cover (%), total			70	20	90	100	20		30	90
herb layer.		25	70	20	90	100	5	20	30	90
floating and submersed layer		—	<5		5				—	5
Ch. Ass.	Sparganium erectum L. ssp. polyedrum (A. et G.) Sch. et Th.	+1	+2	.	+2	1.2	+2	1.2	.	+2
	Sagittaria sagittifolia L.
D.t.	Ch. All. Ranunculus lingua L.	+1	+1	+1	+1	+1	.	.	1.2	.
D.t.+o.	Acc. Equisetum fluviatile L.	+1	2.1	.	.	1.1	2.1	2.1	.
D.t.+c.	Ch. All. Typha angustifolia L.	3.5	.	1.2	2.2	2.2	2.2	+2	2.2
	Typha latifolia L.	+1	+2	.	.	.	2.2	.	.	.
D.o.	Ch. Ord. Oenanthe aquatica (L.) Poir..	+1	.	+1	.	.
D.o.+c.	Ch. Ord. Phalaris arundinacea L.
D.c.	Acc. Caltha palustris L.
	Vaucheria sp.
Ch. All.	Scirpus lacustris L. ssp. lacustris	.	+1	.	.	2.2	+1	.	+1	2.1
Ch. Ord.	Glyc. max. (Hartm.) Holmb..	.	1.1	1.2	.	4.3	.	.	1.2	5.5
	Rorippa amphibia (L.) Besser.	+2	.	.	+1	+1
	Phragmites communis Trin.	3.1	.	2.2	5.5	.	+1	.	.	.
	Alisma plantago-aquatica L. .	.	.	+1	.	+2	.	+2	.	.
	Sium latifolium L.	+1	.	+2	.	+2	+1	.
	Rumex hydrolapathum Huds.	+1	.	+2	+1	+2
	Galium palustre L.	1.2	.	.	1.2	.
	Carex acuta L.	+2	+2	.
D.t.+o.	Acc. Lemna minor L.	+	.	+2	1.2	+	.	1.2
	Lemna trisulca L.	+	+1	.	1.2	+	.	+2
	Spirodela polyrrhiza (L.) Schl.	+2	1.2	.	.	+2
	Hydrocharis morsus-ranae L. .	.	.	1	.	+2	1.2	2	.	.
	Nuphar luteum (L.) Sm..	1.2	+2	.	1.2	.	.	.
	Mentha aquatica L.	+1	.	.	2.2	1.2	.	2.2	+2
	Myosotis scorpioides L.	+1	.	.	+1	+2
	Polyg. amph. L. fo. terr. Leyss.	+2	.	.	.	+2
	Stachys palustris L.	+1	+2	.	.	+1	.
	Lycopus europaeus L.	+1	.	.	+1	.
	Solanum dulcamara L.	+1	.	.	1.2
	Iris pseudacorus L.	1.2
	Symphytum officinale L.

Supplement to the table. Ch. Ass.: *Acorus calamus* L. 1: +1; Ch. All.: *Butomus umbellatus* L. 5: +1, 10: +1, *Scirpus maritimus* L. 10: 1.2, 12: +2, *Cicuta virosa* L. 3: +1; Ch. Ord.: *Glyceria fluitans* (L.) R. Br. 10: +2, *Carex acutiformis* Ehrh. 16: +2; Acc.: *Riccia fluitans* L. 3: 1, 9: 1.3, *Cardamine pratensis* L. 5: +1, 16: +2, *Senecio paludosus* L. 16: 1.2, 20: +2, *Bidens tripartitus* L. 18: +1, 20: +2, *Urtica dioica* L. 20: +2, 21: 1.2, *Lythrum salicaria* L. 3: +1, *Epilobium palustre* L. 3: +1, *Ricciocarpus natans* (L.) Corda 3: 1, *Myriophyllum spicatum* L. 4: +1, *Nymphaea alba* L. 6: +2, *Ranunculus acer* L. 10: +1, *Polygonum persicaria* L. 10: 1.1, *Ranunculus sceleratus* L. 10: +1, *Scutellaria galericulata* L. 12: +2, *Poa palustris* L. 14: +2, *Polygonum amphibium* L. 14: +2, *Elodea canadensis* Michx. 14: 1.2, *Lysimachia vulgaris* L. 16: +2, *Rumex crispus* L. 16: +2, *Viburnum opulus* L. 16: +2, *Polygonum nodosum* Pers. 17: +1, *Poa pratensis* L. 18: +2, *Cardamine amara* L. 18: +1, *Polygonum mite* Schrank 18: 1.1, *Ranunculus repens* L. 18: +1, *Equisetum palustre* L. 20: +2, *Polygonum hydropiper* L. 20: 3.2, *Achillea ptarmica* L. 21: +2.

oecanthetosum						calthetosum						t.	o.	c.	tot.
no tidal influence						tidal influence						P in 41 records	P in 39 records	P in 11 records	P in 145 records
10	11	12	13	14	15	16	17	18	19	20	21				
35	77b	87	39	56	79a	124a	65	65	92	92	94				
W	R	R	W	W	R	IJ	W	W	L	L	L				
25	70	0-50	50-85	>70	>70										
25	20	20	50	100	25	100	1	9	7.5	4	4				
		100	95	90	100	90	70	60	100	80	100				
30	40	95	95	80	90	90	70	60	100	80	100				
30	<5	70	60	40	60	—	—	—	—	—	—				
3.5	+1	1.2	+2	.	+2	III	III		III
+1	.	.	.	2.2	I	I		I
.	II			I
.	+1	1.2	1.2	+2	.	.	III	II	I	II
.	2.2	+2	IV	I	II	II
.	+2	.	.	II		I	I
2.2	+1	+2	4.4	2.2	5.5	I	IV		II
+2	+1	2.1	3.2	+1	.	2.2	2.2		II	IV	I
.	3.2	+1	3.3	3.2	.	.			IV	I
.	3.3			I	I
1.1	3.5	.	+1	III	III		III
.	2.1	3.3	1.1	4.3	+2	.	.	+2	5.5	1.2	.	IV	V		IV
+2	1.2	.	1.2	+2	+2	.	+1	2.2	+2	.	+2	II	IV	II	III
.	4.3	+1	2.2	1.2	+2	.	III	I	III	II
1.2	.	1.2	+1	.	+2	II	II		II
+1	+2	1.2	+1	1.2	+1	1.2	.	1.1	+2	.	.	II	II	II	II
.	+2	1.2	+1	.	+2	II	I	II	II
.	+2	+2	.	.	I	I	I	I
.	+2	1.2	.	.	.	+2	.	.	+2	.	.	I	I	II	I
1	1	+2	4.4	+2	3.3	IV	IV		III
.	+	4.3	1.2	3.3	4.4	II	IV		III
3	+	.	.	+2	+2	I	III		III
.	+	2.2	+2	II	II		II
.	I	I		I
+2	1.2	+2	1.2	.	II	I	I	II
+2	+2	+2	+2	.	.	1.2	2.3	1.2	.	.	.	I	I	II	I
.	.	1.2	.	+2	I	II	I	I
.	1.1	+2	+1	+2	3.2	5.5	I	I	III	I
.	+2	.	+2	.	I		II	I
.	.	+2	+2	.	I	I		I
.	.	.	.	+2	1.2	.	.	I		I	I
.	+2	.	.	+2	+2	.			II	I

1. V 55-75, 13-7-1955

2. S 54-92, 4-8-1954

3. QB 54-273, 30-8-1954

4. V 56-9, 12-6-1956

5. DBH 55-179, 8-9-1955

6. DBH 55-48, 13-6-1955

7. S 54-329, 1-9-1954

8. V 55-124, 26-7-1955

9. D-DBH 55-1029, 20-7-1955

10. QB-S 54-33, 30-7-1954

11. QB-S-V-MB 54-27, 29-7-1954
12. D 55-1116, 31-8-1955

13. D 55-1012, 14-7-1955

14. D 55-1098, 25-8-1955

15. D 55-1065, 16-8-1955

16. D 56-1026, 1-6-1956

17. V 54-211, 16-8-1954

18. QB 54-207, 16-8-1954

19. V 56-98, 17-7-1956

20. V 56-97, 17-7-1956

21. V 56-118, 19-7-1956

and in deep water, usually on a firm soil. The actual depth of the water in which the various facies occur, depends on other factors, like water movement.

One may ask whether the community can be rich in species if it occurs under natural conditions in shallow water. TÜXEN (1947) found that a richly developed vegetation belonging to this association which occurred in a spot that was regularly mowed, developed into a uniform *Phragmites*-field after the mowing was stopped. As a rule in the Netherlands the shallower side of the reed swamps is exploited! (See also WESTHOFF, 1954 b). Anyhow, this does not hold for the tidal *Scirpeto-Phragmitetum* (see p. 32).

The association occurs in the greater part of the former river beds, that is to say in all those with eutrophic, fresh water. Our results concerning the various facies and their ecology are in accordance with the facts known from the literature. Moreover, we found facies of *Equisetum fluviatile* and of *Oenanthe aquatica*. The first occurs both in stagnant water and in the forelands, and may be pioneering. The second is characteristic for former river beds in open connection with the summer bed and/or often inundated and/or exposed to the current during the periods of flood. Maybe, it is also favoured by the treading of cattle. MÖRZER BRUIJNS and WESTHOFF (1951) state that fragments of the *Scirpeto-Phragmitetum* consisting of *Oenanthe aquatica* and some other species come into existence on spots which are regularly dredged. This species can survive the effect of this treatment by its short life cycle. Probably the influences mentioned above have a corresponding effect on the vegetation.

In 1942 TÜXEN and PREISING (see also TÜXEN, 1954) divided the association into two subassociations, viz.

1) Subass. *typhetosum angustifoliae* (the "Teichröhricht", is "pool reed-swamp"), occurring in stagnant water. Differential species: *Typha angustifolia* and *Ranunculus lingua*.

2) Subass. *phalaridetosum arundinaceae* (the "Flussröhricht", is "river reed-swamp"), occurring along streaming water. Differential species: *Phalaris arundinacea* and *Oenanthe aquatica*.

ZONNEVELD described in 1960 a new subassociation, viz. *S.-P. calthetosum* (see also 1952). This community is often dominated by *Typha latifolia*, and *Sparganium erectum* as well as *Glyceria maxima* may be abundant. It further comprises *Typha angustifolia* and *Phalaris arundinacea*, but lacks *Ranunculus lingua* and *Equisetum fluviatile*. Differential species are *Caltha palustris* and *Vaucheria* div. sp. The subassociation has an enormous extension in the Biesbosch, a freshwater tidal delta, but occurs also in the rest of the freshwater tidal area of the rivers (see VAN LEEUWEN, 1954).

ZONNEVELD also gives a new subdivision of the association. Apart from his own observations he disposed of the table of BOER (1942) and of 27 of our own descriptions (with plot records) of the former river beds. His idea was that all records made in the former river beds occurring in the forelands represent the subass. *phalaridetosum*. Starting from this idea he concluded that the subass. *typhetosum* does

not have any differential species, for *Ranunculus lingua* and *Typha angustifolia* occur in the forelands. It would only be possible to determine the subass. *typhetosum* by the absence of the differential species of the other two subassociations. He proposes to change the names of the two first subassociations into resp. *S.-P. typicum* and *S.-P. oenanthetosum*.

With due consideration of the literature mentioned above, we propose to subdivide the *Scirpeto-Phragmitetum* as it occurs in the Netherlands with the aid of differential species in the way indicated in the following table.

Subassociation	typicum	oenanthetosum	calthetosum
<i>Differential species</i>			
<i>Ranunculus lingua</i>	x	.	.
<i>Equisetum fluviatile</i>	x	x	.
<i>Typha angustifolia</i>	x	.	x
<i>Typha latifolia</i>	x	.	x
<i>Oenanthe aquatica</i>	x	.
<i>Phalaris arundinacea</i>	x	x
<i>Caltha palustris</i>	x
<i>Vaucheria</i> div. sp.	x

Subass. *typicum* Zonneveld 1960

This community is identical with the subass. *typhetosum* of TUXEN and PREISING (1942). This name, however, is no longer adequate as the subass. *calthetosum* also contains the two *Typha*-species. The name *ranunculetosum linguae* would be acceptable, but *typicum* seems preferable. Of course, it must not be confused with the variant "*typicum*" of KOCH (1926). The original description given by this author probably includes the subass. *oenanthetosum* as well, but the subass. *typicum* of ZONNEVELD is doubtless the most typical form of the association. Most Dutch literature deals with this form.

This subassociation does not only occur in stagnant water, but also in a number of former river beds in the river forelands (see table). As to the water household these former river beds occupy an intermediary position between the summer bed of the river itself and a pool with permanently stagnant water. This applies to their soils too. Thus the former river beds in the forelands which are not frequently inundated and/or have a sheltered position with regard to the current during high water, normally have a swamp vegetation resembling the *Scirpeto-Phragmitetum* of stagnant pools. This result is in accordance with the data of TUXEN and PREISING (1942).

The subassociation shows a number of facies, but also magnificent mixtures occur. In one of the former river beds, the Kil near Hurwenen (nr. 62), it forms very extensive floatingmat vegetations (rec. nr. 5, see also VAN DONSELAAR-TEN BOKKEL HUININK, 1961).

According to the literature and as confirmed by our own observations, the zone occupied by the community is bordered by the *Myriophylleto-Nupharetum* or by the *Hydrochareto-Stratiotetum* on the deeper

side, and by the *Caricetum gracilis-vesicariae* or by the *Caricetum acutiformo-paniculatae* on the land side.

Subass. oenanthetosum Zonneveld 1960

This community is identical with the subass. *phalaridetosum* of TÜXEN and PREISING (1942). Here too the authors unhappily chose a wrong name, for afterwards it turned out that *Phalaris arundinacea* is a constant species in the subass. *calthetosum*.

It occurs in former river beds which are frequently inundated and/or are exposed to the current during high water. In a few cases there is some tidal movement.

In contrast to those of the subass. *typicum*, the aspect of the vegetation is determined by lower herbs. *Phalaris arundinacea* in this subassociation prefers shallow water.

The most common facies are those of *Oenanthe aquatica* and of *Glyceria maxima*. According to our results *Typha latifolia* is absent. This, however, is not in accordance with the records of TÜXEN and PREISING (1942) and of TÜXEN (1954).

The vegetations are situated between the *Polygoneto-Nymphoidetum typicum* on the one side and the *Sparganieto-Glycerietum fluitantis polygonetosum* or the *Caricetum gracilis-vesicariae* on the other side.

Subass. calthetosum Zonneveld 1960

This subassociation was found in a few former river beds in the freshwater tidal area. In some cases as a result of mowing (see p. 59) its place is taken by a sociation of the *Phragmites-consociation*. In comparison with the Biesbosch our vegetations are poor in species (see ZONNEVELD). As the characteristic species of the association are absent in our records, the community can be referred to the *Scirpeto-Phragmitetum* only because other possibilities can be excluded. If the differential species are absent, the subassociation is indicated by the combination of *Phalaris arundinacea* and *Typha latifolia*. In contrast with the two other subassociations, hydrophytes are, in consequence of the tidal movement, completely absent.

The community is bordered by the *Scirpetum triquetri et maritimi* on the deeper side and by the *Caricetum gracilis-vesicariae* or by the above mentioned *Glycerieto-Sparganion*-community on the land side.

Special attention must be given to record nr. 16. It was made along a former river bed of the IJssel, which up to 1932 has been under the influence of the tides of the Zuiderzee. Then the dam was completed, and the Zuiderzee became a lake, the IJsselmeer. We may suppose that the subass. *calthetosum* was a common community near the mouths of the rivers debouching into the Zuiderzee. It is rather astonishing that after 24 years of "river foreland life" the community still can be recognised.

Recently two associations have been introduced which must be dealt with in connection with the *Scirpeto-Phragmitetum*. Both have

been observed in N.W. Germany (see TÜXEN and PREISING, 1951; TÜXEN, 1955) and in S. Germany (see OBERDORFER, 1957).

LOHMEYER (1950) described the *Association of Oenanthe aquatica and Rorippa amphibia*. This association resembles very much (and may be identical with) the *Oenanthe aquatica*-facies of the *Scirpeto-Phragmitetum oenanthetosum*. It has no *Typha* sp. and no *Ranunculus lingua*, but *Glyceria maxima*, *Oenanthe aquatica* and *Phalaris arundinacea* ($P = V!$) are present. The main differences with our facies of *Oenanthe* are the presence (V) and the high total estimates (2–5) of *Rorippa amphibia*. The community is a “characteristic association” of the valleys of the great rivers in N. and W. Germany. As in summer its habitat mostly runs dry, its position is probably on a higher level than our *Oenanthe*-facies. Nevertheless we have the impression that we better leave this association out of consideration, and stick to the *Scirpeto-Phragmitetum oenanthetosum*. If the *Oenanthe*-facies would be set apart from this subassociation, there would not be left very much of the latter.

TÜXEN (1954) revived the *Glycerietum maximae* Hueck 1931. Its only floristical characterization is that *Glyceria maxima* is dominating. The habitat of the community runs periodically dry. We observed facies of *Glyceria maxima* which thrive in deeper water than the *Glycerietum maximae* of TÜXEN seems to do. However, there is no more reason for us to separate this facies from the *Scirpeto-Phragmitetum* than to do so with any of the other facies. Therefore we prefer to leave the *Glycerietum maximae* out of consideration here.

3. 1. 2. 2. *Cicuteto-Caricetum pseudocyperus* Boer et Sissingh 1942 (Table 10)

In the Synopsis three characteristic species are mentioned for this association, viz. *Cicuta virosa*, *Carex pseudocyperus* and *Caltha palustris*. The community consists of vegetations floating on water or on a soft organic mud. Before its description it was included in the *Scirpeto-Phragmitetum (typicum)*, but afterwards it appeared to occur in all Dutch broads and in many other fenlike habitats, also in Germany. See SCHWICKERATH (1933), VAN ZINDEREN BAKKER (1942), WESTHOFF (1949), TÜXEN and PREISING (1951), MEIJER (1955), KUIPER and SEGAL (1955). Especially BOER (1942), VAN ZINDEREN BAKKER (1947) and VAN DIJK and WESTHOFF (1955) give interesting details concerning the origin of the floating-mat vegetations.

There is some difference of opinion with regard to the position of the association in the order *Phragmitetalia*. Originally BOER (1942) included it in the *Phragmition*, and all Dutch authors agreed to that. TÜXEN and PREISING (1951), however, transferred it to the *Magnocaricion*. Although we never found an argumentation for this transfer, we can see some reason for accepting it. The floating vegetations produce a mat of rhizomes with organic remains in between, found somewhere between the bottom and the water surface or even at the surface. Thus they form a substrate for a number of species which usually occur in less deep water. Among these may be characteristic and differential species of the *Magnocaricion*. Our results prove that the

TABLE 10

<i>Cicuteto-Caricetum pseudocyperus</i>		comaretosum		typicum										com.	typ.	tot.
		stagnant water		river forel.												
mesotrophic		eutrophic														
nr. of record	1	2	3	4	5	6	7	8	9	10	P in 8 records	P in 9 records	P in 24 records			
nr. of former river bed	8	4	10b	10c	126	16a	69	62	124	116a						
river	M	M	M	M	IJ	M	OM	W	IJ	IJ						
P _H open water	5,9	6,2	6,9	6,9	7,2	7,0		7,5		7,5						
area (sq. m)	20	10	4	3	4	4	7,5	9	50	4						
cover (%)	90	100		50	60	70	90	75	70	60						
Ch. Ass.	3.2	2.2	+2	+2	2.2	.	2.2	.	2.2	.				IV	III	III
	.	+2	+1	+1	.	+2	.	1.2	.	1.2				II	IV	III
	.	.	3.3	3.3				II		II
D. com. Acc.	1.2	+2	+1				IV		II
	.	.	+2	+2	II		I			
	.	.	+2	II		I			
D. typ. Ch. Phron.	.	2.2	.	.	+1	+1	3.2	2.2	2.2	.	I	V	II			
Ch. Phra.		+3	1.2	+2	1.2	+1		V	II			
Acc.					+1	+3	.	+2	1.2	.		IV	II			
					.	4.3	.	+2	1.2	.		IV	I			
Ch. Phra.					.	+1	2.2	+2	+2	.		III	II			
Ch. Phron.					.											
					.	+1	.	+1	.	1.1	I	III	II			
					III	I	II			
					.	.	.	1.2	.	.	II	II	I			
					.	1.1			.	.						
Ch. Mg.					.		.	+2	1.2	+1	II	III	III			
					II	I	I			
D. Mg.					.		.	+2	+1	.	II	II	II			

Cicuteto-Caricetum is indeed rather rich in species belonging to the *Magnocaricion* (see table), and this is also obvious in the table of BOER. Nevertheless, in most records the *Phragmition*-species retain their dominating position. Another argument to put the association in the *Phragmition* may be found in its position in the succession. As a rule, vegetations of the *Phragmition* are preceded by a vegetation of the *Potamion*, and succeeded by a vegetation of the *Magnocaricion*. This applies, as a rule, also to the *Cicuteto-Caricetum*. It mostly comes into existence in a mass of floating *Stratiotes aloides* plants, belonging to the *Hydrochareto-Stratiotetum*. After the floating mat has become firmer, the association develops into the *Caricetum acutiformo-paniculatae*.

On the base of our own results, the literature (especially the table of BOER) and some unpublished records of Dr. V. WESTHOFF, we propose to divide the association into two subassociations. These are indicated on the table with their differential species.

Subass. *typicum* subass. nov.

Nearly all Dutch literature deals with this subassociation. It presents all three characteristic species, although *Calla palustris* lacks in our table. The optimum habitat of the community is found in sheltered spots in eutrophic, stagnant, fresh water. Nevertheless we made one record (nr. 7) in water with 200 mg Cl/l. It was also found in a few former river beds in the forelands. Of course these are not inundated very often and they occupy a sheltered position with regard to the current. *Stratiotes aloides*, although not present in the table, may also be considered to be a differential species. The position of the community in the succession has been dealt with above.

Subass. *comaretosum* subass. nov.

This community was found in nearly all mesotrophic former river beds along the Meuse. It occurs above a peat soil. In many cases *Calla palustris* determines the aspect of the vegetation. The community presents less characteristic species of the order and the alliance than the subass. *typicum*. The vegetation is preceded by one belonging to the *Hydrochareto-Stratiotetum* (mesotraphentous variant).

VANDEN BERGHE (1952 b) described the *Calletum palustris* with *Calla* as the only characteristic species. He reckons it, together with the *Caricetum lasiocarpae*, to an alliance called *Caricion lasiocarpae*. Characteristic species of this alliance are *Menyanthes trifoliata*, *Comarum palustre* and *Carex rostrata*. A floristic and ecological comparison of the *Calletum palustris* with the *Cicuteto-Caricetum pseudocyperus comaretosum* leads to the conclusion that the two communities are identical. In this connection it must be mentioned that the *C.-C. p. typicum* does not occur in Belgium, at least was not noticed by LEBRUN c.s. (1949).

3. 1. 2. 3. *Scirpetum triquetri et maritimi* Zonneveld 1960 (Table 11)

In 1933 TÜXEN described the *Scirpetum maritimi*, an association with *Scirpus maritimus* and *Scirpus lacustris* ssp. *glaucus* as characteristic species. It was mentioned from brackish water along the coast and near the

mouths of the rivers in N.W. Germany. Since then this association has been recognised also in Belgium (LEBRUN c.s., 1949) and in the Netherlands (Synopsis). BOER (1942) described the association for the Netherlands, and divided it into a number of subassociations. The greater part of his records, however, were made along the IJsselmeer, the former Zuiderzee, which at that time was desalinating gradually. Therefore his conclusions concerning this community are of little value.

ZONNEVELD (1960, see also 1952) described the communities of the Biesbosch, a freshwater tidal delta. One of these communities resembled the *Scirpetum maritimi*. However, ZONNEVELD's community had its optimum development in the area covered by his investigation, and moreover it differed from the association of TÜXEN a.o. by the enormous extension of *Scirpus triquetra*. This species was accepted already as a characteristic species of the *Scirpetum maritimi* by BOER, and in consequence also by the Synopsis. ZONNEVELD, however, wanted to leave the account of BOER out of consideration for the reasons mentioned above. Therefore, he described his community as a new association, the *Scirpetum triquetra et maritimi*. We fully agree with his argumentation. Characteristic species of the new association are *Scirpus triquetra*, *Scirpus lacustris* ssp. *glaucus* fo. *major* and *Scirpus maritimus* fo. *maritimus*.

Subass. *typicum*, *phalaridetosum* and *senecietosum*
Zonneveld 1960

ZONNEVELD divides the association into three subassociations, viz. *typicum*, *phalaridetosum* and *senecietosum*. The main difference from an ecological point of view is their position with regard to the fluctuating water level.

The three subassociations were found along a few former river beds that were in open connection with the lower course of the river. The water may be fresh or slightly oligohalinic (see rec. nrs. 1-3). The vegetations are not very representative and only a few records were made. They are bordered on the land side by one of the *Caricetum gracilis-vesicariae*, the *Phragmites-consociation* or the *Scirpeto-Phragmitetum calthetosum*.

Subass. *typhetosum* subass. nov.

In the former river beds with stagnant, oligo- to slightly mesohalinic water we found a community which is more or less intermediary between the *Scirpetum triquetra et maritimi* and the *Scirpeto-Phragmitetum typicum*. The main species of it, occurring either in combination or as a facies, are *Scirpus maritimus*, *Scirpus lacustris* ssp. *glaucus* (the formae of these two were not determined), *Typha angustifolia*, *Phragmites communis* and *Glyceria maxima*. A number of hydrophytes too are present. This community probably also occurs in other oligo- to mesohalinic territories in the Netherlands, viz. Botshol (WESTHOFF, 1949), Ilperveld (VAN ZINDEREN BAKKER, 1947), Waterland (see Waterland, 1954), De Liede (REYNDERS, 1952), Zwet (MEIJER, 1953). In these cases, in accordance with our results, it is bordered by a halobious *Potamion-*

TABLE 11

<i>Scirpetum triquetri et martini</i>	typ.			sen.	typhetosum									
	tidal influence				stagnant water									
	1	2	3		4	5	6	7	8	9	10	11		
nr. of record	96	66	66	75	75	76	73	73	73	73	72	P in 14 records		
nr. of former river bed	L	Me	Me	D	D	D	D	D	D	D	D			
river	90	124	124	250	250	2000	686	686	686	686	1252			
mg Cl/l.				40	40	20-35	8	2	15	10	20			
water depth (cm)	6	2.4	9	6	2	3	2	4	4	25	4			
area (sq. m)	20	80	70	100	100	100	95	80	90	90	90			
cover (%), total	20	80	70	50	80	100	70	70	80	90	90			
herb layer	—	—	—	90	90	1	50	—	5	<5	—			
floating/moss layer	—	—	—	—	5	—	—	10	10	—	—			
submersed layer	—	—	—	—	—	—	—	—	—	—	—			
Ch. Ass.	2.2		II II	
<i>Scirpus triquetri</i> L.			
<i>Scirpus lacustris</i> L.	.	3.2	4.3	3.2	2.2	5.5	2.2	2.2	.	.	.			
ssp. glaucus (Smith) Hartman			
<i>Scirpus maritimus</i> L.	IV III II I I I I I		
D. sen. Acc.	.	.	1.2			
<i>Cardamine amara</i> L.			
D. typh. Ch. All.			
Ch. Pot.			
<i>Typha angustifolia</i> L.	5.5	.	+2	+2	+2	3.2	5.5			
<i>Lemna minor</i> L.	5.5	+2	.	.	1.2	+2	.			
<i>Ceratophyllum demersum</i> L.	+2			
<i>Lemna trisulca</i> L.	+2			
<i>Spirodela polyrrhiza</i> (L.) Schleiden	1.2			
<i>Enteromorpha intestinalis</i> Link.			
<i>Potamogeton pectinatus</i> L.			
Ch. All.	.	4.5	+2	IV II II I I		
<i>Scirpus lacustris</i> L. ssp. <i>lacustris</i>			
Ch. Ord.			
<i>Phragmites communis</i> Trin.			
<i>Rumex hydrolapathum</i> Huds.	III II I I		
<i>Carex riparia</i> Curt.			
<i>Sium erectum</i> Huds.			
<i>Glyceria maxima</i> (Hartm.) Holmb.			
Acc.	III II I I		
<i>Myosotis scorpioides</i> L.			
<i>Iris pseudacorus</i> L.			
<i>Vaucheria</i> sp.			
<i>Ranunculus sceleratus</i> L.	I		
	I		
	I		
	I		

or *Ruppion*-community at its deeper side, and often by the *Association of Sonchus paluster* at the land side.

We propose to consider the community to be a subassociation of the *Scirpetum triquetri et maritimi*, and to call it subass. *typhetosum*. It is distinguished from the other subassociations by the absence of *Scirpus triquetra* and by the presence of a number of differential species, viz. *Typha angustifolia* and some characteristic species of the *Potametea*. In contrast with the other three subassociations, it occurs only in oligo- and mesohalinic, stagnant water. From the *Scirpeto-Phragmitetum typicum* it can be distinguished not only by the absence of *Sparganium erectum* ssp. *polyedrum*, but also by that of *Ranunculus lingua* and *Typha latifolia*.

3. 1. 3. Alliance *Magnocaricion elatae* Koch 1926

The Synopsis gives three characteristic species for the *Magnocaricion*. One of these we want to exclude, viz. *Poa palustris*. This species may be regarded as characteristic for the alliance so long as only natural vegetations are taken into account. However, it reaches its optimum in wet meadows (see p. 62). The two remaining species are *Galium palustre* fo. *elongatum* and *Lysimachia thyrsiflora*.

The Synopsis includes four associations in the alliance, but one of them, the *Mariscetum serrati*, may be left out of consideration here, as it does not occur in any of the former river beds. The other three will be dealt with, but we will not enter here in a discussion of the many differences existing between the Dutch, the German and the Belgian subdivision of the *Magnocaricion*. These differences will be mentioned in a separate section (IV. 3. 1. 3. 4).

3. 1. 3. 1. *Caricetum elatae* Koch 1926

A comparison of the literature and our records of the *Caricetum elatae* makes it clear that the association is not homogeneous. The original author distinguished two characteristic species, viz. *Carex hudsonii* and *Senecio paludosus*. The first can be maintained, but the second has its optimum only in apart of the area in which the community occurs. In accordance with the original conception, the community every-

Supplement to the subass. typhetosum. D.: *Hydrochis morsus-ranae* L. I; Ch. Ord.: *Phalaris arundinacea* L. I (8: +.2), *Galium palustre* L. I (8: 1.2), *Veronica anagallis-aquatica* L. I (9: +.2); Acc.: *Drepanocladus fluitans* (Hedw.) Warnst. I (7: 2.2), *Oenanthe fistulosa* L. I (7: +.2), *Poa palustris* L. I (7: +.2).

Supplement to the rest of table 11. Ch. Ord.: *Alisma plantago-aquatica* L. 3: +.2, *Sium latifolium* L. 3: +.2, *Rorippa amphibia* (L.) Besser 3: +.2; Acc.: *Polygonum amphibium* L. fo. *terrestre* Leyss. 2: +.1, *Caltha palustris* L. 3: +.2, *Lythrum salicaria* L. 3: +.2, *Rumex crispus* L. 3: +.2.

- | | |
|------------------------|-------------------------|
| 1. V 56-122, 20-7-1956 | 7. V 56-15, 14-6-1956 |
| 2. V 56-38, 27-6-1956 | 8. V 56-29, 14-6-1956 |
| 3. V 56-39, 27-6-1956 | 9. V 56-30, 14-6-1956 |
| 4. V 56-125, 25-7-1956 | 10. V 56-25, 14-6-1956 |
| 5. V 56-127, 25-7-1956 | 11. V 56-131, 26-7-1956 |
| 6. V 56-144, 6-8-1956 | |

where participates in the hydrosere on sand or peat, and may be succeeded either by the *Alnetum glutinosae* or by a community belonging to the *Caricion fuscae*. For the rest there are many differences. The following subdivision can be made:

Subass. *typicum* subass. nov.

Differential species: *Senecio paludosus*, *Phalaris arundinacea* and *Valeriana officinalis*. This subassociation corresponds with the original description. It is a mainly eutraphentous type of vegetation. Characteristic species of the alliance and the order are not numerous, but anyhow they outnumber the representatives of other groups. This subassociation was found in Switzerland (KOCH, 1926), S. Germany (OBERDORFER, 1957) and Belgium (VANDEN BERGHEN, 1952 a; LEBRUN c.s., 1949).

In this connection it must be mentioned that in the Netherlands *Senecio paludosus* has its optimum in quite a different habitat, viz. the forelands of the upper as well as the lower courses of the larger rivers. Along the lower course it occurs with total estimates of up to 2 in the *Scirpetum triquetri et maritimi senecietosum* and in the adjoining community of *Epilobium hirsutum* and *Phalaris arundinacea* (see ZONNEVELD, 1960). Along the upper courses *Senecio paludosus* has its optimum development together with *Phalaris arundinacea* in the transition of the *Caricetum gracilis-vesicariae* to the *Valerianeto-Filipenduletum senecietosum* (see p. 45).

Subass. *comaretosum* subass. nov. (Table 12)

Differential species: *Lysimachia thyrsiflora*, *Calamagrostis canescens* and the characteristic species of the class *Scheuchzerio-Caricetea*, e.g. *Comarum palustre* and *Epilobium palustre*. This subassociation is more mesotraphentous than the subass. *typicum*. In this connection VAN DIJK and WESTHOFF (1955) state that in the Netherlands *Carex hudsonii* is the mesotraphentous counterpart of the eutraphentous *Carex paniculata*.

The subassociation occurs in the Netherlands (BOER, 1942; DAMMAN, 1954) and in N. Germany (TÜXEN, 1937; PASSARGE, 1955 b). It was found in a number of former river beds along the Meuse with stagnant, mesotrophic water with a P_H of 6,1 to 6,7, above a peat soil. Its position in the hydrosere is usually between the *Cicuteto-Caricetum pseudocyperus comaretosum* and the *Alnetum glutinosae* or the *Caricetum lasiocarpae*.

3. 1. 3. 2. *Caricetum acutiformo-paniculatae* Vlieger et Van Zinderen Bakker 1942 (Table 13)

The *Caricetum acutiformo-paniculatae* has been described in 1942 (VAN ZINDEREN BAKKER, 1942) and since then it has been mentioned in several Dutch publications; see BOER (1942), VAN ZINDEREN BAKKER (1947), WESTHOFF c.s. (1946), MÖRZER BRUIJNS and WESTHOFF (1951), VAN DIJK and WESTHOFF (1955), KUIPER and SEGAL (1955). In Belgium an association of this name is mentioned by LEBRUN c.s. (1949), but it does not correspond with the original description. The community obviously has its optimum development

Caricetum acutiformo-paniculatae		A					B					C					D					A	B	C	D	tot.
		mesotrophic, P _H open water 6,2-6,9					eutrophic, P _H open water 7,2-7,5										eutrophic					P in 10 records	P in 17 records	P in 14 records	P in 10 records	P in 51 records
		open water fresh, <110 mg Cl/l										250-2000 mg Cl/l														
		stagnant water					river foreland					stagnant water														
nr. of record	nr. of former river bed	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20					
river.		11e	12	10a	6	7	63a	126	127	67	68	32	95	64	116d	114a	124	74	74	73	73					
area (sq. m)		M	M	M	M	M	W	IJ	IJ	OM	OM	HM	L	W	IJ	IJ	D	D	D	D	D					
cover (%), herb layer		25	6	10	4	10	3	16	8	4	6	6	25	4	4	6	20	9	9	6	2					
floating layer		95	80	90	30	90	100	100	90	50	100	90	80	40	30	90	90	80	90	100	70					
		—	5	<1	60	—	—	—	5	—	60	—	10	<1	—	—	<1	10	—	—	—					
Ch. Ass.	Carex paniculata Juslen.	.	4.3	4.3	.	4.2	2.2	.	2.2	5.5	.	.	III	II			II
	Carex acutiformis Ehrh.	4.3	.	.	3.2	2.2	.	4.2	.	.	4.5	.	5.2	.	.	.	+2	5.5	5.5	.	.	IV	II			III
	Carex riparia Curt.	3.2	.	.	3.2	+2	5.4	.	2.2	3.3	2.2	2.2	.	.	.	1.2		II	V		III
D. A	Comarum palustre L.	.	+2	1.2	III				I
D. AB	Lycopus europaeus L.	.	+2	.	.	.	+2	1.2	1.2	+2	I	III			I
	Eupatorium cannabinum L.	+2	1.2	.	+1	+2	I	II			I
	Peucedanum palustre (L.) Moench.	.	2.2	.	.	+1	+2	III	I			I
D. ABC	Solanum dulcamara L.	2.2	+2	.	1.2	1.2	+2	1.2	.	.	+2	.	.	1.2	III	III		II	II
(Ch. Ord.)	Glyceria maxima (Hartm.) Holmb.	+2	.	.	1.2	.	.	+1	.	1.2	.	3.2	1.2	I	I		IV	II
	Lythrum salicaria L.	+2	+2	+1	+2	.	+2	+2	I	I		III	I
	Lysimachia vulgaris L.	.	+2	.	+1	1.1	.	+2	+1	+2	II	I		I	I
(Ch. Ord.)	Typha latifolia L.	2.2	1.2	+2	.	+2	+2	.	+2	.	.	+2	III	I		I	I
	Equisetum fluviatile L.	.	.	.	+1	.	.	+2	+1	.	.	+2	+2	.	+1	I	I		II	I
D. B	Angelica sylvestris L.	1.2	.	+1		II			I
D. BC	Stachys palustris L.	3.3	.	.	.	+2	.	+1	.	+2		II		III	I
(Ch. Ord.)	Rorippa amphibia (L.) Besser	+2	+2	.	1.1		I		II	I
(Ch. All.)	Carex acuta L.	+1	+2	+2		I		I	I
D. BCD	Mentha aquatica L.	3.3	.	+2	.	+1	+1	1.2	1.1	+2	.	+2	+2	2.2	3.2	2.2		III		IV	III
(Ch. Ord.)	Sium latifolium L.	1.2	.	+2	1.1	+2	.	+2	.	.	.		II		II	I
(Ch. Ord.)	Scirpus lacustris L. ssp. lacustris	+1	.	.	.	+1	+2		I		II	I
D. C	Polygonum amphibium L. fo. terrestre Leyss.	+1	+2	.	+1				II	I
(Ch. Ord.)	Alisma plantago-aquatica L.	+2	.	+2				II	I
D. D	Festuca arundinacea Schreb.	+2	2.2	.	.				II	I
(Ch. All.)	Galium palustre L.	.	.	+2	.	+2	3.3	2.2	+1	1.2	.	.	+1	.	+1	.	.	+2	.	1.2	.	I	II		II	II
Ch. Ord.	Phragmites communis Trin.	2.2	+1	4.5	2.1	.	4.5	.	.	1.2	2.1	3.2	3.2	3.2	2.2	1.2	2.2	II	V		IV	V
	Rumex hydrolapathum Huds.	.	.	+2	+1	+2	.	+2	+1	.	.	+2	+2	.	+2	+1	.	+2	.	+2	+2	II	II		III	III
	Sparganium erectum L.	.	2.2	.	.	+2	+1	.	.	.	+2	.	.	+2	II	III		I	II
	Typha angustifolia L.	+2	+2	.	.	.	+2	.	.	+2	.	.	.	2.2	.	+2	+2	II	III		II	II
	Sium erectum Huds.	.	.	.	+1	2.2	.	+1	2.2	I			II	I
Acc.	Iris pseudacorus L.	.	.	.	+2	.	.	.	+3	.	.	+2	+2	+2	I	II		II	I
	Epilobium hirsutum L.	+2	1.2	+2	+2	.	I	I		I	I
	Calystegia sepium (L.) R. Br.	+1	.	.	.	+1	.	3.2	I	I		I	I
	Myosotis scorpioides L.	.	.	+2	+2	+2	.	.	.	I	I		II	I
	Agrostis stolonifera L.	.	.	+2	+1	4.2	3.2	.	.	I	I		I	I
	Lychnis flos-cuculi L.	+2	+2	1.2				II	I
	Lemna minor L.	.	1.2	+2	4	4.2	.	.	.	1	.	+2	II	I		III	II

Supplement to the table. Ch. Ord.: Sparganium simplex Huds. 2: +2, Calla palustris L. 3: 1.2, Oenanthe aquatica (L.) Poir. 6: +1, Nasturtium officinale R. Br. 6: 1.2, Phalaris arundinacea L. 9: +2, Acorus calamus L. 12: 2.2, Scirpus lacustris L. ssp. glaucus (Smith) Hartman 17: 1.2, Scirpus maritimus L. 17: +2; Acc.: Epilobium palustre L. 3: +2, 6: +2, Scutellaria galericulata L. 6: +1, 7: 1.2, Epilobium parviflorum Schreb. 6: +2, 9: +2, Poa trivialis L. 7: 1.2, 20: +2, Lysimachia nummularia L. 7: +2, 12: +2, Spirodela polyrhiza (L.) Schleiden 8: 2, 16: +2, Poa palustris L. 9: +2, 19: +2, Salix triandra L. 11: +1, 15: +1, Caltha palustris L. 12: +2, 16: +2, Hydrocharis morsus-ranae L. 14: +, 16: +2, Galium aparine L. 1: 2.2, Galeopsis tetrahit L. 1: +2, Stellaria palustris Retz. 2: +2, Juncus effusus L. 3: 1.2, Bidens tripartitus L. 3: +2, Alnus glutinosa (L.) Gaertn. 4: +1, Rubus caesius L. 4: +1, Rumex crispus L. 8: +2, Cardamine pratensis L. 9: +1, Glechoma hederacea L. 9: +1, Symphytum officinale L. 12: +2, Pedicularis palustris L. 12: +2, Valeriana dioica L. 12: +2, Hottonia palustris L. 13: +1, Equisetum palustre L. 14: +1, Urtica dioica L. 19: +2, Carex otrubae Podp. 19: +2, Oenanthe fistulosa L. 20: 3.2, Calliergon stramineum (Brid.) Kindb. 3: 1.2, Mnium affine Schwaegr. 12: 2.2, Drepanocladus fluitans (Hedw.) Warnst. 17: 2.2, 20: 3.2.

1. D 56-1099, 26-6-1956
2. D 56-1091, 22-6-1956
3. D 56-1090, 22-6-1956
4. V 55-51, 27-6-1955
5. D 56-1074, 20-6-1956
6. D-DBH 55-173, 20-8-1955
7. K 56068, 18-7-1956
8. QB-S-V 54-353, 3-9-1954
9. V 54-215, 17-8-1954
10. V 56-167, 31-8-1956
11. D-K-V 56-1036, 6-6-1956
12. V 56-54, 3-7-1956
13. D-V 56-1003, 23-5-1956
14. QB 54-340 A, 2-9-1954
15. K 56080, 28-8-1956
16. D 56-1023, 1-6-1956
17. V 56-136, 31-7-1956
18. V 56-137, 31-7-1956
19. V 56-28, 14-6-1956
20. V 56-15, 14-6-1956

TABLE 12

Caricetum elatae comaretosum

		1	2	3	4	5	P in 7 records
nr. of record		15	3	3	4	12	
nr. of former river bed		M	M	M	M	M	
water depth (cm)		20	15	0	25	75	
area (sq. m)		10	10	12	5	20	
cover (%)		85	90	100	90	90	
Ch. Ass.	<i>Carex hudsonii</i> A. Benn.	5.3	5.3	3.2	5.4	5.3	V
Ch. All.	<i>Galium palustre</i> L.	2.2	1.2	.	.	1.2	III
(D. subass.)	<i>Lysimachia thyrsiflora</i> L.	.	.	+2	.	.	II
	<i>Carex paniculata</i> Juslen.	+2	I
Ch. Ord.	<i>Cicuta virosa</i> L.	.	+1	.	+2	+2	III
	<i>Typha latifolia</i> L.	+2	.	.	1.2	.	II
	<i>Phragmites communis</i> Trin.	+2	I
Ch. S.-C. D. subass.	<i>Comarum palustre</i> L.	1.2	+2	2.2	+2	+2	V
	<i>Epilobium palustre</i> L.	1.2	+2	.	.	1.2	III
	<i>Hydrocotyle vulgaris</i> L.	.	1.2	1.2	.	.	II
	<i>Stellaria palustris</i> Retz.	.	+2	.	.	+2	II
	<i>Agrostis canina</i> L.	.	+2	1.2	.	.	II
	<i>Viola palustris</i> L.	+2	I
	<i>Eriophorum angustifolium</i> L.	.	.	+2	.	.	I
Acc.	<i>Peucedanum palustre</i> (L.) Moench.	2.2	2.2	2.2	+2	1.2	V
(D. subass.)	<i>Calamagrostis canescens</i> (Web.) Roth.	1.2	+2	+2	2.2	1.2	IV
	<i>Lysimachia vulgaris</i> L.	2.2	+1	+2	+1	.	IV
	<i>Lycopus europaeus</i> L.	2.2	+2	.	+2	.	IV
	<i>Lemna minor</i> L.	+2	+2	.	.	+2	IV
	<i>Bidens tripartita</i> L.	.	.	.	+1	+2	III
	<i>Juncus effusus</i> L.	1.2	.	1.2	.	.	II
	<i>Cardamina pratensis</i> L.	+2	.	.	.	+2	II
	<i>Brachythecium</i> sp.	1.2	.	1.2	.	.	II

Supplement to the table. Ch. Ord.: *Sparganium erectum* L. I, *Rumex hydrolapathum* Huds. I; Ch. S.-C.: *Carex rostrata* Stokes I; Acc.: *Hydrocharis morsus-ranae* L. II (2: 1.2), *Alnus glutinosa* (L.) Gaertn. I (2: 1.2), *Frangula alnus* Mill. I (3: +2), *Salix cinerea* L. I (3: +2), *Sphagnum recurvum* P. de B. I (3: 4.3), *Polytrichum commune* Hedw. I (3: 1.3), *Solanum dulcamara* L. I (5: +2), *Calystegia sepium* (L.) R. Br. I (5: +2), *Cirsium arvense* (L.) Scop. I (5: +1), *Salix triandra* L. I (5: +1).

1. D 56-1116, 27-6-1956

2. D 56-1056, 19-6-1956

3. D 56-1057, 19-6-1956

4. D 56-1068, 20-6-1956

5. D 56-1093, 22-6-1956

in the Netherlands. There it is a very characteristic stage in the autogenic succession in stagnant water. The habitat may be eutrophic or it may tend a little towards mesotrophic, and the water even oligo- to mesohalinic. The soil consists of peat or peaty clay.

The community was found in several of the former river beds. Its floristic composition shows a certain variability in correspondance with differences in the environment. A subdivision of the association into subassociations, however, is as yet not justified; to this end the presence of the species which might be differential ones is too low. Therefore, we only will distinguish some variants (see Table 13).

Attention must be drawn to the fact that the three characteristic species hardly ever occur together. Nevertheless, their actual ecological amplitudes overlap for the greater part. Species which are found more frequently with one of the three than with the other two, could not be detected.

Variant A

In the mesotrophic, stagnant water of the former river beds along the Meuse the association occurs without *Carex riparia*. The presence of *Comarum palustre* and the absence of some purely eutraphentous species indicate a mesotrophic habitat. The soil on which the vegetation occurs and its environment, consists of peat. The vegetation usually forms a floating mat with large tufts of *Carex paniculata*. It is often a succession stage following the *Cicuteto-Caricetum pseudocyperus comaretosum*, but sometimes it directly succeeds a *Potamion*-community. In all cases the next stage is the *Alnetum glutinosae*.

Along some of the former river beds vegetations of *Carex paniculata* and of *Carex hudsonii* may alternate, but they do not intermingle anywhere.

Variant B

This variant corresponds with the greater part of the descriptions of the association given in the literature (e.g. BOER, 1942; VAN ZINDEREN BAKKER, 1942, 1947). It has its optimum development in the Dutch fens and broads and is rich in species. It is probably in some cases hardly separable from the preceding stage, the *Cicuteto-Caricetum*, and may moreover be a combination of the variants A and B (MEIJER, 1955; KUIPER and SEGAL, 1955).

Under natural conditions the community consists in the former river beds of floating mats found between either the *Scirpeto-Phragmitetum typicum* or the *Cicuteto-Caricetum pseudocyperus typicum* and the *Alnetum glutinosae*. If, by human interference, the latter is absent, the community is usually bordered by meadows on the land side. The soil consists of peat or peaty clay, but somewhere the water must be in contact with clay.

Variant C

This community occurs in a number of former river beds in the river forelands which during high water are not strongly influenced by the stream. It is characterized here by the absence of *Carex paniculata* and by the preponderance of *Carex riparia*. The floating mat retains some plant remains, but the subsoil consists of clay. Only in this habitat the association forms a stage in an (at least partly) allogenic succession. It is preceded either by the *Scirpeto-Phragmitetum typicum* or by the *Cicuteto-Caricetum pseudocyperus typicum*, and passes on the land side into the *Caricetum gracilis-vesicariae* or into some other community influenced by man.

Variant D

Along the oligo- and mesohalinic former river beds with stagnant water sometimes a variant of the association occurs in the zone which is situated between the *Scirpetum triquetri et maritimi typhetosum* and the *Association of Sonchus paluster* or the meadow, and which with regard to the water level is somewhat higher than that occupied by the other variants. It consists nowhere of a floating mat. The soil consists of peat or peaty clay. The community lacks many of the common species and is characterized by the presence of *Festuca arundunacea* and possibly also by that of *Sium erectum*. In the table of BOER (1942) one record made by WEEVERS on the island of Goeree belongs to this variant. Perhaps this variant will turn out to be the most clearly definable one and to deserve the status of a subassociation.

3. 1. 3. 3. *Caricetum gracilis-vesicariae* Westhoff 1949 (Table 14)

The *Caricetum gracilis-vesicariae*, not mentioned in the Synopsis, was described by WESTHOFF (1949). Its characteristic species are *Carex acuta* and *C. vesicaria*. The association occurs in the Netherlands and in Belgium, but has usually been described under the name *Caricetum inflato-vesicariae* KOCH 1926 (see e.g. Vlieger, 1937; MEIJER, 1947 a; VAN LANGENDONCK, 1935). VANDEN BERGHEN (1952 a) uses this name too, but his records do not correspond with the original concept.

In the literature the vegetations include the two characteristic species, many species of the *Phragmitetalia*, but also a few species belonging to the class *Scheuchzerio-Caricetea*. The community occurs on a humic clay soil on the banks of stagnant water.

The association was found along many former river beds. In all cases *Carex acuta* dominates; *Carex vesicaria* has a low abundance or is absent, and this applies to all species of the *Scheuchzerio-Caricetea*. The soil is mineral, and consists mainly of clay; the water is eutrophic and fresh or slightly oligohalinic. The vegetations are preceded by one of a *Phragmition*-association, and on the deeper side they may be rich in *Phragmites communis*. Under natural conditions the succeeding stage would be a *Salicion*-community, but in most cases this is replaced either by the *Valerianeto-Filipenduletum* or by a meadow community.

Along former river beds with tidal influence *Carex vesicaria* is absent. There the community is situated between the *Scirpetum triquetri et maritimi*, the *Scirpeto-Phragmitetum oenanthetosum* or the *S.-P. calthetosum* on the outside and a tidal *Salicion*-community or the *Valerianeto-Filipenduletum* subass. of *Heracleum*. At every high water the vegetation is submerged.

In the forelands without tidal influence the community occupies a zone where the water height in summer varies from next to nothing to 50 cm. Here it is an important partner in the allogenic succession. Its position is between the *Scirpeto-Phragmitetum typicum* or the *S.-P. oenanthetosum* and a foreland *Salicion*-community. Where the latter is replaced by the *Valerianeto-Filipenduletum senecietosum* the transition is marked by a high abundance of *Phalaris arundinacea* and *Senecio*

TABLE

<i>Caricetum gracilis-vesicariae</i>		tidal influence		
nr. of record		1	2	3
nr. of former river bed		94	65	25
river		L	W	M
water depth (cm)				
area (sq. m)		4	9	4
cover (%), herb layer		100	90	60
floating and submersed layer		—	—	—
Ch. Ass. <i>Carex acuta</i> L.		5.5	4.2	4.5
<i>Carex vesicaria</i> L.		.	.	.
Ch. All. <i>Galium palustre</i> L.		+2	+2	.
Ch. Ord. <i>Phalaris arundinacea</i> L.		2.2	1.1	+1
<i>Glyceria maxima</i> (Hartm.) Holmb.		.	1.2	1.1
<i>Sium latifolium</i> L.		1.2	.	.
<i>Rorippa amphibia</i> (L.) Besser		.	1.2	.
<i>Phragmites communis</i> Trin.		+2	1.1	.
<i>Rumex hydrolapathum</i> Huds.		.	.	.
<i>Alisma plantago-aquatica</i> L.		.	.	.
<i>Scirpus lacustris</i> L. ssp. <i>lacustris</i>		.	.	.
Acc. <i>Equisetum fluviatile</i> L.		.	+1	.
<i>Senecio paludosus</i> L.		+2	.	.
<i>Polygonum amphibium</i> L. fo. <i>terrestre</i> Leyss.		2.2	.	.
<i>Iris pseudacorus</i> L.		.	.	.
<i>Lythrum salicaria</i> L.		1.2	.	.
<i>Lemna minor</i> L.		.	.	.
<i>Mentha aquatica</i> L.		1.2	.	.
<i>Lysimachia vulgaris</i> L.		.	.	.
<i>Myosotis scorpioides</i> L.		.	1.2	.
<i>Stachys palustris</i> L.		.	.	.
<i>Symphytum officinale</i> L.		.	.	+2
<i>Thalictrum flavum</i> L.		.	.	.
<i>Lemna trisulca</i> L.		.	.	.
<i>Caltha palustris</i> L.		.	3.2	+2
<i>Lysimachia nummularia</i> L.		.	.	.
<i>Carex disticha</i> Huds.		.	.	.
<i>Equisetum palustre</i> L.		.	+1	.

Supplement to the table. Ch. Ord.: *Typha latifolia* L. 7: +1, *Oenanthe aquatica* (L.) Poir. 10: +1, *Sium erectum* Huds. 13: +2, *Ranunculus lingua* L. 13: +2; Acc.: *Agrostis stolonifera* L. 1: +2, 7: 1.2, *Rumex crispus* L. 2: +1, 10: +1, *Cardamine pratensis* L. 2: 1.2, 12: +1, *Calamagrostis canescens* (Web.) Roth. 5: 2.1, 9: +2, *Valeriana officinalis* L. 6: 1.1, 9: +1, *Mentha arvensis* L. 7: +1, 11: +2, *Filipendula ulmaria* (L.) Maxim. 8: +1, 9: +2, *Solanum dulcamara* L. 10: +2, 14: +2, *Hydrocharis morsus-ranae* L. 13: +2, 14: +2, *Lycopus europaeus* L. 1: +2, *Galium aparine* L. 1: +2, *Ranunculus repens* L. 2: 1.3, *Cirsium arvense* (L.) Scop. 6: +1, *Epilobium hirsutum* L. 7: +1, *Scirpus sylvaticus* L. 7: +1, *Myosotis caespitosa* K. F. Schultz 7: 1.2, *Stellaria palustris* Retz. 7: 1.2, *Poa trivialis* L. 10: +2, *Polygonum mite* Schrank 10: +2, *Scutellaria galericulata* L. 11: +1, *Vicia cracca* L. 12: +1, *Amblystegia cf. kochii* Br. et Schimp. 12: 5.5,

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stagnant water				river foreland,					no tidal influence				P in 101 records
4	5	6	7	8	9	10	11	12	13	14	15	16	
102b	18	84	101	32	95	53	47	40	62	61b	104	111	
IJ	M	R	IJ	HM	L	W	W	W	W	W	IJ	IJ	
15						0	0-5	10	25	30	20-	30-	
											40	50	
4	25	4	20	16	9	200	100	25	9	4	25	3	
40	80	50	100	40	100	95	100	100	90	90	70	100	
—	—	—	—	—	20	1	—	—		40	5	20	
3.5	4.4	3.5	2.2	3.2	4.5	3.3	3.3	5.4	4.3	5.2	2.2	3.5	V
.	+1	+2	1.2	1.3	.	.	.	I
+1	+2	1.2	+2	.	.	+2	+2	1.2	1.2	.	+2	.	IV
+1	.	+1	1.2	.	.	2.2	1.1	+2	+2	.	.	+1	IV
.	+1	.	2.2	+1	1.2	1.2	2.2	+1	IV
.	+2	+1	+2	.	+2	.	+2	III
.	+2	.	+1	.	+2	.	.	III
+1	.	.	.	2.1	2.2	5.5	.	3.3	1.1	2.2	+1	1.1	II
.	.	+2	.	.	+2	+2	+1	.	.	.	1.2	.	II
.	+1	.	.	.	+1	.	II
.	.	.	+1	.	.	.	+2	I
+1	.	+1	2.2	+1	.	.	+2	.	1.2	.	+1	+2	III
+1	.	+1	+1	.	1.2	.	+2	1.1	.	+2	.	+1	II
+1	+2	+2	+2	1.2	.	+2	+1	II
+1	.	.	.	+1	.	+2	1.2	+1	+2	+2	2.2	+2	II
.	+2	.	+2	1.2	1.2	.	.	II
.	.	+1	.	.	.	+2	.	.	1.2	2.2	1.2	+	II
.	+2	.	.	1.2	1.2	.	.	II
.	.	+1	1.2	.	.	+2	1.2	1.2	II
.	1.2	II
.	.	+1	.	.	+1	.	+2	.	+2	.	.	.	II
.	.	1.2	+1	+1	.	+1	I
.	.	.	.	+1	.	+1	+2	+1	+2	.	.	.	I
.	1.2	3.3	+2	+	I
+1	+1	.	1.2	+1	I
.	.	1.2	.	+1	+2	+2	.	+2	I
.	+1	+1	.	I

Potamogeton pusillus L. 15: +.2, *Utricularia* sp. 15: +.1, *Spirodela polyrrhiza* (L.) Schleiden 15: +.2, *Ricciocarpus natans* (L.) Corda 16: 2.

- | | | | |
|-------------------|-----------|--------------------|-----------|
| 1. V 56-110 | 19-7-1956 | 9. V 56-52, | 3-7-1956 |
| 2. QB-S-V 54-388, | 10-9-1954 | 10. D 55-1137, | 13-9-1955 |
| 3. QB-V 54-251, | 24-8-1954 | 11. D 55-1052, | 12-8-1955 |
| 4. S 54-287, | 30-8-1954 | 12. D-DBH 55-1021, | 20-7-1955 |
| 5. V 55-103, | 21-7-1955 | 13. DBH 55-94, | 27-6-1955 |
| 6. QB-S-V 54-127, | 18-8-1954 | 14. DBH 55-137, | 19-7-1955 |
| 7. K 56056, | 9-7-1956 | 15. K 56044, | 21-6-1956 |
| 8. V 55-10, | 11-5-1955 | 16. S 54-313, | 31-8-1954 |

paludosus. Sometimes a record can be made with mainly these two species, but usually they are accompanied by species of the preceding and the succeeding stage.

Along the stagnant former river beds the community usually occurs in less deep water. There it is sometimes in contact or mixed with the *Caricetum acutiformo-paniculatae* (see p. 48). At the land side it may be bordered by the *Macrophorbieto-Alnetum* or the *Valerianeto-Filipenduletum*. Possibly in this habitat the community can maintain itself only if it is mowed regularly.

3.1.3.4. *Comparison between various subdivisions that have been proposed for the Magnocarcion*

In Table 15 some of the *Magnocarcion*-associations that have been accepted in Belgium, Germany and the Netherlands are compared.

The *Caricetum inflato-vesicariae*, introduced by KOCH (1926), is a unit that has no value in the Netherlands. The habitat of *Carex rostrata* and the other so-called characteristic species differ too widely. This has been argued sufficiently by WESTHOFF (1949). The subass. of *Carex rostrata* may better be regarded as a community of the *Caricion*

TABLE
Comparison of some associations belonging to

Lebrun c.s. (1949)		Tüxen (1937), Tüxen
<i>Caricetum inflato-vesicariae</i>		
Ch. <i>Carex disticha</i>	subass. of <i>Carex disticha</i>	(Ch. All.)
(Ch. All.)		<i>Caricetum inflato-</i> Ch. <i>Lysimachia thyrsiflora</i> Ch. <i>Peucedanum palustre</i>
Ch. <i>Carex rostrata</i>	subass. of <i>Carex rostrata</i> subass. <i>typicum</i>	Ch. <i>Carex rostrata</i>
Ch. <i>Carex vesicaria</i>	var. of <i>Carex vesicaria</i>	Ch. <i>Carex vesicaria</i>
Ch. <i>Carex acuta</i>		<i>Caricetum</i> Ch. <i>Carex acuta</i>
(Ch. All.)	var. of <i>Carex acutiformis</i>	Ch. <i>Carex acutiformis</i>
Ch. <i>Carex riparia</i>		Ch. <i>Carex riparia</i>
<i>Caricetum acutiformo-paniculatae</i>		<i>Caricetum</i>
Ch. <i>Carex paniculata</i>		Ch. <i>Carex paniculata</i>

fuscae or as a transition to this alliance. A record answering the description of this community is given here as an example:

Fieldnr. V 55-77. Date 13-7-1955. Wychense Ven (nr. 17). Area 5 sq. m. Cover 20 %.

Carex rostrata Stokes 2.2.; Ch. *Phragmitetea*: *Phragmites communis* Trin. 1.1, *Lysimachia thyrsiflora* L. 1.1, *Galium palustre* L. +.1, *Acorus calamus* L. 1.1, *Ranunculus lingua* L. +.1, *Typha latifolia* L. +.1, *Carex pseudocyperus* L. +.2; Ch. *Caricion fuscae*: *Comarum palustre* L. +.1, *Stellaria palustris* Retz. +.2; Acc.: *Oenanthe fistulosa* L. 1.2, *Metnha aquatica* L. 1.1, *Stachys palustris* L. +.2, *Myosotis scorpioides* L. +.1, *Lycopus europaeus* L. +.1, *Peucedanum palustre* Moench. +.1, *Cardamine pratensis* L. +.1.

The (Belgian) subass. of *Carex disticha* was found along several of the former river beds. The vegetations border the *Carex acuta*-zone on places grazed by cattle. The community consists mainly of *Carex disticha*, and contains also several typical meadow species with often high total estimates and very few species of the *Phragmitetea*. Therefore it is regarded here as a wet meadow community (see p. 62 and Table 22 nrs. 4 and 9).

The subass. (or variant) of *Carex vesicaria* probably corresponds with most Dutch descriptions of the *Caricetum inflato-vesicariae*. The

15

the *Magnocaricion* proposed by different authors

and Preising (1951)	Westhoff c.s. (1946), Westhoff (1949), S.O.L.	
<i>vesicariae</i>	(Ch. All.)	(wet meadow vegetation)
subass. of <i>Carex rostrata</i>		(<i>Caricion fuscae</i> community)
	<i>Caricetum gracilis-vesicariae</i>	
subass. of <i>Carex vesicaria</i>	Ch. <i>Carex vesicaria</i>	
<i>gracilis</i>	Ch. <i>Carex acuta</i>	
	<i>Caricetum acutiformo-paniculatae</i>	
	Ch. <i>Carex acutiformis</i>	
	Ch. <i>Carex riparia</i>	
<i>paniculatae</i>	Ch. <i>Carex paniculata</i>	variants A and B

community should be mesotraphentous, and this is more or less in accordance with its floristic composition in the Netherlands (see p. 43).

The *Caricetum gracilis* of TÜXEN seems to show a strong resemblance to the variant of *Carex acutiformis* of LEBRUN c.s. Some records answering the description of this community were made along some former river beds. See the following example:

Fieldnr. K 56078. Date 28-8-1956. Scherpenzeelse Hank (nr. 114). Area 9 sq.m. Water depth 20 cm. Cover 95 %.

Carex riparia Curt. 3.2, *Carex acuta* L. 2.2; Ch. All.: *Galium palustre* L. 2.2; Ch. Ord.: *Phragmites communis* Trin. 2.2, *Rorippa amphibia* (L.) Besser 1.2, *Phalaris arundinacea* L. 1.2; Acc.: *Hydrocharis morsus-ranae* L. 1.2, *Polygonum amphibium* L. fo. *terrestre* Leyss. 1.2., *Iris pseudacorus* L. 1.2., *Poa palustris* L. 1.2., *Mentha aquatica* L. x *Mentha arvensis* L. 1.2., *Carex disticha* L. +.2., *Senecio paludosus* L. +.2.

The occurrence of the combination of *Carex acuta* and *Carex riparia* can, in our opinion, be explained in the two following ways: 1) On some places in the forelands the silting up and the accumulation of plant remains exercise an equally important function in the succession. Then a habitat comes into existence where both species can flourish. 2) If a former river bed is isolated from the river by a dike, the succession in the water changes from allogenic into autogenic. The soil on the deeper side of the *Carex acuta*-vegetation will gradually be covered by plant remains, and possibly even a floating mat vegetation will try to take its place. In consequence, temporarily a mixture of the old and the new community will be present, and this mixture will maintain itself for some time, especially if the vegetation is mowed regularly. We nowhere found the combination of *Carex acuta* and *C. acutiformis*.

The German *Caricetum paniculatae* and the Belgian *Caricetum acutiformo-paniculatae* correspond probably with our variants A and B in so far as they consist mainly of *Carex paniculata* or (in the latter case only) of *Carex acutiformis* (table 13 e.g. nrs. 2-5, 7-8).

The *Cicuteto-Caricetum pseudocyperus*, in our opinion a *Phragmition*-association, is included by TÜXEN and PREISING (1951) in the *Magnocaricion*. This has been discussed on p. 33.

TÜXEN and PREISING also mention a *Caricetum vulpinae*. TÜXEN (1954) gives a description of the association accompanied by one record. It should be "less wet" than the other associations of the alliance, and occur in river valleys with great fluctuations in the ground water level. *Carex vulpina* should be the only characteristic species.

An example of this community was found along one of the former river beds. It is given here:

Fieldnr. D-K-V 56-1035. Date 6-6-1956. Former river bed in the Banwaard (nr. 29). Area 8 sq.m. Soil: wet grey-brown clay. Water level -1 m. Cover 95 %.

Carex vulpina L. 2.2.; Ch. *Phragmitetea*: *Glyceria maxima* (Hartm.) Holmb. 3.2., *Phalaris arundinacea* L. +.2., *Carex acuta* L. +.2., *Galium palustre* L. +.1.; Ch. *Molinieto-Arrhenatheretea*: *Poa trivialis* L. 3.2., *Equisetum palustre* L. +.2., *Taraxacum officinale* Weber +.1., *Rumex acetosa* L. +.1, *Cardamine pratensis* L. +.2; Ch. *Agropyro-Rumicion*: *Ranunculus repens* L. 1.2, *Alopecurus geniculatus* L. +.2, *Potentilla anserina* L. +.2; Acc.: *Polygonum amphibium* L.

fo. *terrestre* Leyss 1.2, *Eleocharis palustris* (L.) R. et Sch. 1.2, *Stellaria palustris* Retz. +.2, *Myosotis scorpioides* L. +.2, *Caltha palustris* L. +.2, *Trifolium* L. sp. +.1.

In our opinion this record can not be regarded as representing a community belonging to the *Magnocaricion*. The part played by species belonging to other units is too large. This also applies to TUXEN's own record.

Our own subdivision of the *Magnocaricion* has some important advantages. By excluding the communities which form transitions to the wet meadows (vegetations of *Carex disticha* and of *Carex vulpina*) we obtain an alliance consisting of swamp associations only. In the hydrosere they are generally preceded by a *Phragmition*-community and succeeded by some carr or by a *Caricion fuscae*-community. The autogenic succession in stagnant water comprises the *Caricetum elatae comaretosum* (mesotraphentous) or the *Caricetum acutiformo-paniculatae* (slightly meso- to eutraphentous). The *Caricetum gracilis-vesicariae* is the community growing on firm mineral soils along the border of pools. Possibly it must be divided into two subassociations. The first is more mesotraphentous, with *Carex vesicaria* and species of the *Caricion fuscae*, and occurs along stagnant water on a humic clay soil. The second is purely eutraphentous, dominated by *Carex acuta*, and occurs especially in the forelands on a purely mineral soil.

The system of LEBRUN c.s. has the advantage that frequently occurring combinations, by others considered as transitions, all may be included in the large *Caricetum inflato-vesicariae*. The system of TUXEN and PREISING makes a clear division between a mesotraphentous *Caricetum inflato-vesicariae* and an eutraphentous *Caricetum gracilis*. Maybe both systems are appropriate in their respective regions. In the Netherlands, however, the *Caricetum acutiformo-paniculatae* with three characteristic *Carices* can not be neglected, and this fact determines the main differences between our system and the other two.

3. 1. 3. 5. *Thelypterideto-Phragmitetum* Kuiper 1957 (Table 16)

KUIPER (1957, see also 1958) introduced a new association of the *Phragmitetalia*: the *Thelypterideto-Phragmitetum*. Up till now he himself did not describe the community, but he refers to a table of MEIJER (1955) indicated as "vegetations of *Dryopteris thelypteris*". The only characteristic species is *Dryopteris thelypteris*. The community may participate in the hydrosere of stagnant, eutrophic fresh water on exposed spots, and is found behind the *Scirpeto-Phragmitetum typicum*. KUIPER is not yet sure whether the association belongs to the *Phragmition* or to the *Magnocaricion*.

In three former river beds a vegetation with much *Dryopteris thelypteris* was found. It is, however, relatively poor in species. The place of the vegetations is more or less in accordance with KUIPER's data. All three records are given in the table. Characteristic species of the *Phragmition*, the *Magnocaricion* and the (meso-oligotraphentous) *Scheuchzerio-Caricetea* are mentioned separately.

TABLE 16

<i>Thelypterideto-Phragmitetum</i>			
nr. of record	1	2	3
nr. of former river bed	6	17	118
river	M	M	IJ
area (sq. m)	6	3	25
cover (%)	25	80	80
Ch. Ass. <i>Dryopteris thelypteris</i> (L.) A. Gray	2.2	3.2	3.2
Ch. Phron. <i>Typha angustifolia</i> L.	+1	.	+2
<i>Typha latifolia</i> L.	+2
<i>Carex pseudocyperus</i> L.	+1
Ch. Mg. <i>Lysimachia thyrsiflora</i> L.	2.2
<i>Galium palustre</i> L.	+2
<i>Carex hudsonii</i> A. Benn.	+2	.
Ch. Ord. <i>Phragmites communis</i> Trin.	4.4	3.2
<i>Sparganium erectum</i> L.	+1	.	+2
<i>Rumex hydrolapathum</i> Huds.	+1	.
Ch. S.-C. <i>Menyanthes trifoliata</i> L.	1.1	.	2.2
<i>Comarum palustre</i> L.	+1	.	.
<i>Epilobium palustre</i> L.	1.2
<i>Carex rostrata</i> Stokes	+1	.	.
Acc. <i>Lycopus europaeus</i> L.	+1	+1
<i>Mentha aquatica</i> L.	+1	1.2
<i>Scutellaria galericulata</i> L.	+1	+1
<i>Equisetum fluviatile</i> L.	1.2	.	.
<i>Calamagrostis canescens</i> (Web.) Roth	2.2	.

Supplement to the table. Acc.: *Lemna minor* L. 1: 1, *Peucedanum palustre* (L.) Moench. 2: +1, *Lysimachia vulgaris* L. 2: +2, *Solanum dulcamara* L. 2: +1, *Stachys palustris* L. 2: +2, *Dryopteris cristata* (L.) A. Gray 3: +2, *Cirsium palustre* (L.) Scop. 3: +1, *Marchantia* sp. 3: +1, *Brachythecium* sp. 3: +2.

1. V 55-49, 27-6-1955
2. V 55-82, 13-7-1955
3. D-K-V 56-1016, 31-5-1956

4. Class MOLINIETO-ARRHENATHERETEA Tüxen 1937

4. 1. ORDER MOLINIETALIA COERULEAE Koch 1926

4. 1. 1. Alliance Filipendulo-Petasition Braun-Blanquet 1947

In 1947 BRAUN-BLANQUET separated the *Filipendulo-Petasition* from the alliance *Molinion coeruleae* Koch 1926. The new alliance, observed in N.W. and S. Germany (see TUXEN, 1955; OBERDORFER, 1957) and also mentioned by DUVIGNEAUD (1949), seems to be acceptable in the Netherlands too (see SEGAL and WESTHOFF, 1959).

In the Netherlands the *Molinion* comprises four associations. After a complete revision of the classes *Molinieto-Arrhenatheretea* and *Scheuchzerio-Caricetea fuscae* (which certainly is necessary, see LEBRUN c.s.,

1949; DUVIGNEAUD, 1949), none of these four would be left in it. According to SEGAL and WESTHOFF (1959) the *Cirsieto-Molinietum* might be transferred to the *Eriophorion latifolii*. This probably holds for the *Juncetum acutiflori* too. The two other communities, the *Valeriano-Filipenduletum* and the *Association of Sonchus paluster*, may be regarded belonging to the *Filipendulo-Petasition* (see also DUVIGNEAUD, 1949).

If this is accepted, the alliance would merely consist of "replacing-communities" of carrs (*Alnetum glutinosae*, *Salicion* and *Alnion glutinoso-incanae*). Their habitat generally would come into existence by the cutting down of the trees, or else by an artificial heightening of the substrate. See e. g. WESTHOFF (1949) and Waterland (1954). A natural factor which prevents the growth of trees and shrubs, may be ice drift (ZONNEVELD, 1960).

Although future changes are not excluded, we propose for the moment the following species as characteristic (within the formation) of the *Filipendulo-Petasition* in the Netherlands: *Valeriana officinalis*, *Epilobium hirsutum*, *Eupatorium cannabinum* and *Angelica sylvestris*.

4. 1. 1. 1. *Valeriano-Filipenduletum* Westhoff 1949 (Table 17)

According to the Synopsis and WESTHOFF (1949) the characteristic species of the association are: *Valeriana officinalis*, *Hypericum maculatum*, *Euphorbia palustris*, *Stachys palustris*, *Crepis paludosa*, *Veronica longifolia*, *Lathyrus paluster* and *Festuca arundinacea*. Some alterations are recommendable. *Valeriana officinalis* also occurs in the *Association of Sonchus paluster* and must be regarded as a characteristic species of the alliance.

Supplement to table 17. Ch. All.: *Eupatorium cannabinum* L. 1: +.1; Ch. Cl.: *Holcus lanatus* L. 1: +.2, 3: +.2, *Dactylis glomerata* L. 12: +.2, 14: +.2, *Lathyrus pratensis* L. 8: 1.2; Acc.: *Viburnum opulus* L. 1: +.2, 4: +.1, *Lychnis flos-cuculi* L. 1: 1.1, 8: +.2, *Ranunculus repens* L. 1: +.1, 14: 3.2, *Rubus idaeus* L. 2: +.2, 3: 1.2, *Lotus uliginosus* Schkuhr. 2: +.2, 4: +.1, *Galium aparine* L. 3: +.2, 12: +.1, *Epilobium parviflorum* Schreb. 4: +.1, 8: +.2, *Mentha arvensis* L. 5: +.1, 7: 2.2, *Stellaria palustris* Retz. 5: +.2, 7: 1.2, *Mentha aquatica* L. 6: +.1, 10: +.2, *Potentilla reptans* L. 10: +.2, 11: +.1, *Rubus* sp. 3: +.2, *Scirpus sylvaticus* L. 3: 1.2, *Lycopus europaeus* L. 3: +.2, *Galeopsis tetrahit* L. 3: +.2, *Cirsium palustre* (L.) Scop. 4: 2.1, *Carex pseudocyperus* L. 4: 2.2, *Carex elongata* L. 4: +.1, *Salix cinerea* L. 4: +, *Alnus glutinosa* (L.) Gaertn. 4: 1, *Sambucus nigra* L. 4: +, *Athyrium filix-femina* (L.) Roth 4: 1.2, *Stellaria alsine* Grimm. 4: +.1, *Rorippa amphibia* (L.) Besser 5: +.1, *Sium latifolium* L. 5: +.1, *Scirpus lacustris* L. ssp. *lacustris* 6: +.1, *Rumex hydrolapathum* Huds. 6: +.2, *Trifolium repens* L. 7: +.1, *Achillea ptarmica* L. 8: +.2, *Rumex obtusifolius* L. 9: +.1, *Myosotis caespitosa* K. F. Schultz 10: +.2, *Salix triandra* L. 10: +.2, *Artemisia vulgaris* L. 12: +.1, *Tanacetum vulgare* L. 12: +.2, *Cirsium arvense* (L.) Scop. 13: +.1, *Myosotis scorpioides* L. 13: +.1, *Rumex conglomeratus* Murr. 13: +.1, *Typha latifolia* L. 13: +.2, *Plantago major* L. 14: +.2, *Festuca gigantea* (L.) Vill. 14: +.2, *Lolium perenne* L. 14: +.2, *Senecio jacobaea* L. 14: +.2.

- | | | | |
|------------------|-----------|--------------------|-----------|
| 1. V 55-68, | 30-6-1950 | 8. D-DBH 55-1028, | 20-7-1955 |
| 2. V 55-57, | 29-6-1955 | 9. D-V 56-1004, | 23-5-1956 |
| 3. K 56092, | 5-9-1956 | 10. K 56050, | 27-6-1956 |
| 4. V 55-43, | 27-6-1955 | 11. QB-S-V 54-362, | 6-9-1954 |
| 5. D 55-1114, | 31-8-1955 | 12. V 55-137, | 5-8-1955 |
| 6. QB-S-V 54-54, | 3-8-1955 | 13. QB-S-V 54-255, | 25-8-1954 |
| 7. D 55-1095, | 24-8-1950 | 14. V 56-125, | 20-7-1956 |

<i>Valerianeto-Filipenduletum</i>		juncetosum			
		mesotrophic			
		stagnant water			
nr. of record		1	2	3	4
nr. of former river bed		12	11a	11h	7
river		M	M	M	M
area (sq. m)		4	3	12	100
cover (%)			90	100	95
Ch. Ass.	Filipendula ulmaria (L.) Maxim.	+3	4.4	4.2	2.2
	Thalictrum flavum L.
D. junc.	Juncus effusus L.	+2	+2	+2	2.2
	Juncus conglomeratus L.	+1	+2	.	.
D. sen.	Senecio paludosus L.
	Polygonum amphibium L. fo. terrestre Leyss.
	Lysimachia nummularia L.
D. her.	(Ch. Cl.) Heracleum sphondylium L.
	(Ch. All.) Epilobium hirsutum L.
	Anthriscus sylvestris Hoffm.
	Agrostis stolonifera L.
not junc.	Phalaris arundinacea L.
	Phragmites communis Trin.
	Symphytum officinale L.
	(Ch. Cl.) Vicia cracca L.
	Glyceria maxima (Hartm.) Holmb.
not sen.	(Ch. All.) Angelica sylvestris L.	+1	.	+1
not her.	Lysimachia vulgaris L.	+1	+1	1.2	.
	Calamagrostis canescens Roth.	3.3	+2	.
Ch. All.	Valeriana officinalis L.	3.2	.	.	4.3
Ch. Cl.	Poa trivialis L.	2.2	.	.	.
	Cardamine pratensis L.
Acc.	Rubus caesius L.	+1	.	2.2
	Lythrum salicaria L.	+1	.	+2	.
	Iris pseudacorus L.	+1	.	+2	.
	Stachys palustris L.	+2	.
	Calystegia sepium R. Br.	+1	.	2.2	.
	Urtica dioica L.	2.2	.
	Carex acuta L.
	Galium palustre L.	1.1	.	.	+2
	Glechoma hederarcea L.	+1	.	.	.
	Equisetum palustre L.	+1	+2	.
	Solanum dulcamara L.	1.1
	Rumex crispus L.	+1	.	.	.
	Equisetum fluviatile L.

senecietosum							subass. of Heracleum			junc.	sen.	her.	tot.
eutrophic										P in 5 records	P in 30 records	P in 3 records	P in 46 records
stagnant water or river foreland, no tidal influence							tidal influence						
5	6	7	8	9	10	11	12	13	14				
86	36	44	40	64	101	99	21	26	96	V	III IV	2	III III
R	W	W	W	W	IJ	IJ	M	M	L				
100		50	400	4	25	12	6	6	3				
90	50	100	100	90	100	80	80	80	100				
2.2	2.3	3.3	4.4	1.2 2.2	+2 +2	4.4 +2	.	+2 .	2.2 .	V II	IV II II	1	III I I I
.				
1.2 +2 .	.	1.2 .	1.2 +1 +2	.	+1 +2 .	1.2 +2 .	.	+2 .	.				
.	+1	.	+2	+2				
.	.	.	+1	.	+1	.	1.1 .	+2 3.3 +1 .	2.2 .	I	3 1 1 1	I I I I	
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4.3 2.2 2.2 .	+2 +1 .	2.2 3.2 .	+2 . 2.2 .	+2 +1 +1 .	+2 . 1.1 +2 2.2	+1 +1 +2 .	4.4 +1 .	+2 1.1 +2 .	+2 . 1.2 .				
.	1.1				
							.	+1	+2	II		2	I
2.2 .	.	+2 .	1.2 .	1.2 4.2	.	.				III II	III II		III II
.	.	.	+2	.	2.2	+2	2.2	+2	+2	III	III	3	III
.	.	.	+2 +2	.	2.2	II	II I		I I
2.2 +2 +2 2.2 .	.	2.2 .	+3 +2 1.2 +2	.	2.2 +1 +2 .	+2 +2 .	.	2.3 +2 .	.	III II II I III I	III III III III II II I II I I I I	1 1 1 2 2 1 1 1 1 1	III III III III II I I I I I I I I I
.	.	+2	1.2	.	+1	+2	1.2 +1 .	1.2 +2 +2	.	II I III I	II II I I I I I I I I I	1 1 1 2 2 1 1 1 1 1 1 1 1	I I I I I I I I I I I I I I I
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Stachys palustris must be eliminated: it is just as important in the *Phragmitetea*. *Thalictrum flavum* and *Filipendula ulmaria* occur in the *Cirsieto-Molinietum*, but undoubtedly have their optimum in the *Valerianeto-Filipenduletum*. Moreover, it seems better to transfer the *Cirsieto-Molinietum* to the *Eriophorion latifolii*, and if this is done, they may be accepted as characteristic species of the *Valerianeto-Filipenduletum*.

The association shows a remarkable variability which corresponds more or less with the differences in the undergrowth of the replaced carrs. Along the former river beds we found three communities which must be regarded as subassociations. In the Dutch literature, moreover, the presence of two other subassociations (though not described as such; see also WESTHOFF, 1951 a) is indicated, viz. one along the broads in the Haf district, and one along brooks.

In table 18 are listed all species which in one way or another are useful as differential species. The characteristic species are indicated separately. Remarks in the literature concerning the occurrence of *Crepis paludosa* and *Hypericum maculatum* are not clear. Anyhow, these species do not occur in the subassociations *juncetosum* and *senecietosum* and the subass. of *Heracleum*.

The subassociations of the broads and the brooks will be left out of consideration now. They are not found along the former river beds. See the publications and tables dealing with the broads: VAN ZINDEREN BAKKER (1942, 1947), DE JONG (1943), WESTHOFF (1949), REYNOLDERS (1952), VAN DIJK and WESTHOFF (1955), MEIJER (1955); dealing with the brooks: KLINKENBERG (1943).

In Belgium, where the association occurs also, HEINEMANN (see LEBRUN c.s., 1949) distinguishes four subassociations viz. 1) with *Carex disticha*, 2) *typicum*, 3) with *Holcus lanatus*, 4) with *Urtica dioica*. This subdivision corresponds in no way with ours. Maybe it can be applied in the Netherlands too, but for the moment our subdivision seems better founded.

Subass. *juncetosum* subass. nov.

This subassociation was found along the mesotrophic former river beds, on a peaty soil. It replaces the mesotraphentous variant of the *Alnetum glutinosae*, and may border the *Caricetum acutiformo-paniculatae*.

DAMMAN (1953) gives two records of this community made in the same region as ours.

Subass. *senecietosum* subass. nov.

Outside the tidal area the forelands have their own subassociation of the *Valerianeto-Filipenduletum*. There it replaces a foreland *Salicion*-community. In some cases not the cutting down of the trees but the ice drift in winter may prevent the development of a marsh-carr.

Many of the former river beds with stagnant and eutrophic, fresh water, found inside the dikes, have this community along their borders. There it is a relic from the situation before the dike was constructed, and usually is preserved by mowing. It corresponds with

TABLE 18

<i>Subassociation</i>	juncetum	broads	brooks	senecietum	of Heracleum
<i>Characteristic and differential species</i>					
Ch. <i>Crepis paludosa</i>
Ch. <i>Hypericum maculatum</i>
<i>Juncus effusus</i>	x
<i>Juncus conglomeratus</i>	x
<i>Lotus uliginosus</i>	x	X	.	.	.
<i>Calamagrostis canescens</i>	x	x	x	x	.
<i>Lysimachia vulgaris</i>	x	x	x	x	.
Ch. <i>Filipendula ulmaria</i>	x	x	x	x	x
<i>Angelica sylvestris</i>	x	x	x	.	x
<i>Scutellaria galericulata</i>	x	x	.	x
<i>Vicia cracca</i>	x	x	x	x
Ch. <i>Thalictrum flavum</i>	x	x	x	x
<i>Symphytum officinale</i>	x	x	x	x
<i>Phragmites communis</i>	x	x	x	x
<i>Glyceria maxima</i>	x	x	x	x
<i>Phalaris arundinacea</i>	x	x	x
Ch. <i>Euphorbia palustris</i>	x	.	.	.
Ch. <i>Lathyrus paluster</i>	x	.	.	.
<i>Succisa pratensis</i>	x	.	.	.
Ch. <i>Veronica longifolia</i>	x	.	.
<i>Achillea ptarmica</i>	x	.	.
<i>Polygonum amphibium</i>					
fo. <i>terrestre</i>	x	.
<i>Senecio paludosus</i>	x	.
<i>Lysimachia nummularia</i>	x	.
<i>Rubus caesius</i>	x	.	.	x	x
<i>Heracleum sphondylium</i>	x
<i>Anthriscus sylvestris</i>	x
Ch. <i>Festuca arundinacea</i>	x
<i>Cardamine amara</i>	x
<i>Agrostis stolonifera</i>	x
<i>Epilobium hisutum</i>	x

carrs belonging to the *Salicion* or to the *Alion glutinoso-incanae* and usually borders the *Caricetum gracilis-vesicariae*.

Along former river beds which have been isolated very long ago from the river, and which are found in places where in the surrounding soil the profile-formation has reached an advanced stage, *Angelica sylvestris* and *Eupatorium cannabinum* (both lacking in the subass.

senecietosum) may occur. Eight records with these species were left out of account in the subdivision of the association.

Subass. of *Heracleum Zonneveld* 1960

ZONNEVELD described a provisional subassociation occurring in the tidal area. It has quite a number of differential species, and its habitat totally differs from that of the other subassociations. Therefore we propose to accept it as a distinct subassociation.

The community was found along a number of former river beds with tidal influence. There it replaces a tidal variant of the *Salicion*. Only three records were made, which are all three included in the table. The differential species and the species not occurring in this community have not been taken from our own records, but from ZONNEVELD's table.

4. 1. 1. 2. Association of *Sonchus paluster* Vlieger et Van Zinderen Bakker 1942 (Table 19)

VLIEGER and VAN ZINDEREN BAKKER (see VAN ZINDEREN BAKKER, 1942) described a community of *Sonchus paluster* which they did not (yet) propose as an association. In our opinion two of the three records which are given by them must be referred to the *Valerianeto-Filipenduletum*, but the third represents a community which afterwards was mentioned by others under the name "community of *Sonchus paluster*". See VAN ZINDEREN BAKKER (1947), WESTHOFF (1949), REYNDERS (1952), MEIJER (1953), Waterland (1954). This same community was found along the halinic former river beds with stagnant water.

In our opinion the community deserves the status of an association. It is sufficiently distinct from the *Valerianeto-Filipenduletum*, the community which it resembles most, by characteristic species of its own, and by the very particular character of its habitat. There is, however, a transition between the two.

Sonchus paluster is a characteristic species, and this applies also to *Althaea officinalis*, as suggested by the Synopsis. *Epilobium hirsutum* (also suggested), however, is much more common in the subass. of *Heracleum* of the *Valerianeto-Filipenduletum*. *Eupatorium cannabinum* may be used as a differential species to distinguish it from the subassociations of the *Valerianeto-Filipenduletum* occurring along stagnant waters. Two differential species by which it differs from the whole of the *Valerianeto-Filipenduletum* are *Sium erectum* and *Carex riparia*; it differs from this association also by the absence of *Calamagrostis canescens*, *Lysimachia vulgaris*, *Vicia cracca* and *Glyceria maxima*. Apart from *Eupatorium cannabinum*, a high presence is also shown by *Poa trivialis*, *Angelica sylvestris*, *Phragmites communis* and *Mentha aquatica*.

The association has its optimum development along mesohalinic stagnant water. Only there *Althaea officinalis* is present, whereas *Valeriana officinalis* is lacking. The community also occurs along oligohalinic waters. There it may be mixed with the *Valerianeto-Filipenduletum* or it may be bordered by this community on the land side.

TABLE 19

Association of Sonchus paluster

nr. of record	1	2	3	4
nr. of former river bed	76	74	74	72
river	D	D	D	D
mg Cl/l in open water	2000	672	672	1252
area (sq. m)	4	6	500	16
cover (%)	100	100	100	100
Ch. Ass. <i>Sonchus paluster</i> L.	+2	2.2	2.2	1.2
Ch. All. <i>Eupatorium cannabinum</i> L.	5.5	.	1.2	4.5
<i>Valeriana officinalis</i> L.	2.2	3.2	4.3
<i>Epilobium hirsutum</i> L.	+2	.	.	.
<i>Filipendula ulmaria</i> (L.) Maxim.	+2	.
D. Ass. <i>Carex riparia</i> Curt.	2.2	.	.	2.2
Acc. <i>Phragmites communis</i> Trin.	3.2	4.5	4.5	1.2
<i>Poa trivialis</i> L.	3.2	+2	.
<i>Rumex hydrolapathum</i> Huds.	+2	.	.
<i>Cirsium palustre</i> (L.) Scop.	+2	.	.
<i>Festuca arundinacea</i> Schreb.	+2	.	.
<i>Epilobium parviflorum</i> Schreb.	1.2	.	.
<i>Typha angustifolia</i> L.	1.2	.	.
<i>Carex acutiformis</i> Ehrh.	3.2	.
<i>Galium palustre</i> L.	+2	.
<i>Symphytum officinale</i> L.	+2	.
<i>Urtica dioica</i> L.	+2
<i>Rumex conglomeratus</i> Murray	+2
<i>Pulicaria dysenterica</i> (L.) Bernh.	+2
<i>Rubus caesius</i> L.	1.2

1. V 56-150, 6-8-1956
2. V 56-139, 31-7-1956
3. V 56-141, 31-7-1956
4. V 56-134, 26-7-1956

The association is generally preceded by the *Scirpetum triquetri et maritimi typhetosum*. According to our data, however, the *Caricetum acutiformo-paniculatae* (variant D) may be interposed between them. A similar zonation was also observed in some broads by VAN ZINDEREN BAKKER (1947). Possibly this zonation will be found only along oligohalinic waters. The drier side of the community may replace a eutraphentous variant of the *Alnetum glutinosae*.

4. 1. 1. 3. *Community of Epilobium hirsutum and Phalaris arundinacea*
Zonneveld 1960 (Table 20)

ZONNEVELD (1960) distinguishes a community of *Epilobium hirsutum* and *Phalaris arundinacea* found in the Biesbosch. It is situated between the *Scirpetum triquetri et maritimi senecietosum* and the *Valerianeto-Filipenduletum* subass. of *Heracleum*. The community has no characteristic species of its own, whereas characteristic species of the *Phragmition* and the *Molinion* (*Filipendulo-Petasition*) are equally important. Without

TABLE 20

Community of Epilobium hirsutum and Phalaris arundinacea

nr. of record	1	2	P in 6 records
nr. of former river bed	94	65	
river	L	W	
area (sq. m)	6		
cover (%)	100	80	
<hr/>			
Phalaris arundinacea L.	2.2	5.5	V
Stachys palustris L.	5.5	1.2	V
Phragmites communis Trin.	.	+1	III
Senecio paludosus L.	+2	+1	II
Urtica dioica L.	1.2		II
Calystegia sepium (L.) R. Br.	.	1.2	II
Rorippa amphibia (L.) Besser	+2	.	I
Sium latifolium L.	+2	.	I

1. V 56-119, 19-7-1956

2. S 54-205, 16-8-1954

TABLE 21

Phragmites-consociation

nr. of record	1	2	3	4	5	6
nr. of former river bed	96	66	70	71	71	66
river	L	Me	OM	OM	OM	Me
area (sq. m)	25	16	4	9	25	25
cover (%)	100	100	100	100	100	100

Species of the Phragmites-consociation

Phragmites communis Trin.	5.5	5.5	5.5	5.5	4.3	5.5
Caltha palustris L.	+2	2.2	5.5	2.2	+2	2.2
Cardamina amara L.	3.2	2.2	3.2
Ranunculus ficaria L.	+2	2.2	.
Poa trivialis L.	1.2	.	2.2
Leucorum aestivum L.	+2	.	.

Other species

Polygonum amphibium L.						
fo. terrestre Leyss.	+2	.	.	.	2.2
Valeriana officinalis L.	+2	.
Calystegia sepium (L.) R. Br.	+1	.
Phalaris arundinacea L.	1.2	2.2
Galium aparine L.	+2	+2
Urtica dioica L.	+2
Equisetum arvense L.	+

1. V 56.129, 20-7-1956

2. V 56-36, 27-6-1956

3. D-K-V 56029, 8-6-1956

4. D-K-V 56-41, 7-6-1956

5. D-K-V 56-40, 7-6-1956

6. D-K-V 56-191, 5-6-1956

taking a definite decision, ZONNEVELD is inclined to reckon it to the *Phragmition*.

In two of the former river beds with tidal influence a community was found resembling the just mentioned one, not only in composition but also with regard to its position. Two records are given as examples.

4. 1. 1. 4. *Phragmites-consociation* Zonneveld 1960 (Table 21)

In the reed swamps and in the adjacent communities in the tidal area *Phragmites communis* may come to absolute dominance. This is caused either by its enormous competing force or by human interference, mainly regular mowing. The few species occurring in these very dense *Phragmites*-fields have their flowering period early in spring or do not flower at all in this habitat.

ZONNEVELD (1960) describes the dominance of *Phragmites* in the Biesbosch. There the *Phragmites*-fields may occupy the place of the *Scirpeto-Phragmitetum calthetosum*, the community of *Epilobium hirsutum* and *Phalaris arundinacea* and the *Valerianeto-Filipenduletum* subass. of *Heracleum*. The floristic differentiation of the *Phragmites*-fields does not correspond with the various communities which they replace. Therefore it is not allowed to designate it as the *Phragmites*-facies of a special community. Moreover the character of these vegetations hardly permits to describe them as vegetation units in the sense of BRAUN-BLANQUET. Therefore ZONNEVELD designates the whole group of *Phragmites*-fields as the *Phragmites-consociation*, and divides it in sociation-groups and sociations in the sense of DU RIETZ (1930).

Vegetations representing this consociation play an important part in a number of former river beds in the tidal area. As in the Biesbosch they occupy in the first place the basins. The records nrs. 2, 1 and 3 represent the *Phragmites-Caltha-sociation*, respectively in its normal form, in one that is poorer in *Caltha* and in one that is richer in *Caltha*. These sociations replace parts of the *Scirpeto-Phragmitetum calthetosum*, the *Scirpetum triquetri et maritimi senecietosum* and even transitions to the community of *Epilobium hirsutum* and *Phalaris arundinacea*. The records nrs. 4, 5 and 6 are probably more or less transitional between one of ZONNEVELD's sociations and the communities they replace.

In only one of the former river beds, viz. the Kooigat near Rhoonse Veer (nr. 71), *Leucojum aestivum* was found. This species, which is very rare in the Netherlands, occurs also in other places along the Oude Maas (VAN LEEUWEN, 1954), but is absent in the Biesbosch. Along the Kooigat its occurrence is restricted to the vegetations of the *Phragmites-consociation*. Though not numerous, the plants had flowers and fruits, and made a healthy impression.

5. WET MEADOW VEGETATIONS (Table 22)

Many former river beds are surrounded by meadows. These meadows may occur in places which under fully natural conditions would be occupied either by a carr, or by a vegetation of the *Valerianeto-Filipenduletum* or one of the *Caricetum gracilis-vesicariae*.

TABLE 22

wet meadow vegetations															P in 40 records
nr. of record	1	2	3	4	5	6	7	8	9						
nr. of former river bed.	104	23	84	103	116d	123	91	102b	5						
river	IJ	M	R	IJ	IJ	IJ	L	IJ	M						
area (sq. m)	12	4	0,8	3	4	12	9	4	4						
cover (%)	100	70	100	100	90	100	100	50	40						
<i>Ch. Ass. of Rumex crispus and Alopecurus geniculatus</i>															
<i>Lysimachia nummularia</i> L.	+1	1.1	+1	+2	+2						
<i>Carex hirta</i> L.	+2	.	2.2	+1	.						
<i>Potentilla reptans</i> L.	+2						
<i>Rorippa sylvestris</i> (L.) Besser	1.1						
<i>Ch. All. Agropyro-Rumicion crispis and Cl. Plantaginea majoris</i>															
<i>Ranunculus repens</i> L.	2.2	1.2	1.1	1.2	1.1	1.2	2.2	.	.						
<i>Agrostis stolonifera</i> L.	1.2	2.2	.	3.5	5.5	.	.	.						
<i>Potentilla anserina</i> L.	+2	+1	1.2	+1	2.3						
<i>Rumex crispus</i> L.	+2	+1	.	+2						
<i>Lolium perenne</i> L.	2.2						
<i>Leontodon autumnalis</i> L.	1.1						
<i>Plantago major</i> L.	+2						
<i>Sagina procumbens</i> L.	1.2						
<i>Ch. All. Magnocaricion elatae and Cl. Phragmitetea</i>															
<i>Galium palustre</i> L.	+2	.	1.2	+2	1.2	2.2	+2	.	.						
<i>Phalaris arundinacea</i> L.	1.2	.	.	+2	+1	.	+2	1.1	.						
<i>Glyceria maxima</i> (Hartm.) Holmb.	+1	+1	.	3.2	.	.	.						
<i>Carex acuta</i> L.	+2	.	.	+2	.	.						
<i>Ch. Cl. Molinieto-Arrhenatheretea</i>															
<i>Equisetum palustre</i> L.	1.2	+1	+1	.	1.1	+2	+1	.	.						
<i>Cardamine pratensis</i> L.	+1	+2	.	+2	.	.						

<i>Poa trivialis</i> L.	2.2	.	.	4.2	.	.	3.1	II
<i>Rumex acetosa</i> L.	1.2	+1	+	II
<i>Taraxacum officinale</i> Weber	+1	+1	.	.	.	II
<i>Thalictrum flavum</i> L.	+1	.	.	.	+2	I
<i>Vicia cracca</i> L.	+1	.	.	+2	.	+	I

Other species

<i>Carex disticha</i> Huds.	3.2	.	.	3.2	1.2	.	2.2	2.2	2.1	III
<i>Polygonum amphibium</i> L. fo. <i>terrestre</i> Leyss.	1.2	+1	+2	1.2	.	.	1.2	+2	+1	III
<i>Mentha aquatica</i> L.	1.2	+2	2.2	+2	2.2	1.1	.	III
<i>Eleocharis palustris</i> (L.) R. et Sch.	1.2	.	+2	1.1	+2	2.2	.	.	.	III
<i>Myosotis scorpioides</i> L.	+2	+	+	.	III
<i>Trifolium repens</i> L.	1.2	2.1	+1	+1	1.1	.	.	.	3.3	II
<i>Juncus articulatus</i> L.	1.2	+2	.	+	+2	.	.	1.2	II
<i>Oenanthe fistulosa</i> L.	+2	+1	+2	1.2	.	.	.	II
<i>Stellaria palustris</i> Retz.	+	+	+	+2	+	+	.	II
<i>Equisetum fluviatile</i> L.	1.1	.	1.2	+2	.	.	.	II
<i>Caltha palustris</i> L.	+	+	.	1.2	.	II
<i>Poa palustris</i> L.	1.1	1.2	II
<i>Poa pratensis</i> L.	2.2	2.2	.	I

Supplement to the table. Ch. *Phragmitetea*: *Phragmites communis* Trin. 6: +1, 7: 2.1, *Rorippa amphibia* (L.) Besser 1: +1, *Typha latifolia* L. 3: 1.1, *Glyceria fluitans* (L.) R. Br. 5: +, *Rumex hydrolapathum* Huds. 6: +2; Ch. *Molinieto-Arrhenatheretea*: *Prunella vulgaris* L. 2: +1, 8: +2, *Juncus conglomeratus* L. 2: 1.2, 5: +2, *Cerastium caespitosum* Gilib. 3: +1, 8: +2, *Lysimachia vulgaris* L. 7: +1, 8: 2.3, *Festuca pratensis* Huds. 8: 1.2, 9: +1, *Lathyrus pratensis* L. 8: 1.1, 9: +1, *Valeriana officinalis* L. 1: +2, *Chrysanthemum leucanthemum* L. 2: 2.1, *Lotus uliginosus* Schkuhr. 2: +1, *Ranunculus acer* L. 2: +1, *Achillea ptarmica* L. 2: +1, *Cynosurus cristatus* L. 2: 1.1, *Filipendula ulmaria* (L.) Maxim. 8: 1.2, *Alopecurus pratensis* L. 9: +1, *Holcus lanatus* L. 9: +1; other species: *Deschampsia caespitosa* (L.) P. B. 1: +2, 7: +2, *Lycopus europaeus* L. 1: +1, 8: +1, *Mentha arvensis* L. 1: +2, 2: 1.1, *Carex otrubae* Podp. 2: +1, 5: +2, *Euphrasia odontites* L. 3: 2.1, 5: 1.2, *Lythrum salicaria* L. 5: +1, 7: +1, *Glechoma hederacea* L. 1: +2, *Stellaria graminea* L. 1: +1, *Carex nigra* (L.) Reichard 1: +1, *Plantago lanceolata* L. 2: +1, *Senecio jacobaea* L. 2: +1, *Scutellaria galericulata* L. 3: +1, *Calliergonella cuspidata* (Hedw.) Loeske 5: +, *Juncus compressus* Jacq. 5: +2, *Senecio paludosus* L. 7: 1.2, *Symphytum officinale* L. 7: +2, *Lychnis flos-cuculi* L. 7: +2, *Rhinanthus glaber* Lam. 7: +1, *Equisetum arvense* L. 7: +1, *Iris pseudacorus* L. 8: +1.

- K 56037, 20-6-1956
- S 54-249, 24-8-1954
- QB-S-V 54-137, 18-8-1954
- K-V 56035, 30-5-1956
- QB-S-V 54-347, 2-9-1954
- V 56-64, 12-7-1956
- V 56-13, 12-6-1956
- S 54-289, 30-8-1954
- V 55-35, 17-6-1955

Though a number of species of the replaced communities may be present, the flora of the wet meadows has a specific composition. In this connection three species deserve our special attention, viz. *Oenanthe fistulosa*, *Poa palustris* and *Carex disticha*. In the Synopsis and in other papers too they are considered to be characteristic species of the *Phragmitetalia* or of one of its lower units. In our opinion these species have their optimum development in wet meadow communities not belonging to the *Phragmitetalia* (see also p. 23, 39 and 47).

Constant species which may reach high abundances are *Carex disticha*, *Agrostis stolonifera* and *Eleocharis palustris*. It can be seen from the table that there are other species which are either constant or which may reach high abundances. It also appears that there is a great variability in the floristic composition. It is not possible to find any correlation between the presence or absence of a species or a group of species and one of the environmental factors that could be studied at the time the records were made. This is not surprising, for there are a number of other factors which may influence or even dominate the effect of the latter. TÜXEN (1950) and OBERDORFER (1957) state that in river forelands the composition of some meadow communities may vary greatly from year to year according to differences in the length of the inundation period. Other factors of great importance that were not investigated, are grazing and mowing (see VAN WOERDT and DE VRIES, 1948).

It is not possible to identify all records with one of the vegetation units that so far have been described and that are acceptable to us. Certainly, a number of our records agree with the *Caricetum inflatovesicariae* subass. *Carex disticha* (see a record by VANDEN BERGHEN, 1952 a), but we prefer to exclude this possibility (see p. 47). The greater part of the records, however, shows affinity to the *Association of Rumex crispus and Alopecurus geniculatus*. This association belongs to the *Agropyro-Rumicion crispi*, an alliance of the *Plantaginetalia majoris*, which is the only order of the class *Plantaginetea majoris*. Before TÜXEN (1950) proposed this classification, the *Association of Rumex crispus and Alopecurus geniculatus* was known under the name *Association of Ranunculus repens and Alopecurus geniculatus*, and included in the *Arrhenatherion elatioris* (TÜXEN, 1937; WESTHOFF c.s., 1946). MÖRZER BRUIJNS (1947) is the only author who described the community in the Netherlands, viz. in the valley of the IJssel.

In our opinion the new classification of TÜXEN (1950) may be useful in the Netherlands too. We therefore include the characteristic species of the *Association of Rumex crispus and Alopecurus geniculatus* in the table; some corrections given by TÜXEN (1954) in a later publication are taken into account.

6. Class SCHEUCHZERIO-CARICETEA FUSCAE (Nordhagen) Tüxen 1937

In different countries the class *Scheuchzerio-Caricetea fuscae* has been subdivided in very different ways. A review of the various systems will not be given here, because the class is represented in the former

river beds by three associations only. Attention must be drawn, however, to the main Belgian literature dealing with this class, viz. DUVIGNEAUD (1949), DUVIGNEAUD and VANDEN BERGHEN (1945), LEBRUN c.s. (1949) and VANDEN BERGHEN (1952b). The first-mentioned author gives a complete revision of the classification of all plant communities occurring in Europe on a more or less peaty soil. He unites them in a new class, the *Sphagno-Caricetea fuscae*, which comprises the *Scheuchzerio-Caricetea*, the *Oxycocco-Sphagnetes* and parts of the *Moliniato-Arrhenatheretea*.

Though it is not sure that the subdivision given in the Synopsis is the best one for the Netherlands, it will be used here.

6. 1. ORDER CARICETALIA FUSCAE Koch 1926

6. 1. 1. Alliance Caricion fuscae Koch 1926

The position of *Carex rostrata*, in the Synopsis a characteristic species of the *Caricetum inflato-vesicariae*, has been discussed by WESTHOFF (1949; see also p. 46). We add it to the characteristic species of the *Caricion fuscae*, a possibility already suggested by WESTHOFF.

6. 1. 1. 1. *Caricetum lasiocarpae* Koch 1926 (Table 23)

In the Synopsis the *Caricetum lasiocarpae* is given with three characteristic species, viz. *Carex lasiocarpa*, *C. diandra* and *Eriophorum gracile*. In the Netherlands this association occurs along pools and broads, and participates in the hydrosere starting in mesotrophic water. Its composition is very variable; and this variability is related with its stage of development and with the properties of the water. It may be preceded by a community of the *Potamion*, of the *Littorellion* or by the community of *Juncus subnodulosus* and *Menyanthes trifoliata*. Sometimes it succeeds a *Magnocaricion*-community. It is itself succeeded either by the *Caricetum canescentis-fuscae*, by a carr or (if the vegetation is mowed and the soil drained) by the *Cirsieto-Molinietum*. See VAN ZINDEREN BAKKER (1942), MÖRZER BRUIJNS and WESTHOFF (1951), KUIPER (1957), KUIPER and SEGAL (1955), VAN DIJK and WESTHOFF (1955), DE WIT (1951, 1955).

The association occurs in a number of isolated former river beds. In this habitat it is, however, very poor in species in comparison with those given in the Dutch literature quoted above. Two of the three characteristic species, *Carex diandra* and *Eriophorum gracile*, are absent, and this applies also to several other species, e.g. to the greater part of the mosses.

There are different opinions with regard to the question in which way the great variability of the *Caricetum lasiocarpae* should be dealt with. SCHWICKERATH (1942) uses this association as a good example to demonstrate the way in which differential species may be used. He lets the association intact, but introduces many differential species to indicate e.g. its imperceptibly changing character from eutraphentous to obligotraphentous. The Synopsis places itself on the same standpoint. Other authors divide the association into two parts:

TABLE 23

<i>Caricetum lasiocarpae oligomesotrophicum</i>		1	2	3	4	5	6	7	8	9	10	P in 14 records
nr. of record		24	11	13b	3	15	13c	10	17	14	3	
nr. of former river bed		M	M	M	M	M	M	M	M	M	M	
river												
water depth (cm)		20	5	35	5	30	2		5			
area (sq. m)		15	20	25	20	50	100	12	16	6	12	
cover (%), total		80	95	90	80	75	95	50			100	
herb layer		75	90	80	80	70	95	50	50	80	70	
floating layer		25	10	25	20	<5	<1	—	<5	—	—	
moss layer		—	—	—	—	—	—	—	—	60	95	
Ch. Ass. <i>Carex lasiocarpa</i> Ehrh.		•	4.2	•	4.3	4.5	5.5	2.2	3.5	4.2	3.2	IV
Ch. All. <i>Carex rostrata</i> Stokes		4.5	3.2	4.5	+2	3.2	+2	1.2	+1	•	•	IV
<i>Epilobium palustre</i> L.		•	•	•	•	•	+2	+1	•	•	•	I
<i>Drepanocladus exannulatus</i> (Gümb.) Warnst.		•	•	•	•	•	•	•	•	3	•	II
<i>Calliergon cordifolium</i> (Hedw.) Kind.		•	•	•	•	•	•	•	•	+	•	I
<i>Sphagnum platyphyllum</i> Warnst.		•	•	•	•	•	•	•	•	1	•	I
<i>Carex curta</i> Good.		•	•	•	•	•	•	•	•	•	+2	I
Ch. Ord. <i>Comarum palustre</i> L.		+2	1.2	1.2	1.2	2.2	2.2	2.3	•	2.3	2.2	V
<i>Campyllum polygamum</i> (Br. eur.) Bryhn.		•	•	•	•	•	•	•	•	3	•	I
Ch. Cl. <i>Menyanthes trifoliata</i> L.		•	•	+2	•	+2	+2	1.2	2.2	•	+2	III
<i>Eriophorum angustifolium</i> Honcken.		•	•	•	•	•	•	•	•	•	+2	II
<i>Agrostis canina</i> L.		1.2	•	•	•	•	•	•	•	•	1.2	I
Acc. <i>Hypericum elodes</i> L.		+2	•	1.2	•	•	•	•	•	•	•	II
<i>Hydrocharis morsus-ranae</i> L.		1.2	2.2	•	2.2	•	•	•	•	•	•	II
<i>Juncus effusus</i> L.		+2	•	1.2	1.2	+2	•	•	•	•	+2	III

one part corresponding with the variant occurring in our former river beds, and the other one with the variant described in most Dutch literature (this is also the one to which the original description by KOCH applies). LEBRUN c.s. (1949) call the parts respectively "variant with *Sphagnum*" (D. *Sphagnum cuspidatum* and *S. recurvum*) and "variant with *Scorpidium scorpioides*" (D. *Carex diandra*, *Eriophorum gracile* and *Scorpidium scorpioides*). These two variants correspond with two subassociations described by DUVIGNEAUD and VANDEN BERGHEN (1945), viz. subass. *oligomesotrophicum* and subass. *eutrophicum*. These subassociations are included by them in two different alliances, corresponding respectively with the *Caricion fuscae* and the *Caricion davallianae*. In a subsequent paper DUVIGNEAUD (1949) puts the two parts once more in these two alliances, but here he gives them the position of associations, the *Caricetum lasiocarpae acidoclinum* and the *Caricetum diandro-lasiocarpae basiclinum*.

As far as we can judge our association seems to be different from the original *Caricetum lasiocarpae*. The best solution may be to accept the two subassociations proposed by DUVIGNEAUD and VANDEN BERGHEN, but to keep them together in one alliance, the *Caricion fuscae*. It should be emphasized, however, that this is but a preliminary decision.

The *Caricetum lasiocarpae oligomesotrophicum*, as we found it, in the former river beds also shows a remarkable variation (see the table). In the initial stage in water up to 25 cm deep, *Carex lasiocarpa* itself may be absent and completely replaced by *Carex rostrata*. In this stage characteristic species of the preceding *Potamion* and the *Eleocharetum multicaulis* may be frequent. The following (optimum) stage is much richer in helophytes, and usually forms a floating mat. It usually is succeeded by the *Caricetum elatae comaretosum*. Record nr. 10 presents a variant, which was found only once, behind a zone of the *Caricetum elatae* and passing into the *Caricetum canescentis-fuscae*.

6. 1. 1. 2. *Caricetum canescentis-fuscae* (Braun-Blanquet 1915) Vlieger 1937 (Table 24)

In the Netherlands the *Caricetum canescentis-fuscae* has, according to the Synopsis, two characteristic species, viz. *Carex curta* and *C. echinata*. It is usually found between a *Magnocaricion*-community and the *Betuleto-Salicetum*. See VLIEGER (1937), VAN ZINDEREN BAKKER (1942, 1947), MÖRZER BRUIJNS and WESTHOFF (1951).

The community was found in some of the isolated meso- to oligotrophic former river beds of the Meuse. In these localities its composition corresponds fairly well with the descriptions given by other Dutch authors (see e.g. the records of VLIEGER, 1937, and of VAN ZINDEREN BAKKER, 1942). In one case it followed the *Caricetum lasiocarpae oligomesotrophicum* (with *Spagnum recurvum*), in the other cases it was preceded by a floating-mat vegetation resembling or corresponding with the *Cicuteto-Caricetum pseudocyperus comaretosum*. The community was succeeded by a vegetation of the *Sphagnion* or the *Betuleto-Salicetum*.

TABLE 24

<i>Caricetum canescentis-fuscae</i>				
nr. of record	1	2	3	P in 5 records
nr. of former river bed	8	3	17	
river	M	M	M	
area (sq. m)	100	25	10	
cover (%), total.	100	90		
herb layer	70	70	60	
moss layer	90	50	40	
Ch. Ass. <i>Carex curta</i> Good.	4.2	1.2	3.2	V
Ch. All. <i>Carex rostrata</i> Stokes	1.2	1.2	+2	V
<i>Carex lasiocarpa</i> Ehrh.	+2	+1	II
<i>Drepanocladus exannulatus</i> (Gümb.) Warnst.	1.2	.	.	II
<i>Stellaria palustris</i> Retz.	+1	I
Ch. Ord. <i>Comarum palustre</i> L.	+1	2.2	.	III
Ch. Cl. <i>Agrostis canina</i> L.	+1	2.2	+1	II
<i>Menyanthes trifoliata</i> L.	3.2	2.2	II
<i>Eriophorum angustifolium</i> Honckeney . .	+2	.	.	II
<i>Hydrocotyle vulgaris</i> L.	+2	.	I
Acc. <i>Lysimachia thyrsiflora</i> L.	+1	2.2	1.2	IV
<i>Polytrichum commune</i> Hedw.	2.2	1.2	.	IV
<i>Sphagnum recurvum</i> P. de B.	5.5	2.3	.	IV
<i>Typha latifolia</i> L.	3.2	.	+1	IV
<i>Calliergon stramineum</i> Lindb.	2.2	1.2	.	II
<i>Galium palustre</i> L.	2.2	+1	II
<i>Carex hudsonii</i> A. Benn.	+2	+2	II
<i>Cicuta virosa</i> L.	2.2	.	I
<i>Brachythecium</i> sp.	2.2	.	I
<i>Calamagrostis canescens</i> (Web.) Roth. .	.	.	2.1	I
<i>Sphagnum squarrosum</i> Pers.	3	I

Supplement to the table. Acc.: *Betula pendula* Roth (juv.) 1: +1, *Betula pubescens* Ehrh. (juv.) 1: +1, *Salix cinerea* L. (juv.) 1: +1, *Drosera rotundifolia* L. 1: +1, *Pohlia nutans* (Hedw.) Lindb. 1: 1.2, *Acorus calamus* L. 2: 1.2, *Iris pseudacorus* L. 2: +2, *Juncus effusus* L. 2: 1.2, *Lycopus europaeus* L. 2: +1, *Polygonum amphibium* L. fo. *terrestre* Leyss. 2: +1, *Lysimachia vulgaris* L. 2: +2, *Eleocharis palustris* (L.) R. et Sch. 2: +2, *Phragmites communis* Trin. 2: 1.1, *Calliergonella cuspidata* (Hedw.) Loeske 2: 1, *Caltha palustris* L. 3: +1, *Lotus uliginosus* Schkuhr. 3: +2, *Juncus articulatus* L. 3: +1, *Rumex hydrolapathum* Huds. 3: +1, *Mentha aquatica* L. 3: +1.

1. D 56-1075, 21-6-1956
2. D 56-1051, 19-6-1956
3. V 55-80, 13-7-1955

6. 1. 1. 3. *Juncetum acutiflori* Braun-Blanquet 1915 (Table 25)

In the Synopsis the *Juncetum acutiflori* is mentioned under the alliance *Molinion*. According to the authors, their material presented a majority of *Molinietalia* species. They state, however, that the *Juncetum acutiflori sphagnetosum* of DUVIGNEAUD and VANDEN BERGHEN

TABLE 25

<i>Juncetum acutiflori sphagnetosum</i>		
nr. of record	1	2
nr. of former river bed	3	8
river	M	M
area (sq. m)	2	9
cover (%), total		100
herb layer	25	75
moss layer	75	90
Ch. Ass. <i>Juncus acutiflorus</i> Ehrh.	3.1	3.2
Ch. All. <i>Stellaria palustris</i> Retz.	+1	.
<i>Epilobium palustre</i> L.	+1	.
<i>Carex curta</i> Good.	+2	.
Ch. Ord. <i>Comarum palustre</i> L.	1.2	.
Ch. Cl. <i>Eriophorum angustifolium</i> Honckeney	+1
<i>Hydrocotyle vulgaris</i> L.	2.1	.
Acc. <i>Sphagnum recurvum</i> P. de B.	5	3.5
<i>Juncus effusus</i> L.	+1	.
<i>Lysimachia vulgaris</i> L.	+1	.
<i>Galium palustre</i> L.	2.1	.
<i>Carex elongata</i> L.	+1	.
<i>Polytrichum commune</i> Hedw.	3.5
<i>Oxycoccus palustris</i> Pers.	4.5
<i>Erica tetralix</i> L.	+2
<i>Pinus sylvestris</i> L. (juv.)	+1

1. V 55-30, 16-6-1955

2. D 56-1081, 21-6-1956

(1945) should certainly be included in the *Caricion fuscae*. Here too a way out of this unsatisfactory situation may perhaps be found by adopting the completely revised classification of DUVIGNEAUD (1949). This author removes the whole *Juncetum acutiflori* to a new alliance, the *Molinio-Juncetum acutiflori*, and distinguishes some subassociations among which the oligotraphentous *J. a. sphagnetosum recurvi*.

Along some of the isolated meso- to oligotrophic former river beds a vegetation occurred corresponding with the *Juncetum acutiflori sphagnetosum recurvi*. It more or less alternated with vegetations of the *Caricion fuscae* and of the *Sphagnion*.

7. Class OXYCOCCO-SPHAGNETEA Braun-Blanquet et Tüxen 1943

7. 1. ORDER ERICETO-SPHAGNETALIA (Braun-Blanquet 1915)
Schwickerath 19407. 1. 1. Alliance *Sphagnion europaeum* (Braun-Blanquet 1915) Schwickerath 1940

Sphagnum recurvum is mentioned in the Synopsis as a characteristic species of the *Sphagnion*. This certainly is not correct. Our tables 23, 24 and 25 and the Belgian literature prove that this species is common in communities of the *Scheuchzerio-Caricetea fuscae*, at least in the South of the Netherlands.

In two of the meso- to oligotrophic former river beds the *Caricetum canescentis-fuscae* passed into a community of the *Sphagnion*. The vegetations, usually occupying small territories, could not be identified with a well-defined association. An example of a well-developed vegetation is given here.

Fieldnr. V 55-31. Date 21-6-1955. Klopven (nr. 3). Area 200 sq.m. Cover herb layer 40 %, moss layer 40 %.

Eriophorum vaginatum L. 3. 2., *Peucedanum palustre* (L.) Moench. 2. 2., *Lysimachia thyrsoflora* L. 2. 1., *Lysimachia vulgaris* L. +. 1., *Comarum palustre* L. +. 2., *Menyanthes trifoliata* L. +. 2., *Juncus effusus* L. +. 2., *Sphagnum recurvum* P. de B. 3.

8. CARRS

In order to understand the next chapter it is necessary to know the classification of the carrs used by KOP (1961). It is reproduced here in short.

Class	Order	Alliance	Suballiance	Association	Variant
Alnetea glutinosae	Alnetalia glutinosae	Alnion glutinosae		Betuleto- Salicetum Alnetum glutinosae	mesotraphentous
Querceto Fagetea	Populetales albae	Alno- Ulmion	Salicion		eutraphentous foreland
			Alnion glutinoso- incanae	Macrophorbieto- Alnetum (?)	tidal

V. THE TYPES OF FORMER RIVER BEDS
AND THEIR DISTRIBUTION

1. CHARACTERIZATION OF THE TYPES

The classification of the 127 former river beds investigated by us resulted in the creation of 11 types and subtypes; only 12 examples could not be included in these 11 groups and are classified as transitions between two of them. See the list on p. 78-80.

Every type is characterized by a definite set of communities cor-

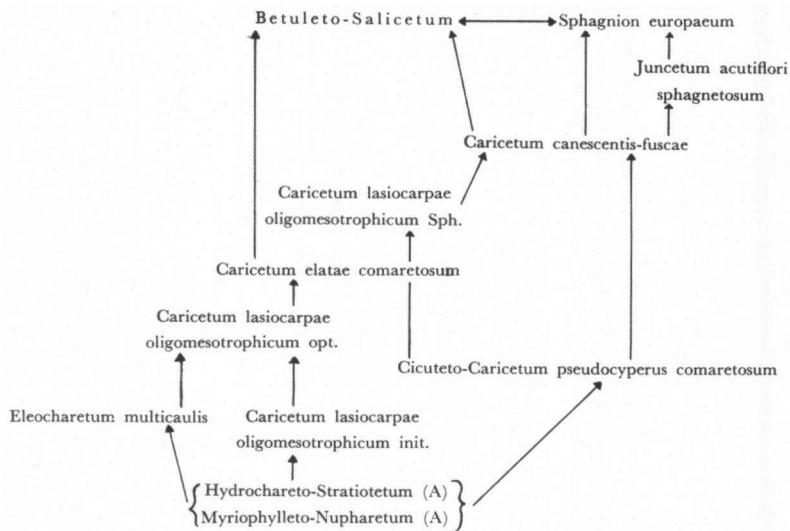
responding with a more or less distinct set of abiotical features. All this is summarized in table 26. This table also compares the types with the numbers of the former river beds mentioned in fig. 1. All information with regard to the communities can be found in the preceding chapter and (with regard to the carrs) in the publication of Kop (1961).

In the table subtype 4 b is left out of account. This is explained on p. 73. There is also a number of communities not included in the table, viz. 1) some rare or rather indistinct communities; 2) the wet meadow vegetations and the *Phragmites-consociation* (because they are strongly influenced by man); 3) the carrs on the borders of the isolated former river beds belonging to the *Salicion* or the *Alnion glutinoso-incanae*; at present they do not form a stage in the hydrosere of the former river bed.

The communities belonging to the same type form a succession. The vegetation of a type is described (apart from Table 26) mainly by a succession diagram. In the diagrams again a number of communities is left out of account for the sake of clearness. However, the carrs on the borders, which do not participate in the hydrosere, are indicated separately.

1.1. TYPE ZWART WATER

The *type Zwart Water* is very clearly defined. Three classes are represented solely in this type or nearly solely. For the rest the type has some communities in common with the *type Meerlo*. In the course



of the succession the habitat changes from mesotrophic to oligotrophic. The most oligotrophic spots are occupied by vegetations of the *Sphagnion*.

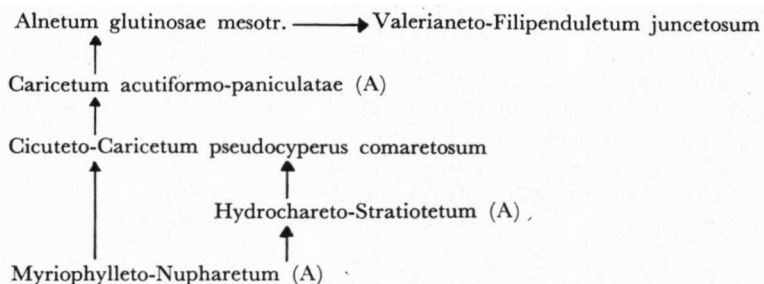
This type is the only one which shows in this case starting with the *Caricetum elatae comaretosum* the series *Magnocaricion* → *Caricion fuscae* →

Sphagnion, which is mentioned in the literature dealing with the Dutch broads, especially with those found in N.W. Overijssel (VLIEGER, 1937; BOER, 1942; MÖRZER BRUIJNS and WESTHOFF, 1951; DE WIT, 1955; VAN DIJK and WESTHOFF, 1955; KUIPER and SEGAL, 1955). There, however, a stage with *Carex diandra*, sometimes called *Caricetum diandrae* (VLIEGER, 1937) is interposed between the *Caricetum lasiocarpae* (*eutrophicum*) and the *Caricetum canescentis-fuscae*.

In the Dutch literature there is only one description of a habitat which corresponds with this type, viz. the Tuspeel near Ittervoort (DAMMAN, 1953). This is not surprising, for this locality is situated in the same region (the middle of the province of Limburg), and offers the same ecological environment as five of the six representatives of the type *Zwart Water*. On the ground of the similarity between some communities found in this type and some others found in Belgium, it may be supposed that in Belgium too habitats referable to this type are present.

1.2. TYPE MEERLO

The type *Meerlo* is not very clearly defined by specific vegetation units. It has some communities in common with the type *Zwart Water*, but on the other hand several of its communities are the mesotraphentous equivalents of more generally known eutraphentous communities.



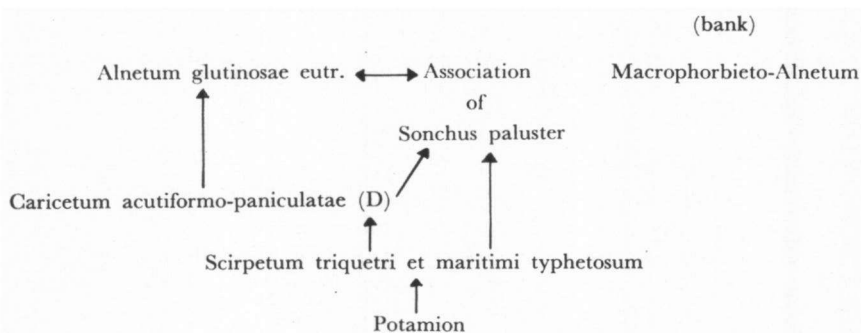
The type as a whole can be characterized best as a more mesotrophic counterpart of the eutrophic *subtype Tuil* (4 a). The character of the vegetation, however, does not fully justify the conclusion that the habitat is mesotrophic in the sense in which this term is generally understood. Perhaps the best way to characterize it, is "meso- to eutrophic".

Table 26 does not reveal the presence of an environmental factor which would explain the differences in mineral content and in P_H of the types *Zwart Water* and *Meerlo*. The explanation, however, must be found in some incidentally effective factors. This will not be described in detail here. The main factor is apparently the composition of the water supply derived from the surroundings. The composition of the latter depends e.g. on the elevation, the vegetation and the exploitation, of the surrounding country (alder wood, pine wood, manured arable land, etc.).

There are no descriptions of other territories in the Netherlands which show a strong resemblance to the *type Meerlo*. Its presence in Belgium may be supposed on the same grounds as brought up for the *type Zwart Water*.

1. 3. TYPE SPUI

The only community which the *type Spui* has in common with any other type is the *Alnetum glutinosae*. For the rest the nature of its communities is determined by the oligo- to mesohalinic habitat. The *Macrophorbieto-Alnetum* on the banks does not participate in the autogenic succession.



The succession diagram corresponds very well with that of the mesohalinic pools given by MÖRZER BRUIJNS and WESTHOFF (1951). The description of the Botshol by WESTHOFF (1949) indicates that at that place locally the same succession of communities is found. For the rest no other halinic broads in the Netherlands seem to correspond with the *type Spui*. Judging from the descriptions given by VAN ZINDEREN BAKKER (1947) many of them must be intermediate between the *types Spui* and *Tuil*.

1. 4. TYPE TUIL

The *type Tuil* represents all isolated former river beds with stagnant, eutrophic, fresh water. In such a water floating-mat communities may play an important part in the autogenic succession, especially in small pools and in isolated spots. The ideal hydrosere is demonstrated in the succession diagram of the *subtype Tuil*.

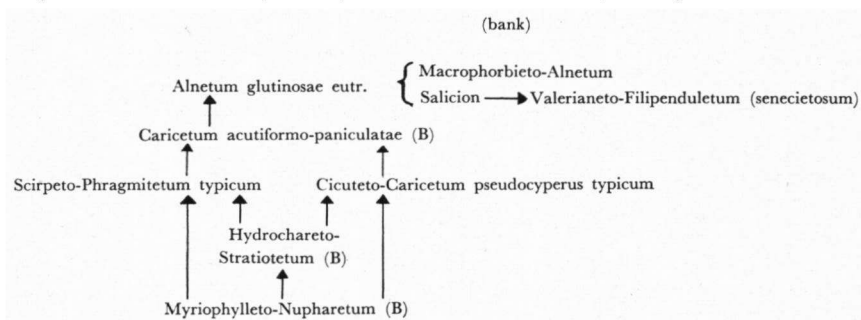
However, before their isolation, all former river beds of this type were situated in the forelands; in some cases they were even under the influence of the tide. At that time their hydrosere was different, and the succession mainly allogenic. After the isolation the succession in the water changed rather rapidly and now the development of a peat layer started. On the part of the bank above the water surface, however, no longer any silt was deposited, and here no development of a peat layer took place; this part therefore changed only slowly on account of a slight increase of the humus content and by the development of the soil profile. As a consequence the vegetation on

nr. of type	1	2	3	4a	5	6a	6b	6c	7	8
nr. of representatives, total	6	6	5	5	40	13	8	8	6	8
Meuse	6	6			4				3	
Heusdense Maas					4				3	1
Waal (and the one of the Merwede)				1	6	9	3	7		2
Oude Maas				1						2
rest of delta W. of Dordrecht			5							
Rhine					2	4	5	1		
Lek					3					3
IJssel				3	21					
best representatives	8, 3-4	11, 9-10	73, 76	63	19, 40, 62, 124-125	39, 77	42	46	27, 29	31, 65, 70
corresponding number(s) of former river beds in fig. 1	1	1	11, 12	6, 10	2, 4, 8	3	3	5	7	9, 13
soil	peat layer on , river "loam" and/or sand			various soil types	clay and/ or sand	clay and/or sand			clay	
relation to river	isolated				in river foreland					
					usually no open commun.	open commun. or no open communication		open communication		
water movement	stagnant or incidentally exposed to a very slow current caused by sluicing				inundation by annual floods			no annual floods		
					less frequent than in 6, and/or no strong cur- rent during inund. period	more frequent than in 5, and/or strong current during inundation period		tidal movement with an amplitude smaller than in 8		greater than in 7, ev. inund. by high tide
general mineral content	meso- to oligotrophic	meso- to eutrophic	eutrophic							
P _H of open water	5,9-6,2	6,5-7,0	? (>7,0)	7,0-7,3	6,9-7,6	7,0-7,5			7,1-7,3	? (>7,0)
Cl-content of open water in mg/l	? (low)	23-49	250-2000	33-104 (nr. 69:200)	22-110	41-96	32-40	76-96	82-100 (nr. 25:42)	90-124
Class	Order	Alliance	Suball.	Association (or "community")	Subass. (or variant)					
Litt.	Litt.	Litt.		Eleocharetum multicaulis						
Pot.	Pot.	Pot.		Hydrochareto-Stratiotetum	mesotraphentous (A) eutraphentous (B)					
				Myriophylleto-Nupharetum	mesotraphentous (A) eutraphentous (B)					
				halobious vegetation						
				Potametum lucentis						
				Polygoneto-Nymphoidetum	typicum					
				Comm. of Ran. circ. and El. can.						
				undet. vegetation						
Phr.	Phr.	Phr.		Cic.-Caricetum pseudocyp.	comaretosum typicum					
				Scirpeto-Phragmitetum	typicum oenanthesosum calthetosum					
				Scirpetum triquetri et mar.	typhetosum other subass.					
		Magn.		Caricetum elatae	comaretosum					
				Caricetum acut.-paniculatae	mesotraphentous (A) halobious (D) eutraphentous (B) foreland (C)					
				Caricetum grac.-vesicariae						
		Glyc.-Sparg.		Sparg.-Glyc. fluitantis	polygonetosum					
				undet. community						
Sch.-C. f.	Car. f.	Car. f.		Caricetum can.-fuscae						
				Juncetum acutiflori	sphagnetosum					
				Caricetum lasiocarpae	oligomesotrophicum					
Ox.-Sph.	Er.-Sph.	Sph.		undet. vegetation						
Mol.-Arrh.	Mol.	Fil.-Pet.		Valerianeto-Filipenduletum	juncetosum senecietosum subass. of Heracleum					
				Ass. of Sonchus paluster						
Aln.	Aln.	Aln.		Betuleto-Salicetum						
				Alnetum glutinosae	mesotraphentous eutraphentous					
Q.-Fag.	Pop.	A.-Ulm.	Sal.	foreland						
				tidal						

this part of the bank changed but slowly. The drier side of the *Caricetum gracilis-vesicariae* passed into the adjoining *Salicion*-community, and this community gradually passed into a vegetation belonging to the *Alnion glutinoso-incanae*, which probably has to be referred to the *Macrophorbieto-Alnetum* (see KOP, 1961). Many former river beds of the type *Tuil* retain on their banks vegetations of the *Valerianeto-Filipenduletum senecietosum*, the *Salicion* and its transitions to the *Macrophorbieto-Alnetum* as relics of their former condition.

a. Subtype *Tuil*

The succession diagram of the *subtype Tuil* corresponds with the description of the succession by floating-mat vegetations in most of the Dutch broads and in pools with eutrophic, fresh water, especially those in N.W. Overijssel (see MÖRZER BRUIJNS and WESTHOFF, 1951; VAN ZINDEREN BAKKER, 1942; V Lieger, 1937; BOER, 1942; VAN DIJK and WESTHOFF, 1955; KUIPER and SEGAL, 1955).



b. Subtype *Ossermeer*

The *subtype Ossermeer* is not included in table 26. Therefore the peculiarities are given here in so far as they are different from those of the *subtype Tuil*.

Number of representatives:	10
Best representative	: nr. 102
Rivers	: Meuse 3, Waal 1, Oude Maas 2, Rhine 1, IJssel 3.
Soil	: peat layer locally present and then thinner than in the <i>subtype Tuil</i>
P _H of open water	: 6,8–7,7
Cl-content of open water	: 28–71 mg/l

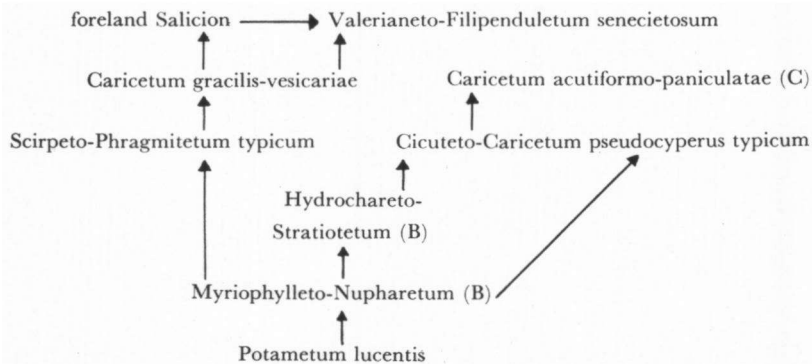
The former river beds belonging to this subtype are intermediate between the types from which they originate (*Hurwenen*, *Kekerdome* and *Krook*) and the *subtype Tuil*. It may be expected that under natural circumstances the greater part of them would develop into the latter. Their actual properties and vegetation are a stage in a relatively rapid evolution. However, in the case of other and older former river beds anthropogenous factors disturb the development. Cleaning of the water and removal of the talus along the banks prevent the development of floating-mat vegetations. Mowing of the vegetation on the banks prevents the formation of carrs, and maintains in this

way the *Caricetum gracilis-vesicariae*. Especially in such a habitat vegetation units belonging to more or less different hydroseres occur together and intermingle. This is the reason why this subtype is not included in table 26.

1.5. TYPE HURWENEN

Most numerous are the representatives of the *type Hurwenen*. They form nearly one third of all investigated former river beds. The type includes those former river beds in the forelands which are not very intensively influenced by inundation and by currents.

Whereas the nature of many of the water and swamp communities is determined mainly by the mineral content of the water and to a lesser degree by the soil type, it is not surprising that the vegetation in the *type Hurwenen* as far as it consists of plants rooting under water corresponds fairly well with that found in the *subtype Tuil*. The communities above the water surface, however, resemble or are identical with those of the other foreland types.



The ecological and floristical description given by LAUTERBORN (1917) of former river beds of the Rhine, suggest that a number of those found between Basel and Bonn may resemble our *type Hurwenen*.

1.6. TYPE KEKERDOM

The former river beds of the *type Kekerdom* are strongly influenced by inundation and currents. In consequence floating-mat vegetations are absent. The only community which nearly all representatives of this type have in common is the *Polygoneto-Nymphoidetum typicum*. The *Scirpeto-Phragmitetum oenanthetosum* occurs in two of the three subtypes.

a. Subtype Kekerdom

In the *subtype Kekerdom* the hydrosere is complete from the submersed *Potametum lucentis* up to the *Salicion-carr*.

LAUTERBORN's (1917) descriptions seem to indicate that this subtype is present along the Rhine in Germany, at least below Bingen.

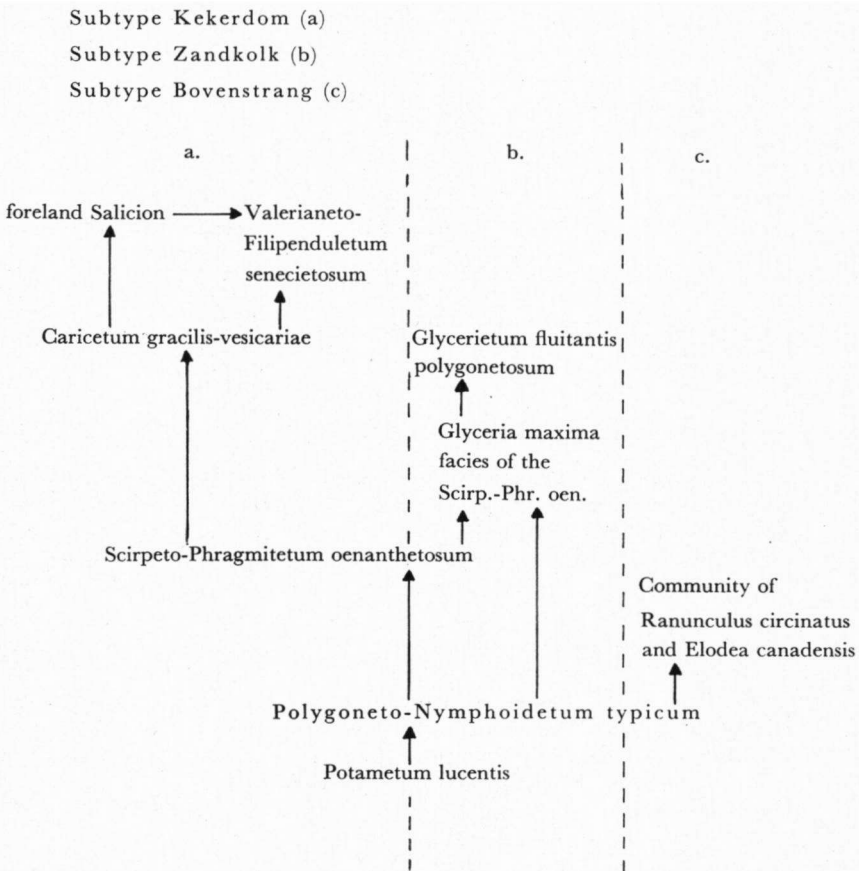
b. Subtype Zandkolk

The representatives of the *subtype Zandkolk* are bordered by meadows

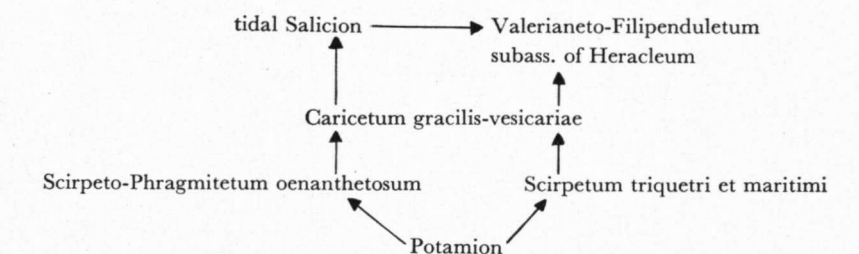
which reach up to the edge of the water. Usually cattle can graze the vegetation. Perhaps this causes the deviation noted in the succession.

c. Subtype Bovenstrang

The former river beds of the *subtype Bovenstrang* are situated very near to the river. Maybe that the strong current during the inundation time and the ice drift prevent the formation of reed swamps.



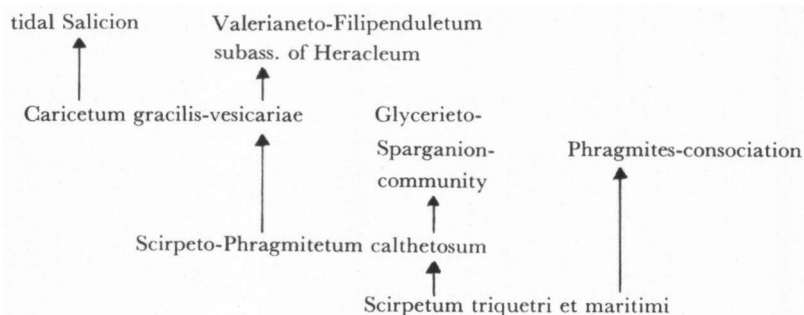
1. 7. TYPE KROOK



The *type Krook* consists of former river beds with very little tidal movement. It is more or less intermediate between the *type Kekerdom*, with no tidal movement, and the *type Bloemstrang*, with more tidal movement. It has no characteristic communities of its own.

1.8. TYPE BLOEMSTRANG

The *type Bloemstrang* is clearly defined by some communities which are restricted to the fresh water tidal area. The type corresponds completely with that of many creeks in the Biesbosch (ZONNEVELD, 1960). There, however, all communities are much better developed.



2. THE DISTRIBUTION OF THE TYPES

The distribution of the types along the various rivers can easily be understood if one compares fig. 1 with the head of table 26.

However, some interesting facts in relation to the distribution of the *types Hurwenen* and *Kekerdom* may be stressed. The differences between these two types are correlated with the frequency of the inundations by annual floods and with the strength of the current during the inundation. In this connection the water household of the large rivers must be recalled to memory (see p. 5). The forelands of the Meuse and the IJssel are inundated less frequently than those of the Rhine-Lek and the Waal. Moreover the forelands of the IJssel form a relatively wide zone, so that in many places there is hardly any current during the inundation. In correspondence with these facts the *type Kekerdom* does not occur along the Meuse and the IJssel.

Along the Rhine-Lek and the Waal the frequency of the inundations of the forelands by the annual floods decreases down the river, as indicated on p. 5. As a consequence towards the West the *type Kekerdom* gradually disappears, whereas the *type Hurwenen* becomes a little more frequent. This can be seen from the list on p. 78–80, where the former river beds of every river are arranged in accordance with the direction of the stream.

VI. SUMMARY

This study deals with the vegetation of about 125 former beds of the larger rivers in the Netherlands. It includes all communities of higher plants except the carrs, which are dealt with in a separate paper by KOP (1961).

The investigation of the communities aimed at a knowledge of their floristic composition as well as at a definition of their habitat. The description and the classification of the units was carried out according to the concepts and methods of the Braun-Blanquet school (BRAUN-BLANQUET, 1932, 1951; BECKING, 1957). Moreover, among the former river beds types were recognized, characterized by a special set of communities and by correlated abiotical properties.

A number of vegetation-units are described here for the first time, viz.

The *Polygoneto-Nymphoidetum* (alliance *Potamion*) with the subass. *typicum* and the subass. *potametosum pectinati*. According to descriptions of vegetations found in the literature the subass. *typicum* is also present in former river beds of the Rhine in Germany about up to Bingen (LAUTERBRON, 1917); more to the south it is replaced by the *Trapo-Nymphoidetum* (OBERDORFER, 1957).

The *Sparganieto-Glycerietum fluitantis polygonetosum* (alliance *Glycerieto-Sparganion*). The main difference with the habitat of the other subassociations (see MAAS, 1959), where the water is moving either permanently (brooks) or at least now and then (ditches), is that the vegetation is influenced by the current only during the short-lasting annual floods.

The *Cicuteto-Caricetum pseudocyperus* (alliance *Phragmition*) is to be divided into two subassociations, viz. the subass. *typicum* and the subass. *comaretosum*. The main difference between the habitats of the two subassociations appears to be that the first is eutrophic and the second more mesotrophic.

The *Scirpetum triquetri et maritimi typhetosum* (alliance *Phragmition*). In contrast with the other subassociations (see ZONNEVELD, 1960), this one occurs only in oligo- to mesohaline, stagnant water.

The *Caricetum elatae* (alliance *Magnocaricion*) is revised. *Carex hudsonii* is the only characteristic species found throughout the area in which the association occurs. The community everywhere participates in the hydrosere on sand or peat. The following subdivision was made: Subass. *typicum*; the community is eutraphentous; according to the literature it is found in Switzerland (KOCH, 1926), S. Germany (OBERDORFER, 1957) and Belgium (LEBRUN c.s., 1949; VANDEN BERGHEM, 1952 a). Subass. *comaretosum*; more mesotraphentous than the subass. *typicum*; found in N. Germany (TÜXEN, 1937; PASSARGE, 1955 b) and the Netherlands.

Of the *Valeriano-Filipenduletum* (alliance *Filipendulo-Petasion*) two new subassociations are established, viz.: Subass. *juncetosum*; it is the replacing-community of a mesotraphentous variant of the *Alnetum glutinosae*. Subass. *senecietosum*; represented in the river forelands outside the tidal area; it replaces there an eutraphentous *Salicion*-community, and may be natural if the development of trees is prevented by ice-drift.

Eight types of former river beds were distinguished. Two of these could be subdivided into some subtypes. Their classification according to their communities and their abiotical properties is summarized in table 26.

Descriptions of habitats which more or less resemble one of these types of former river beds, are known from other parts of the Netherlands and from the adjoining parts of Germany and Belgium. However, as far as we know, of the types described by us, viz. those represented in the river forelands along the upper courses of the rivers, seem to differ from all habitats that have been described so far.

VII. LIST OF FORMER RIVER BEDS INCLUDED IN THIS STUDY

<i>nr. former river bed(s)</i>	<i>municipality(s)</i>	<i>map(s)</i>	<i>type</i>
MEUSE			
1. f.r.b. (wood) in river foreland . . .	Obbicht-Papenhoven	60 C	—
2. f.r.bs. in Grote Beemd	Maasbracht	58 D	5
3. Klopven	Horn	58 D	1
4. Houterven	Horn	58 D	1
5. f.r.b. in Weerd	Beesel-Reuver	58 E	5
6. Koelbroek and environs	Maasbree	52 G	2
7. Tangkoel near Hout-Blerick . . .	Maasbree	58 E	2
8. Zwart Water	Arcen-Velden and Venlo	52 H	1
9. Lottummer Schuitwater	Grubbenvorst	52 G	2
10. Broekhuizer Broek	Broekhuizen	52 E, G	2
11. Schuitwater between Meerlo and Broekhuizervorst	Meerlo	52 E	2
12. Schuitwater S.E. of Meerlo . . .	Meerlo	52 E	2
13. Rozendaal	Wanssum	52 B, E	1
14. Vilt	Beugen	46 D	1-2
15. Lange Ven	Bergen (L.)	46 D	1
16. Wychense Meer	Wychen	46 A	4 b
17. Wychense Ven	Wychen	45 F	1-2
18. Balgoijse Meer	Overasselt	45 F	4 b
19. Oude Maas	Megen-Haren- Macharen	39 G, 45 E	5
20. Ossermeer	Megen-Haren- Macharen	45 E	4 b
21. f.r.b. E. of Hedel	Hedel and Maasdriel	45 A	7
22. f.r.b. W. of Empel	Empel-Meerwijk	45 A	5-6
23. Hedikse Maas	Haarsteeg	45 A	5
24. Galgenwiél	Loon op Zand	44 H	1
25. Oude Maasje near Drongelen . .	Drongelen	44 E, F	7
26. Oude Maasje between Haagoord and Keizersveer	Capelle, Waspik and Raamsdonksveer	44 E	7
HEUSDENSE MAAS			
27. Krook	Ammerzoden	45 A	7
28. f.r.b. in Doornwaard	Heusden	44 F, 45 A	5
29. f.r.b. in Banwaard	Wijk-Aalburg	44 F	7
30. f.r.b. in Wijkse Waard	Wijk-Aalburg	44 F	5
31. f.r.b. along Zandplaat	Brakel	44 F	8
32. Del	Brakel	44 F	5
33. f.r.b. in De Waarden	Brakel	44 F	5
34. Oude Maasje near Loevestein . .	Brakel	38 G, 44 E	7
WAAL			
35. Oude Waal W. of Lobith	Herwen-Aerd	40 G	5-6 a
36. Oude Waal near Kekerdom . . .	Ubbergen	40 D	6 a
37. Ooijse Graaf	Ubbergen	40 D	4 b
38. Strang in Sophia's Kamp	Ubbergen	40 D	6 b
39. Strang	Bemmel	40 C	6 a
40. Oude Waal E. of Nijmegen . . .	Ubbergen	40 C, D	5
41. Zeumke	Nijmegen	40 C	6 a
42. Zandkolk	Valburg	40 C	6 b
43. Strang S.E. of Slijk-Ewijk . . .	Valburg	40 C	6 c
44. Strang in Loenense Buitenpolder	Valburg	40 C	6 a

45. Strang near Hien	Dodewaard	39 H	5
46. Bovenstrang near Hien	Dodewaard	39 H	6 c
47. f.r.b. near Afferden	Druten	39 H	5
48. Strang and Weeversgat near Turksweerd	Druten	39 H	6 a
49. Goudmijn	Druten	39 G, H	6 c
50. Hoek van de Lange Krib	Echteld	39 G	6 c
51. Oude Waal E. of Ochten	Echteld	39 G	5-6 a
52. Oude Waal S.W. of Ochten . . .	Echteld	39 G	6 c
53. Kil near Ooy	Echteld	39 G	6 a
54. Kil E. of Tiel	Tiel	39 D, G	5
55. f.r.b. in Uiterwaarderpolder . .	Wamel and Dreumel	39 D	6 c
56. f.r.b. S.W. of Tiel	Tiel	39 D	6 b
57. Kil in Dreumelse Waard	Dreumel	39 D	5-6 a
58. Kil in Stifse Uiterwaarden . . .	Ophemert and Varik	39 D	6 a
59. f.r.b. W. of Heerewwaarden . . .	Heerewwaarden	39 D, 45 B	6 c
60. Weiwaardsgat	Heerewwaarden	45 B	6 a
61. Kil	Waardenburg	39 C	5-6 a
62. Kil van Hurwenen	Zaltbommel and Hurwenen	45 A	5
63. Wiel near Tuil.	Haften	39 C	4 a
64. Kil in Broomwaard	Zuilichem	38 H	5
65. Bloemstrang	Brakel and Woudrichem	38 H, 44 F	8

MERWEDE

66. Avelingerdiep	Gorinchem and Hardinxveld	38 G	8
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OUDE MAAS

67. Voordevel.	Heerjansdam	37 H, 38 C	4 b
68. Waal	Heerjansdam, Baren- drecht, Ridderkerk and Hendrik Ido Ambacht	37 H, 38 C	4 b
69. Binnenbedijkte Maas	Westmaas, Mijnsheren- land and Maasdam	43 F	4 a
70. f.r.b. E. of Heinenoord	Heinenoord	37 H	8
71. Kooigat and environs	Poortugaal	37 G, H	8

REST OF THE DELTA W. OF DORDRECHT

72. Grote Gat.	Zuid Beijerland	43 E	3
73. Oostenrijk (Vierambachten- boezem)	Geervliet	37 D	3
74. Holle Mare	Heenvliet	37 D	3
75. Spui near Brielle	Nieuwenhoorn	37 D	3
76. Meertje van Rockanje (Waal) . .	Rockanje	37 C	3

RHINE

77. Oude Rijn between Spijk and Duiven	Herwen-Aerdt	40 D, G	6 a
78. f.r.b. S. of Loover	Huissen	40 B	6 c
79. Strang in Huissense Waarden . .	Huissen	40 B	5-6 a
80. f.r.b. S.W. of Renkumse Veer . .	Heteren	39 F	6 b
81. f.r.b. S.W. of Lexkes Veer . . .	Heteren	39 F	6 b
82. f.r.b. W. of Oude haven.	Wageningen	39 F	5
83. Strang in Maneswaard	Kesteren	39 F	6 b
84. Oude Rijn	Kesteren and Lienden	39 E	4 b
85. f.r.b. S.E. of Elst	Rhenen	39 E	6 b
86. f.r.b. in Waterschap Bovenpolder	Amerongen	39 B	5

87. Kil in Polder Koornwaard . .	Amerongen	39 B	6 a
88. Kilsloot in Polder Koornwaard	Amerongen	39 B	6 a
89. f.r.b. N. of Eck en Wiel . . .	Maurik	39 B	6 b
90. f.r.b. near Roodvoet	Maurik	39 B	6 a

LEK

91. Kleine Lek	Vianen	38 F	5
92. f.r.b. in Bolswaard (open part)	Lexmond	38 E, F	8
93. f.r.b. in Bolswaard (closed part)	Lexmond	38 E, F	5
94. Binnenlek	Lopik	38 E	8
95. f.r.b. in Binnen Nes	Groot Ammers	38 B	5
96. Kil along island Hoop	Lekkerkerk	38 C	8

IJSEL

97. Rhedense Laak	Rheden	40 B	5
98. Lamme IJsel	Doesburg	33 G, 40 E	5
99. Dierense Hank	Doesburg	40 E	5
100. f.r.b. S.W. of Gelderse Toren .	Rheden	33 G	5-6 a
101. Vreekolk and environs	Steenderen	33 G	4 b
102. Oude IJsel and Hoender- nesterbeek	Zutfen	33 E, G	4 b
103. Blanke Hank	Voorst	33 E	5
104. f.r.bs. near Wilp	Voorst and Deventer	33 E	5-6 a
105. f.r.b. in Ossenswaard	Deventer	33 E	5-6 a
106. f.r.b. near Ter Cera	Voorst	27 G	5
107. Munnikenhank	Diepenveen	27 G	5
108. f.r.bs. in Olster en Hengvorder Waarden S. of Olst	Olst	27 G	5
109. Hank S. of Welsum	Olst	27 G	5
110. Barlose Kolk (Southern of the two)	Olst	27 G	4 b
111. f.r.b. in Olster Waard N. of Olst	Olst	27 G	5
112. Hank near Veessen (open part)	Heerde	27 E, G	5
113. Hank near Veessen (closed part)	Heerde	27 E, G	5
114. Scherpenzeelse Hank	Wijhe and Olst	27 E, G	5
115. f.r.b. near Vorchten	Wijhe and Heerde	27 E	5
116. f.r.bs. S. of Herkeloo	Zwollerkerspel	27 E	5
117. Hanskolk	Hatterm	27 E	5-6 a
118. Scheller Wade (Kolk van Greve)	Zwollerkerspel	21 G, 27 E	4 a
119. Spoolderhank	Zwollerkerspel	27 F, G	5
120. f.r.b. near Doornik	Oldebroek	21 D	5
121. Hank near Zalk (open part) .	IJsselmuiden	21 D	5
122. Hank near Zalk (closed part)	IJsselmuiden	21 D	5
123. Koeluchtergat	IJsselmuiden	21 D	5
124. Hank near Wilsum (open part)	IJsselmuiden	21 D	5
125. Hank near Wilsum (closed part)	IJsselmuiden	21 D	5
126. Oude IJsel in Onderdijkse Polder	Kampen	21 D	4 a
127. Noorderdiep	Kampen	21 A, C	4 a

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EXPLANATION TO THE TABLES AND THEIR SUPPLEMENTS

The species are arranged in groups. These groups consist of characteristic and differential species of units of various ranks, and of accompanying species. Sometimes a characteristic species of a unit is also present in another unit. Then the species is listed in the table of the latter as characteristic of the unit of the next higher rank to which both units belong. E.g. *Carex acuta* is a characteristic species of the *Caricetum gracilis-vesicariae*, and this association belongs to the alliance *Magnocaricion*. However, the species is present also in the *Scirpeto-Phragmitetum*, which is an association belonging to the *Phragmition*. *Magnocaricion* and *Phragmition* both belong to the order *Phragmitetalia*; consequently *Carex acuta* is listed in the table of the *Scirpeto-Phragmitetum* as a characteristic species of the order *Phragmitetalia*.

The abbreviated indications placed in front of the species refer to the whole of a group or to a part of a group. An indication between brackets, however, refers only to the species in front of which it is placed.

As a rule the records on the table of a unit are selected from the total number of records which are available of that unit. The presence (P) of a species which is placed at the end of its line, does not refer to the number of records present in the table, but to the total number available; the latter number is mentioned above the line of Roman figures which indicate the presence of the species.

Some tables represent a unit which is subdivided in a number of units of lower rank. In this case the number of records available for the whole unit may be somewhat higher than the sum of the available records of its lower units. This is caused by the circumstance that not every record could be identified with one of the lower units.

If less than 5 records of a unit are available, the presence of a species is not indicated by a Roman figure, but by an Arabic figure, which indicates the real number of records in which the species is present.

ABBREVIATIONS USED IN THE TABLES AND THEIR SUPPLEMENTS

Acc.	accompanying species	MB.	Mörzer Bruijns
All.	alliance	Me.	river Merwede
Ass.	association	Mg.	Magnocaricion
Ch.	characteristic species	OM.	river Oude Maas
Cl.	class	Ord.	order
c.	subass. calthetosum	o.	subass. oenanthetosum
com.	subass. comaretosum	P.	presence
D.	1) differential species	Phra.	Phragmitetalia
	2) rest of delta area W. of Dordrecht	Phron.	Phragmition
	3) J. van Donselaar	QB.	A. J. Quené-Boterenbrood
DBH.	W. A. E. van Donselaar-ten Bokkel Huinink	R.	river Rhine
forel.	foreland	S.	P. J. Schroevens
HM.	river Heusdense Maas	S.-C.	Scheuchzerio-Caricetea fuscae
her.	subass. of Heracleum	sen.	subass. senecietosum
junc.	subass. juncetosum	t(yp.)	subass. typicum
K.	L. G. Kop	typh.	subass. typhetosum
L.	river Lek	V.	E. E. van der Voo
M.	river Maas	W.	river Waal
		IJ.	river IJssel