

## SYNTAXONOMY AND SYNECOLOGY OF THE LOLIO-POTENTILLION TÜXEN 1947 IN THE NETHERLANDS\*

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### SUMMARY

From 1978 to and including 1980 the author studied Dutch pastures inundated in winter and spring. The ecology and taxonomy of the following communities are described in this paper:

Class: *Plantaginetea majoris* R. Tüxen and Preising 1950

Order: *Agrostietalia stoloniferae* Oberdorfer, Müller and Görs 1967

Alliance: *Lolio-Potentillion anserinae* Tüxen 1947

*Ranunculo-Alopecuretum geniculati* Tüxen 1937

Subassociations: *typicum* subass.nov.

*rorippetosum sylvestris* subass.nov.

*equisetetosum palustris* subass.nov.

*Nasturtio-Alopecuretum geniculati* ass.nov.

*Triglochino-Agrostietum stoloniferae* Konczak 1968

Subassociations: *ranunculetosum repens* subass.nov.

*juncetosum gerardii* subass.nov.

*inops* subass.nov

*Agrostio-Trifolietum fragiferi* ass.nov.

Subassociations: *typicum* subass.nov.

*festucetosum rubrae* subass.nov.

*inops* subass.nov.

Derivate community of *Festuca arundinacea*-[*Lolio-Potentillion*]

Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*]

Community of *Scirpus maritimus* and *Alopecurus geniculatus*

Class: *Asteretea tripoliae* Westhoff and Beaufort 1962

Order: *Glauco-Puccinellietalia* Beaufort and Westhoff 1962

Alliance: *Armerion maritimae* Brauna-Blanquet and De Leeuw 1936

*Ononido-Caricetum distantis* Runge 1966

*Juncetum maritimi* Bilik 1956

Besides some comments are made on the *Alopecurus arundinaceus* community, observed in Sweden, which is unclear syntaxonomically. The relation of these communities to one another and to the two major environmental factors – salt influence and the position of the ground-water level during the growing season – are discussed on the basis of an ordination diagram.

### 1. INTRODUCTION

Because of the great difference in floristic composition and habitat the communities of inundated pastures (*Lolio-Potentillion anserinae* Tüxen 1947) and the communities occurring on organic drift material along the coasts of the northern part of Europe (*Agropyro-Rumicion crispae* Nordhagen 1940), previously

\*Dedicated to Prof. V. Westhoff on the occasion of his retirement from the University of Nijmegen.

combined in the *Agropyro-Rumicion crispis* Nordhagen 1940 em. Tüxen 1950, have been separated by SÝKORA (1980).

As the *Lolio-Potentillion* had been studied insufficiently (WESTHOFF & DEN HELD 1969, WILMANNS 1978), a study into the syntaxonomy and syncology of the *Lolio-Potentillion* in some countries of Western Europe was started in 1978. Relevés were made in The Netherlands (1978, 1979 and 1980), Ireland (1979), Belgium and the northern part of France (1980), England and Wales (1981) and South Sweden (1978). In order to study the long term dynamics of the hydrology determining the occurrence of the alliance, permanent transects were investigated during these years. Papers about the data from Ireland, Belgium, France and from the transects are in preparation.

## 2. METHODS

During the analytical phase 428 relevés were made according to the Braun-Blanquet method (WESTHOFF & VAN DER MAAREL 1973). For estimation of the quantitative occurrence of each species the Braun-Blanquet scale as refined by BARKMAN et al. (1964) was used. The location of the sites visited is shown in fig. 1. A few relevés from Sweden have been added to the table (column 29). The size of the sample plots varied from 1 to 25 square meters, most of them being 4 square meters or more. According to various sources (see WESTHOFF & VAN DER MAAREL 1973) the minimal area values for pastures (*Lolio-Cynosuretum*) varies between 5 and 10 sq.m. Very often the shape of the plots was oblong, for instance 2 × 10 or 0,5 × 10 m, parallel to the waterline. The sites were selected using the knowledge already existing in phytosociological literature (e.g. PASSARGE 1964, WESTHOFF & DEN HELD 1969, OBERDORFER 1977, ELLENBERG 1978, RUNGE 1980) about the floristic composition and habitat of the *Lolio-Potentillion* and of the adjacent communities belonging to the alliances found on sites with a different hydrology and management (e.g. *Arrhenatherion*, *Phragmition*, *Magnocaricion*, *Bidention*). No relevés were made of the *Poo-Lolietum* D. M. de Vries and Westhoff n.n. apud Bakker 1965 because this association developing out of the *Lolio-Cynosuretum* when excessive manuring with nitrogen is applied, usually with an increase in grazing intensity, should be assigned to the *Lolio-Plantaginion* (FOERSTER 1968, WESTHOFF & DEN HELD 1969). The *Poo-Lolietum* occurs on sites which are too dry for the *Lolio-Potentillion*.

An auger was used to take soil samples in order to determine the soil texture and the organic material content. Besides grazing and poaching intensity, soil moisture, height above and distance from open water and salt influence were recorded.

In the synthetical phase the Tabord program was used for structuring the rough table (VAN DER MAAREL et al. 1978). The scale of BARKMAN et al. (1964) was transformed according to the ordinal transformation (VAN DER MAAREL 1979a, b). The similarity ratio (WISHART 1969) was used to measure similarities between relevés and clusters. The relevés were divided into two tables. In the



Fig. 1. Map of The Netherlands on which the localities where relevés were made are indicated with an asterix.

Table 1. Synoptic table of communities assigned to the *Lolio-Potentillion anserinae* Tx. 1947 occurring in The Netherlands as well as some other communities.

- 1-11 Ranunculo-Alopecuretum geniculati Tx. 1937
- 1-5 Subass. roripetosum sylvestris
- 6 Subass. typicum
- 7-11 Subass. equisetetosum palustris
- 12-13 Derivate community of *Festuca arundinacea*-[*Lolio-Potentillion*]
- 14 Nasturtio-Alopecuretum geniculati ass.nov.
- 15 Community of *Scirpus maritimus* and *Alopecurus geniculatus*
- 16-17 Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*]
- 18-22 Triglochino-Agrostietum stoloniferae Konczak 1968
- 18 Subass. *inops*
- 19-20 Subass. ranunculetosum *repentis*
- 21-22 Subass. juncetosum *gerardii*
- 23-25 Agrostio-Trifolietum *fragiferi* ass.nov.
- 23 Subass. *inops*
- 24 Subass. *typicum*
- 25 Subass. festucetosum *rubrae*
  
- Other communities**
- 26 Ononido-Caricetum *distantis* Runge 1966
- 27-28 Juncetum *maritimi* Bilik 1956
- 29 Alopecurus *arundinaceus* community

**Table 1.** Legend on preceding page.

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Cluster number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
number of relevés	5	16	15	11	7	39	30	4	51	8	14	12	9	16	17	14	12	11	10	4	26	12	17	14	10	6	4			
Plantae-Potentillietalia	IV	II	IV	IV	III	IV	III	III	IV	II	II	III	II	III	III	IV	V	III	V	IV	V	II	V	V	IV	IV	III			
Potentillietalia	II	I	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Plantae-Potentillietalia	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Lolium perenne	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Pea annua	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Polygonum aviculare	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Geochloë-Cladoniae	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Geochloë-Polygonetalia - a constant companion	V	IV	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Arenaria stolonifera	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Oedemera trivialis	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Alopeurus geniculatus	V	IV	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Rubus fruticosus	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Garrigue	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Janetiella	I	II	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Ranunculus aquatilis																														
Phalaris arundinacea	IV	V	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Polygonum amphibium	II	III	III	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Potentilla repens	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Paracotula officinalis	II	III	III	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Erysimum cheiranthoides	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Carex hirta	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Lysimachia nummularia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Myosotis scorpioides	IV	V	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Berberis vulgaris	IV	V	IV	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Juncus effusus	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Agrostis capillaris	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Bulettia salinaria	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Glechoma hederacea	II	III	III	IV	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II							
Glyceria maxima	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Mentha pulegium	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
India brasiliana	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Abutilon theophrasti	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III	II	V	II	II	III	II	IV	IV	II	IV	II	II	IV	II	II	II								
Plantae-Potentillietalia	I	II	III	III	IV	III																								

definite table the threshold value was 0.35 in both tables, the fusion level 0.67 and 0.77 respectively. After removing the rest group and the clusters clearly belonging to associations from other alliances (*Lolio-Cynosuretum*, *Sagino maritimae-Cochlearietum danicae*), 401 relevés remained. Only the synoptic table is presented here (table 1). Apart from this general table, four synoptic tables of lower units were constructed in order to show their internal structure (tables 2, 4, 5 and 6).

The cluster centroids, that is the mean of the transformed cover abundance values of each species belonging to one cluster, were used in a principal components analysis. For this ordination the Ordina program (ROSKAM 1971, see also VAN DER MAAREL 1979a) was used.

Names of phanerogams are according to the Flora Europaea (TUTIN et al. 1964–1980). The mosses are named according to LANDWEHR (1966).

### 3. RESULTS

#### 3.1 THE ALLIANCE *Lolio-Potentillion* Tüxen 1947.

Synonym: *Agrostion stoloniferae* Görs 1966, *Agropyro-Rumicion crispis* Nordhagen 1940 em. R. Tüxen 1950 pro parte. Non *Agropyro-Rumicion crispis* Nordhagen 1940 (see Sýkora 1980)

Syntaxonomy (table 1): The *Lolio-Potentillion* as studied in The Netherlands is characterized by the presence of the character-species *Agrostis stolonifera*, *Alopecurus geniculatus* and *Rumex crispus*, and the constant companion *Poa trivialis*. Constant companions are species which have a presence of more than 60% but cannot be designated as character-species or differential species (BRAUN-BLANQUET 1925, 1928, 1959, 1964).

*Carex otrubae* and *Juncus inflexus* are placed under the heading *Lolio-Potentillion* in the table because they have a clear preference for some of the lower units in the Belgian, French and Irish material. In the Dutch material these species do not show any obvious preference. *Lymnaea truncatula* Müll., the liver fluke snail, occurs with preference in the *Lolio-Potentillion* (OVER 1967) as its occurrence is promoted by grazing, ground-water fluctuation and poaching (see Synecology).

In 1970 TÜXEN separated the *Lolio-Plantaginion majoris* Sissingh 1969 and the *Lolio-Potentillion* (called Agropyro-Rumicion in his paper) and put them into separate orders which he placed into the class *Molinio-Arrhenatheretea* Tüxen 1937. Whereas the first alliance remained in the *Plantaginetalia majoris* R. Tüxen (1947) 1950, the *Lolio-Potentillion* was placed into the *Trifolio fragiferi-Agrostietalia* (Oberdorfer 1967 em. Tüxen 1970). In 1971 OBERDORFER abandoned the unit *Lolio-Plantaginetum* (Linkola 1921) Beger 1930 em. Sissingh 1969 (*Lolio-Plantaginion* Sissingh 1969), and after dividing this community into three subassociations, one of which he assigned to the *Cynosurion* (Tüxen 1937), her renamed it the *Matricario-Polygonetum* Müller mscr. In the same paper he stated that *Lolium perenne* is not a character-taxon of the *Plantaginetea majoris* Tüxen et Preising 1950, but of the *Cynosurion*.

In 1972 KRIPELOVÁ divided the *Lolio-Plantaginetum* into the subassociations *typicum* Krippelová 1972, *poetosum annuae* Krippelová 1972 and *potentilletosum anserinae* Krippelová 1972. Besides she recognized within this association the stadium of *Polygonum aviculare* (comparable to the *Matricario-Polygonetum typicum* described by Oberdorfer 1971) and the stadium of *Plantago major*. As *Lolium perenne* occurs with high coverage and high frequency (100%) in the subassociation *typicum* and as species of the *Cynosurion* are almost absent in this community, the unit *Lolio-Plantaginetum* should be maintained. Although *Lolium perenne* occurs with a high presence in communities belonging to the *Cynosurion*, it is obviously a character-species of the *Lolio-Plantaginetum typicum* (KRIPELOVÁ 1972, KOPECKÝ 1978).

The assignment of the *Plantagineta majoris* to the *Molinio-Arrhenatheretea* can by no means be justified. The same applies for the *Lolio-Potentillion*. This alliance differs considerably in floristic composition from the *Molinio-Arrhenatheretea*. In this class the species *Cynosurus cristatus*, *Phleum pratense*, *Plantago lanceolata*, *Poa pratensis*, *Festuca rubra*, *Festuca pratensis*, *Cerastium fontanum*, *Ranunculus acris*, *Trifolium pratense*, *Rumex acetosa*, *Holcus lanatus*, *Vicia cracca*, *Lathyrus pratensis*, *Trifolium dubium*, *Alopecurus pratensis*, *Arrhenatherum elatius*, *Bellis perennis*, *Prunella vulgaris*, *Leucanthemum vulgare*, *Veronica chamaedrys* and *Trisetum flavescens* are frequent. On the contrary they are almost absent in the *Lolio-Potentillion*, whereas the opposite applies for a lot of species which are characteristic for this alliance.

As the character-species of the *Plantaginetea*, *Potentilla anserina*, *Plantago major*, *Lolium perenne* and *Poa annua* occur in the *Lolio-Potentillion*, often with high presence degrees in most (*Potentilla anserina*, *Plantago major*) or in some of the communities (*Lolium perenne* and *Poa annua*), I consider this alliance to belong to this class. Besides the *Lolio-Plantaginetum* and the communities of the *Lolio-Potentillion* are ecologically related by their occurrence on soils which are frequently treaded and are deficient in oxygen. In the *Lolio-Plantaginon* the oxygen deficiency is caused by the compaction of the soil whereas in the *Lolio-Potentillion* it is mainly caused by inundation and waterlogging. Since, on the other hand, the difference in floristic composition and in habitat is obvious, I adopt the opinion of OBERDORFER et al. (1967) to assign the *Lolio-Potentillion* (called *Agropyro-Rumicion* by them) to a separate order, the *Agrostietalia stoloniferae* Oberdorfer, Müller & Görs 1967 (see also GÖRS 1968, MÜLLER & GÖRS 1969). In my opinion the suggested division of the *Lolio-Potentillion* into three suballiances, *Juncion effusi*, *Loto-Trifolion* and *Eu-Agro-pyro-Rumicion* (WESTHOFF et al. 1961, WESTHOFF & VAN LEEUWEN 1962, 1966, WESTHOFF & DEN HELD 1969) does not apply for the atlantic domain of Europe.

The *Lolio-Potentillion* occurs in almost all countries of Europe. It is found in the southern part of Sweden, but its northern limitation is still unclear. In the Mediterranean region it is replaced by the vicariant alliance *Trifolio-Cyndontion* Braun-Blanquet & Bolos 1957, which is found under similar ecological conditions, e.g. moist soils poor in oxygen, inundated in winter, grazed by cat-



Fig. 2. The *Lolio-Potentillion* is restricted to the low-lying inundated zone (January 1980) in a pasture on the bank of a former creek. During summer the water table will be below the soil surface. Just outside the fence where grazing pressure is absent the vegetation is dominated by *Phragmites australis*.



Fig. 3. The *Agrostio-Trifolietum fragiferi* inundated by slightly brackish water on an upper salt marsh in The Netherlands (February 1980). The little hummocks are caused by poaching. The little bushes on the small dunes consist of *Ononis spinosa* and *Salix repens*.

tle and often poached. In arid or semi-arid climates it is restricted to places where the ground-water level is constantly very high e.g. along rivers with low banks and on frequently inundated islands. It is therefore rather rare and occupies only small areas. The *Caricetum divisae*, subassociation of *Leucojum aestivum* and *Galium constrictum* as described by DONKER & STEVELINK 1961, should be assigned to the *Trifolio-Cynodontion* (BRAUN-BLANQUET & BOLOS 1957, TÜXEN & OBERDORFER 1958, BOLOS 1967, RIVAS-MARTINEZ 1968, BOLOS et al. 1970). J. TÜXEN (1966) is of the opinion that the floristic differences between these two alliances is insufficient and he therefore proposes to abandon the alliance *Trifolio-Cynodontion*. As this alliance has been studied insufficiently no definite enunciation can be made.

**Synecology:** The communities belonging to the *Lolio-Potentillion* are mainly composed of reptant hemicryptophytes and rhizome-geophytes. These plants have a capacity for rapid vegetative spread and are efficient colonizers of temporary gaps. They occur in water meadows, river forelands, along former river beds, beside pools resulting from dike bursts, in or along depressions containing stagnant water, at the edge of drinking pools for cattle, along ditches, on higher salt marshes and along former creeks, now surrounded by polders. They are found on all kinds of relatively nutrient-rich, hydromorphic soils, varying from sand to heavy clay soils and soils with a peaty top soil layer of about 10 cm consisting for almost 100% of organic material. Most of the species characterizing this alliance have their optimal occurrence on soils moderately rich to rich in nitrogen (ELLENBERG 1978). A mean C/N ratio of 13 ( $n = 16$ ,  $\sigma = 2$ ) measured in the *Ranunculo-Alopecuretum*, the *Nasturtio-Alopecuretum* and the *Agrostio-Trifolietum fragiferi* indicates a rather rapid mineralization. The main factors associated with their occurrence are winter and spring inundation (often with silt or sand deposition) and grazing. The composing species belong to the trichohygrophyta (HEJNY 1960); germination, flowering and maturation of the seed take place in the terrestrial phase when the soil is still moist. A long limose phase offers favourable conditions and a secondary flooding is tolerated.

The flooding (figs. 2 and 3) leads to oxygen depletion of the soil which again causes the formation of  $Mn^{++}$ -ions,  $Fe^{++}$ -ions and reduction of sulphate into sulphides.  $CO_2$ , organic acids and for instance methane are produced by decomposition of organic material (BRÜMMER 1974). While lack of oxygen can seriously trouble the respiration in the cell, the substances mentioned above are toxic to many species. Under anaerobic conditions phosphorus is easily available (SCHEFFER et al. 1976). This is in concordance with the fact that most of the species characteristic for the *Lolio-Potentillion* have their highest relative average frequencies on soils with a rather high (P-citric acid 51–80) to high (P-citric acid  $> 80$ ) phosphorus status (KRUYNNE et al. 1967). Flood sensitive species appear to be excluded from frequently flooded habitats due to the production of increased amounts of ethanol resulting from an increased rate of glycolysis induced by the anaerobic conditions. This accumulation of toxic quantities of

ethanol does not occur in flood-tolerant species. According to some evidence a metabolic switch in the latter species may lead to the accumulation of mainly the non-toxic malic acid (HENSHAW et al. 1962, CRAWFORD & MC MANNON 1968, CRAWFORD & TYLER 1969, CRAWFORD 1966, CRAWFORD 1969, MC MANNON & CRAWFORD 1971).

Various plant species avoid oxygen stress by means of oxygen diffusion through stems, rhizomes and roots. *Lolio-Potentillion* species possessing aerenchymous tissues in stem and roots are for instance *Alopecurus geniculatus*, *Inula britannica*, *Agrostis stolonifera* and *Potentilla anserina* (WALTHER 1977). Radial oxygen loss from the roots of these plants is of considerable benefit to wetland species as it oxydises the reduced soil toxins (CONWAY 1940, ARMSTRONG 1964, 1967, 1971; BRÄNDLE 1980a, b). Of course this oxygen transport is only possible if the plants are partly emerged. As plant activity is stimulated by higher temperatures, inundation during the summer season is of more influence than winter inundation. According to KLAPP (1971) in a temperate climate growth of grassland species starts at 5°C and abundant growth only above 10°C. By growing on frequently inundated sites, the *Lolio-Potentillion* species avoid competition from flood-sensitive grassland species (DIERSCHKE & JECKEL 1980). Species selection is probably already taking place in the seed bank. Most seeds will not normally germinate if the oxygen tension is decreased below that in the atmosphere and after some time their viability becomes impaired (MAYER & POLJAKOFF-MAYBER 1963). Other species can only germinate if the seeds are shed in a very moist habitat. In years of excessive rainfall and flooding a marked general reduction of the abundance and cover of species which cannot survive prolonged inundation periods (e.g. numerous species of the *Molinio-Arrhenatheretea*) can be observed (STOFFERS & KNAPP 1962, KLAPP 1965, BALATOVA-TULAČKOVA 1972, WALTHER 1977). The fluctuations resulting from climatological differences from year to year (ecotypic oscillations) were called "Harmonika-Sukzession" by TÜXEN (1950). For the species in question the flooding (in some communities even with sea water) is a perturbation i.e. a significant deviation from the nominal state (the normal operating range). For the grassland species sensitive to flooding, the oxygen depletion induced by the inundation is a severe unfavourable deflection or stress (sensu ODUM et al. 1979). In the *Lolio-Potentillion* the fluctuation in the hydrology does not act as a stress but as a subsidy i.e. it improves the performance of the ecosystem. The elimination of these natural pulses will severely perturb the "perturbation-dependent" ecosystem (VAN LEEUWEN 1958, VAN LEEUWEN & WESTHOFF 1961, WESTHOFF et al. 1961, WESTHOFF & VAN LEEUWEN 1966, BAKKER 1965).

The species composing the *Lolio-Potentillion* belong to the category of ruderal-perennial herbs (GRIME 1979). Ruderals sensu Grime are species that thrive under conditions of low stress (sensu Grime) and high disturbance. Grime has unfortunately broadened the concept ruderal. It is used in botanical literature for species growing on rubble (latin: rudus) and disturbed road sides, e.g. *Sisymbrium* and *Onopordietalia* (ELLENBERG 1978, WILMANNS 1978). The communities to which they belong are strongly influenced by man. The term ruder-

al sensu Grime also comprises communities where disturbances have a natural cause as for instance flooding in the case of the *Lolio-Potentillion*. The anthropogenic influence here is grazing but as will be stated further down, this alliance can also occur under conditions of natural grazing. By preventing the establishment of tall growing species, grazing is advantageous to the low creeping hemicryptophytes and rhizome-geophytes (KLAPP 1971).

Although deep and often numerous hoofprints are seldom absent, poaching is not a necessary condition for the development of the *Lolio-Potentillion*. Totally untrampled but short-grazed sites often occur immediately outside the pasture fence bearing excellently developed *Lolio-Potentillion*. In ELLENBERG 1978 an outline is given of the influence of trampling on the vegetation (see also KLAPP 1971). Soil compaction resulting from this phenomenon again reduces the aeration of the soil.

As grazing by wild herbivores and frequent inundation along uncontrolled rivers were common in the European lowland, this alliance must have existed in prehistoric times (LOHMEYER 1954, WESTHOFF & VAN LEEUWEN 1966, GROENMAN-VAN WAATERINGE 1968, KLAPP 1971, Anonymous 1979). Nowadays human pressure has increased so severely that this alliance although very characteristic for the North European lowland, is declining in a considerable way (FRILEUX 1976, DIERSCHKE 1978, DIERSCHKE & JECKEL 1980). The main factor involved in this process is the drastic land drainage and the consequent lowering of the water tables. Wetlands present the most obvious of challenges to the farmer intent on agricultural intensification (SMEETS et al. 1980). Anything that is wet can be drained – at a price (SHOARD 1980).

In Europe in general the last two decades have witnessed a very impressive increase in field drainage to such an extent that it now is one of the leading factors in rural environmental change (GREEN 1980). Besides drainage the intensive use of herbicides, the large scale use of inorganic fertilizers, overgrazing and an increase in salt influence (MEULEMAN & JOANKNECHT 1980) are detrimental to the *Lolio-Potentillion*.

### 3.1.1. The lower units

I *Ranunculo-Alopecuretum geniculati* Tüxen 1937.

Synonym: *Rumici-Alopecuretum geniculati* Tüxen 1950.

Syntaxonomy (table 1 and 2, clusters nr. 1–11):

Character-species: *Potentilla reptans*, *Carex hirta*, *Rorippa sylvestris*, *Juncus compressus*, *Inula britannica* and *Mentha pulegium*.

Differential species: *Phalaris arundinacea*, *Polygonum amphibium*, *Taraxacum officinale* group, *Elymus repens*, *Lysimachia nummularia*, *Myosotis scorpioides*, *Rorippa amphibia*, *Alopecurus pratensis*, *Equisetum palustre*, *Glechoma hederacea* and *Glyceria maxima*.

Constant companion: *Ranunculus repens*.

*Inula britannica* and *Mentha pulegium* respectively, are rather rare and very rare in The Netherlands (VAN DER MAAREL 1971a, ARNOLDS et al. 1976). *Mentha pulegium* reaches its north-western boundary in Ireland, South England

Cluster number	1	2	3	4	5	6	7	8	9	10	11
<u>Plantaginetea and Lolio-</u>											
Potentillion											
<i>Agrostis stolonifera</i>	V	IV	IV	V	V	V	V	V	V	V	V
<i>Rumex crispus</i>	V	V	V	V	III	V	IV	IV	III	III	III
<i>Plantago major</i>	II	V	IV	III	IV	V	III	V	IV	II	III
<i>Poa annua</i>	II	III	IV	II	I	I	III	III	I	I	II
c.e. <i>Poa trivialis</i>	I	V	IV	III	V	V	V	V	V	V	V
c.c. <i>Ranunculus repens</i>	I	V	IV	IV	IV	V	V	V	V	V	V
<i>Alopecurus geniculatus</i>	II	V	V	IV	V	III	II	V	IV	V	V
<i>Rorippetosum sylvestris</i>	IV	IV	V	II	V	IV	I	II	II	I	I
<i>Rorippa sylvestris</i>	V	V	V	V	V	IV	III	II	II	I	III
<i>Elymus repens</i>	III	IV	V	IV	V	II	II	III	I	I	I
Potentilla reptans											
<u>Equisetum palustre</u>							II	IV	III	I	IV
<i>Trifolium repens</i>	II	III	II	II	I		III	IV	IV	IV	IV
<i>Cardamine pratensis</i>							I	II	III	III	II
<i>Equisetum fluviatile</i>							I	I	II	I	III
<u>Variancia + subvariancia</u>											
<i>Potentilla anserina</i>	IV	II	IV	IV	II	IV	III	III	III	I	II
<i>Cirsium arvense</i>	III	V	I	II	IV	II	III	III	II	I	I
<i>Phalaris arundinacea</i>	IV	V	IV	II	II	V	IV	III	III	I	I
<i>Polygonum amphibium</i>	II	III	III	I		IV	IV	IV	IV	I	I
<i>Glechoma hederacea</i>	II					II	II	III	I		
<i>Mentha aquatica</i>	I		I		I		II	IV	III	I	I
<i>Carex hirta</i>	I	I	II	IV	V	II	IV	IV	III	II	III
<i>Myosotis scorpioides</i>	I	I	II	V	II	III	IV	V	III	I	
<i>Holcus lanatus</i>							I	I	V	V	
<i>Artemisia vulgaris</i>	II										
<i>Taraxacum officinale</i> gr.	II	V		III	II	I	III	II	III	II	III
<i>Alopecurus pratensis</i>	I	IV	I	II		II	II	I	I	I	I
<i>Juncus compressus</i>	I		I	II	IV	I	II	II	I		
<i>Mentha pulegium</i>											
<i>Calliergonella cuspidata</i>	I	I	I			I	I		I	I	I
<i>Lolium perenne</i>	I	I	I	III	II	II		V	II	I	III
<i>Lysimachia nummularia</i>	II	I	I			III		V	III	I	
<i>Bellis perennis</i>	I	I	I				V	I	II	I	
<i>Festuca pratensis</i>	II		II			II	II	V	I	III	II
<i>Prunella vulgaris</i>							I	III	I	I	I
<i>Cerastium fontanum</i>						I	I		III	IV	I
<i>Glyceria maxima</i>						I	I		IV	IV	II
<i>Juncus articulatus</i>	I	I	III	I	I	IV	IV	IV	IV	IV	II
<i>Glyceria fluitans</i>	I		I	I	I			IV	V	IV	
<i>Galium palustre</i>	I	I	I	I	I	II	II	IV	II		
<u>Remaining species</u>											
<i>Eleocharis palustris</i>	I	II	I	III	II		III	II	III	II	II
<i>Veronica catenata</i>	I	I	II	III	II	I	II	II	I	I	I
<i>Poa pratensis</i>	II	I	I	II	III	I	I	III	I		
<i>Rorippa amphibia</i>	I	II	I	II	III	I	I	II	I		
<i>Leontodon autumnalis</i>	III	I	II	I		I	I	III	II		I
<i>Equisetum arvense</i>	III	I	I	III	I		I		I		
<i>Polygonum aviculare</i>	I	I	II	II	I	II	I		I	I	
<i>Stellaria media</i>	I					III	II	I			
<i>Juncus bufonius</i> gr.			I	II	I	I	II	II	II	I	I
<i>Plantago lanceolata</i>	I	I	I	I	I	I	I	II	I	I	I
<i>Polygonum hydropiper</i>	I	I	I	I	I	I	I	II	I	I	I
<i>Ranunculus sceleratus</i>	I	I	I	II	I	I	I	I	I	I	I
<i>Myosotis laxa</i> ssp. <i>caespitosa</i>	I				I	I	II	I	I	I	I
<i>Oenanthe aquatica</i>	I		I		I	I	II	I		I	
<i>Rumex obtusifolius</i>	II	II	I			II			I	I	
<i>Trifolium fragiferum</i>					I	I	I		II		
<i>Urtica dioica</i>	II	I			I	I		I			
<i>Trifolium pratense</i>	I				I	I		II	I		
<i>Mentha arvensis</i>			II		I	I		I			
<i>Phleum pratense</i>		I			I			II	II		
<i>Iris pseudacorus</i>	II				I	I		I			
<i>Veronica serpyllifolia</i>					I	I	II	I		I	
<i>Butomus umbellatus</i>	II				I	I			I		
<i>Oenanthe fistulosa</i>							II	II	I		
<i>Ranunculus acris</i>						I	II	II			
<i>Rumex conglomeratus</i>	I	I				I	I	II	I		
<i>Carex otrubae</i>						I	I	II	I		
<i>Juncus inflexus</i>						I	I	II	I		
<i>Lychnis flos-cuculi</i>						I		II			

and The Netherlands. In The Netherlands it has been recorded only in nine hoursquares since 1950. A new locality has been found in 1981 (ADEMA 1981). Its decline from 47 hoursquares before 1950 is probably due to a change in water control (ADEMA 1980). In the literature (WESTHOFF & DEN HELD 1969, OBERDORFER 1970, VICHEREK 1973, KNEEPKENS & VERHOEVEN 1975, ELLENBERG 1978) these species are considered to be character-species of the *Lolio-Potentillion* (*Agropyro-Rumicion crispi* sensu Tüxen 1950); in *table 1* they are represented in the *Ranunculo-Alopercuretum* only, so that they are considered to be characteristic for this association.

*Elymus repens* and *Ranunculus repens* are neither character-species of the alliance nor of the *Ranunculo-Alopercuretum*. *Elymus repens* has a wide ecological amplitude and occurs with presence class IV or V in several communities (see *table 3*). These communities occur on arable lands, recently disturbed soils, ruderal and otherwise anthropogenically influenced sites.

According to PALMER & SAGAR (1963) *Elymus repens* is usually found in waste places and on arable land where tree or shrub cover is not continuous. It is a common component of lightly grazed grassland communities of basic soils in Britain, a pioneer plant in the colonization of waste places, a pest of agriculture, especially associated with arable land. In case of disturbance of the vegetation cover this species is quickly colonizing the gaps by means of its prolific vegetative reproduction through rhizomes (PALMER & SAGAR 1963). *Elymus repens* is both very resistant against drought and against flooding (KRUYNE & DE VRIES 1968). It has been observed to spread impressively as a reaction to overfertilization with nitrogen (LAMBERT 1979). MÜLLER & GÖRS (1969) consider it to be a character-species of the *Convolvulo-Agropyron repens* Görs 1966, *Agropyretea intermedii-repentis* Oberdorfer, Müller & Görs 1967, semi ruderal grasslands from dry and medium dry sites. Originally, before the creation of these anthropogenic habitats, the optimal occurrence of *Elymus repens* must have been in natural *Lolio-Potentillion* communities where open places were created by the influence of inundation (e.g. sedimentation, erosion) or poaching.

*Ranunculus repens* occurs with high presence class in some *Magnocaricion*-communities, especially in the *Phalaridetum arundinaceae* Libb. 1931 and the *Caricetum gracilis* (Graebn. & Hueck 1931) Tüxen 1937 as well as in several communities of the *Calthion palustris* Tüxen 1937 em. 1951, especially in the *Cirsietum oleracei* Tüxen (1937) 1951 and the *Juncetum subnodulosi* Koch 1936 (PASSARGE 1964). It is a weed of grassland and arable land and of recently disturbed ground. *Ranunculus repens* is especially abundant where drainage is impeded and is found mainly on heavy wet soils. Colonization of open ground is quickly effected by the production of long stolons (HARPER 1957). These conditions explain its high presence in the *Lolio-Potentillion*.

- a) Subassociation *typicum* (cluster nr. 6). This subassociation takes a central position between the other subassociations.
- b) Subassociation *rorippetosum sylvestris* (clusters nr. 1-5). Differential spe-

Table 3. Communities in which *Elymus repens* is found with presence class IV or V (PASSARGE 1964, WESTHOFF & DEN HELD 1969, KOPECKÝ 1978, RUNGE 1980).

I	Polygono-Chenopodion W. Koch 1926 em. Sissingh 1946 denuo em. Oberd. 1957.
1.	Chrysanthemo-Sperguletum (Br.-Bl. & De Leeuw 1936) Tx. 1937
2.	Chenopodietum albi Pass. 1955
3.	Digitarietum ischaemi Tx. & Prsg. (1942) 1950
4.	Lycopsetum arvensis Raabe 1944
5.	Mercuriali-Fumarietum (Kruseman & Vl. 1939) em. Tx. 1950
6.	Veronico-Lamietum hybriди Kruseman & Vl. 1939
II	Sisymbrium Tx., Lohm. & Prsg. 1940
1.	Agropyro-Convolvuletum arvensis Feldföldy 1943
III	Arction (Tx. 1937) em. Sissingh 1946
1.	Lamio-Conietum Oberdorfer 1957
2.	Artemisieturn vulgaris (Br.-Bl. '31) Tx. 1942
IV	Aegopodium podagrariae Tx. 1967
1.	Aegopodietum Tx. 1967
V	Trifolion medi Th. Müller 1961
1.	Urtico-Cruciatetum laevipes Dierschke 1973
VI	Derivate community of [Agropyron repens-Arrhenatheretalia] Kopecký 1978.

cies: *Rorippa sylvestris*, *Elymus repens* and *Potentilla reptans*.

Variant with *Phalaris arundinacea* and *Polygonum amphibium* (clusters nr. 1–3).

Variant with *Carex hirta* and *Myosotis scorpioides* (clusters nr. 4 & 5).

c) Subassociation *equisetetosum palustris* (clusters nr. 7–11). Differential species: *Equisetum palustre*, *Trifolium repens*, *Cardamine pratensis* and *Equisetum fluviatile*.

Variant with *Polygonum amphibium* and *Phalaris arundinacea*, (clusters nr. 7–9).

Variant with *Holcus lanatus* (clusters nr. 10 & 11).

Within the *Ranunculo-Alopecuretum* each cluster represents a unit below the variant. These units will not be discussed here. The differential species are apparent from table 2.

**Synecology:** The subassociation *rorippetosum sylvestris* is confined to sites with a low ground water table and a dry top soil after the retreat of the water. The water table is often situated more than one meter below the ground level. This subassociation is found on sandy ridges and sandy river shores (cluster 1), in pastures in the river forelands mainly on heavy clay and sometimes on sandy clay. In summer the clay becomes very hard and fissured by desiccation. It also occurs on steep banks along pools resulting from former dike bursts and on the foot of dikes with only five to ten centimeter of soil (clay, sometimes sand) on a stoney or asphalt underground.

The two variants mainly result from a difference in grazing intensity. The variant with *Phalaris arundinacea* is mainly found in alternate pastures and in hay pastures. This is in concordance with the results of KRYUNE et al. (1967), which demonstrate that *Phalaris arundinacea* and *Polygonum amphibium* have their highest relative average frequencies in pure hayfields and hay pastures

and the lowest in alternate pastures and pure pastures.

The variant with *Carex hirta* and *Myosotis scorpioides* on the contrary is found in pure pastures. Concerning *Carex hirta* this is again in concordance with the data from KRUYNE et al. 1967. *Myosotis scorpioides* on the other hand has a highest relative average frequency in hay pastures. In this case it is confined to the variant with *Carex hirta* and *Myosotis scorpioides*, a community from pastures with a slightly higher water table and a somewhat moister top soil.

In the subassociation *equisetetosum palustris* the water table is a long time above the surface and close to the soil surface even in the driest period. In almost all cases it has been found adjacent to open water, along former river beds, pools resulting from dike bursts, marshy, severely poached ditch banks, on the bottom of ditches and drainage furrows. Measurements revealed that the ground-water level was always within 30 cm from the soil surface, in many cases at the same level as, or even sometimes  $\pm$  5 cm above the soil surface. The *Ranunculo-Alopecuretum geniculati equisetetosum palustris* occurs on heavy clay, sandy clay and peaty soils. Because of the high water content these soils are very soft resulting in the presence of many, often deep hoofprints.

The variant with *Phalaris arundinacea* and *Polygonum amphibium*, is almost restricted to the river forelands where the hydrological dynamics are more pronounced than in the sites where the variant of *Holcus lanatus* is found. While the former variant is yearly inundated by a deep water layer, the depth of the water in the latter is always restricted to about 20 cm, permitting species like *Holcus lanatus* to be emerged during the greater part of the growing season. The variant with *Holcus lanatus* was not found in river forelands but in moist pastures mostly in the polder areas, mainly on peaty soils, on soils consisting of 5–10 cm of organic material on clay or sand, on sandy clay and on clay.

The subassociation *typicum* is intermediate in its hydrological characteristics. It occurs in river forelands, mainly on heavy clay, sandy clay and sometimes on sand.

## II Association group with *Eleocharis uniglumis*.

### Syntaxonomy:

Character-species: *Eleocharis uniglumis*.

Differential species: *Phragmites australis*, *Festuca arundinacea*.

These three taxa combine the three associations:

*Nasturtio-Alopecuretum geniculati*

*Triglochino-Agrostietum stoloniferae*

*Agrostio-Trifolietum fragiferi*.

**Synecology:** The associations belonging to this group are restricted to habitats where the top soil never desiccates. The hydrology is considerably less dynamical than in the river forelands.

### A. *Nasturtio-Alopecuretum geniculati* ass.nov.

#### Syntaxonomy (table 1):

Local character-species: *Ranunculus sardous*.

Differential species: *Nasturtium microphyllum*, *Ranunculus sceleratus*, *Veronica catenata*, *Epilobium parviflorum*.

Constant companions: *Ranunculus repens* and *Glyceria fluitans*.

Nomenclatural type:

Locality: Zeeuws Vlaanderen, "Cambronkreek", a former creek;

Date: 15th of June 1978;

Size: 5 m<sup>2</sup>; Total cover 95%; height 20–50 cm; soil type: sandy clay.

*Ranunculus sardous* +, *Nasturtium microphyllum* 1, *Ranunculus sceleratus* +, *Veronica catenata* +, *Epilobium parviflorum* +, *Ranunculus repens* +, *Glyceria declinata* 1, *Alopecurus geniculatus* 2a, *Rumex crispus* 3, *Agrostis stolonifera* 5, *Juncus articulatus* +, *Eleocharis uniglumis* 1, *Poa trivialis* 2a, *Festuca arundinacea* +, *Trifolium fragiferum* +, *Phragmites australis* +, *Scirpus lacustris* ssp. *tabernaemontani* 1, *Phalaris arundinacea* +, *Oenanthe aquatica* +, *Mentha aquatica* 2, *Brachythecium rutabulum* +.

Relevés of this community have also been made by me in Belgium, N.W. France, Britain and Ireland. The *Nasturtio-Alopecuretum* is transitional to the *Helosciadetum nodiflori* Braun-Blanquet 1931 and the *Nasturtietum officinalis* Seib. 1962 (*Glycerio-Sparganion* Braun-Blanquet et Sissingh 1942). It is often adjoined by these communities and by the *Bidention* Nordhagen 1940. Although *Apium nodiflorum* rarely occurs in the Dutch material, it is regularly found in the relevés made abroad. This species reaches its northern limit in The Netherlands and is rather rare (TUTIN et al. 1968, ARNOLDS et al. 1975).

Synecology: The association occurs along ditches and along former creeks now lying inland. The very soft, severely poached sandy clay soils are water saturated throughout the year. The top soil consists of slime mixed with organic material. The water level is situated at 10–20 cm above the soil surface during the greater part of the year. The presence of shells in the soil indicates a high calcium content.

#### B. *Triglochino-Agrostietum stoloniferae* Konczak 1968.

Syntaxonomy (tables 1 and 4):

Character-species: *Triglochin palustris*.

Differential species: *Juncus articulatus*, *Galium palustre*, *Ranunculus flammula*, *Hydrocotyle vulgaris*, *Carex nigra*, *Myosotis laxa* spp. *caespitosa*. Lectotype: relevé nr. 5, table 18 from KONCKZAK 1968. The table given by Konczak (1968) is somewhat complex and the floristic composition of this table is not sufficiently characteristic for this association. This is probably caused by the fact that his relevés are made on relatively dry sites (water table at a depth of 60 cm on 20-8-1964) and originate from a restricted locality, viz. the Havelseen near Potsdam. *Triglochin palustris* has been considered a character-species of the *Scheuchzerio-Caricetea fuscae* Nordhagen 1939 (KRAUSCH 1968, OBERDORFER 1970 and 1977, ELLENBERG 1978). Close examination of published synoptic tables shows that this does not apply. It is absent in most of the communities belonging to that class, while in the other communities its presence class does

	cluster number				
	18	19	20	21	22
<i>Agrostis stolonifera</i>	V	V	V	V	IV
<i>Potentilla anserina</i>	V	III	V	V	V
<i>Eleocharis uniglumis</i>	II	II	IV	III	III
<i>Juncus articulatus</i>	IV	V	V	V	V
<i>Galium palustre</i>	IV	V	V	IV	II
<i>Alopecurus geniculatus</i>	III	V	IV	I	II
<i>Ranunculus flammula</i>	IV	III	V	III	V
<i>Hydrocotyle vulgaris</i>	IV	III	V	V	II
<i>Carex nigra</i>	V		V	V	V
<i>Ranunculus eschscholtzii</i> and <i>Juncetosum gerardii</i>					
c.c. <i>Poa trivialis</i>	I	V	III	I	IV
<i>Phragmites australis</i>	I	III	V	IV	III
<i>Triglochin palustris</i>	V		III	II	IV
<i>Ranunculus eschscholtzii</i>					
<i>Ranunculus repens</i>	II	V	V	II	
<i>Lolium perenne</i>		III	II		
<i>Juncetosum gerardii</i>					
<i>Juncus gerardi</i>	I	II	I	V	V
<i>Glaux maritima</i>	I			IV	V
<i>Inona</i>					
<i>Stellaria palustris</i>	II				
<i>Carex panicea</i>	II				
<i>Variants</i>					
<i>Cardamine pratensis</i>	II	V	IV	III	
<i>Juncus bufonius group</i>	II	I	II	III	
<i>Mentha aquatica</i>	I	IV	III	II	
<i>Leontodon autumnalis</i>	II	III	IV	III	I
<i>Myosotis laxa</i> ssp. <i>caespitosa</i>	I	IV	V	III	
<i>Plantago major</i>	I	IV	I	II	
<i>Holcus lanatus</i>	II	IV		I	I
<i>Scirpus lacustris</i> ssp. <i>tubernaemontani</i>		IV			
<i>Festuca arundinacea</i>		III			
<i>Senecio aquaticus</i>		III			
<i>Berula erecta</i>		III			
<i>Lysimachia nummularia</i>		II			
<i>Epilobium palustre</i>		II			
<i>Eleocharis palustris</i>			V		
<i>Rumex crispus</i>	I	I		III	
<i>Carex disticha</i>			III		
<i>Plantago lanceolata</i>			II		
<i>Vicia cracca</i>			II		
<i>Calliergonella cuspidata</i>			IV		
<i>Carex serotina</i>			II		
<i>Anagallis minima</i>			II		
<i>Centaurea pulchellum</i>			II		
<i>Trifolium fragiferum</i>				V	
<i>Eleocharis quinqueflora</i>				IV	
<i>Brachythecium rutabulum</i>				IV	
<i>Remaining species</i>					
<i>Trifolium repens</i>	II	IV	II	II	IV
<i>Glyceria fluitans</i>	I	III	II		
<i>Polygonum amphibium</i>	I	I	II		
<i>Ranunculus sceleratus</i>		II		I	
<i>Triglochin maritima</i>		I		I	II
<i>Lotus corniculatus</i>	II	II		I	
<i>Foa pratensis</i>	I		II	I	I
<i>Cerastium fontanum</i>		II	I		
<i>Mentha arvensis</i>	II		I		III
<i>Equisetum arvense</i>			II	I	
<i>Sagina procumbens</i>	I	III			III
<i>Lycopus europaeus</i>	II	I	II	I	
<i>Veronica scutellata</i>	II		I	I	
<i>Juncus effusus</i>	II	II		I	
<i>Drepanocladus aduncus</i>	I	II	II	I	II

not exceed II (PASSARGE 1964, KRAUSCH 1968, OBERDORFER 1977, ZIJLSTRA 1981). In TÜXEN (1937) *Triglochin palustris* is absent from the *Scheuchzeriella*, but occurs in the *Ranunculus repens-Alopecurus geniculatus* association, subassociation of *Eleocharis uniglumis* Tüxen et Hintz 1937, with presence class IV.

In agreement with VAN OOSTSTROOM (1954) I consider the species to have its optimal occurrence in the *Lolio-Potentillion* (*Agropyro-Rumicion crispis* Tüxen 1950 p.p.) and more in particular as a character-species of the *Triglochino-Agrostietum stoloniferae* (compare table 1).

a) Subassociation *ranunculetosum repentis* (19–20)

Differential species: *Ranunculus repens*, *Lolium perenne*.

b) Subassociation *Juncetosum gerardii*

Differential species: *Juncus gerardi*, *Glaux maritima*.

c) Subassociation *inops*: This species-poor community is characterized by the absence of differential species.

**Synecology:** The *Triglochino-Agrostietum stoloniferae* is restricted to pastures without any artificial manuring. Consequently the nutrient status is low and the soil is moderately acid. The character- and differential species have their highest presence on wet, moderately to strongly acid, peaty to pure peat soils, with a rather low to low (P-citric acid 0–20 and 21–32 respectively) phosphorus status (KRUYNE et al. 1967, KRUYNE & DE VRIES 1968); their optimal occurrence is on soils which are poor to very poor in nitrogen (ELLENBERG 1978). Throughout the year the water table stands just above or just beneath the soil surface.

The association has an affinity to the *Caricion curto-nigrae* W. Koch 1926 em. Nordhagen 1936, the small sedge communities, peat building, mesotraphent communities from calcium-poor soils (WESTHOFF et al. 1969, OBERDORFER 1977). In The Netherlands these communities as well as the *Triglochino-Agrostietum* are very rare at present, because of the extensive use of artificial fertilizers, often in combination with drainage.

The subassociation *ranunculetosum repentis* is confined to marshy fresh soils. It has been found in and along ditches, along former creeks in a pasture grazed by pigs, along dune slacks and in a ditch shaded by *Pinus sylvestris*. The soil consists of brown peaty clay, peat, clay, sandy clay or sand rich in organic material.

The subassociation *juncetosum gerardii* occurs under slightly brackish conditions. Two samples taken from water inundating this community on the 27th of February, each contained 0.46‰ Cl<sup>-</sup>. It occurs on the higher saltmarshes where it is inundated with seawater during high water spring tides, but only when there is a considerable influence of fresh water from lateral seepage out of surrounding dunes or from stagnant rain water. It is also found on saltmarshes nowadays inaccessible for the sea where the salt has partly been washed out of the soil. The top soil (5–10 cm) consists of peat, sometimes mixed with sand, on grey, reduced sand. Compared to the situation in the other subassociations, the top soil of the subassociation *inops* is drier in summer. In some

	cluster number			
	23	24	25	26
<i>Agrostis stolonifera</i>	V	V	V	V
<i>Potentilla anserina</i>	V	II	V	V
<i>Juncus gerardii</i>	V	V	V	V
<i>Glauca maritima</i>	IV	V	II	V
<i>Eleocharis uniglumis</i>	IV	V	I	III
C.o. <i>Trifolium repens</i>	II	IV	V	V
<u>Typeicum, festucetosum rubrae and Ononido-Caricetum.</u>				
<i>Carex distans</i>	IV	IV	IV	
<i>Leontodon autumnalis</i>	III	III	III	
<i>Triglochin maritima</i>	II	II	I	
<u>Typeicum and festucetosum rubrae</u>				
<i>Trifolium fragiferum</i>	I	V	III	II
<i>Centaurea pulchellum</i>	I	V	III	
<u>Typeicum</u>				
<i>Plantago major</i>	II	IV	II	
<i>Phragmites australis</i>	II	IV	II	II
<i>Drepanocladus aduncus</i>		IV		
<i>Poa trivialis</i>	I	III	I	
<i>Carex otrubae</i>	I	III		
<i>Samolus valerandi</i>		III		
<i>Lotus tenuis</i>		III	I	
<i>Bellis perennis</i>		III		
<u>Festucetosum rubrae and Ononido-Caricetum</u>				
<i>Festuca rubra</i>	I	V	V	
<i>Holcus lanatus</i>	I	I	V	V
<i>Poa pratensis</i>	I	I	IV	V
<i>Plantago coronopus</i>	I	I	III	III
<i>Odontites vernae ssp serotina</i>	II		III	III
<i>Plantago maritima</i>	I	I	III	III
<i>Centaurea littoralis</i>			II	II
<u>Ononido-Caricetum</u>				
<i>Ceratium fontanum</i>			III	V
<i>Ononis spinosa</i>		I	I	V
<i>Armeria maritima</i>			II	IV
<i>Lotus corniculatus</i>			I	IV
<i>Trifolium pratense</i>		I	I	III
<i>Cochlearica danica</i>				II
<i>Elymus pungens</i>				II
<u>Remaining species</u>				
<i>Lolium perenne</i>	I	II	I	
<i>Festuca arundinacea</i>	II	III	II	I
<i>Scirpus maritimus</i>	II	III		
<i>Juncus articulatus</i>	I	III	II	I
<i>Galium palustre</i>	II	I		
<i>Triglochin palustris</i>	I	II	II	
<i>Carex nigra</i>	I		II	I
<i>Cirsium arvense</i>	I		II	I
<i>Juncus bufonius group</i>	I	III	II	I
<i>Sagina procumbens</i>		I	II	II
<i>Alopecurus geniculatus</i>	II			
<i>Scirpus lacustris ssp tabernaemontani</i>	I	II		
<i>Leontodon taraxacoides</i>		I	II	II
<i>Salix repens</i>	I		I	II
<i>Brachythecium rutabulum</i>	II	III	III	III

cases it even runs fully dry, i.e. a layer of dry papery organic material is formed on a moist sandy subsoil.

*C. Agrostio-Trifolietum fragiferi* ass.nov. (cluster nr. 23–25). Synonym: community of *Agrostis stolonifera* subvar. *salina* and *Trifolium fragiferum* Westhoff 1947.

Syntaxonomy (tables 1 and 5):

Character-species: *Trifolium fragiferum*.

Differential species: *Juncus gerardi*, *Glaux maritima*, *Carex distans*, *Centaurium pulchellum*.

Constant companion: *Trifolium repens*.

Nomenclatural type:

Locality: Noord-Beveland.

Date: 27th of July 1978.

Size: 9 m<sup>2</sup>; total cover 98%; height 10–25 cm; soil type: 5 cm organic material on grey reduced sand.

*Agrostis stolonifera* 4, *Trifolium repens* 2b, *Trifolium fragiferum* 3, *Festuca arundinacea* 2b, *Carex distans* 2a, *Carex otrubae* +, *Centaurium pulchellum* 1, *Lotus tenuis* +, *Triglochin maritima* +, *Scirpus maritimus* +, *Plantago major* +, *Ononis spinosa* +, *Juncus gerardi* 3, *Phragmites australis* 1, *Bellis perennis* +, *Samolus valerandi* 1, *Juncus articulatus* +, *Poa trivialis* 1, *Lolium perenne* +, *Glaux maritima* 1, *Poa annua* 1, *Leontodon autumnalis* +, *Drepanocladus aduncus* 4, *Brachythecium rutabulum* 1.

a) Subassociation *typicum* (cluster nr. 24).

Differential species: *Plantago major*, *Phragmites australis*, *Drepanocladus aduncus*, *Poa trivialis*, *Carex otrubae*, *Samolus valerandi*, *Lotus tenuis*, *Bellis perennis*.

*Carex otrubae* is probably a character-species of the *Agrostio-Trifolietum fragiferi*; in this association it has a high presence in Belgium and France too. Its status will be decided after the interpretation of the relevés made in these countries.

b) Subassociation *festucetosum rubrae* (cluster nr. 25).

Differential species: *Festuca rubra*, *Holcus lanatus*, *Poa pratensis*, *Plantago coronopus*, *Odontites verna* spp. *serotina*, *Plantago maritima*, *Cerastium fontanum*, *Centaurium litorale*.

The *festucetosum rubrae* is a transition community between the subassociation *typicum* and the *Onido-Caricetum distantis* Tüxen 1955.

c) Subassociation *inops* (cluster nr. 23). Synonym: *Agrostis stolonifera-Potentilla anserina* community Runge 1966.

This subassociation is negatively characterized by the absence or very low presence of the differential species of the other subassociations and of *Carex distans*, *Leontodon autumnalis*, *Triglochin maritima*, *Trifolium fragiferum* and *Centaurium pulchellum*.

Synecology: The habitats of the subassociations *typicum* and *festucetosum rubrae* differ mainly in salt influence. The subassociation *typicum* has only been

found on slightly brackish soils out of reach of the sea. The *festucetosum rubrae* is inundated irregularly in winter during high water spring tides by sea water. The former occurs on sites adjacent to the inland slopes of sea dikes through which sea water is percolating and on primary dune slacks. The latter is restricted to higher salt marshes (fig. 3) and to so called "sluftervlakten" i.e. salt marshes of restricted surface behind the dunes in connection with the sea through a narrow inlet. Three samples taken from water inundating the subassociation *festucetosum rubrae* on the 27th of February 1980 contained 1.23, 1.93 and 2.13 ‰ Cl<sup>-</sup> respectively. Both habitats have the same soil composition viz. 5–10 cm of silt rich in organic material, on grey, reduced sand.

The subassociation *inops* experiences very low grazing pressure. On some sites the vegetation was grazed very extensively by sheep, on other sites by cattle and sometimes even by rabbits only. It often occurs as low lying patches surrounded by a stand dominated by *Juncus maritimus*, *Calamagrostis epigejos*, *Schoenus nigricans* or *Festuca rubra* (fig. 4).

### III Other units.

A. *Ononio-Caricetum distantis* Runge 1966. Synonym: *Ononis spinosa-Carex distans* association Tüxen 1955 nomen nudum.

Syntaxonomy (tables 1 and 5, cluster nr. 26).

Local character-species: *Ononis spinosa*.

WESTHOFF & DEN HELD (1969) assigned this association to the *Agropyro-Rumicion* (*Lolio-Potentillion*). Although it has a strong affinity to the *Agrostio-Trifolietum fragiferi* (table 5), the preponderance of *Glauco-Puccinellietalia* and *Armerion* species, like *Plantago maritima*, *Armeria maritima*, *Festuca rubra* ssp. *litoralis*, *Centaurium litorale*, *Juncus gerardi*, *Carex distans* and *Glaux maritima*, justifies its classification into the *Armerion*, as has been done by TÜXEN (1955) and RUNGE (1980). The *Ononio-Caricetum* has only been recorded on the Wadden islands and along the coast of the Baltic Sea.

Synecology: The *Ononio-Caricetum distantis* occurs as a zone above the *Agrostio-Trifolietum fragiferi festucetosum rubrae* on small dunes in extensively grazed upper salt marshes. The soil is composed of a top layer of about 5 cm which is very rich in organic material, lying on sand. The colour of the sandy subsoil is yellow indicating that reduction of the soil is considerably less severe than in the grey subsoil of the *Agrostio-Trifolietum*. The association occurs 40–60 cm above mean high tide level (RUNGE 1980). The vegetation is hardly grazed due to the protection given by the spines of the *Ononis spinosa* bushes.

B. Derivate community (Derivatgesellschaft sensu Kopecký & Hejný 1978) of *Festuca arundinacea-[Lolio-Potentillion]*.

Syntaxonomy (tables 1 and 6, clusters nr. 12 and 13): This community is characterized by the high presence and high coverage of *Festuca arundinacea*. As character-taxa of lower units are hardly present and as this community has no character-taxon of its own, it can be considered a derivate community of the alliance (KOPECKÝ & HEJNÝ 1974, 1978). Within this community two types

	cluster number	
	12	13
<i>Festuca arundinacea</i>	V	V
<i>Agrostis stolonifera</i>	V	V
<i>Poa trivialis</i>	IV	V
<i>Rumex crispus</i>	III	IV
<i>Potentilla anserina</i>	III	II
<i>Carex otrubae</i>	II	III
<i>Ranunculus sardous</i>	II	III
<i>Phragmites australis</i>	II	I
<i>Lolium perenne type:</i>		
<i>Lolium perenne</i>	IV	II
<i>Elymus repens</i>	IV	
<i>Ranunculus acris</i>	II	
<i>Urtica dioica</i>	II	
<i>Alopecurus geniculatus type:</i>		
<i>Trifolium repens</i>	III	V
<i>Ranunculus repens</i>	III	V
<i>Plantago major</i>	II	IV
<i>Alopecurus geniculatus</i>	II	IV
<i>Taraxacum officinale group</i>	I	III
<i>Carex hirta</i>		III
<i>Eleocharis uniglumis</i>	I	III
<i>Equisetum palustre</i>		II
<i>Nasturtium microphyllum</i>		II
<i>Eleocharis palustris</i>		II
<i>Glyceria fluitans</i>		II
<i>Remaining species</i>		
<i>Holcus lanatus</i>	III	IV
<i>Bellis perennis</i>	II	III
<i>Cirsium arvense</i>	III	II
<i>Ceratium fontanum</i>	III	II
<i>Rumex conglomeratus</i>	I	II
<i>Scirpus maritimus</i>	I	II
<i>Juncus articulatus</i>	I	II
<i>Trifolium fragiferum</i>	I	II
<i>Mentha aquatica</i>	I	II
<i>Cardamine pratensis</i>	I	II
<i>Brachythecium rutabulum</i>	I	II

can be distinguished:

- a) the *Lolium perenne* type is characterized by the presence of *Lolium perenne*, *Elymus repens*, and, with a lower presence, *Ranunculus acris* and *Urtica dioica*.
- b) the *Alopecurus geniculatus* type is characterized by the higher presence of *Trifolium repens*, *Ranunculus repens*, *Plantago major*, *Alopecurus geniculatus*, *Taraxacum officinale* group, *Carex hirta*, *Eleocharis uniglumis*, *Nasturtium microphyllum*, *Eleocharis palustris* and *Glyceria fluitans*.

As *Festuca arundinacea* can be found with high coverage in all kinds of grasslands under special management conditions, it is neither a character-species of this community nor of the *Potentillo-Festucetum arundinaceae* Tüxen 1950, or of any other community within the *Lolio-Potentillion*. *Festuca arundinacea* dominated vegetation types are of common occurrence on most of the dikes in The Netherlands. These sites are never inundated, ungrazed, irregularly burned and they contain a heavy clay soil. Under these conditions *Festuca arundinacea* tussocks are accompanied by *Molinio-Arrhenatheretea* species while *Lolio-Potentillion* species are hardly present or altogether absent. This situation can be found both in ruderal forms of *Arrhenatheretum* as well as in irregularly grazed *Lolio-Cynosuretum* communities (SÝKORA & SÝKORA-HENDRIKS 1977, SÝKORA-HENDRIKS & SÝKORA 1973 and many unpublished relevés).

That management (selective irregular grazing) rather than hydrology determines the spreading of *Festuca arundinacea*, can be seen in pastures consisting of both a dike and a piece of river foreland. In the same pasture the facies of this species occurs both in the inundated *Lolio-Potentillion* as well as in the adjoining *Lolio-Cynosuretum*.

**Synecology:** The D.c. *Festuca arundinacea-[Lolio-Potentillion]* was found in irregularly grazed pastures inundated or waterlogged in winter. *Festuca arundinacea* seems especially favoured by irregular horse grazing, but the community also occurs in pastures irregularly grazed by cattle and sheep (KLAPP 1965, 1971). The community occurs on various soils, e.g. peaty soils, on heavy clay, sandy clay and sand. The habitats of the two types differ in hydrology. The *Lolium perenne* type is restricted to sites which are considerably drier during the growth season than those occupied by the *Alopecurus geniculatus* type.

#### C. Community of *Scirpus maritimus* and *Alopecurus geniculatus*.

**Syntaxonomy (table 1, cluster nr. 15):** This community is a transition between the *Lolio-Potentillion* and the *Scirpetum maritimii* (W. Christ. 1934) Tüxen 1937. Although *Potentilla anserina*, *Agrostis stolonifera*, *Alopecurus geniculatus* and *Eleocharis uniglumis* are still frequent the occurrence of *Scirpus maritimus* with presence class V and *Scirpus lacustris glaucus* (presence class III) indicates its affinity with the *Scirpetum maritimii*.

**Synecology:** This community was found on low lying parts of pastures where the water remains above soil level for most of the year. It occurs under slightly brackish conditions on peaty soils, sandy clay soils, clay and sand. The *Scirpetum maritimii* is permanently inundated by brackish water with a depth of 5 to maximally 100 cm (WESTHOFF & DEN HELD 1969, OBERDORFER 1977, RUNGE 1980).

#### D. Basal community (Basalgesellschaft sensu Kopecký & Hejný 1978) of *Agrostis stolonifera-[Lolio-Potentillion]*.

**Syntaxonomy (table 1, clusters nr. 16, 17):** On floristic criteria this community cannot be assigned to one of the associations. Two types can be distinguished. The *Scirpus maritimus-Juncus bufonius* type (nr. 17) is almost exclusively composed of the class and alliance character-species *Potentilla anserina*, *Agrostis stolonifera* and *Alopecurus geniculatus*. Also *Scirpus maritimus* and *Juncus bufonius* occur in this type (presence class III). The *Trifolium fragiferum-Ranunculus sardous* type (cluster nr. 16) is somewhat less severely disturbed and apart from the class and alliance species mentioned for the *Scirpus maritimus-Juncus bufonius* type, it contains *Plantago major* and *Lolium perenne*. Besides *Poa trivialis*, *Festuca arundinacea*, *Ranunculus sardous*, *Juncus gerardi*, *Trifolium fragiferum* and *Trifolium repens* also occur (with presence class III or more).

**Synecology:** The main factor in the development of the basal community is disturbance. In some sites the disturbance was caused by severe treading and overgrazing, the vegetation having a height of only 5 cm and in extreme situations scoring only 30% total coverage. In other localities herbicides were used,



Fig. 4. The *Agrostio-Trifolietum fragiferi* is often constricted to grazed patches between a hardly grazed vegetation in which *Juncus maritimus* is the dominant species.

a thick layer of organic material was deposited on the pasture, a grazing regime had just recently been started in a formerly unmanaged grassland, a recently reclaimed soil was in the process of desalination, or a pasture was overfertilized with artificial fertilizers or by the droppings of a colony of seagulls.

#### E. *Juncus maritimus* dominated communities.

In many cases the *Agrostio-Trifolietum fragiferi* can be found as a mosaic of grazed low lying patches between a vegetation dominated by *Juncus maritimus*. The units 27 and 28 (*table 1*) result from relevés made in this adjoining vegetation in order to study its syntaxonomical position. *Juncus maritimus* has been considered to be a differential species with special affinity to the *Agropyro-Rumicion crispis* Nordhagen 1940 em. Tüxen 1950 (WESTHOFF et al. 1961, WESTHOFF & DEN HELD 1969) and some other authors even considered the species to have its optimum in the alliance (WESTHOFF & VAN LEEUWEN 1966, BEEFTINK 1968). According to BEEFTINK (1968) on the European Atlantic coast *Juncus maritimus* is only a facultative halophyte, with an optimum in the *Agropyro-Rumicion crispis*.

As can be seen in *table 1* the *Juncus* dominated vegetation adjoining the *Agrostio-Trifolietum fragiferi* clearly belongs to the *Juncetum maritimi* Bilik 1956 (*Armerion maritimae* Braun-Blanquet & De Leeuw (1936) and *Juncus maritimus* is by no means characteristic for any of the *Lolio-Potentillion* communities. Moreover one of the essential factors for the development of the *Lolio-Potentillion* is grazing. This is considerably restricted or even prevented be-

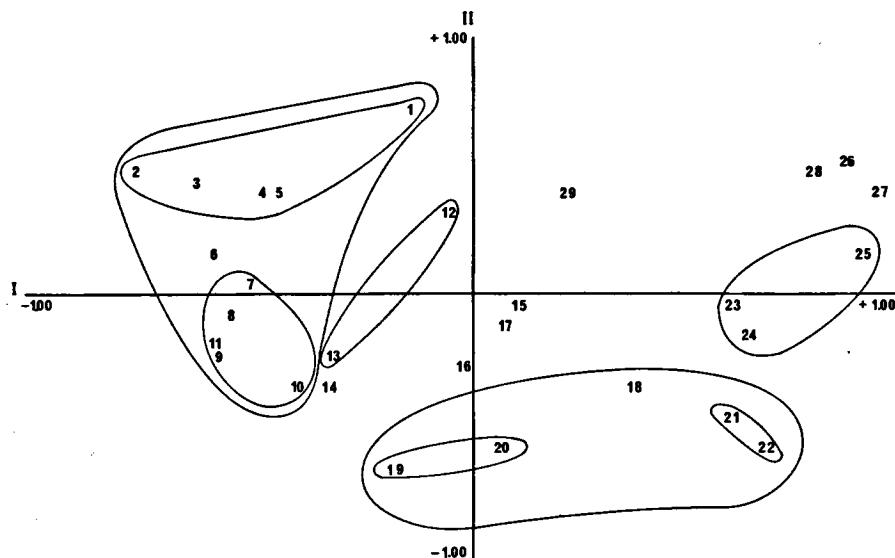
tween the coarse *Juncus* bushes. Only on the lower-lying patches where the vegetation is kept short by a sufficiently high grazing pressure, the *Agrostio-Tri-folietum fragiferi* is optimally developed (fig. 4). The boundary between the two vegetation types is very sharp, forming a convergent limit: limes convergens or ecotone (VAN LEEUWEN 1966, BECKING 1968, VAN DER MAAREL 1971b, SHIMWELL 1971).

#### F. *Alopecurus arundinaceus* community.

The syntaxonomic position of this community still remains unclear. It has been compared to an *Alopecurus geniculatus* community by TYLER (1969). The absence of a sufficiently strong grazing pressure enables the development of tall *Alopecurus arundinaceus* and *Festuca arundinacea* clumps, thus leading to a more or less ruderal tall forb community. The relevés presented in *table 1* were made near the Baltic Sea on an upper salt marsh. The soil respectively consisted of an upper layer of organic material, litter and even a decaying faggot on a sandy soil. The *Alopecurus arundinaceus* community (see also NORDHAGEN 1954) can certainly not be assigned to the *Lolio-Potentillion*.

#### 3.2. Principal components analysis (fig. 5)

*Fig. 5* is the result of the ordination of the units represented in *table 1*. The first two dimensions (percentage extracted variance respectively 28 and 12%) illustrate the relations of the units to one another and to the two main environmen-



*Fig. 5.* Ordination of the clusters presented in *table 1*. The numbers used in this figure correspond with the cluster numbers in *table 1*. Dimension 1 corresponds with the salt influence, dimension 2 with the depth of the water table during the growth season. For explanation of the numbers see text and *table 1*.

tal factors. Ecological interpretation of dimension 3 and 4 appeared to give difficulties. Dimension 1 corresponds with an increase in salt influence. The *Ranunculo-Alopecuretum geniculati* (clusters 1–11), the *Nasturtio-Alopecuretum geniculati* (cluster 14) and the derivate community of *Festuca arundinacea-[Lolio-Potentillion]* (cluster 12–13) on the left side of the diagram, are restricted to fresh soils. The *Agrostio-Trifolietum fragiferi* (cluster 23–25), *Juncetum maritimi* (clusters 27–28) and *Ononido-Caricetum distantis* (cluster 26) on the right side are restricted to brackish sites, whereas the community of *Scirpus maritimus* (cluster 15) and the *Alopecurus arundinaceus* community (cluster 29) take an intermediate position.

From the *Triglochino-Agrostietum* the subassociation *ranunculetosum repens* (clusters 19–20), growing on fresh soils, is found on the left hand side, whereas the subassociation *juncetosum gerardii* (clusters 21–22) from brackish sites occurs in the right hand side of the diagram.

Because the basal community of *Agrostis stolonifera-[Lolio-Potentillion]* (clusters 16–17) and the *Triglochino-Agrostietum inops* (cluster 18) are very poor in species as well as poor in indicative species, their position in the diagram does not clearly show their relation to the salt influence.

The second dimension corresponds with the depth of the water table during the growth season and consequently the extent to which the top soil is desiccating. Within the *Ranunculo-Alopecuretum* the *rorippetosum sylvestris* (clusters 1–5), growing on sites with a low water table in summer, is situated in the upper part of the diagram while the *equisetetosum palustris* (clusters 7–11) is found considerably lower. The subassociation *typicum* (cluster 6) takes an intermediate position. The *Nasturtio-Alopecuretum* (cluster 14) and the *Triglochino-Agrostietum* (clusters 18–22) from sites with a very moist top soil throughout the year, are presented in the lower half of fig. 5. The same applies for the brackish communities. While the *Ononido-Caricetum distantis* (cluster 26) and the *Juncetum maritimae* (clusters 27–28) occur in the upper half, the *Agrostio-Trifolietum fragiferi* (clusters 23–25) is represented lower down.

The two types of the D.C. of *Festuca arundinacea-[Lolio-Potentillion]* also show this configuration, the drier *Lolium perenne* type (cluster 12) above the wetter *Alopecurus geniculatus* type (cluster 13). The *Triglochino-Agrostietum* subassociation *inops* (cluster 18), having a dry topsoil in summer, is positioned above the two other subassociations. The community of *Scirpus maritimus* and *Alopecurus geniculatus* (cluster 15), a community of low lying parts in pastures inundated for most of the year, is located too high in the diagram.

## APPENDIX

Species with presence restricted to class I, with the cluster numbers: *Achillea millefolium* 2 and 6; *Achillea ptarmica* 2, 7, 9, 6, 3, 1; *Agrostis canina* 18; *Alisma lanceolatum* 7, 9, 6, 3; *Alisma plantago-aquatica* 9, 6, 15; *Allium vineale* 2, 12; *Alopecurus aequalis* 9; *Anthoxanthum odoratum* 7, 11, 9, 20, 19; *Apium graveolens* 25; *Apium nodiflorum* 7, 9; *Artemisia maritima* 26; *Atriplex patula* 26; *Bidens cernua* 19; *Bidens frondosa* 6; *Bidens tripartita* 2, 4, 6, 3, 20, 19; *Brachythecium velutinum* 1; *Bryum* species 6; *Calamagrostis epigejos* 23, 24; *Capsella bursa-pastoris* 6; *Carduus crispus*

12, 17, 25; *Carex acuta* 7, 9, 6, 14; *Carex arenaria* 23, 21; *Carex curta* 18; *Carex ovalis* 9; *Carex riparia* 19; *Carex trinervis* 26; *Centaurea debeauxii* ssp. *thuillieri* 20; *Ceratodon purpureus* 25; *Chamomilla recutita* 4; *Cicuta virosa* 10; *Cirsium palustre* 23, 26, 28, 19; *Cirsium vulgare* 12, 25; *Convolvulus arvensis* 2, 9; *Coronopus squamatus* 3; *Crepis capillaris* 4; *Dactylis glomerata* 12; *Danthonia decumbens* 16, 18, 23; *Deschampsia caespitosa* 2, 7, 6; *Eleocharis acicularis* 4; *Epilobium hirsutum* 9, 6; *Equisetum variegatum* 18; *Eriophorum angustifolium* 7; *Eupatorium cannabinum* 12; *Euphorbia esula* 2, 6, 1; *Eurhynchium praelongum* 19; *Filaginella uliginosa* 18; *Filipendula ulmaria* 18, 20; *Galium aparine* 12; *Galium mollugo* 2; *Galium uliginosum* 24; *Geranium dissectum* 9; *Herniaria glabra* 3; *Hippophae rhamnoides* 25; *Hordeum secalinum* 12, 15; *Hypochoeris radicata* 21; *Juncus alpinus* 27, 21; *Juncus conglomeratus* 20; *Juncus filiformis* 18; *Lemna minor* 14; *Limonium vulgare* 23; *Linum catharticum* 23, 25, 24; *Linum usitatissimum* 16; *Lotus uliginosus* 11, 10, 9, 23, 28; *Lysimachia vulgaris* 9, 6, 1; *Lythrum salicaria* 2, 7, 11, 9, 4, 6, 18; *Matricaria maritima* 2, 6, 5, 3; *Medicago lupulina* 3, 26; *Menyanthes trifoliata* 23; *Myosoton aquaticum* 2, 9; *Nardus stricta* 18; *Ophioglossum vulgatum* 18, 26, 21, 20; *Parapholis strigosa* 23, 25, 24; *Poa palustris* 9; *Polygonum mite* 10, 9, 6; *Polygonum persicaria* 11, 13, 18; *Potentilla supina* 7; *Puccinellia distans* 16, 12, 17, 15; *Radiola linoides* 21; *Ranunculus circinatus* 7, 11, 3; *Ranunculus ficaria* 2; *Rhinanthus angustifolius* 5, 21; *Rhytidadelphus squarrosus* 18, 25, 21, 19; *Rhynchosstiella curviseta* 25, 27; *Rorippa islandica* 2, 7, 17, 9, 6, 3, 14; *Rumex x abortivus* 6; *Rumex acetosa* 11, 13, 20; *Rumex hydrolapathum* 19; *Sagina nodosa* 26, 24; *Salix cinerea* 12; *Salix triandra* 7; *Schoenus nigricans* 23, 25, 27, 21, 28; *Scirpus lacustris* ssp. *glaucus* x *triquerter* 13; *Scirpus setaceus* 24; *Senecio vulgaris* 2; *Spergularia marina* 16, 14, 23, 21; *Spergularia media* 12, 17; *Sympyrum officinale* 2, 7, 6, 20, 28; *Tanacetum vulgare* 3, 1; *Thalictrum flavum* 2, 7; *Trifolium arvense* 25, 28; *Trifolium dubium* 23; *Typha latifolia* 19; *Veronica beccabunga* 11, 9, 6; *Vicia sativa* ssp. *nigra* 6, 12, 23; *Vicia sativa* ssp. *sativa* 12.

#### ACKNOWLEDGEMENT

I am greatly indebted to the following persons: Professor Dr. V. Westhoff and Professor Dr. M. J. A. Werger for critically examining the text, the various officers of the Dutch State Forest Service (Staatsbosbeheer) and "Naturmonumenten" for their advice in finding suitable study areas and for their permission to enter the reserves.

I am also greatly indebted to Drs. O. van Tongeren for the kind and pleasant way in which he helped me in using the computer programs.

I wish to thank Dr. H. J. Over; I very much appreciated the excursions we made together. Finally I thank Conny Sýkora for reading and typing the manuscript.

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