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ARONIA MEDIK. IN THE NETHERLANDS II. ECOLOGY OF A. × PRUNIFOLIA (MARSH) REHD. IN THE DUTCH HAF DISTRICT

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SUMMARY

Aronia × *prunifolia* has run wild in a number of reed marsh nature reserves in the western part of The Netherlands. Both in open *Sphagnum*-dominated communities and below the canopy of woodland the bushes can maintain themselves and reproduce, although performance in open vegetation seems to be better. On gaining dominance in the vegetation both the herb and the bryophyte layer become strongly reduced.

From laboratory experiments environmental circumstances as encountered in reed marshes do not seem to affect the germination of *Aronia* adversely. No significant relations could be detected between the composition of the vegation and the amounts of nutrients available in the ground water at sites where *Aronia* was present. Only high cover percentages of *Aronia* were correlated with elevated amounts of NH_4^+. The species may be found over a wide range from more or less oligotrophic conditions to slightly brackish and moderately eutrophic conditions.

Factor analysis of the vegetation data produced no obvious relations with abiotic conditions. The density of *Aronia* and the structure of the vegetation dominated the first two factors, accounting for 47% of the variance in the data.

1. INTRODUCTION

Species from the North American genus *Aronia* (Rosaceae) were recorded in The Netherlands from 1875 on. In the first decades of the present century they spread to a number of nature reserves in the western part of the country (VLIEGER 1947). In 1911 THIJSSE (1911) welcomed *Aronia* as an addition to the flora of the Naardermeer (N.-Holland), but in the second half of this century it turned out to be a serious pest in several nature reserves (FRENKEN 1975, VAN DER VELDE & BRAND 1974, WERKGROEPEN K.N.N.V. AFD. AMSTERDAM 1973). Problems in the management of nature reserves suffering from fast growing *Aronia*-populations led to investigation of the presence of *Aronia* in The Netherlands and some aspects of its ecology (BEENTJES 1979), especially in reed marshes where rapidly expanding shrubs were suppressing the reed marsh vegetation.

A first result of the inventory of *Aronia*-populations in the Haf District was, that the plants cannot be treated as belonging to one or more "true" species, but that they belong to a hybrid complex for which the name *Aronia* × *prunifolia* (Marsh.) Rehd. is appropriate (WIEGERS 1983).

The present paper deals with the types of vegetation invaded by *Aronia* in nine reed marsh nature reserves in the Dutch Haf District, changes in the vegeta-

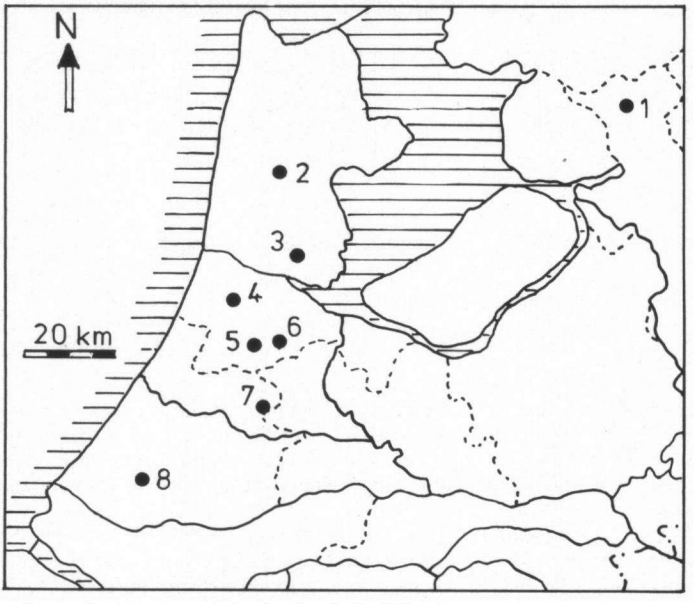


Fig. 1. Sites where relevés were made in the Dutch Haf District.
1. Weerribben
2. Ursem
3. Ilperveld
4. Binnenliede/Buitenliede
5. Oosteinderpoel
6. Amstelveense Poel
7. Nieuwkoopse Plassen
8. Delft (Tweemolentjesvaart)

tion following this invasion, some aspects of the ecology of this hybrid complex and a brief survey of the ecological position of *Aronia* in North America.

2. MATERIALS AND METHODS

Relevés were made in nine areas where *Aronia* was present, according to the methods of the French-Swiss tradition (BRAUN-BLANQUET 1964), using the cover/abundance scale of LONDO (1976). Relevés were made both in stands with *Aronia* and in adjacent stands of the same vegetation lacking this species. The relevés were ordered by hand into a structured table. Here only the relevés with *Aronia* will be presented.

Nomenclature of higher plants follows HEUKELS-VAN OOSTSTROOM (1977), of bryophytes MARGADANT & DURING (1982), and of syntaxa WESTHOFF & DEN HELD (1969).

The areas of investigation are marked in *fig. 1*. Samples of the ground water were taken at a depth of c. 25 cm at 28 sites of relevés with *Aronia* and at 18 sites adjacent to these sampling sites in the same plant community but lacking *Aronia*. These water samples were taken in the first half of June 1977. The results of their analysis hence only illustrate differences or similarities between the sites

at the moment of sampling. The substrate at all sites was peat (80–95% organic matter).

The water samples were filtrated (filter pore diameter 0.45μ) and subsequently the following measurements were carried out. Electric Conductivity was assessed with an electrode coupled to a Philips PW9505 conductivity meter; pH and concentration of NH_4^+ were measured with specific electrodes coupled to an Orion 701 meter. Alkalinity was determined by titration to pH 4.6 with 0.01N HCl. Concentrations of PO_4^{3-}, NO_3^-, NO_2^- and SO_4^{2-} were measured with a Beckman Acta V spectrophotometer. Cl^- concentration was assessed potentiometrically by means of an $AgNO_3^-$ solution. Concentration of Na^+ and K^+ were determined using an Eppendorf flame-photometer, and those of Mg^{2+} and Ca^{2+} with a Perkin Elmer Absorption Spectrophotometer 290 B.

A subset of 28 relevés was submitted to factor analysis using a BMDP4M-routine available at the Botanical Institute of the University of Rome. A cluster analysis using a routine from ORLOCI & BOWLES (1982) was carried out on the results from the water analysis for evaluation of the resemblances in ecological conditions between the different sites.

From the investigated sites samples were taken of *Aronia* stems at 25 cm above soil level to determine relations between age, stem density and stem diameter in five *Aronia*-populations. In September 1978 sites were visited to collect branches with ripe fruit from plants growing scattered in reed marsh vegetation, from closed scrub in woodland margins, and from plants growing under a tree canopy to measure the diameter of the fruit produced under these different ecological conditions.

Using seeds harvested from a population at Nieuwkoop germination experiments were carried out at the laboratory to test the influence of pH of the substrate on the germination percentage and to assess the rate of germination at an optimum level of pH. The seeds used in these experiments were stored at 10 °C after being harvested. In a first experiment a pretreatment to break dormancy (14 days at 4 °C under moist conditions) was applied to one half of the seed lot and the influence of different levels of pH was tested. The seeds were put onto filter paper in Petri dishes wetted with distilled water brought to pH 3, 4, 5, 6 or 7 by means of an acetic acid resp. sodium phosphate buffer solution. Each combination of cold pretreatment and pH was tested for two batches of ten seeds. The filter paper was wetted twice per week and pH was checked and, if necessary, adjusted. The experiment was terminated after 15 weeks. In a second experiment only pH 4 was used and all seeds received a cold pretreatment as described above. Ten Petri dishes each containing 20 seeds were used. For 15 weeks the number of germinated seeds was counted weekly. The germinated seeds were removed from the Petri dishes.

In both experiments the Petri dishes were placed in a growth chamber. During the light period (16 hours per day, $\pm$ 6,000 lux) the temperature was kept at 25 °C, whereas during the dark period (8 hours/day) this was lowered to 15 °C.

Table 1. Germination of *Aronia* × *prunifolia* at different levels of pH, with or without a cold pretreatment of 14 days at 4 °C. Each sample contained 20 seeds.

pH	3	4	5	6	7	3	4	5	6	7
cold pretreatment	.....no.....					.....yes.....				
number of seeds germinated	2	–	1	1	–	10	8	9	8	11

3. RESULTS

3.1. Germination experiments

The results of the first experiment are presented in *table 1*. The positive effect of the cold pretreatment is obvious throughout the pH range tested. Differences in pH of the medium seem to be of no importance between pH 3 and 7, levels of pH met with by *Aronia* at the investigated sites, and in most reed marshes in The Netherlands.

The results of the second experiment are given in *table 2*. Within 6 ± 2 weeks 70% of the seeds germinated. The total germination percentage after 15 weeks was 44%, which does not differ significantly from the 46% attained in the previous experiment.

3.2. Relations between stem density, age, and stem diameter

The results of the measurements and the counting of year rings in five populations are graphically presented in *fig. 2*. In the dense populations (stem densities 50–200 stems/m²) sampled at the sites Delft, Buitenliede, and Weerribben no shoots older than 8 years were found. At the other sites (stem densities < 50 stems/m²) individual shoots with an age of 13 years could be sampled. The regression lines for the five populations sampled indicate a lower increment rate in the dense populations and higher variation of this feature, indicated by lower correlation coefficients for the regression lines.

3.3. Diameter of the fruit in relation to the site

The diameter of fruits from different site types is summarized in *fig. 3*. Site conditions clearly influence fruit size. Under a tree canopy fruit size is distinctly smaller (8.7 ± 1.0 mm) than in plants from open habitats (10.2 ± 1.0 mm). Plants growing in woodland margins exhibit a fruit size that is intermediate (9.6 ± 1.0 mm).

Table 2. Germination rate of *Aronia* × prunifolia at pH 4, following a cold pretreatment (14 days at 4 °C). In this experiment 10 Petri dishes each containing 20 seeds were used.

week number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
number of seeds germinated	–	5	9	8	16	15	16	4	6	4	2	1	1	1	–

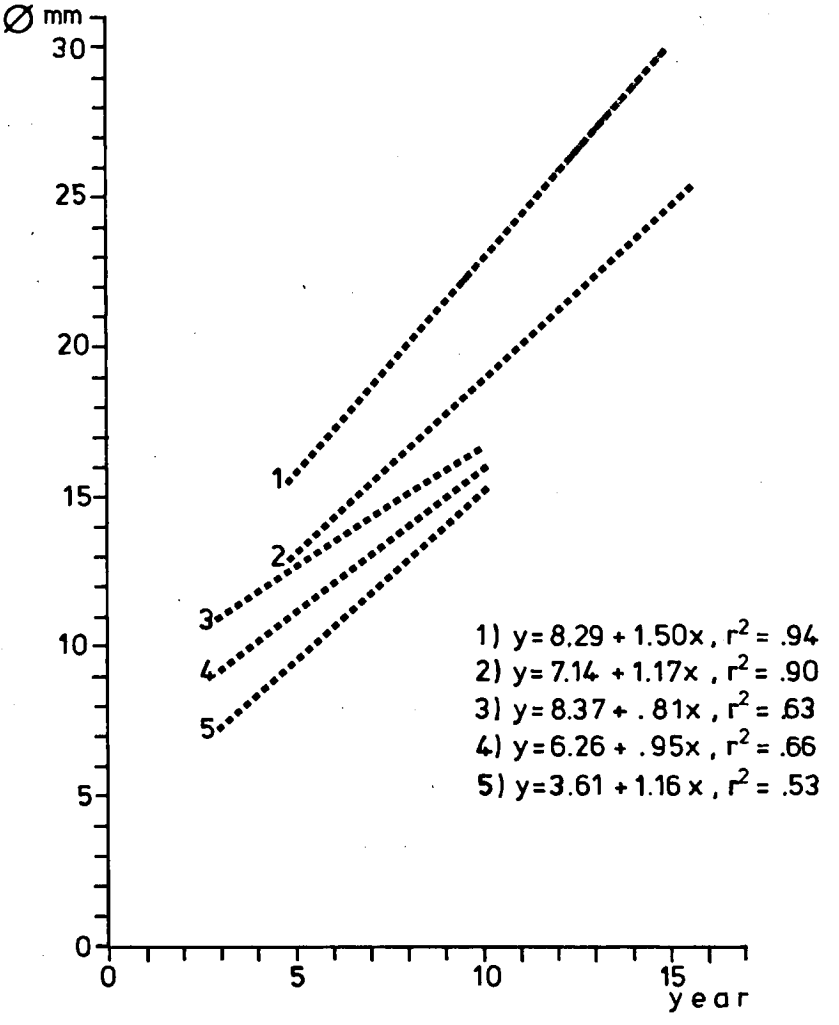


Fig. 2. Relations between stem diameter and age in five populations of *Aronia* × *prunifolia* in the Dutch Haf District. 1: Nieuwkoop, stem density up to 50 stems/m², n = 15; 2: Binnenliede, stem density up to 50 stems/m², n = 30; 3: Delft, stem density 50–100 stems/m², n = 15; 4: Buitenliede, stem density 80–200 stems/m², n = 15; 5: Weerribben, stem density 50–150 stems/m², n = 30.

3.4. Vegetation analysis

In the structured table (*table 3*) six groups of relevés are delineated on the basis of differential species groups in five groups. The sixth group has no differential species.

Group A (rel. 1–28) shows a good resemblance with the *Sphagnetum palustri-papillosi*, in this table characterized by the differential species *Eriophorum angustifolium*, *Oxycoccus palustris*, and *Vaccinium vitis-idaea*, the presence of *Calypo-*

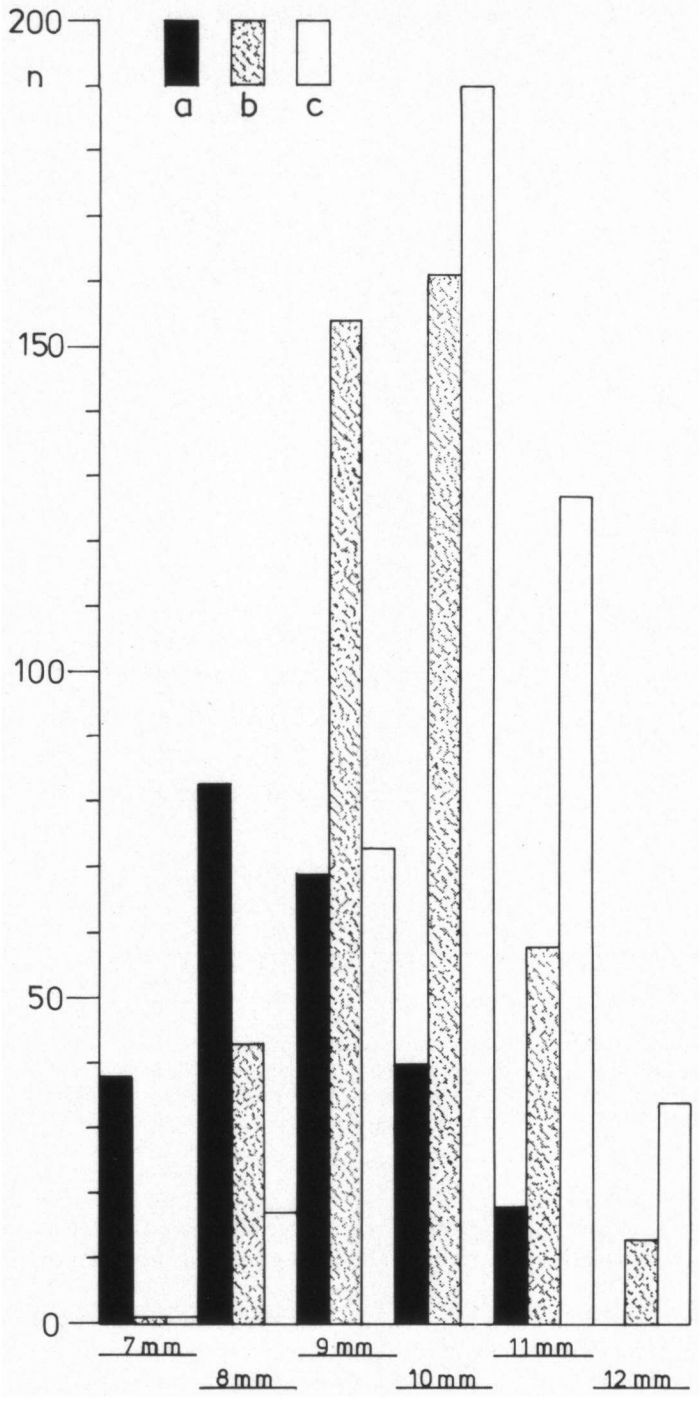


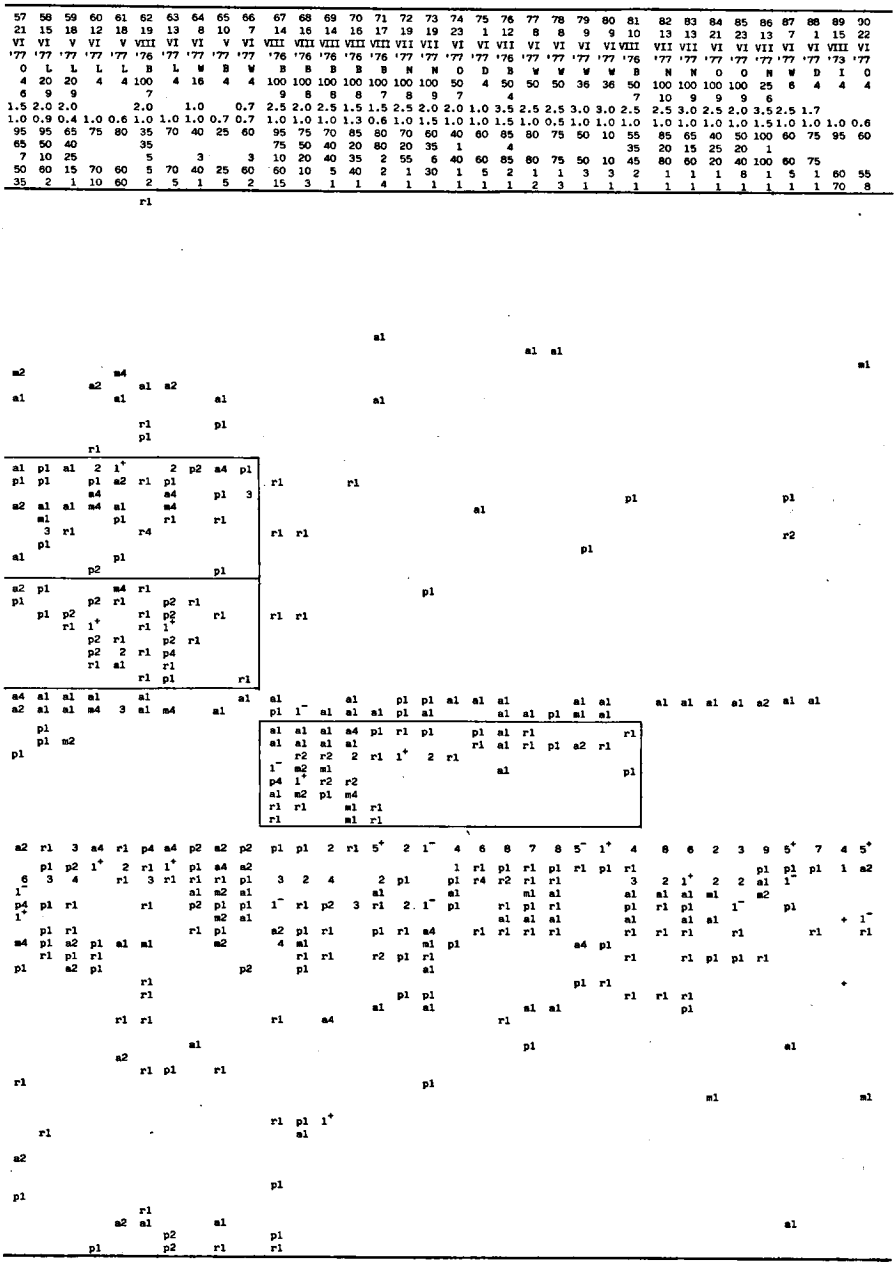
Fig. 3. Diameter of the fruit of *Aronia* × *prunifolia* from three different site types. a. under a tree canopy in woodland, b. in dense scrub in woodland margins, c. in tall herb vegetation.

Table 3. Legend on p. 316.

Relevé 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
Date day	11	10	17	17	17	18	20	22	20	21	21	21	21	27	22	20	20	16	14	14	14	27	19	25	6	9	9	27
month	VI	VI	VI	VI	V	V	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VIII	IX	IX	IX	VI	VI	VIII	VII	VII	VII	VI
year	'76	'76	'76	'76	'77	'77	'77	'77	'77	'77	'77	'77	'77	'77	'77	'77	'77	'82	'74	'74	'74	'77	'77	'81	'82	'82	'82	'77
Site	B	L	L	L	B	L	0	0	0	0	0	0	0	0	0	0	0	P	P	P	P	0	0	P	P	P	P	0
Area (m^2)	4	4	4	4	4	4	4	4	4	100	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Height tree layer (m)										6																		
" shrub " (m)	1.8						1.7	1.5	1.8	2.5	1.2	1.2	1.3	1.2		1.4	1.5	0.4					2.0	0.2	0.3	0.6	0.4	1.0
" herb " (m)	1.0	1.0	0.3	0.4	0.6	0.4	1.2	1.2	1.8	0.5	1.2	1.2	1.2	1.3	0.6	1.2	1.2	1.2				1.5	2.0	1.2	0.2	0.5	0.5	1.0
Cover, total (%)	70	75	80	85	75	95	95	50	90	80	95	95	75	70	90	95	90	100				90	80	100	100	95	80	65
" tree layer (%)										50																		
" shrub " (%)	20						20	1	20	30	7	8	2	5		25	50	15	20	50	60		60	2	3	70	5	3
" herb " (%)	50	50	65	60	55	85	80	55	30	30	45	30	7	60	45	60	15	20	45	50	70	15	10	5	5	10	15	60
" moss " (%)	25	50	50	55	30	55	25	1	60	20	65	85	70	30	45	60	70	100	75	90	85	85	35	100	100	85	75	7
Oxycoccus macrocarpos	a2	2	7	6	5¯	8	7	5¯	p1																			
Eriophorum angustifolium			a2	p1	p2	p2	a1	m2	a1	m2	r1	p1	p1		a1	a1		1¯	2	1	2	m2	a2	m1	a1	1¯	1¯	p1
Calluna vulgaris							m4	p1	1	1+	a1	a2																
Vaccinium vitis-idaea										2	4	1¯	p2	r1														
Oxycoccus palustris												2	p1	6	4	5¯	1+											
Drosera rotundifolia									r1			p1	p1		p1	1¯		1¯	1	+	1	1+						
Juncus subnodulosus											p1																	
Molinia caerulea																												
Potentilla erecta																												
Polytrichum commune	1+	2	a1	m2	a1	a1			a1		1¯		a1	a1				2+	2	2	2	1¯	1	9	8+	r1		
Pallavicinia lyellii	a1	a1	a1	a1	m1																							
Pohlia nutans									a1		m2				p1	m1							a1		m2	a1	m1	
Sphagnum flexuosum		2	3	4	3	5	2	a1	2	2	7	7	m2	4	4	7	9¯	4	5	5	6	2	p1		6¯	3+	1¯
Anthoxanthum odoratum		p1	p1	p1	p1	r1			a1					p1	r1	p1	a1					p1	p1	a1	m2	1¯		
Calypogeia fissa	a1			a1	a1	a1	a1		a1	a1	m1		a2				p1									a1	m1	
Sphagnum fimbriatum	m2		a1	a1	m2	m2	m2		m4	m4			a1													1¯	r1	
Luzula multiflora					r1																				a1	a1	a1	
Dryopteris cristata																				r					pl			
Hierochloë odorata					p1																							
Lysimachia vulgaris		p2																							r1			
Peucedanum palustre											r1																	
Carex scutiformis							r1																					
Brachythecium rutabulum																												
Rumex acetosa																												
Salix cinerea																												
Carex riparia																												
Agrostis tenuis																												
Iris pseudacorus																												
Calystegia sepium																												
Lythrum salicaria																												
Valeriana officinalis																												
Lysimachia thyrsiflora		pl																										
Lychnis flos-cuculi																												
Filipendula ulmaria																												
Mentha aquatica																												
Viola palustris		pl																										
Mnium hornum																												
Eurhynchium praelongum																												
Solanum dulcamara																												
Stellaria media																												
Alnus glutinosa																												
Poa trivialis																												
Sambucus nigra																												
Melandrium rubrum																												
Ilex aquifolium																												
Crataegus monogyna																												
Aronia x prunifolia	2	p2	e4	p2	1¯	2	1	a1	1	p1	e4	1¯	r1	a2	p1	2	5	a1	+	+	1	p2	6	a1	p1	e4	a2	e4
Phragmites australis	a2	p2	p1	p1	p1	p1	m4	a1	1+	p1		a2	a1		p1	a2	a4	a2		+	+	a1	a1	a1	m4	a2	a2	p1
Betula pubescens	1+		r1	p1	r1	r1	1	a1	1	5		p1	p1	6		1+	p1	1+	2	1	1	1	1	r1	a2	6+	a2	r1
Aulacomnium palustre	a1	m4	a1	a1	a1	a1	a1		m2	a1	a2	m1	m1	r1				a1						p1	a1	m4	a2	
Rubus fruticosus s.l.	r2	r1			r1				p1	r1	r1	r1													p1	r1		
Sphagnum palustre	1						m4	m1	m2	a1				1¯				r1	2	5	5			p1	3¯	2¯	4¯	
Dryopteris carthusiana	p2	r1	r1													p1	r1						r1	p1	p1			
Calamagrostis canescens											a1											p1	r1	p1				
Sorbus aucuparia											r1	r1		r1									r1	r1	p4			
Holcus lanatus	a1	a1																					r1					
Juncus subuliflorus									p1		p1								+			r1		p1	a1			
Frangula alnus	p2																									p1		
Lophocolea bidentata																												a1
Cirsium palustre																			r									
Juncus effusus											a1												r1		p1			
Sphagnum squarrosum																			3	2								
Typha angustifolia				r1		r1												r1			1							
Dryopteris dilatata	r1																											
Epilobium hirsutum																												
Calypogeia muelleriana																											a1	
Quercus robur															m1													
Sambucus racemosa																									r1			
Hydrocotyle vulgaris																												
Cephalozia connivens																												
Lotus uliginosus																1¯												
Agrostis canina																			r									
Angelica sylvestris																					+				a1			
Thalictrum flavum																												
Plagiothecium sylvaticum																												
Plagiothecium denticulatum																												
Lycopus europaeus																												
Stachys palustris																												

Table 3, continued.

Relevé number	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Date day	14	29	14	20	15	18	13	1	13	28	11	24	23	7	11	17	16	1	1	15	2	9	14	7	16	11	15	8
month	V	VI	VII	VII	VII	VII	VII	VI	VII	VI	V	VI	VI	IX	V	VIII	VI	VI	VI	VI	V	V	VIII	VII	VI	V	VII	VI
year	'77	'77	'77	'77	'77	'77	'77	'82	'77	'77	'77	'82	'77	'82	'77	'76	'76	'76	'76	'77	'77	'77	'76	'82	'76	'77	'77	'77
Site	B	O	N	W	N	N	N	P	N	O	B	P	O	P	B	B	I	D	D	L	U	B	B	P	I	B	N	W
Area (m^2)	4	4	4	4	4	4	4	4	4	100	4	4	100	4	4	100	4	4	4	4	10	4	4	4	4	4	4	36
Height tree layer (m)										8			7			7											4	2
" shrub " (m)		1.0	2.5						2.5	2.5		0.2	2.5	0.5		1.5	1.0				2.0						1.5	1.0
" herb " (m)	0.7	1.0	1.5	1.0	2.0	1.0	0.5	0.3	1.5	1.2	0.8	0.3	1.0	0.3	0.7	0.6	1.0	1.0	1.0	1.0	0.3	0.8	1.2	0.4	0.5	0.7	1.0	1.0
Cover, total (%)	45	85	80	65	90	80	60	100	80	80	35	95	60	90	65	80	70	65	60	35	35	40	80	100	50	35	30	30
" tree layer (%)										20			25			80											3	3
" shrub " (%)		4	75						80	2		8	1	55		2	10				15						2	3
" herb " (%)	8	4	7	20	90	30	20	20	5	85	6	10	1	10	55	2	30	10	10	30	10	25	75	15	15	6	25	30
" moss " (%)	40	80	1	55	6	60	50	100	2	2	30	95	50	90	20	4	40	60	60	10	15	25	20	100	40	30	5	5
Oxycoccus macrocarpos																												
Eriophorum angustifolium																												
Calluna vulgaris																												
Vaccinium vitis-idaea																												
Oxycoccus palustris																												
Drosera rotundifolia	r1	p1	a2	a2																								
Juncus subnodulosus	r1	m4	p1	r1		p4	p1	m2	p1						p1		r1		p1									
Molinia caerulea			a4	1	8	m4			a2	1^{+}	p1																	
Potentilla erecta			r1	a1	r1	p1	p2																					
Polytrichum commune	m2	a1	m2	1	p1	2	2	2	m1	a4		3^{-}	a1	1^{-}	p1		2	2	2	m2	1^{+}	m4		5^{+}	2	m4		
Pallavicinia lyellii	m1				a1	a1									a1	a1		2	a1	a1	a1	a1	m1		a1			
Pohlia nutans	a1	a1			a1							r1	a1	a1			1^{+}							a2	1^{+}	a1		
Sphagnum flexuosum		7	p1	4		a1	2		a1	a2		p1	a1	5^{-} 8^{+}			m2	2	2	a1			1^{-}		a1			
Anthoxanthum odoratum				p1	p1	m4	a2	m1			p1	a1	m2	p1			m2	a1		r1	p2		a2	a2	a1			
Calypogeia fissa				a1	a1	a1	a1					r1			m1	a1	a1					a2						
Sphagnum fimbriatum							a1	a1		p1					a1							a1						a2
Luzula multiflora	a1			p1				a1				a1			r1		p1	p1	p1	r1	r1			a1	p1	a1		
Drepopteris cristata										p2		r1												a2				
Hierochloë odorata																				r1					p1			
Lysimachia vulgaris								a1		r1	p1				r1	r1	p1	p2	r1	p2								r1
Peucedanum palustre										p1								r1	r1	r1					r1		p1	r1
Carex acutiformis								r1												a4	r1		r1					
Brachythecium rutabulum																					a1	p1						
Rumex acetosa																					r1	a1						
Salix cinerea																				r1								r1
Carex riparia																				p1					a2	a1		
Agrostis tenuis																						p1		a1	p1			
Iris pseudacorus																						p1						
Calystegia sepium										r1																1^{-}	r1	
Lythrum salicaria																										p2		
Valeriana officinalis																												
Lysimachia thyrsiflora										p1																		
Lychnis flos-cuculi													•															
Filipendula ulmaria																												
Mentha aquatica																												
Viola palustris																												
Mnium hornum																a1					a1				a1		a1	
Eurhynchium praelongum																					a1					a1		
Solanum dulcamara																												
Stellaria media																												
Alnus glutinosa																										r4		
Poa trivialis																												
Sambucus nigra																												
Melandrium rubrum																												
Ilex aquifolium																												
Crataegus monogyna																												
Aronia x prunifolia	m2	a4	7	p1	r1	p4	1	r1	7	r1	a2	a1	p2	p1	4	5^{-}	2	a4	p1	1^{+}	1^{+}	p1	7	r1	1^{+}	a1	r1	a1
Phragmites australis	a2	3	p1	p1	a2	1^{+}	1^{+}	m2	p1	p2		m4	r1	a2	a4	r1	p1	p2	p2	p2	a1	a4	p1	1^{-}	p1	a1	1^{-}	a1
Betula pubescens	r1	a2	r1	r1		p2	p1		r1	2	r1	1^{-}	2	5^{-}	r1	r1	r1		r1	r1		r1	r2	p1	p4			r4
Aulacomnium palustre	m2		a1	a1		m2	a2	a2	a1	r1	a1	a1		a1	a2	2	m4		a1	a2	a1	m4	a1	a1	m4	a2		
Rubus fruticosus s.l.	p1		p1		p1		r1		r1	p1	r1	r1			r1	r1			r1			p1	r1	r1		p1		r1
Sphagnum palustre	3	p1	m1		m4	4	m1	9	m1		2	8^{+}		p1	1^{+}	1^{+}	m2	2	2			2		6^{+}	a1	2		m1
Dryopteris carthusiana	r1		p1		r1		r1			r1							p1	p1	p1	p1		p1		p1	r1		p1	r1
Calamagrostis canescens								r1		6												a2		p1				r2
Sorbus aucuparia												r1									r1			p1				
Holcus lanatus	r1						p1				p1						p1	a1		a2		m4			r1	r1		
Juncus subuliflorus		m2						p1			p1		p1											a1				
Frangula alnus					r1				r1	r1				p2														r1
Lophocolea bidentata							a1				a1						a1	a1	p1						a1			
Cirsium palustre	r1																				p1	r1						
Juncus effusus										p1							p1				r1				p1			
Sphagnum squarrosum																							1^{+}					
Typha angustifolia																											a2	
Dryopteris dilatata	p1																											
Epilobium hirsutum										p1					p1	a1												
Calypogeia muelleriana	a1																											
Quercus robur										r1		p1	r1													a1		
Sambucus racemosa																								r1				
Hydrocotyle vulgaris																			r1									
Cephalozia connivens								p1									p1								p1			
Lotus uliginosus							a1						a1															
Agrostis canina								a1									r1											
Angelica sylvestris										r1																		
Thalictrum flavum																												
Plagiothecium sylvaticum										r1						a2												
Plagiothecium denticulatum										a1																		
Lycopus europaeus																										a1		
Stachys palustris																												



Group	A	B	C	D	E	F
Number of relevés	28	14	12	12	15	9
Oxycoccus macrocarpos	II			+		
Eriophorum angustifolium	V					
Calluna vulgaris	II					
Vaccinium vitis-idaea	I					
Oxycoccus palustris	II					
Drosera rotundifolia	II	II				
Juncus subnodulosus	+	III				
Molinia caerulea		III	II	+		
Potentilla erecta		II				
Polytrichum commune	IV	V	V		+	
Pallavicinia lyellii	I	II	IV		I	
Pohlia nutans	II	III	II			+
Sphagnum flexuosum	V	IV	III	I		
Anthoxanthum odoratum	III	III	IV	II		
Calypogeia fissa	III	II	II	II	+	
Sphagnum fimbriatum	II	II	I	+		
Luzula multiflora	I	II	IV	I		
Dryopteris cristata	I	I	+	+		
Hierochloe odorata	+		I	+		
Lysimachia vulgaris	I	II	III	V		
Peucedanum palustre	+	+	II	IV	I	
Carex acutiformis	+	+	II	II	+	+
Brachythecium rutabulum			I	III	+	
Rumex acetosa			I	II		
Salix cinerea			+	II	I	+
Carex riparia			I	I	+	
Agrostis tenuis			II	I		
Iris pseudacorus			+	I		
Calystegia sepium		+		III	+	
Lythrum salicaria				III		
Valeriana officinalis				III	I	
Lysimachia thyrsiflora	+	+		II		
Lychnis flos-cuculi				II		
Filipendula ulmaria				II		
Mentha aquatica				II		
Viola palustris	+			II		
Mnium hornum			II	III	IV	IV
Eurhynchium praelongum			+	IV	V	
Solanum dulcamara				+	IV	
Stellaria media				I	IV	
Alnus glutinosa				I	III	
Poa trivialis					II	
Sambucus nigra					II	
Melandrium rubrum					II	
Ilex aquifolium					II	
Crataegus monogyna					II	
Aronia x prunifolia	V	V	V	V	V	V
Phragmites australis	V	V	V	V	III	III
Betula pubescens	V	V	IV	V	IV	IV
Aulacomnium palustre	IV	IV	V	II	II	III
Rubus fruticosus s.l.	II	III	III	IV	V	III
Sphagnum palustre	III	IV	IV	II	II	III
Dryopteris carthusiana	II	II	III	III	IV	III
Calamagrostis canescens	I	I	I	IV	III	
Sorbus aucuparia	II	+	I	II	III	III
Holcus lanatus	I	II	III	II	I	
Juncus subuliflorus	II	II	+	+	I	+
Frangula alnus	I	II		I	II	II
Lophocolea bidentata	+	I	II		II	+
Cirsium palustre	+	+	I	I	II	
Juncus effusus	I	+	II			
Sphagnum squarrosum	I		+	+	+	+
Typha angustifolia	I			I		
Dryopteris dilatata	+	+		II		
Epilobium hirsutum	+	+	I	+	+	
Calypogeia muelleriana	+	+	+			II
Quercus robur	+.	II	+			
Sambucus racemosa			+	+	II	
Hydrocotyle vulgaris		+	I		+	
Cephalozia connivens	+	+		+		
Lotus uliginosus	+	+	+			
Agrostis canina	I	+				
Angelica sylvestris		+		+	+	
Thalictrum flavum		+	+	+		
Plagiothecium sylvaticum		+		I		
Plagiothecium denticulatum			+	+		+
Lycopus europaeus				I	+	
Stachys palustris				I	+	

Table 3. Relevés with *Aronia* × *prunifolia*, made at the following sites: B = Buitenliede, L = Binnenliede, O = Oosteinderpoel, P = Amstelveense Poel, N = Nieuwkoop, I = Ilperveld, D = Delft (Tweemolentjesvaart), U = Ursem, W = Weerribben.

ADDITIONAL SPECIES: *Acer pseudoplatanus* 25: rlk; *Agrostis stolonifera* 25: pl, 52: pl; *Amelanchier lamarckii* 25: rlj, 88: rl; *Bryum pseudotriquetrum* 27: ml; *Calliergon stramineum* 18: al; *Calypogeia trichomanis* 6: al; *Carex curta* 42: m4; *C. elongata* 62: rl; *C. hudsonii* 87: rl; *C. lasiocarpa* 56: pl; *C. nigra* 40: 1^-; *C. paniculata* 36: pl; *Chamaenerion angustifolium* 1: pl, 81: rl; *Chiloscyphus polyanthus* 2: pl, 61: pl; *Dicranella cerviculata* 90: pl; *Dicranum bonjeanii* 12: ml; *D. scoparium* 40: rl; *Drepanocladus fluitans* 45: +; *Empetrum nigrum* 28: 6; *Epilobium palustre* 1: rl; *Erica tetralix* 8: 1^-, 9: pl; *Eupatorium cannabinum* 39: rl, 73: rl; *Euphorbia palustris* 66: rl; *Funaria hygrometrica* 27: al; *Galium palustre* 57: al, 61: al; *Hypochaeris radicata* 36: rl; *Leptobryum pyriforme* 27: m2; *Lonicera periclymenum* 38: rl, 55: rl; *Lophocolea heterophylla* 26: al, 27: ml; *Myosotis palustris* 41: rl; *Orchis praetermissa* 4: pl; *Oxalis europaea* 70: a2; *Pedicularis palustris* 61: a2; *Pellia epiphylla* 11: al; *Phalaris arundinacea* 61: pl; *Poa palustris* 50: pl; *P. trivialis* 61: al; *Polytrichum longisetum* 52: pl; *Potentilla anglica 52: rl; P. palustris* 56: rl; *Prunus serotina* 64: rl; *Ranunculus repens* 19: +; *Ribes nigrum* 68: rl, 70: rl; *Rumex hydrolapathum* 58: rl; *Salix aurita* 88: p2; *Scirpus maritimus* 18: al, 19: +; *Sphagnum nemoreum* 9: 5^+, 12: m4; *S. papillosum* 11: 1^-, 12: m2; *Thelypteris palustris* 32: pl; *Typha latifolia* 19: +; *Urtica dioica* 63: rl, 80: pl.

geia fissa, Drosera rotundifolia and *Pallavicinia lyellii*, and the abundance of *Polytrichum commune* and *Sphagnum flexuosum*. Mean cover percentage of *Aronia* in this group is c. 10%.

Group B (rel. 29–42) cannot be assigned to any single syntaxon on the basis of its differential species group (*Juncus subnodulosus, Molinia caerulea*, and *Potentilla erecta*). From the species group shared with the relevé groups A and C it might be named a poorly developed and relatively dry variant of the *Thelypterido-Phragmitetum*. Mean cover of *Aronia* is slightly over 10%.

Group C (rel. 43–54) has no differential species but is characterized by the combination of species that are also present in the relevé groups A and B, or more optimally represented in relevé group D. It shows both characteristics of the *Thelypterido-Phragmitetum* and the *Valeriano-Filipenduletum*. Mean cover of *Aronia* is almost 20%.

Group D (rel. 55–66) represents the *Valeriano-Filipenduletum*. Its characteristic species *Lychnis flos-cuculi, Lysimachia vulgaris*, and *Lythrum salicaria* have their optimum in this group. With the remaining relevé groups it shares the presence of *Eurhynchium praelongum* and *Mnium hornum*, species very common on a raw litter layer. This group is considerably richer in species (56) than the relevé groups A, B, C, and E (41–46 species). *Aronia* is often limited to scattered shoots (mean cover percentage less than 5%).

Group E (rel. 67–81) unites woodland and shrub communities, generally with a well-developed shrub layer of *Aronia*. It can be judged to belong partly to the *Carici elongatae-Alnetum* by the presence of *Betula pubescens, Cirsium palustre, Solanum dulcamara*, and *Sphagnum palustre* and partly to the *Salicion cinareae* (the shrub communities in this relevé group). Transitions to communities belonging to the *Alno-Padion* are visible from the presence of *Crataegus monogyna, Melandrium rubrum, Poa trivialis*, and *Sambucus nigra*. Mean cover percentage of *Aronia* in this relevé group is over 25%.

Group F (rel. 82–90) is very poor in species (18), which may be partly related to the dominance of *Aronia* (mean cover percentage over 50%). From the, sometimes sparse, presence of *Betula pubescens, Frangula alnus, Salix cinerea, Sphagnum palustre*, and *S. squarrosum* a weak affinity to the *Franguletea* can be concluded.

Factor analysis carried out on a subset of 28 relevés, considered as fairly good representants for the six relevé groups, indicated the same separation into groups as presented in *table 3*. It revealed a major separation into two groups, one with positive loadings on the second axis (A, B, and C) and one with negative loadings on this axis (D, E, and F) (*fig. 4*). Within both groups there is a strong correlation between the loading on the first axis and the cover percentage of *Aronia*, relevés with high quantities of this species receiving high positive values. The second factor is closely related to the structure in the vegetation. Relevés with only a herb layer generally have high positive loadings on this factor whereas woodland communities receive high negative loadings. These two factors account for 47% of the variance in the data.

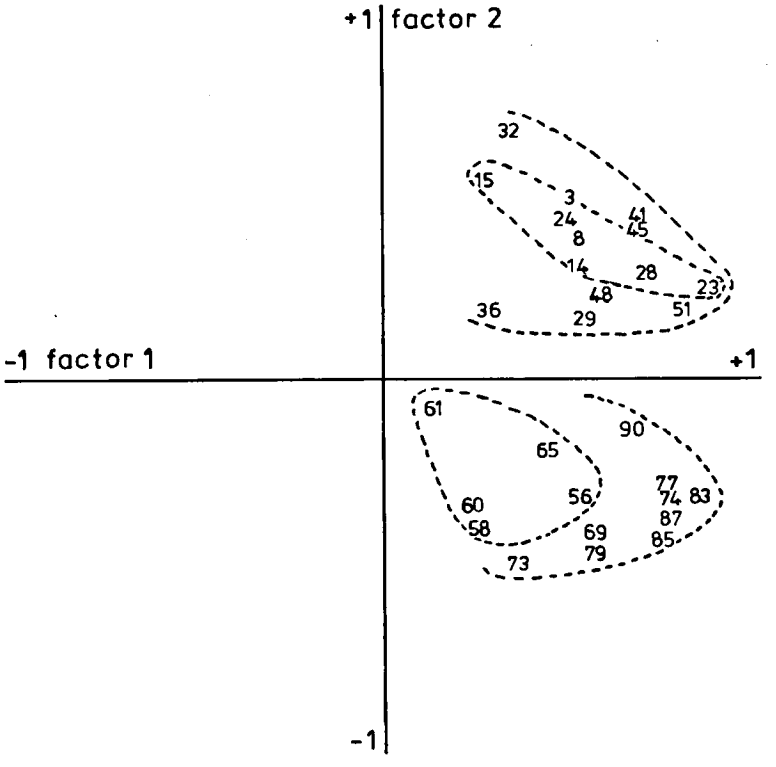


Fig. 4. Projection of a subset of 28 releves on the first two axes determined by factor analysis. These two axes account for 47% of the variation in the data. The first factor is correlated with the density of *Aronia* in the vegetation, the second with the structure of the vegetation.

3.5. Ecological factors

The results of the water analyses from sites with *Aronia* and comparable sites lacking this species are given in *table 4*. For relevé group F no equivalent of this vegetation type lacking *Aronia* could be sampled. No differences in the ground water properties measured could be found between sites with *Aronia* and sites lacking this species. Alkalinity could only be measured in several samples from group C and D and NO_3^- was detectable in only five samples. These two factors are not included in *table 4*.

In all relevé groups ground water levels varied between -10 and -15 cm. Electric Conductivity varied between 132 μS/cm and 950 μS/cm. Mean values for the six relevé groups varied slightly, but ranges for all groups showed considerable overlap. There were no obvious differences in pH of the ground water of all the samples. The values ranged between 3.3 and 6.3, low values being more frequent in relevé groups A and F and high values being more frequent in relevé groups D and C.

Table 4. Results of water analysis from sites belonging to the six vegetation types from *table 3*, with (+) or without (−) *Aronia*. n = number of samples, n.d. = not detectable. Ion concentrations in mg/l.

Relevé group		n	pH	Cl^-	PO_4^{3-}	NO_2^-	SO_4^{2-}	NH_4^+	Ca^{2+}	Mg^{2+}	Na^+	K^+
A	+	7	3.4–3.5	71.0±25.9	.53±.26	.03±.02	12.0± 1.6	.78± .12	9.0± 4.2	4.0±1.4	32.8±10.4	6.3±1.5
	−	3	3.3–4.2	25.0± 4.2	.50±.14	n.d.	39.0±28.6	.97± .30	12.0± 4.2	3.0±2.8	13.5± 3.5	6.0±3.5
B	+	4	4.5–4.9	58.3±24.5	.40±.20	.03±.02	32.0±25.5	.44± .27	11.3± 7.1	4.7±2.3	29.0±11.4	3.7±2.9
	−	3	3.9–5.2	66.0±29.5	.17±.04	.05±.04	32.3±19.5	.61± .05	30.0±16.5	6.0±5.3	18.5± 6.4	3.0±1.8
C	+	3	5.4–5.6	93.3± 5.8	.83±.12	.03±.02	51.0±10.2	1.23± .15	16.3± 4.0	8.0±4.1	39.0±16.8	13.0±2.8
	−	3	4.4–6.3	67.5±24.8	.72±.54	.10±.05	26.7±16.0	.93± .15	12.5± 6.4	9.3±5.0	36.0±15.0	7.3±2.1
D	+	5	3.7–4.8	34.7± 9.1	.35±.07	.09±.02	53.0±19.5	.79± .31	13.7± 5.9	5.7±2.1	21.3± 5.0	9.0±2.8
	−	5	3.7–6.3	69.7±26.1	.70±.29	.06±.03	56.2±34.2	1.08± .57	27.3± 9.7	9.5±4.1	41.3±10.2	8.4±4.9
E	+	5	3.4–407	83.8±42.3	.67±.29	.03±.02	43.3± 8.6	2.72± .41	23.0± 4.8	6.6±3.8	42.0±22.0	8.0±4.9
	−	3	4.0–5.0	65.3±16.2	.78±.30	.08±.05	55.7±14.5	1.31± .69	13.0± 1.0	7.0±3.5	43.0±16.6	3.0±1.0
F	+	4	3.6–4.3	111.0±55.2	.60±.41	.06±.04	29.3±15.5	2.73±1.46	20.7± 3.1	7.5±3.7	62.3±15.3	12.0±2.2

Table 5. Groups of water samples emerging from a cluster analysis using average linkage clustering. The interpretation of the main discriminating factor is indicated

group	relevé numbers	interpretation
I	8, 14, 15, 23, 28 29, 56, 65, 77, 79	Cl^- < 55 mg/l
II	3, 24, 36, 41, 45, 48 51, 58, 60, 61, 74, 90	Cl^- 55–100 mg/l
III	32, 69, 73, 83, 85, 87	Cl^- > 100 mg/l

NH_4^+-concentrations were significantly higher in E and F (ranging from 0.82 to 4.3 mg/l) than in the other groups (0.14–1.4 mg/l), both in samples with and in samples without *Aronia*. Ca^{2+}-concentrations varied between 5 and 42 mg/l. Mean values for the groups did not differ significantly. The same holds for Mg^{2+}-concentrations (1–14 mg/l), Na^+-concentrations (11–74 mg/l), and K^+-concentrations (1–15 mg/l).

Anion concentrations also show considerable overlap between the relevé groups. Cl^--concentrations varied from 22 till 150 mg/l, PO_4^{3-}-concentrations from 0.2 till 1.2 mg/l, NO_2^--concentrations from 0.01 till 0.19 mg/l, and SO_4^{2-}-concentrations from 8 till 110 mg/l. No significant differences were found between the relevé groups or between samples from sites with *Aronia* and sites lacking this species.

Cluster analysis of the 28 water samples from sites with *Aronia* rendered three groups at a fusion level of 4.0 (*table 5*). The division into these three groups appears to be caused mainly by the Cl^--concentration. In the first group all values are lower than 55 mg/l and in the third group they are higher than 100 mg/l. All samples but one in the second group have intermediate Cl^--concentrations. Sample 58 has a lower value, but has obviously been linked to sample 61 on the basis of its high SO_4^{2-}-concentration. Only in these two samples it exceeds 100 mg/l. This subdivision does not correspond with the division into six groups based on floristic composition and shows no relation with the ordination of the 28 relevés.

Ranking the relevé groups on the basis of mean ion concentrations in the water samples produces a sequence that is equal to the ranking based on mean kation concentrations. In this sequence A and B are the least minerotraphentous communities and C and F are the richest in mineral nutrients. Ranking on the basis of NH_4^+-concentrations has the highest correlation with average cover values of *Aronia*.

4. (SYN-)ECOLOGICAL POSITION OF ARONIA IN NORTH AMERICA

In North America *Aronia* is a common element of shrub communities on ombrotrophic bogs and their woodland fringes (GAUTHIER & GRANDTNER 1975, KNAPP

1965, POLLETT & BRIDGEWATER 1973, POTONIÉ 1912), but it is also present in moderately rich fen vegetation and their corresponding woodlands (POLLETT & BRIDGEWATER 1973, ROUSSEAU 1974, UPHOF 1932). Following disturbance of a bog site, e.g. by a fire, it may exhibit an aggressive growth habit comparable to its behaviour in the Dutch Haf District.

5. DISCUSSION AND CONCLUSIONS

Information about the presence of *Aronia* at other sites in Europe is very scarce. SUKOPP(1959/'60, 1962) mentions it to be present in the woodland fringes of bogs and at slightly eutrophicated sites in ombrotrophic bogs.

In The Netherlands *Aronia* × *prunifolia* is present in a wide range of peatland ecosystems in the western part of the country. Germination seems not to be affected adversely be a closed *Sphagnum* layer resulting in a low pH of the substrate. Following germination the plants remain vegetative in their first growing season, flowering in the next year for the first time.

Differences in ecological conditions between sites with *Aronia* in a range of vegetation types were only gradual. High densities of the shrub are correlated with NH_4^+-concentrations in the ground water between 1.0 and 4.5 mg/l.

In all relevé groups high cover values of *Aronia* involve a reduction of the total number of species. The communities in relevé group F could have been evolved from any of the communities in the other relevé groups. The strong dominance of *Aronia*, forming a dense shrub, reduced the available light at soil level apparently so strongly that the development of many species is prohibited. Bryophyte cover of the soil and litter layer, which may reach well over 50% in peatland ecosystems is also strongly reduced.

The tendency to gain dominance in widely different vegetation types presents a potential threat to quite a few nature reserves where the species is not yet present. Although fruiting of the species can effectively be suppressed by yearly mowing, expansion of existing bushes is not affected by this type of management. Just below the surface of the soil or the moss cover horizontal shoots are produced, resulting in a network of underground stems. Abandoning mowing management at sites where the species has built up a dense undergroud shoot system may result in rapid development of dense bushes, suppressing the original local vegetation.

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