Ecological notes on Carex aquatilis communities

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Abstract

Carex aquatilis spp. *aquatilis* grows in mesotrophic fens and has a boreal circumpolar distribution. The species is most frequent in areas north of the 66° N line. In Europe the southern limits of its distribution is ca 53° N. Here *Carex aquatilis* is found in eutrophic flood plains. However, mesotrophic communities of *C. aquatilis* have been reported from these areas as well. Nowadays the peripheral populations in NW Europe appear to be relics of former mesotrophic communities which at present are under heavy pressure from human activities such as drainage and fertilizing. In the northern part of the Netherlands *C. aquatilis* stands are restricted to areas with a steady supply of cool groundwater. A decreased groundwater discharge has a negative influence on the development of inflorescences. It is expected that further interference with the hydrology will promote a further decline of the peripheral populations. The species will not be able to survive in drained, eutrophic, warmed up habitats.

Introduction

Carex aquatilis Wahlenb. is a swamp species with a boreal circumpolar distribution (Cajander, 1903; Alechin, 1927; Andreas, 1951; Kern & Reichelt, 1954; Churchill, 1955; Bakker & Westhoff, 1957; Neumann, 1957; Hultén, 1962; Komarov, 1964; Tutin *et al.*, 1980; Dierssen, 1982).

Three subspecies of *Carex aquatilis* have been distinguished (Hultén, 1962; *Carex aquatilis* ssp. *stans* (Drejer) Hultén, *Carex aquatilis* spp. *altior* Rydb., and *Carex aquatilis* spp. *aquatilis*. Subspecies *stans* has a more northern distribution than ssp. *aquatilis*, while the American ssp. *altior* has a more southern distribution. In Europe ssp. *altior* is absent. This article deals with *C. aquatilis* ssp. *aquatilis* only (see Fig. 1).

In Europe the main distribution of *Carex aquatilis* is north of the 66° N line (Dierssen, 1982) where the species grows in reed swamps, fens, wet meadows and even in relatively saline habitats (Siira,

* Nomenclature of phanerogams follows Heukels – van Ooststroom (1977), that of Bryophytes Smith (1978). Nomenclature of northern plant communities follows Dierssen (1982), that of Dutch and NW German communities Westhoff & den Held (1969) and Ellenberg (1978).

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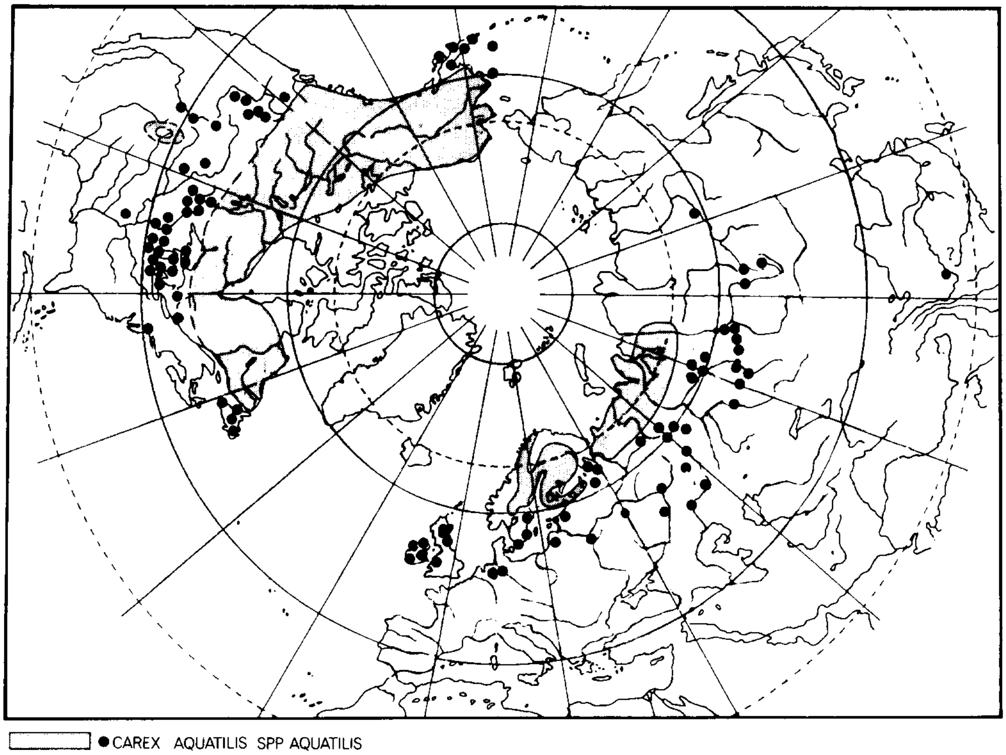

Fig. 1. Distribution of *Carex aquatilis* spp. *aquatilis* in the northern hemisphere. In America the distribution of *Carex aquatilis* includes both *C. a.* ssp. *aquatilis* and *C. a.* ssp. *altior* (after Hultén, 1962).

1970; Jefferies, 1977). In northern Sweden the species has a remarkable peat-forming ability (Elveland, 1976; Waldemarson-Jensén, 1979).

In the Netherlands and in NW Germany *C. aquatilis* was known only as a sub-fossil remain until 1948 (Andreas, 1951). In the period 1951–1955 many localities of *C. aquatilis* were discovered (Andreas, 1951; Küsel, 1956 pers. comm.; Bakker, 1957; Neumann, 1957; Dierschke, 1968). Before 1951 the species must have been confused with *Carex acuta*. Up to now the most southern locality of *C. aquatilis* in Europe appears to be the Overijsselse Vecht in the Netherlands at 53° N.

In this article we will discuss how *C. aquatilis* is able to survive at the southern border of its distribution, where conditions are quite different from those in the main distribution area. The occurrence of differences in the ecology of central and peripheral populations has been suggested (Bakker, 1979; Schmidt, 1969; see also Hengeveld & Haeck, 1982). Thus the NW European lowland habitats of the species may differ from those of more northern localities. The synecological conditions of *Carex aquatilis* stands were studied on the Drenthian Plateau, N Netherlands, which is similar to several Pleistocene plateau's in the NW German lowland.

The species composition and performance of *C. aquatilis* stands were studied in relation to hydrological features. The results are compared with published research on *C. aquatilis* communities in NW Germany, Norway, N Sweden and Scotland.

Materials and methods

The study area is situated south of Groningen (53°08′N, 6°37′E) in the catchment of the Drentse Aa, which drains 30 000 ha of a pleistocene landscape. Detailed information on hydrological and pedological aspects of this region was presented by Gischler (1967) and de Gans (1982). The vegetation of the Drentse Aa catchment area has been discussed by de Bruijn (1980), Everts *et al.* (1980) and Grootjans (1980).

In 1978 *Carex aquatilis* stands in this area were described according to the Braun-Blanquet approach, using the scale of Londo (1976). Below 5% cover a combination of letter and number is given: *p* = less than 20 individuals on 4 m^2, *a* = 20–100, *m* = more than 100; 1 = less than 1% cover, 2 = 1–3%, 3 = 3–5%. Above 5% cover only a number is given: 1 = 5–15%, 2 = 15–25%, ..., 9 = 85–95%, 10 = 95–100%).

The performance of *C. aquatilis* was estimated by assessing the percentage of flowering shoots and the cover of the species. The percentage of flowering shoots is thought to be a measure of the vitality of the plants. For sedge species this may not always be a correct assumption. For instance shoots of *Carex lacustris* remain vegetative in most years (Bernard, 1975). Flowers were formed only during one summer following severe flooding. In *C. rostrata* all vegetative mature shoots will flower; the number of flowering shoots is dependent on shoot mortality (Bernard & Gorham, 1978). *C. aquatilis* has a life cycle similar to that of *C. rostrata* (Gorham & Somers, 1973), so the percentage of flowering shoots appears to be a good measure of the vitality of the plants.

Observations of the water table were made in a number of *C. aquatilis* stands. The measurements were carried out in PVC tubes (40 mm diameter) every two weeks. All the data have been transformed to cumulative frequency histograms. These lines represent the residence time of groundwater in the soil profile (for more detailed information see Niemann, 1973; Grootjans & ten Klooster, 1980).

Results

Carex aquatilis *in Dutch catchment areas*

In the Netherlands *Carex aquatilis* is restricted to the northeastern part of the country (Fig. 2). The main distribution area is the fringe of the Drenthian Plateau where deep groundwater, originating from the plateau, emerges. In Figure 3 the distribution of *Carex aquatilis* is shown. Seepage areas and flow patterns of deep groundwater are shown too (see Working Group Geohydrological Research in Drenthe, 1978).

Carex aquatilis seems to prefer seepage areas in the lower reaches of the Drenthian streams. This suggests a preference of the species for enriched groundwater.

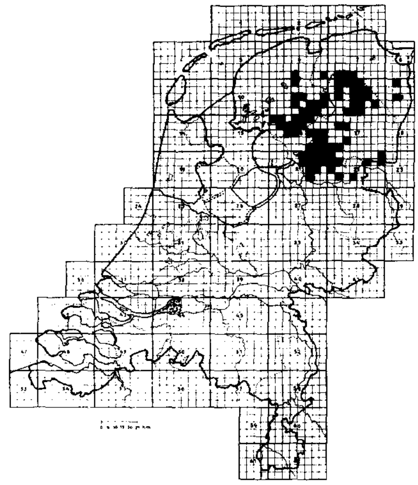

Fig. 2. Distribution of *Carex aquatilis* in the Netherlands. Each square represents 28 km^2.

Although the preference of *Carex aquatilis* for certain seepage areas is clear, the species is absent from areas where agricultural improvement projects have been carried out. Some stream systems have been devastated almost completely, leaving none of the marsh vegetation.

In the eastern part of Drenthe, the absence of *Carex aquatilis* is probably due to the presence of extensive oligotrophic bog complexes preventing the mineral rich deep groundwater from reaching the surface. Most of these mires have been reclaimed for agricultural purposes, and only small remnants of more natural vegetation are still present. Relevés of *Carex aquatilis* from Dutch stream basins are shown in Table 1. Five groups have been distinguished (A–E); they will be discussed only briefly here. Figure 4 presents a sketch of hydrological conditions and occurrence in the landscape.

Carex aquatilis is most abundant in the lower basins where the species is able to form extensive mats on soils that are rich in silt and organic material and which are flooded regularly. The relevés of group A must be classified as *Lysimachio–Caricetum aquatilis inops*. The species richness of these *Magnocaricion* stands is very low. The rest of the relevés of the lower basin (group B) and the majority of the relevés of the middle basin (groups D and E) belong to the *Senecioni–Brometum racemosi*

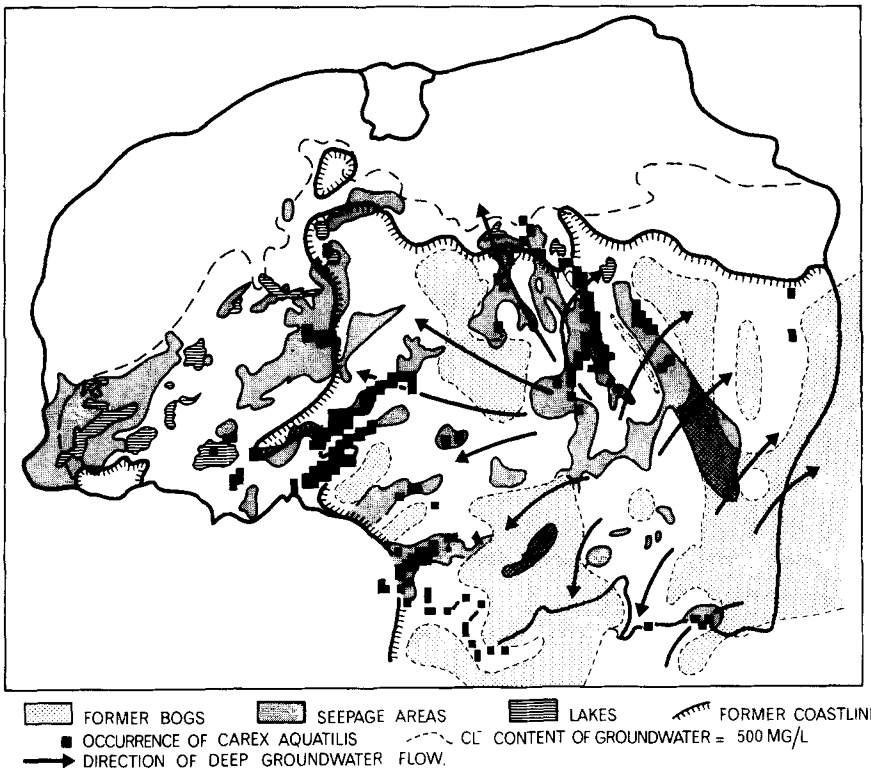

Fig. 3. Distribution of *Carex aquatilis* in the N Netherlands. Each square represents 1 km^2. Indicated are seepage areas, former bogs and flow direction of the deep groundwater. The former coastline is thought to correspond to the present 2 m above Amsterdam ordnance datum (NAP) line. The occurrence of brackish groundwater is indicated by the 500 mg/l Cl^- line.

and are rich in species. Relevés from group C belong to the *Caricetum curto-echinatae* and are rich in species as well.

Carex aquatilis stands in the lower basins are bordered by *Carex acuta* stands belonging to the *Caricetum gracilis* and by communities of small sedges (*Caricion curto-nigrae*).

In the middle reaches of undisturbed catchments *C. aquatilis* is fairly common. It grows in damp depressions just behind the stream banks. In these stands *Caltha palustris, Myosotis scorpioides, Lychnis flos-cuculi, Filipendula ulmaria* and many more species of the *Molinio-Arrhenatheretea* are frequent.

In the upper reaches *C. aquatilis* stands are rare. They can be classified as *Calthion palustris* as well.

Summarizing it can be said that most of the *C. aquatilis* stands of the middle and upper reaches belong to the *Calthion palustris* alliance, while quite a number of stands in the lower basin can be assigned to the *Magnocaricion* alliance. This points to prevailing less wet conditions in the middle and upper reaches compared to the lower basin. To verify this the groundwater regime of *Carex aquatilis* stands will be considered.

Carex aquatilis *and groundwater regime*

From the catchment area of the Drentse Aa, all available measurements of groundwater tables in *Carex aquatilis* stands were gathered. The data have been transformed into cumulative frequency histograms (Fig. 5). Unfortunately few series of measurements were available, so a direct comparison of *C. aquatilis* stands of lower and middle basins was not possible from a statistical point of view. We can however compare the grouped frequency lines with references from the literature (Grootjans, 1980; Grootjans & ten Klooster, 1980). For that purpose we chose the *Senecioni-Brometum race-*

Table 1. Relevés of *Carex aquatilis* stands in the middle and lower reaches of the catchment of the Drentse Aa (N Netherlands).

Group code	A							B										C			D						E					
Relevée 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	30	31	32
L = lower basin, M = middle basin	L	L	L	L	L	L	L	M	M	M	L	L	L	L	L	L	L	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Surface in m²	4	4	4	4	4	4	4	2	2	2	4	4	4	4	4	4	4	4	4	2	4	4	4	4	2	2	4	4	4	4	4	4
Cover (%) of phanerogams	30	30	50	50	35	80	30	30	40	95	30	35	30	30	35	30	60	40	60	40	60	50	15	40	70	50	40	85	95	70	70	60
Cover (%) of mosses	-	-	-	-	-	-	-	3	5	<1	10	3	20	50	50	85	25	1	2	2	5	2	5	25	10	35	20	20	<1	6	<1	2
Number of taxa	13	5	7	6	7	6	9	16	20	15	16	17	21	17	15	14	17	16	23	29	33	29	25	27	28	29	33	36	34	33	23	33
Carex aquatilis	1	3	3	4	2	7	3	1	2	4	1	1	2	2	2	3	5	2	m2	1	1	2	1	2	3	3	2	3	2	1	1	1
Equisetum fluviatile	a1	a1	1	p1	m2	p1	a1	a1		r	p1	p1	a1	p1	p1	p1	p1	m1	p1	m1	m4	m1	m1	m1	p1	p1		p1	m1	m2	p1	a1
Galium palustre	r		p1	p1			p1		a1		a1	a1	m1	m1	m2	m1	a1	m1		m1	m1	a1	a1	m1	a1	a1	m1	m1	m1	m1		
Glyceria maxima	m2	m2		1	a2	p1	m2	a1	p1	p1		1	a1	a1			p1	p1		p1	r	p1	r						r	p1		
Carex rostrata			m4						1			p1	p1			p1	p1				p1		p1	m1			p1		p1			
Phalaris arundinacea		a1				a4		a1	p1	a2	p1	p1	p1	a1	a1	a1	p1			p1	p1	r			p1		p1					
Lysimachia vulgaris	a1			r	r		r	p1												r	r	p1	p1	r								
Agrostis stolonifera									p1		p1	m2	m1	m1	m1	m1	m2	m1			a1		a1	m2								
Myosotis palustris									p1	a1	p1	p1	a1	a1	m1	m2	p1				a1	a1	a1		p1	p1	p1	p1	a1	p1		p1
Caltha palustris								p2	p2		r	p1	r	a2	p1		r	r		m2	p2	p1	p1	1	p2	1	a2	p1	1	a2	p1	p1
Ranunculus repens									a2	a2		r	r	m2	a1	p1	p1	r		p1		1	r		p1	p1	a1	m4	m4	1	1	a1
Poa trivialis								m1		m2				m1	a1	m1			p1		a1	m4		m1	m2	m1	m1	m2	1	m2	m1	m1
Holcus lanatus									a1	m4					a1			m2	a1	1	a1	m2	r	a1	a1	m4	m4	m2	a1	m2	2	2
Calliergon cordifolium									m4		m1	m1	m1	m2	m1	m1	1	a1	a1	m2	m2	m2		m1	m4	m2				m4	p1	
Calliergonella cuspidata									a1		m1		m1	a1			1			a1	m2		m2	m4	m4	1	2	1		m2		m2
Plagiomnium affine								a1	m2		a1		p1							p1	m1	a1	m1	2	m1	m2		a1	m1	m1		p1
Brachythecium rutabulum								m2		m1	m1										m1	a1	m2	m2		p1	m1	1	a1	a1	m1	
Amblystegium riparium								m1			1	m2	2	5	5	8					m2											
Calamagrostis canescens											m1	r	a1	a1	1	a1																
Cardamine pratensis ssp. palustris											p1	p1	a1	a1	m2	p1	p1															
Ranunculus flammula												p1	p1	p1		m1	m1															
Agrostis canina																		2	4	a1												
Viola palustris																		a1	r	r												
Hydrocotyle vulgaris																		m2	m2													
Filipendula ulmaria										3										m2	a1	p1	a2	a2		p2	a1	1	r	a2	a4	p1
Rumex acetosa										p1											p1	a1				r	p1	p1	a1	r	a1	p1
Cardamine pratensis ssp. pratensis																		r		m2		m2	r	r	p1	p1	m1	a1	p1	m2	a1	a1
Anthoxanthum odoratum																		p1	1	a1				p1	r	m2	m1	p1	m4	a1	1	1
Lychnis flos-cuculi																				a1		a2	p1		p1	p1	m2	1	p1	m2	p1	
Cirsium palustre																			r	r	p1	p1		r	r	r	p1	p2	p1		r	r
Mentha aquatica							p1														p1	a1	a1	a1		p1	m2	p1	r			a1
Equisetum palustre																		a1			p1	p1			a2	a1	m1	r		r		r
Lotus uliginosus																			r		a1	a1	a1	a1				1		m2		a1
Stellaria palustris									p1											p1	p1	r		r	p1				r	a1		r
Galium uliginosum																				m1	a1			m4				a1				m1
Cynosurus cristatus																									p1	p1	p1	m2	2			
Cardamine amara								p1													a1	a1	a1	a1								
Menyanthes trifoliata												p1									2				1	p1						
Carex nigra																			p1				p1	a1	p1	p1		m2				r
Trifolium repens																											m2	p1	p1	a1	r	1
Cerastium holosteoides																											a1	m1	a1	r		
Festuca pratensis																									p1		p1	p1	m2	p1	a1	p1
Ranunculus acris																						p1				p1	m2	m4	a1	p1	p1	p1
Festuca rubra																			a1					a1			r	p1		a1	p1	p1
Plantago lanceolata																										p1	r	p1	m4	p1		
Trifolium pratense																												a1	a1	m2		
Rhinanthus serotinus																				r			a1					a2	m2	m4	p1	

Addenda: other accompanying species

Peucedanum palustre 1/p1, 5/r; Rorippa amphibia 1/p1, 3/2; Cicuta virosa 1/p1, 6/r; Iris pseudacorus 1/p1, 7/r; Typha latifolia 2/r, 4/p1; Carex disticha 5/1, 7/m2, 13/a1; Carex hudsonii 1/1, 5/a2, 12/a1, 13/1; Stellaria alsine 8/p, 9/r, 18/m, 19/m1; Carex acutiformis 8/2, 10/p1, 18/p1, 22p1; Juncus effusus 7/r, 8/r, 9/a1,26/a, 27/a, 28/p1, 29/aa, 31/a1; Lythrum salicaria 21/p1, 22/r, 24/r, 29/p1; Taraxacum sect. vulgaria 19/p1, 24/p1, 25/r, 26/p1, 29/r, 32/p1; Achillea ptarmica 19/a1, 24/m2, 25/p1; Carex curta 21/r, 29/r, 30/a1; Climacium dendroides 22/p1, 26/a1, 32/a1; Rhytidiadelphus squarrosus 23/a1, 26/a1, 31/m1; Senecio aquaticus 28/a1, 29/r, 32/r.

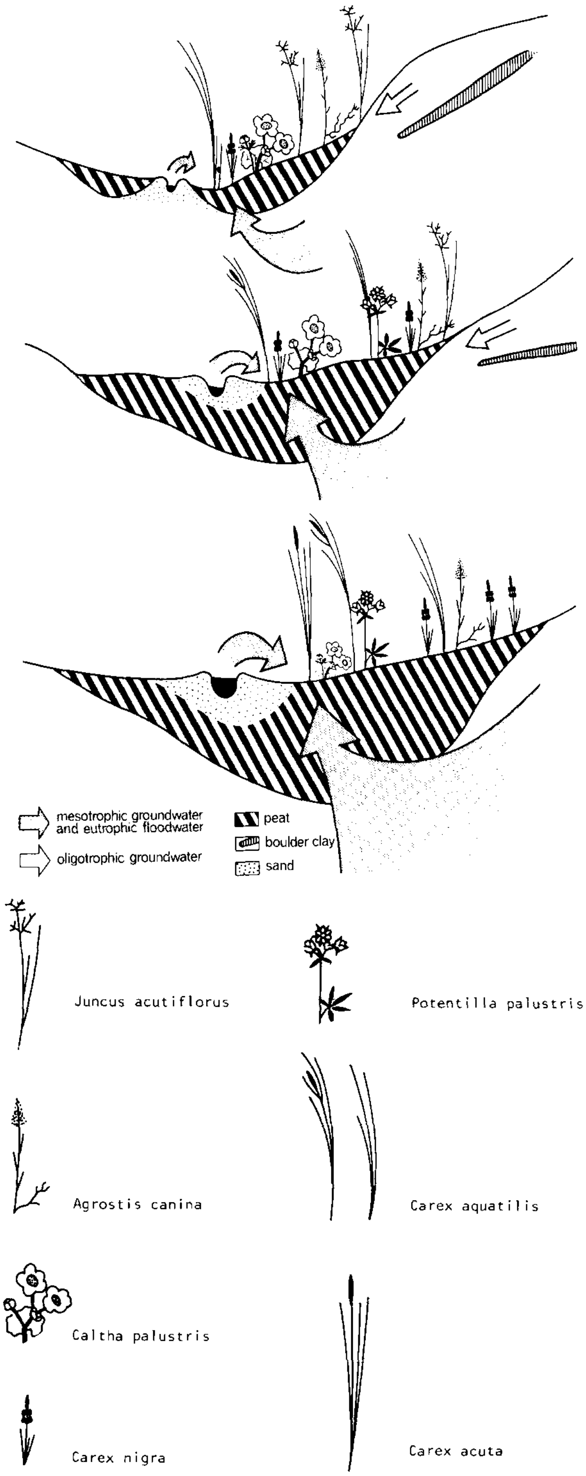

Fig. 4. Occurrence of *Carex aquatilis* stands in upper, middle and lower reaches of Drenthian streams. Shaded arrows indicate mesotrophic groundwater or eutrophic floodwater. Light arrows indicate oligotrophic subsurface groundwater above boulder clay lenses.

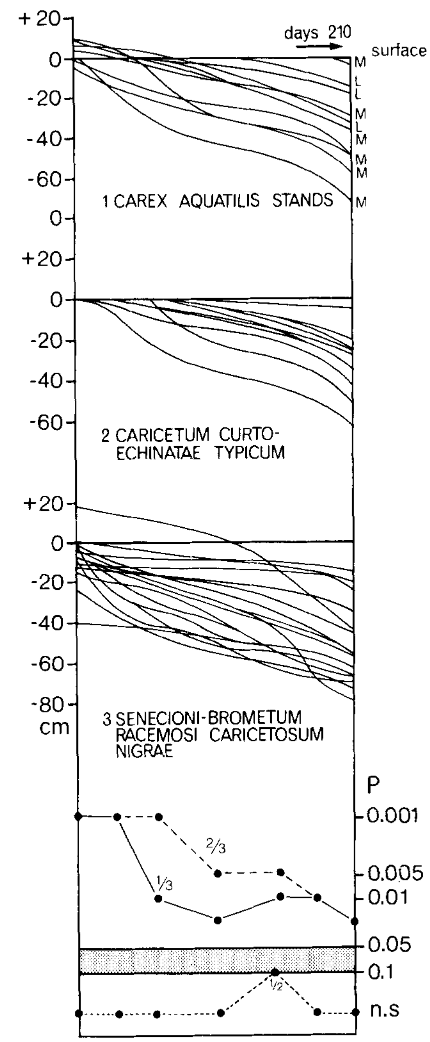

Fig. 5. Cumulative frequency histograms of groundwater tables ((Dauerlinien) of three plant communities during the vegetation period. The lines represent the residence time of groundwater in the soil profile. The results of a statistical analysis (using the Wilcoxon-Mann-Whitney test) are at the base of the figure. L = lower reaches; M = middle reaches.

mosi (a wet *Calthion palustris* community) and the *Caricetum curto-echinatae* (a very wet *Parvocaricetea* community). In our region both communities are found in close contact with *Carex aquatilis* communities. The data from these communities include a wet (1979) and a dry (1976) year.

From the statistical analysis of the data, it can be concluded that the groundwater regime of the *Carex aquatilis* and the *Caricetum curto-echinatae* community are very similar.

Although some of the *Carex aquatilis* stands (especially those in the lower reaches) show more profound flooding than the small sedge community, these differences are not significant. Groundwater regimes of both communities differ, however, from the *Senecioni–Brometum racemosi* association in all levels. The differences in the highest levels are most pronounced. In contrast to what would be expected, the analysis shows that the cumulative frequency lines of the *Caricetum curto-echinatae* are more different from the *Senecioni–Brometum* lines, than from those of the *Carex aquatilis* groups, especially in water levels slightly below the surface. So the groundwater regime of *Carex aquatilis* stands have more in common with that of the drier *Calthion palustris* association then with that of the wetter *Pervocaricetea* community. Figure 5 shows that the lines from the middle basin are responsible for this effect.

As most *Carex aquatilis* stands of the middle reaches are situated just behind the stream banks, drainage is most probably caused by the stream itself. Superficial drainage by ditches, discharging in the stream, may enhance this effect.

Recent hydrological studies (Streefkerk & van Hoorn, 1984) have shown that after radical interference with the hydrology during the last 30 years, the stream levels in the middle course have indeed been lowered, especially in spring and winter. These lower levels may well be responsible for the unexpected results of the analysis of groundwater levels and may account for the many *Carex aquatilis* stands that must be classified as *Calthion palustris*.

Observations on reproduction in Carex aquatilis *stands*

If the supposition presented above is correct, one would expect that the habitats of *Carex aquatilis* stands in the middle reaches has become less favourable. If so, *Carex aquatilis* plants in the lower basin would perform better in some way than the plants in the middle reaches. To test this we estimated the cover percentage and the percentage of flowering shoots in 32 *Carex aquatilis* stands. If the percentage of flowering shoots and the percentage cover would be a measure of the vitality of the plants, one would expect this to be lower in the middle reaches than in the lower reaches.

The results show that in 1978 the percentage of flowering shoots in the middle basin was indeed lower than in the lower basin (Table 2). In the middle reaches only 2% of the shoots had inflorescences, while in the lower reaches this was 12–28%.

In 1980 the same plots were visited again. In the lower basin the percentage of flowering shoots was almost the same as in 1978. The flowers however, withered before maturing as a consequence of a very dry period in spring. In the middle reaches the percentage of flowering shoots had increased considerably (to 13%) and the flowers did not wither. Although the high values of the lower basin were

Table 2. Percentage of flowering shoots and cover of *Carex aquatilis*. The group codes (A–E) correspond to those mentioned in Table 1.

Group code (see Table 1)	A	B	C	D	E
L = Lower basin / M = Middle basin	L	L/M	M	M	M
Average % cover of C. aquatilis	32	23	11	21	18
% of flowering shoots					
1978 mean	28.3	11.6	0.3	2.1	1.5
S.D.	9.8	21.8	0.6	2.3	1.8
1980 mean	20–30	10–15	13.0	6.8	2.8
S.D.			6.9	7.8	4.2

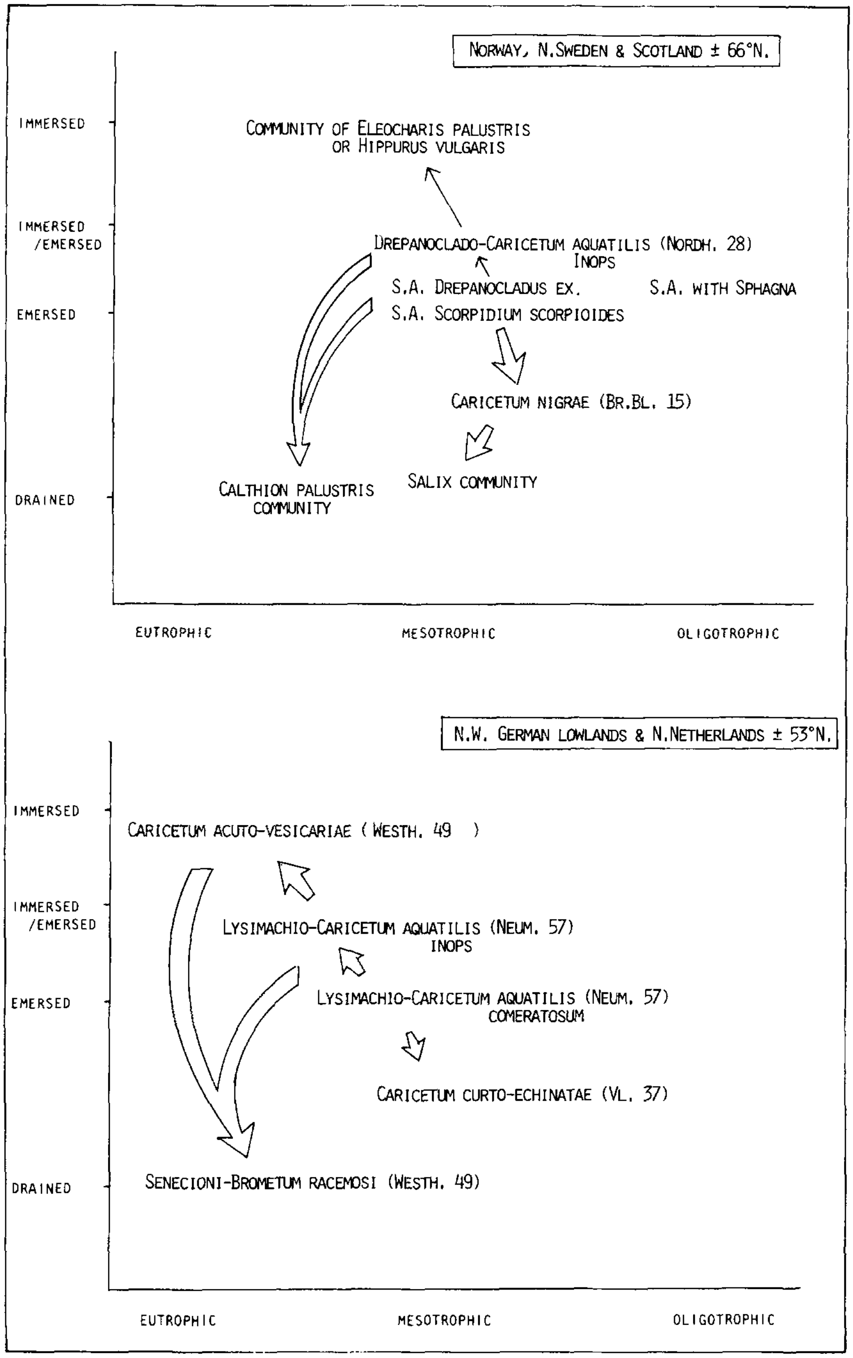

Fig. 6. Synecological conditions of *Carex aquatilis* communities in N and NW Europe. Eutrophic corresponds to substrates rich in silt and groundwater rich in dissolved minerals (high pH and E.C.). Oligotrophic corresponds to nutrient-poor organic substrates influenced by mineral-poor groundwater. The wetness gradient ranges from drained to immersed (flooded). In N Sweden flooding may occur by brackish water (Elveland, 1976). Double arrows indicate predominant vegetation development in the region. Information on ecological conditions in N European communities has been derived from Elveland (1976), Waldemarson-Jensén (1979), and Dierssen (1982). Additional information on NW European *C. aquatilis* communities originate from Neumann (1957), Dierschke (1968), and Tüxen & Dierschke (1975).

not reached, the flowering plants were well developed. The observed phenomena could be related to a gradual increase in precipitation since 1978 after the exceptionally dry year 1976; this led to higher water tables in the Drenthian Plateau. Higher water tables in the plateau were associated with increased water discharge of deep groundwater in the river valleys, especially in the middle reaches of the Drentse Aa, where the seepage is more intense and where fewer drainage channels (adjacent land consolidation) are present. Thus the effect of the dry spring period of 1980 was better compensated by the higher groundwater discharge in the middle reaches than in the lower reaches. In the middle reaches *Carex aquatilis* stands responded with an increased percentage of flowering shoots compared with 1978 and the flowers remained in good condition. Despite this the plants did not subsequently form ripe seed in either area.

Carex aquatilis *in NW Europe*

Communities of *Carex aquatilis* have been reported mainly from areas north of the 66°N line (Cajander, 1903; Alechin, 1927; Elveland, 1976; Waldemarson-Jensén, 1979; Dierssen, 1982). More to the south *Carex aquatilis* communities are described from subalpine and alpine areas (McVean & Ratcliffe, 1962; Dierssen, 1982) or from river valleys in lowland areas (Küsel, 1956; Bakker, 1957; Neumann, 1957; Dierschke, 1968; Tüxen & Dierschke, 1975).

Since most authors present rather limited information on habitat characteristics we will compare synecological conditions of the different communities in the following way. The associations with *C. aquatilis* have been ranked along two environmental gradients (see Fig. 6):

- A trophic gradient, from eutrophic to oligotrophic. By eutrophic we mean that the substrate is rich in silt and the groundwater is rich in minerals (E.C. 25 °C > 300 μS/cm). Oligotrophic means: the substrate is poor in silt and the groundwater is poor in minerals (E.C. 25 °C < 150 μS/cm).
- A wetness gradient, from immersed to drained. Immersed means: high groundwater levels and frequent flooding by (stream) overflow (see Kulczynski, 1949). Emersed means: high, but usually constant groundwater levels sustained by groundwater emerging at the surface. Flooding can occur, but silt precipitation is of minor importance. Drained means that on average the groundwater table is more than 20 cm below the surface throughout the year.

When we compare the northern *Carex aquatilis* communities with the ones more to the south, large differences and only a few similarities can be observed. In Norway and N Sweden eutrophic floodplain communities such as the *Caricetum acuto-vesicariae* (= *Caricetum gracilis*) and the *Lysimachio-Caricetum aquatilis* are not present. In both the north and the south *Carex aquatilis* is found in *Calthion palustris* meadows which emerge from a very wet fen vegetation dominated by *Carex aquatilis*, after drainage and fertilization (Siira, 1970; Tüxen & Dierschke, 1975; Dierssen, 1982).

The northern *Drepanoclado–Caricetum aquatilis* is a distinct mesotrophic *Caricion lasiocarpae* community (Dierssen, 1982) and lacks *Phragmitetea* species like *Glyceria maxima* and *Rumex hydrolapathum*. The southern *Lysimachio–Caricetum aquatilis* belongs to the *Magnocaricion*, while many *Phragmitetea* species are present. Only the mesotrophic subassociation with *Potentilla palustris, Menyanthes trifoliata, Lysimachia thyrsiflora* and *Carex rostrata* is almost identical to the *Drepanoclado–Caricetum aquatilis* (see also Dierssen, 1982). This subassociation is very rare in NW Germany and has not yet been found in the Netherlands.

The *Caricetum nigrae* and the *Caricetum curto-echinatae* mentioned in Figure 6 are identical as well. *Carex aquatilis* has a reduced performance here.

Carex aquatilis thus has its optimum in habitats where enriched groundwater emerges and where frequent flooding occurs. In northern Europe natural and semi-natural *Carex aquatilis* communities with a distinct mesotrophic character are most frequent according to the literature. Eutrophic floodplain communities with *Carex aquatilis* seem to be rare and lack the *Phragmitetea* species which are characteristic for the NW German and Dutch floodplain communities.

At the southern border of the distribution area, mesotrophic *Carex aquatilis* communities have been registered, but are rare. Most frequent here are eutrophic sedge communities with *Carex acuta*.

Despite the pronounced differences in species composition between northern and southern *Carex aquatilis* communities, there appears to be little evidence that in former days the species occupied an essentially different habitat at the border of its distribution area compared to the center. At present populations of *Carex aquatilis* in NW Germany and in the Netherlands seem to be under heavy pressure of human activities, which are giving rise to more eutrophic and to drier conditions.

This process of eutrophication in the lowlands is stimulated by both drainage and increased flooding. Drainage of mesotrophic *Carex aquatilis* communities has led to species-rich *Calthion palustris* communities, in which *C. aquatilis* has a reduced fertility. Almost all *C. aquatilis* stands in the middle reaches of Dutch catchments are probably degenerate stages of former mesotrophic communities. Furthermore drainage in upstream areas leads to increased rates of water discharge in the wet season and this is followed by increased flooding of the downstream areas. Thus the downstream areas experience more eutrophic conditions mainly because of the increased silt deposition.

Consequently the *Lysimachio–Caricetum aquatilis comaretosum* is replaced by the *L. – C. a. inops*, or even by the *Caricetum gracilis* (Bakker & Boedeltje, 1980; Brouwer & van den Hof, 1981).

The water surcharge promotes further interference with the hydrology. The construction of large canals with a regulated water discharge will eventually diminish both emersion of groundwater and immersion by floodwater. As a result the disappearance of *Carex aquatilis* stands is almost inevitable.

In former days *Carex aquatilis* communities belonging to the *Caricion lasiocarpae* must have been more widespread in the Dutch and German lowlands. Oligo- and mesotrophic conditions probably prevailed in most of the European brooks, rivulets and lowland marshes (cf. Succow, 1971, 1982; Kulczynski, 1949). These conditions were sustained by a very regular supply of cool groundwater. Because of this welling up of groundwater with a temperature of 9–10 °C the habitat of *C. aquatilis* in the Netherlands is much colder than would be expected climatologically. The findings of Conolly & Dahl (1970) that *C. aquatilis* is not present in areas where summer maximum temperatures exceed 28 °C is no doubt correct, but the temperature in the root zone of *C. aquatilis* is, in fact, at least 10 °C lower. The maximum temperatures do not exceed 15–17 °C and may be only slightly higher than the maximum temperatures in northern stands. Yet the species seems to be unable to form ripe seeds. Up to now utricles collected in the Netherlands have only been found to contain undeveloped fruits. This might be caused by climatic and/or genetic factors. As the species is at the southern limit of its range the sedge may well be outside the area within which the climate permits regular fruit production. A similar case has been presented by Shaver *et al.* (1979), who found a population of *Carex aquatilis* in the Alaskan tundra that persisted only by means of vegetative propagation. Their research showed distinct ecotypic differentiation in nutrient uptake between the different populations. So gene exchange must have taken place in the distant past and natural selection subsequently gave rise to edaphic ecotypes.

It would be very interesting to center on ecotypical differentiation in Europe and find out exactly by what mechanisms the populations of *Carex aquatilis* are able to survive in habitats characterized by rather eutrophic conditions. Experiments with reciprocal transplantation both here, in N Sweden, and in Alaska, would make a good start to solving these problems (see Chapin & Chapin, 1981).

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