

Quantifying seed transport in the river Drentse Aa

a pilot study



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To be a successful hydrochore it is not necessary for a species to have well-developed morphological adaptations for water dispersal.

Johansson *et al.*, 1996

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Abstract

In this study we tried to quantify seed transport in the small river Drentse Aa, and to relate this to the adjacent vegetation. This was done by placing seed traps upstream and downstream of a regularly flooded nature reserve. We assumed that downstream of the nature reserve more species and more seeds would be intercepted than upstream. We did not find large differences between the number of species found at the downstream and upstream site. Also no apparent difference in number of seeds caught at the downstream and upstream site was found. From this study it is clear that a nature reserve like the Kappersbult area is not a large source for seed dispersal through the river Drentse Aa during the summer season, probably through lack of flooding. Although part of the area is continuously inundated it does not add many seeds to the river. We assume that a great deal of seeds in the river originates from riverbank vegetation and therefore it is important to protect these banks in nature conservation policies. We consider a flood to disperse large quantities of seeds. If this hypothesis turns out to be true, it would be of importance to bring back rivers in their original state in restoration projects along river corridors.

Introduction

Recently a lot of attention is paid to nature conservation and nature restoration. In the Netherlands an attempt is made to restore or enlarge several stream-valley landscapes. These systems were formerly used as agricultural grassland. As in any other system, apart from optimized abiotic conditions, establishment of characteristic species during restoration is essential in these systems (Bakker *et al.*, 1996). When viable diaspores of plants are not available in seed banks, success of regeneration depends on dispersal of seeds, spores or vegetative plant parts (Bakker *et al.*, 1996; De Bruijn & Hofstra, 1996). Potential dispersal agents are wind, animal, water and self dispersal (explosive fruits) (Howe & Smallwood, 1982).

Seed dispersal by water (hydrochory) is considered to be the most important dispersal mechanism for riparian species (Cook, 1987; Nilsson *et al.*, 1991). In this way, continuous river corridors are important for maintaining regional biodiversity (Tabacchi *et al.*, 1990; Johansson *et al.*, 1996). Rivers can transport seeds, as well as vegetative plant parts (Johansson & Nilsson, 1993). After flooding some diaspores are likely to remain in the flooded areas. This could be a major advantage in restoration projects in stream-valleys, where desired species are still present upstream. Several studies have examined buoyancy of seeds and some of these have tried to relate this to processes like structuring riverbank vegetation or the distribution of species along riverbanks (e.g. Skoglund, 1990; Schoof, 1998; Nilsson *et al.*, 1991). Danvind & Nilsson (1997) found that seed buoyancy varies considerably between species, ranging from a few days to over one year. Nilsson *et al.* (1991) concluded that species with high seed floating capacity were always more common along river corridors than species with lower seed buoyancy. They found no difference between species with and without specific dispersal devices. In contrast, Danvind & Nilsson (1997) did not find a significant relationship between buoyancy and the distribution of plant species. Nilsson & Grelsson (1990) observed that after the retreat of the flood, some riverbank sites showed large accumulations of organic debris, including large numbers of seeds, whereas other sites are eroded and devoid of loose organic material. Skoglund (1990) concluded that over a longer period of time (years), it is possible for seeds of most species to reach any flooded part of the transects and germinate or be incorporated into the seed bank.

In Poschlod & Bonn (1998) results are presented of a study performed by Fuchs (in Poschlod *et al.*, 1997). The number of species with germinable diaspores found in drifted material and in the sediment of the upper Loire was determined. In the drifted material 42 species were found, originating from diverse vegetation types like freshwater and peatland vegetation, vegetation of disturbed places, grassland, fringe and shrubland and woodland. Of the total number of 63 species, only four were known to disperse by water. In a study by Poschlod & Bonn (1998) up to 80.000 diaspores per day were caught.

Several studies (Schneider & Sharitz, 1988; Skoglund, 1989; Nilsson *et al.*, 1991; Danvind *et al.*, 1997) have mentioned the potential seed dispersal by water and the importance of hydrochory for regeneration of nature reserves. In spite of its ecological significance, very few of these studies (e.g. Poschlod & Bonn, 1998) however focussed on quantifying seed-transport by a river. Apart from seed buoyancy, clearly the number of seeds transported is as important for a successful establishment of species. The more viable seeds will reach a potential habitat, the bigger the chance for successful establishment. Therefore we tried to quantify the transport of viable seeds by a small river and to relate this amount to the adjacent vegetation. We hypothesize that with increasing water levels, more seeds will end up in the river, because a larger area will be flooded. Since dispersal by water is directional and downstream (Schneider & Sharitz, 1988) it is expected that downstream of a flooded nature reserve more seeds will pass through the river than upstream.

Methods

Site description

All experiments were carried out in the Kappersbult nature reserve, which is situated in northern Drenthe in the Netherlands (fig. 1).

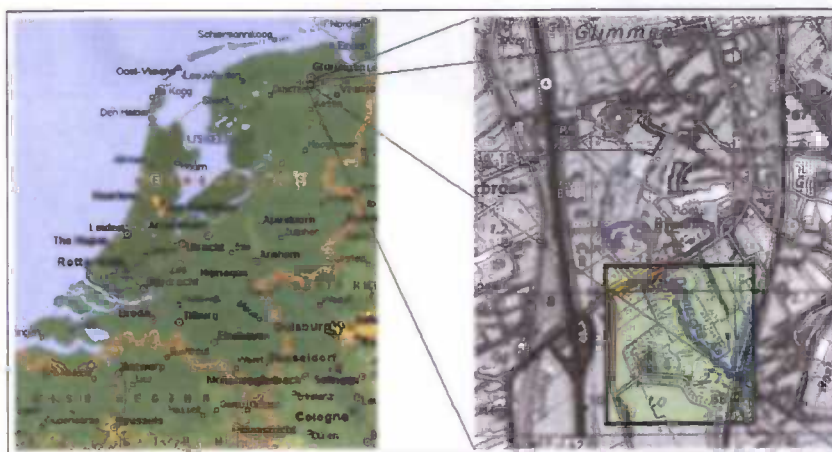


Figure 1: Location of the Kappersbult nature reserve in the Netherlands.

The Kappersbult is a floodplain area of 27 ha, adjacent to the western bank of the downstream part of the river Drentse Aa (Gabel, 1996). The Drentse Aa is a small river with a generally low discharge (approx. $30 \text{ m}^3 \text{ s}^{-1}$) and a flow rate of approximately 1 m s^{-1} (in the summer season).

Vegetation map

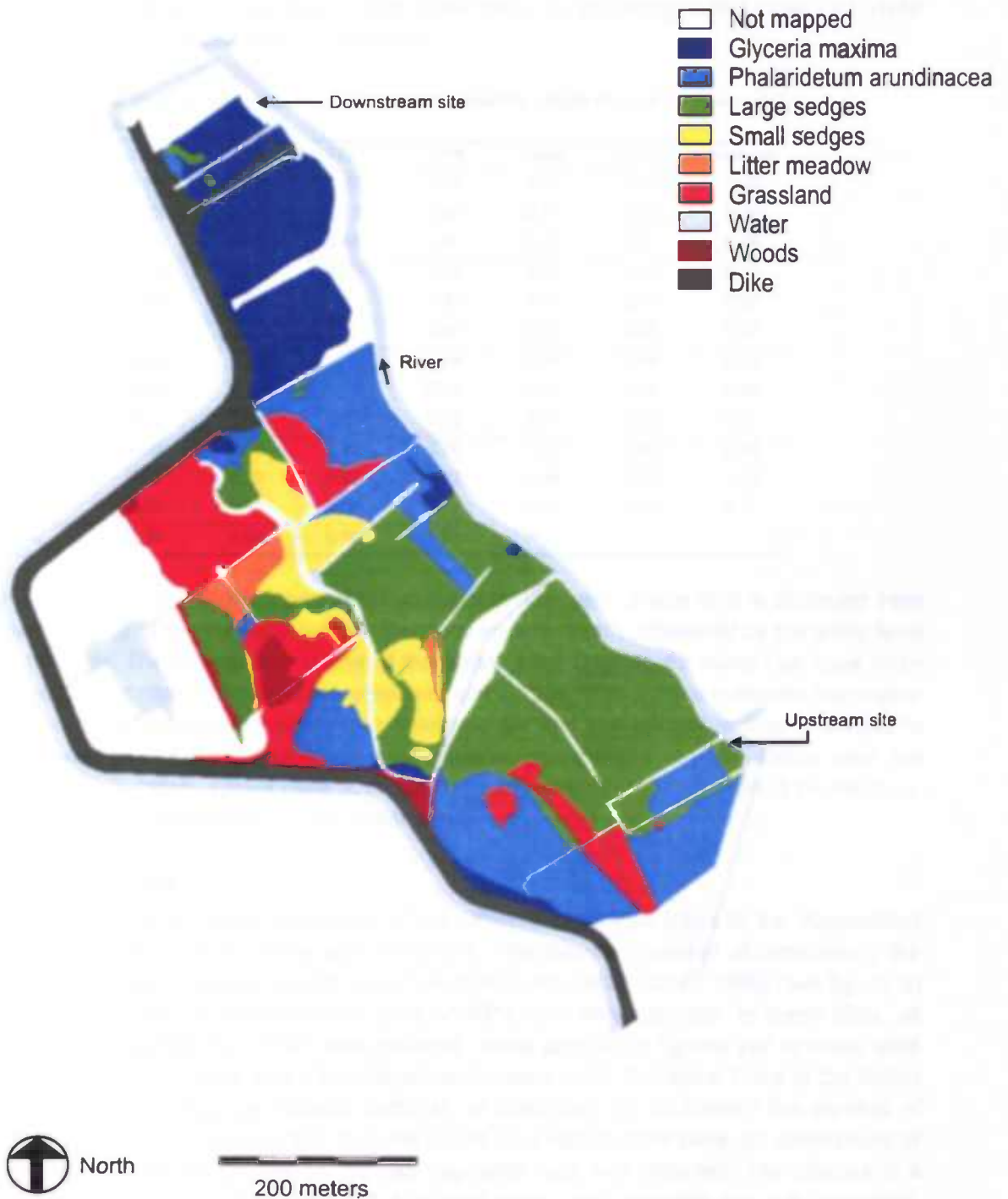


Figure 2: The different communities of the Kappersbult nature reserve and the location of the seed traps

The water level in the river itself is not regulated, but the water in which the Drentse Aa discharges is. This damps the water level fluctuations in the Drentse Aa near the Kappersbult nature reserve. In appendices 1A to 1D the water-level fluctuations for four years are presented. Usually, the water level is around 0.60-0.70m +NAP, but this level can reach extreme values up to more than 1.20m +NAP (table 1). In October 1998 even 1.52 +NAP was reached, but these values rarely occur.

Table 1: Water levels (m +NAP) of the river Drentse Aa near the Kappersbult nature reserve (* indicates a missing value).

	1995	1996	1997	1998	mean	lowest	Highest
Jan	0,84	0,69	0,69	0,66	0,72	0,66	0,84
Feb	0,79	0,69	0,70	0,62	0,70	0,62	0,79
March	0,79	0,70	0,68	0,67	0,71	0,67	0,79
April	0,72	0,68	0,65	0,69	0,69	0,65	0,72
May	0,69	0,69	*	0,64	0,67	0,64	0,69
June	0,72	0,7	*	0,64	0,69	0,64	0,72
July	0,68	0,69	*	0,64	0,67	0,64	0,69
Aug	0,68	0,70	*	0,64	0,67	0,64	0,68
Sept	0,70	0,68	0,63	0,65	0,67	0,63	0,70
Oct	0,69	0,68	0,63	0,78	0,70	0,63	0,78
Nov	0,69	0,70	0,63	0,63	0,66	0,63	0,70
Dec	0,68	0,71	0,65	*	0,68	0,65	0,71
max	1,30	0,93	0,88	1,52			

A dike borders the western part of the study area. This way, arable land is protected from river flooding, while the water table in the study area is directly influenced by the water level in the river. The Kappersbult is one of the areas in the Drentse Aa valley that have been protected for nature conservation purposes since 1965. Therefore a complete vegetation gradient has developed, ranging from relatively dry and low-productive litter meadows to very wet and very productive *Glyceria maxima* communities (fig. 2). Every year the vegetation is mown. This is done at the end of the growing season (in 1998 in September), so most of the species will be able to set seed.

Seed availability

In order to quantify seed production of the different vegetation types in the Kappersbult nature reserve, a field survey was performed. This survey consisted of determining the number of seed producing plants per m² per community (after Gabel, 1996) (see fig. 2). In every community 10 representative plots of 90*90 cm were selected. In these plots, all plants in a reproductive state were counted. Seed production figures per species were determined by counting, taken from literature (Brienen, 1997; Biological Flora of the British Isles, *Journal of Ecology*, several authors), or estimated. By multiplying the number of seeds per plant with the number of plants per m² in a reproductive state, an assessment of seed production per species per m² per vegetation type was obtained. The species in a reproductive state occurring on the riverbank were also recorded but not quantified, because the banks contain highly heterogeneous vegetation.

Data processing and potential seed dispersal

The methods used and calculations on data are partly rough and some data are estimates. The number of viable seeds caught in the traps was extrapolated to the whole width of the

river and to a period of two weeks. This resulted in multiplication factors between 31 and 152 (mean is 66). Because of the large correction factors, the estimated numbers of seeds per plant and non-replicate measurements, it was not possible to do any useful statistical analyses.

In order to calculate the inundation surface at several water levels (per community), flooding maps of the nature reserve were created with the GIS package Idrisi for Windows (version 4.0). The maps were produced by overlaying the vegetation map with an elevation map (by Gabel, 1996) (app. 2) and refer to the following water levels: 0.50-0.60m +NAP; 0.60-0.70m +NAP; 0.70-0.80m +NAP; 0.80-0.90m +NAP (app. 4 A-D).

By multiplying the surface of an inundated area of a community with the seed production per square meter in that community, an indication of the number of seeds which are available in the nature reserve for transport by the river was obtained.

The estimates of seed availability in the nature reserve were coupled to flooding events. This resulted in an assessment of potential dispersal of seeds at different water levels. According to our hypotheses, the vegetation in the Kappersbult area should be reflected in differences in species composition and number of seeds trapped between the downstream and the upstream trapping-site. Therefore we simulated some events that actually do take place from time to time. An event consists of a date and a flood of a certain height.

It is assumed that during floods, all the seeds will be taken up from the soil and eventually end up in the river. This is included in calculations as a bipartite process. When water levels in the river rise, the flooded area will expand and more seeds will end up in the river. The first flood was defined on the 10th of July and the second after the 1st of October. After this date all plants found in the Kappersbult have set seed. All water levels discussed in the 'Data processing' section were used. These scenarios have been worked out for 8 species: *Holcus lanatus*, *Anthoxanthum odoratum*, *Glyceria maxima*, *Lychnis flos-cuculi*, *Plantago lanceolata*, *Festuca pratensis*, *Carex panicea* and *Succisa pratensis*.

Actual seed dispersal

In order to quantify seed transport by the river, six seed traps were constructed. These traps consisted of a wooden frame, a fine-meshed net and two wooden floats of 60 cm length (fig. 3). The frames were 53 cm wide and 50 cm high. The surface of the net was about nine times the surface of the frame, to minimize flow-resistance caused by the net. If the net was as big as the frame, the total surface of the perforation in the net would have been too small to filter all of the entering water.



Figure 3: One seed trap, as used in the seed trapping experiment.

One set of frames was placed at the upstream site of the nature reserve and the other set at the downstream site (fig. 2). At each site, three traps were placed in the river at equal distance from each other and from the riverbanks. This was done two times a week, overnight, for about 20-24 hours. The propagule-drift experiment started mid-June 1998 and continues until the present day. We intend to measure seed transport every week during one entire year. In the present report data from the period of mid-June 1998 until the end of August 1998 were used.

In June and July the riverbanks were mown by a mowing-boat. The hay ended up in the river where it was collected downstream and pulled out. This hay in the river caused a lot of trouble and interference with the seed-trapping experiment. Often, large piles of hay were found in the traps. This kept going on until August, even when mowing was stopped at the end of July, because a lot of hay had gathered in meanders in the river. With turning wind directions the hay was blown out of the refuges and floated downstream. To determine if mowing dispersed any seeds, a few samples of the hay were taken.

Propagule identification

Trapped seeds were rinsed out of the nets with water using a large funnel (fig. 4), put in plastic bags and stratified at 4 °C in a dark room for at least 10 days. After stratification, the seeds were sown on sterile soil covered with a thin layer of sand and placed in a greenhouse at 25 °C and 12 hours of light. Temperature at night was maintained at 15 °C. Water was added daily to create field-like conditions. Germinated seeds were determined and quantified.



Figure 4: *Funnel, used to rinse the nets.*

Results

Seed production

In table 2 the results of the field survey are listed. Here, the different reproductive states, which were observed in the field, are combined and recalculated to the number of seeds produced during this season. Appendices 3 A&B present the numbers of plants in different reproductive states. The *Carex*, *Phalaris arundinacea* and *Glyceria* communities produce between 24.000 and 83.000 seeds per m² (table 2 & 3). The litter meadow and the grassland produce respectively 250.000 and 545.000 seeds per m². Multiplying these values with the total area of the communities produced numbers of hundreds of millions to a few billions of seeds per community (table 3).

Table 3: Area (m²), calculated number of seeds per m² and calculated total number of seeds in the different communities in the Kappersbult nature reserve.

Community	area (m ²)	# seeds / m ²	total # seeds
<i>Glyceria maxima</i>	32.817	24.608	807.560.736
<i>Phalaris arundinacea</i>	48.342	83.052	4.014.899.784
large sedges	71.006	100.646	7.146.469.876
small sedges	16.495	30.612	504.944.940
poor meadow	3.768	251.969	949.419.192
grassland	28.797	545.770	15.716.538.690

Also species in a reproductive state occurring on the riverbank were recorded. The species composition on the riverbank was highly heterogeneous on a small scale, varying from meadow species like *Cirsium palustre* to species from very wet communities like *Glyceria maxima* or *Phalaris arundinacea*. The 33 species listed in table 4 were found.

Table 4: Species in a reproductive state found on the riverbanks.

<i>Acorus calamus</i>	<i>Eupatorium cannabinum</i>	<i>Persicaria hydropiper</i>
<i>Agrostis canina</i>	<i>Filipendula ulmaria</i>	<i>Peucedanum palustre</i>
<i>Agrostis tenuis</i>	<i>Glyceria maxima</i>	<i>Phalaris arundinacea</i>
<i>Alopecurus pratensis</i>	<i>Holcus lanatus</i>	<i>Philipendula ulmaria</i>
<i>Angelica sylvestris</i>	<i>Iris pseudacorus</i>	<i>Phragmites australis</i>
<i>Anthriscus sylvestris</i>	<i>Lycopus europaeus</i>	<i>Poa palustris</i>
<i>Calamagrostis canescens</i>	<i>Mentha aquatica</i>	<i>Rumex spec.</i>
<i>Carex elata</i>	<i>Mentha arvensis</i>	<i>Solidago canadensis</i>
<i>Cicuta virosa</i>	<i>Myosotis laxa</i>	<i>Typha latifolia</i>
<i>Cirsium palustre</i>	<i>Myosotis scorpioides</i>	<i>Urtica spec.</i>
<i>Epilobium hirsutum</i>	<i>Persicaria amphibia</i>	<i>Veronica beccabunga</i>

species	counted	#	n	source	large sedges	P. arundinaceae	grassland	small sedges	G. maxima	litter meadow
<i>Agrostis canina</i>	seeds/plant	180	2	C	1,178	1,639	778	9,267	0	8,311
<i>Agrostis capillaris</i>	seeds/plant	350	3	C	0	0	11,451	86	0	0
<i>Agrostis stolonifera</i>	seeds/plant	200		E	0	0	0	25	0	0
<i>Alopecurus pratensis</i>	seeds/plant	160	5	C	0	49	514	0	0	0
<i>Anthoxanthum odoratum</i>	seeds/plant	58	5	C	0	0	3,867	14	0	2,893
<i>Calamagrostis canescens</i>	seeds/plant	698	2	C	3,749	9,694	172	172	0	0
<i>Caltha palustris</i>	seeds/flower	8	3	C	1	0	0	1	0	0
<i>Cardamine pratensis</i>	seeds/plant	21		B	1	0	0	0	0	0
<i>Carex acuta</i>	seeds/plant	175		E	0	27	0	0	0	0
<i>Carex aquatilis</i>	seeds/plant	312	3	C	520	626	0	347	0	0
<i>Carex curta</i>	seeds/plant	50		E	0	0	0	6	0	0
<i>Carex elata</i>	seeds/plant	183	3	C	768	0	0	0	0	0
<i>Carex nigra</i>	seeds/plant	135		B	292	0	117	5,100	0	133
<i>Carex panicea</i>	seeds/plant	40		E	0	0	0	10	0	0
<i>Cirsium palustre</i>	seeds/flower	52	5	C	0	0	899	0	0	1,207
<i>Deschampsia cespitosa</i>	seeds/plant	658		B	0	0	487	0	0	2,437
<i>Eleocharis palustris</i>	seeds/plant	25		E	184	0	0	633	0	0
<i>Enophorum angustifolium</i>	seeds/flower	12	10	C	0	28	0	338	0	68
<i>Festuca pratensis</i>	seeds/plant	74		B	0	0	292	0	0	0
<i>Festuca rubra</i>	seeds/plant	54		B	0	0	853	140	0	0
<i>Filipendula ulmaria</i>	seeds/plant	1,201		B	74	0	0	0	0	0
<i>Galium palustre</i>	seeds/plant	2,500		E	38,426	8,488	3,085	9,568	0	0
<i>Glyceria fluitans</i>	seeds/plant	400		E	0	1,605	0	0	0	0
<i>Glyceria maxima</i>	seeds/plant	620	2	C	0	1,052	0	0	7,119	0
<i>Holcus lanatus</i>	seeds/plant	168	3	C	0	0	17,298	124	0	4,729
<i>Juncus acutifloris</i>	seeds/plant	16,300	3	C	3,019	0	414,543	0	0	0
<i>Juncus articulatus</i>	seeds/plant	5,900	3	C	0	0	14,568	0	0	0
<i>Juncus conglomeratus</i>	seeds/plant	10,000		E	0	0	33,333	0	0	4,938
<i>Juncus effusus</i>	seeds/plant	10,000	1	C	0	50,926	40,741	2,469	0	224,691
<i>Lychnis flos-cuculi</i>	seeds/flower	50		E	0	131	0	0	0	0
<i>Mentha aquatica</i>	seeds/plant	1,320	3	C	0	0	0	0	16,296	0
<i>Myosotis laxa</i>	seeds/plant	44		E	1,075	122	0	60	0	0
<i>Myosotis scorpioides</i>	seeds/plant	44		B	0	0	0	0	152	0
<i>Pedicularis palustris</i>	seeds/plant	20	5	C	210	0	0	521	0	0
<i>Persicaria amphibia</i>	seeds/plant	1,000		E	0	0	0	0	247	0
<i>Phalaris arundinaceae</i>	seeds/plant	290	2	C	161	7,877	215	0	36	0
<i>Plantago lanceolata</i>	seeds/plant	41	3	C	0	0	1,109	0	0	1,336
<i>Poa palustris</i>	seeds/plant	100	3	C	123	0	0	0	0	0
<i>Poa trivialis</i>	seeds/plant	106		B	137	0	0	0	0	0
<i>Potentilla palustris</i>	seeds/flower	20		E	0	0	0	2	0	0
<i>Ranunculus acris</i>	seeds/flower	36	3	C	0	0	262	0	0	0
<i>Ranunculus flammula</i>	seeds/flower	23	5	C	226	699	142	1,627	0	318
<i>Ranunculus repens</i>	seeds/flower	26		C	0	0	385	0	0	64
<i>Rhinanthus angustifolius</i>	seeds/flower	18	3	C	0	0	107	0	0	0
<i>Rumex acetosa</i>	seeds/plant	30		E	0	0	493	0	0	281
<i>Stachys palustris</i>	seeds/mullei	192	3	C	178	0	0	0	759	0
<i>Stellaria palustris</i>	seeds/flower	8	10	C	1	88	59	102	0	0
<i>Succisa pratensis</i>	seeds/flower	71	4	C	0	0	0	0	0	561
<i>Veronica scutellata</i>	seeds/flower	2		E	1	0	0	0	0	0
total # seeds/m2					50,324	83,052	545,770	30,612	24,608	251,969

Table 2: Results of the field survey in number of seeds per m² listed per community. Counted 'seeds/b' refers to the numbers of seeds per plant part (b) counted during the field survey; '#' is the number of seeds per plant part (b); 'n' is the number of replicates counted; 'source' is the source of '#', where 'C' stands for counted, 'E' stands for estimated and 'B' is taken from Brien (1997).

Potential seed dispersal

From the flooding maps (app. 4A-D), table 5 and appendix 5 it is clear that the higher the water level in the river, the larger the inundated area. Wet communities like *Glyceria maxima* and *Phalaridetum arundinacea* are inundated even when water levels of the Drentse Aa are lower than average (0.50-0.60m +NAP). At normal water levels (0.60-0.70m +NAP) large sedges swamp and small sedges swamp are inundated too. When flooding occurs (>1.00 m +NAP) the entire area will be submerged.

Table 5: Inundated areas as a percentage of the total surface of the community.

Community	Area (m ²)	Percentage inundated			
		river-water level (m +NAP)			
		0.50-0.60	0.60-0.70	0.70-0.80	0.80-0.90
<i>Glyceria maxima</i>	32.817	86	100	100	100
<i>Phalaris arundinacea</i>	48.342	17	69	95	99
large sedges	71.006	1	77	97	100
small sedges	16.495	0	59	98	100
poor meadow	3.768	0	7	74	100
grassland	28.797	1	12	58	76

For four species, the results of the events described in the 'scenario definition' section are listed in table 6. Appendix 6 deals with 8 species. These tables imply that timing of a flood determines the number of seeds and species composition in a river to a large extent. At the 10th of July, 80% of the seeds of *Plantago lanceolata* are mature, while *Festuca pratensis* lost only 30% of its seeds. This means that the ratio *P. lanceolata*/*F. pratensis* seeds in a flood at the 10th of July would be larger than in a second flood (in autumn) when of *F. pratensis* still 70% of its seeds are present in the area and of *P. lanceolata* only 20%.

Table 6: Calculated number of seeds that can potentially be transported by the river after inundation at the 10th of July and the calculated number of seeds are available for dispersal during a flood after the 1st of October (the same water levels in the two boxes correspond to each other).

	<i>Plant. lanc.</i>	<i>Anth. odor.</i>	<i>Fest. prat</i>	<i>Succisa prat.</i>
Seed release	80%	75%	30%	0%
Water level	calculated # of seeds in river after inundation at 10-7			
50-60 cm	142.839	466.940	14.104	0
60-70 cm	3.348.830	10.709.147	303.534	0
70-80 cm	17.679.629	54.281.015	1.452.058	0
80-90 cm	23.463.129	71.883.973	1.919.053	0
	calculated # of seeds available for flood after 1-10			
50-60 cm	35.710	155.647	32.908	0
60-70 cm	837.207	3.569.716	708.246	144.177
70-80 cm	4.419.907	18.093.672	3.388.134	1.560.702
80-90 cm	5.865.782	23.961.324	4.477.791	2.113.848

Actual transport of propagules

At the downstream site of the study area a total of 19,486 seeds was intercepted in 10 weeks, while at the upstream site 16,712 seeds were caught. These figures imply that per day the number of seeds lies in the order of a few hundred. Table 7 shows that in almost every period more seeds were intercepted at the downstream site than at the upstream site. The downstream site also yielded a few more species.

Table 7: Calculated number of seeds and number of species intercepted by the seed traps per period of two weeks, downstream and upstream of the study area.

Week	# seeds		# species	
	downstream	upstream	downstream	upstream
25-26	6675	5817	13	10
28-29	1312	4362	10	12
30-31	5568	3373	20	15
32-33	3882	1384	18	17
34-35	2049	1777	12	11
Total	19.486	16.712	38	33

Propagule identification

In table 8 the species are shown of which viable seeds have been trapped from mid June up to the end of August 1998. A total of 52 species was trapped. Species trapped at the downstream site and species trapped at the upstream site were rather different. Nineteen species were found at both sites, 19 species were found exclusively at the downstream site while the upstream site yielded another 14 species. Table 8 also gives an indication of the magnitude of the calculated number of seeds intercepted. The calculated amount of seeds varied considerably from some 38 to a few thousands of seeds per species. In appendix 7, the original numbers per species per period are listed.

Table 8: Species trapped in the propagule-drift experiment from mid June up to the end of August 1998 in the Drentse Aa near the Kappersbult area (-: no seeds caught; +: up to 200 seeds caught; ++: 200 to 1000 seeds caught; +++: >1000 seeds caught).

Species	downstream	upstream	Species	downstream	upstream
<i>Betula pubescens</i>	+++	+++	<i>Conyza canadensis</i>	+	-
<i>Holcus lanatus</i>	+++	+++	<i>Dactylis conglomer.</i>	+	-
<i>Juncus effusus</i>	+++	+++	<i>Glyceria maxima</i>	+	-
<i>Poa trivialis</i>	+++	+++	<i>Gnaphalium ulig.</i>	+	-
<i>Epilobium spec.</i>	+++	++	<i>Juncus bufonius</i>	+	-
<i>Epilobium hirsutum</i>	++	++	<i>Mentha aquatilis</i>	+	-
<i>Lycopus europeus</i>	++	++	<i>Rumex hydrolap.</i>	+	-
<i>Rumex acetosa</i>	++	++	<i>Sagina procumbens</i>	+	-
<i>Salix spec.</i>	++	++	<i>Salvia pratensis</i>	+	-
Unknown 1	++	++	<i>Stellaria aquatica</i>	+	-
<i>Ranunc. scleratus</i>	++	+	<i>Stellaria spec.</i>	+	-
Unknown 2	++	+	<i>Typha latifolia</i>	+	-
<i>Rorippa sylvestris</i>	+	++	<i>Rorippa palustris</i>	-	++
<i>Carex disticha</i>	+	+	<i>Agrostis capillaris</i>	-	+
<i>Cirsium palustre</i>	+	+	<i>Agrostis stolonifera</i>	-	+
<i>Epilobium ciliatum</i>	+	+	<i>Alopecurus genic.</i>	-	+
<i>Myosotis laxa</i>	+	+	<i>Anth. odoratum</i>	-	+
<i>Ranunculus repens</i>	+	+	<i>Bidens cernua</i>	-	+
<i>Carex nigra</i>	+++	-	<i>Crataegus monog.</i>	-	+
<i>Carex pseudocyp.</i>	+++	-	<i>Epilobium tetrag.</i>	-	+
<i>Carex spec.</i>	+++	+	<i>Festuca pratensis</i>	-	+
<i>Agrostis canina</i>	++	-	<i>Festuca rubra</i>	-	+
<i>Phalaris arundin.</i>	++	-	<i>Hypoch. radicata</i>	-	+
<i>Veronica beccab.</i>	++	-	<i>Rorippa spec.</i>	-	+
<i>Berula erecta</i>	+	-	<i>Urtica spec.</i>	-	+
<i>Cicuta virosa</i>	+	-	<i>Viola palustris</i>	-	+

To determine if mowing of the riverbanks dispersed any seeds, a few samples of the hay were taken of which the results are shown in table 9. Nine species were determined in the drifted material of which 4 in a considerable amount. Especially *Juncus effusus* was present in a large amount.

Table 9: Species found in drifted material released by mowing; sample taken at 16-7-98.

Species	#
<i>Holcus lanatus</i>	18
<i>Juncus effusus</i>	> 100
<i>Bidens cernua</i>	1
<i>Glyceria maxima</i>	40
<i>Phalaris arundinacea</i>	15
<i>Betula pubescens</i>	2
<i>Poa trivialis</i>	2
<i>Glyceria fluitans</i>	1
<i>Epilobium spec.</i>	2

Discussion

Theoretically, species from a *Glyceria maxima* or large sedges vegetation have a greater possibility to reach the river than species from a meadow, because of the difference in elevation and thus inundation frequency. But the number of seeds captured during this experiment was low, even though *Glyceria maxima*, *Phalaris arundinacea* communities and the large sedges swamp were inundated most of the time. This means that despite the fact that several thousands of seeds per m² are present, these have large difficulties of getting into the river. This can be due to several reasons. First, seeds can be immobilized by surrounding vegetation. Inundation levels during the summer season were only a few centimeters above ground level so the water surface never reached the top of the vegetation. The sometimes-dense vegetation causes a barrier for floating seeds at low water levels. Secondly, the inundation water generally seemed stagnant water. An explanation for this could be that at these water levels, inundation water originates from groundwater or rainwater, and no connection to the river is present. This would imply that when the river floods the area after the reproductive season, a lot of seeds would still be present in the area. At such an event seeds are more likely to disperse by water, because of the higher water levels and increased current velocities. This phenomenon can be considered as a 'threshold' effect.

In this study we assumed that during a flood, all seeds released by the vegetation would be transported out of the study area. However, a study by Cellot *et al.* (1998) indicated that the number of seeds estimated in drift material during a flood is only a fraction of the number of seeds present in the area.

In the seed transport experiment, large multiplication factors were used. This means that species of which just one seed was trapped, appears in the results as several tens of seeds. If in the propagule drift experiment only species are considered of which a reasonable amount of seeds was caught (>200 during the experiment, see table 3) the difference between species captured at the downstream site and the upstream site is rather well explained by the vegetation in the Kappersbult area. In numbers, *Carex spec.* were trapped more at the downstream site than at the upstream site. A large part of the study area consists of *Carex* vegetation which is submerged most time of the year. Also the riverbank consists of some *Carex* species. Three other abundant species in the seed traps were *Agrostis canina*, *Phalaris arundinacea* and *Veronica beccabunga*, which were all common in the area and on the riverbank. At the upstream site on the other hand, no species were trapped in a considerable amount, which were not trapped at the downstream site, except for *Rorippa spec.* A lot of species that were trapped at both sites were trapped in a considerable amount and no general differences were found between the downstream and upstream site for these species. It can be assumed that these species were already present in the river before entering the study area, and therefore the vegetation in the nature reserve did not have an evident effect on the quantity of these species in drifted material.

In the seed transport experiment, of some species large amount of seeds (>1000) were caught. These species are actually species that produce large numbers of seeds (e.g. grasses and *Carex* species) and are common species in these kind of systems. Obviously such quantities of seed production offer a great advantage in successful hydrochory for these species. In an abiotic optimized area the few seeds of rare species have to compete with large amounts of seeds of common species. This would mean an extra barrier for successful establishment of rare species.

From the former we assume that under normal (non-flooding) conditions, most of the seeds in a river probably originate from riverbank vegetation and plants along ditches discharging in the river. As listed under 'Seed production' in the 'Results' section, a riverbank vegetation is highly heterogeneous and therefore a riverbank can provide a considerable amount of species for dispersal through the river. Another important factor is that these species can relatively easily enter the river because of its vicinity. Data of Fuchs (in Poschlod *et al.*, 1997) indicate that species with germinable diaspores in the river not only originate from riverbank vegetation. However, no quantification was given so the impact of these diaspores in structuring plant communities is hard to assess.

It is generally assumed that seeds with short buoyancy will not disperse very successfully in water. But, in a river with a current velocity of 1 m/s (estimated for the Drentse Aa at a water level of 0.60-0.70 m +NAP) seeds can travel up to 86 km in 24 hours. When flooding occurs, current velocities are much higher due to the increased discharge and thus, seeds will be transported even further. Buoyancy of more than a few days or even more than one day is thus not essential for a seed to travel large distances.

The results of the scenario calculations indicate that when a river floods an area after most plants have set seed, large quantities of seeds can be expected in a river. Together with large current velocities at such events, seeds are expected to travel long distances. In this study we did not quantify such events, but visual observations confirmed this suggestion. In week 44 in 1998 the Kapppersbult area was flooded (up to 1.50m +NAP) and heaps of seeds were drifting around, especially at land-water interfaces.

Seed transport in rivers is heavily influenced by environmental conditions like shape of the river or wind directions. Many floating diaspores are trapped in eddies and along outer curves of rapids (Nilsson *et al.*, 1991); in lakes and slow-flowing stretches the wind may easily catch drifting objects (Cook, 1987). Like Danvind & Nilsson (1997) discussed, floating seeds are easily trapped by litter packs. Mowing of the riverbanks as observed in this study caused the formation of large litter packs in the river. These litter packs are heavily under the influence of winds or obstacles and increase the risk of stranding (Danvind & Nilsson, 1997). On the other hand, if hydrochory was not to be stopped, seeds would flow downstream with the river and eventually end up in the sea. So, we assume that the risk of stranding might also be interpreted as a possibility for seeds to find new habitats.

References in Skoglund (1990) state that *Juncus* species produce non-buoyant seeds. In this study however, two *Juncus* species were trapped of which one (*Juncus effusus*) in a considerable amount and during the entire period of propagule trapping. We think that these results indicate that either seeds of some *Juncus* species are buoyant, or that another process produced these results. For now, we have no indication what such kind of process may be.

Schneider & Sharitz (1988) stated that timing and magnitude of hydrologic events determine the results of hydrochory to a great extent. The results of this study confirm this suggestion firmly. The results of the scenarios have shown that timing is especially important for the ratio of different species in the river and magnitude for the quantity of seeds. Timing of a hydrologic event might be very important for the establishment of different species and communities. If a flood would occur early in the reproductive season, it would only favor early flowering species that have already released seeds. For example, *Carex* species would be favored by such early events, and seeds of late flowering species like *Glyceria maxima* would not be present in the water.

From this study it is clear that a nature reserve like the Kappersbult area is not a large source for seed dispersal through the river Drentse Aa during the summer season, probably through lack of flooding. Although part of the area is continuously inundated it does not add many seeds to the river. Since we assume that a great deal of seeds in the river originates from riverbank vegetation it is important to protect these banks in nature conservation policies. An important topic to study is the dispersal of seeds after flooding, because we consider a flood to disperse large quantities of seeds. If this hypothesis turns out to be true, it would be of importance to bring back rivers in their original state in restoration projects along river corridors.

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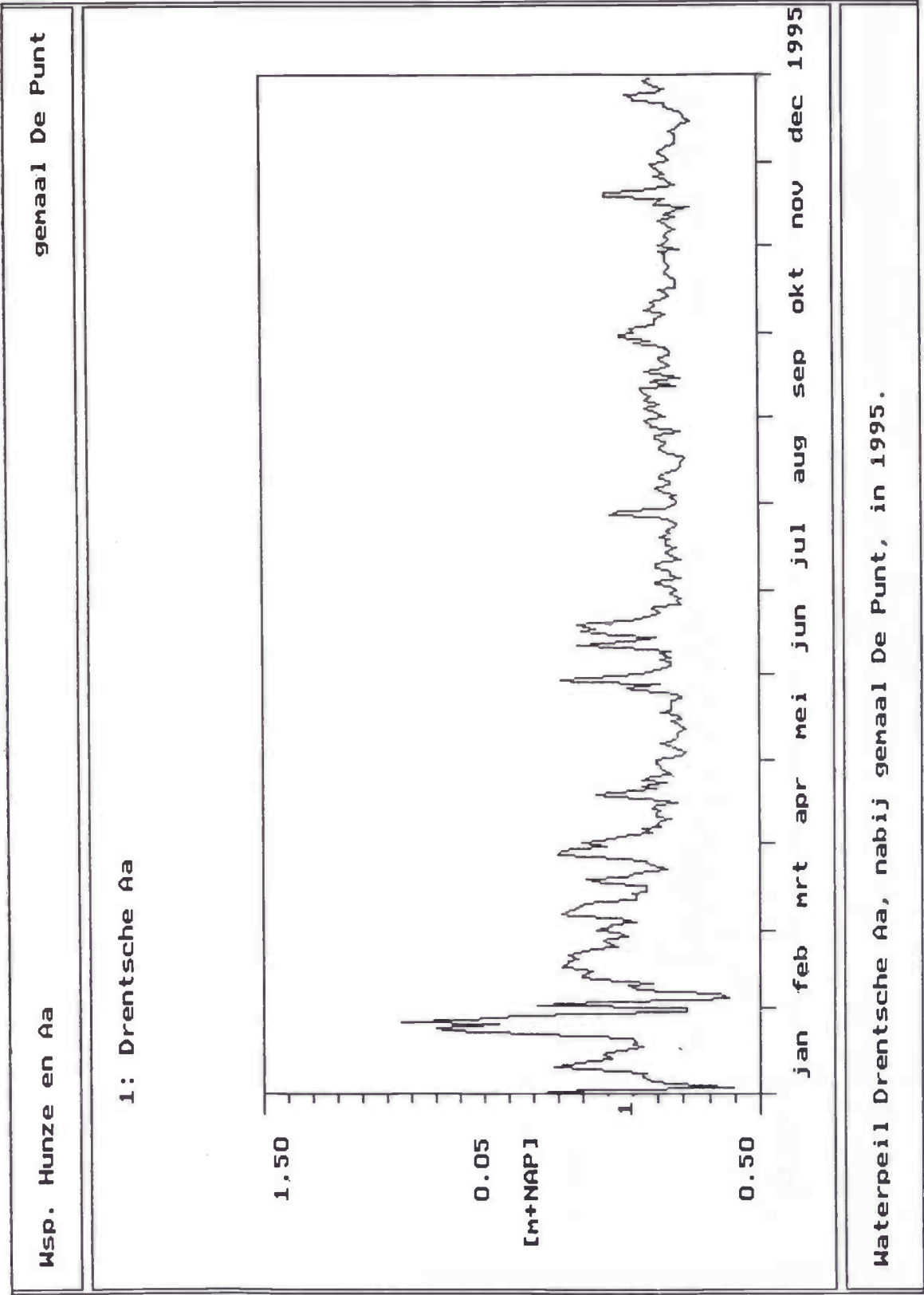
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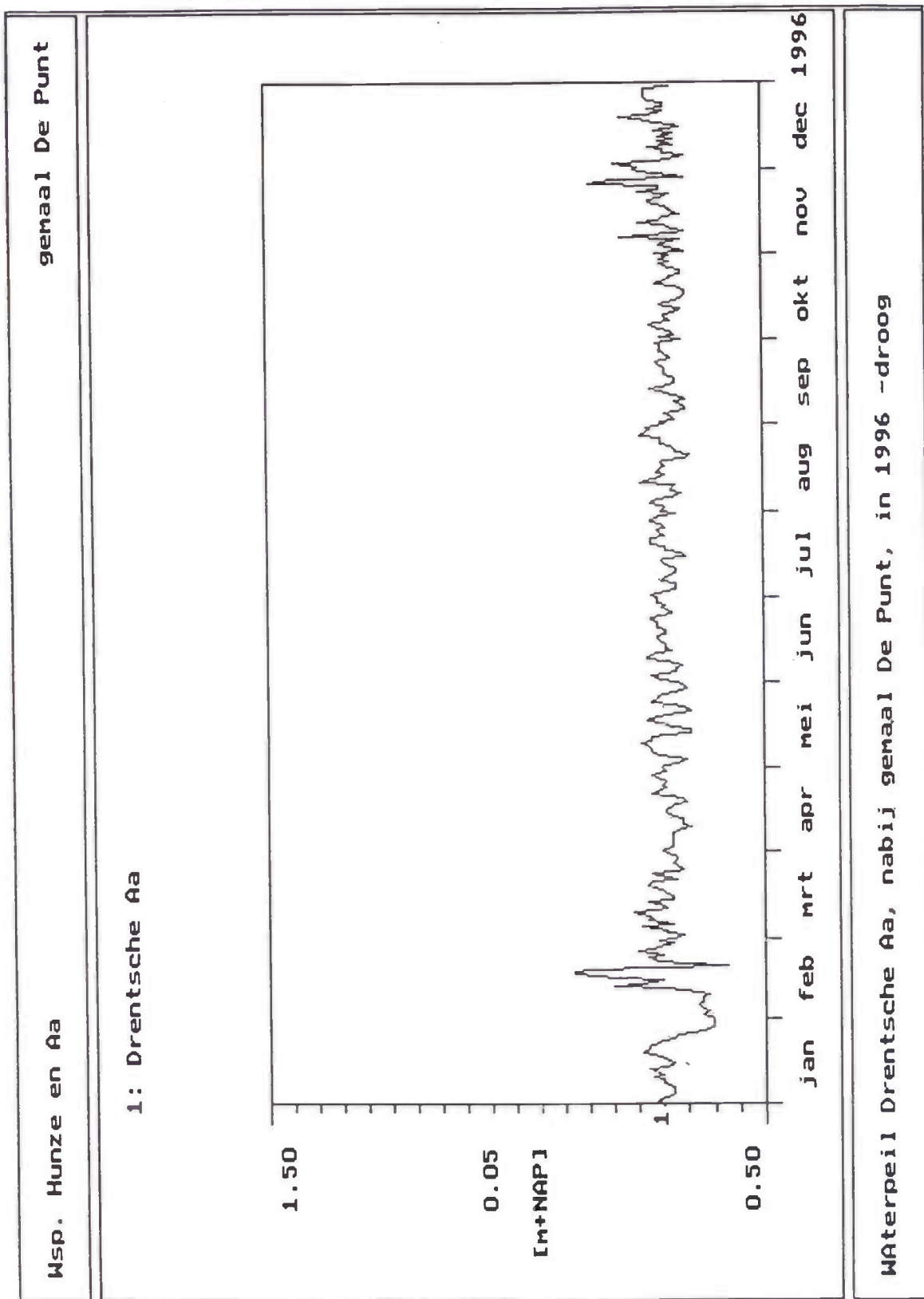
Appendix

Appendices

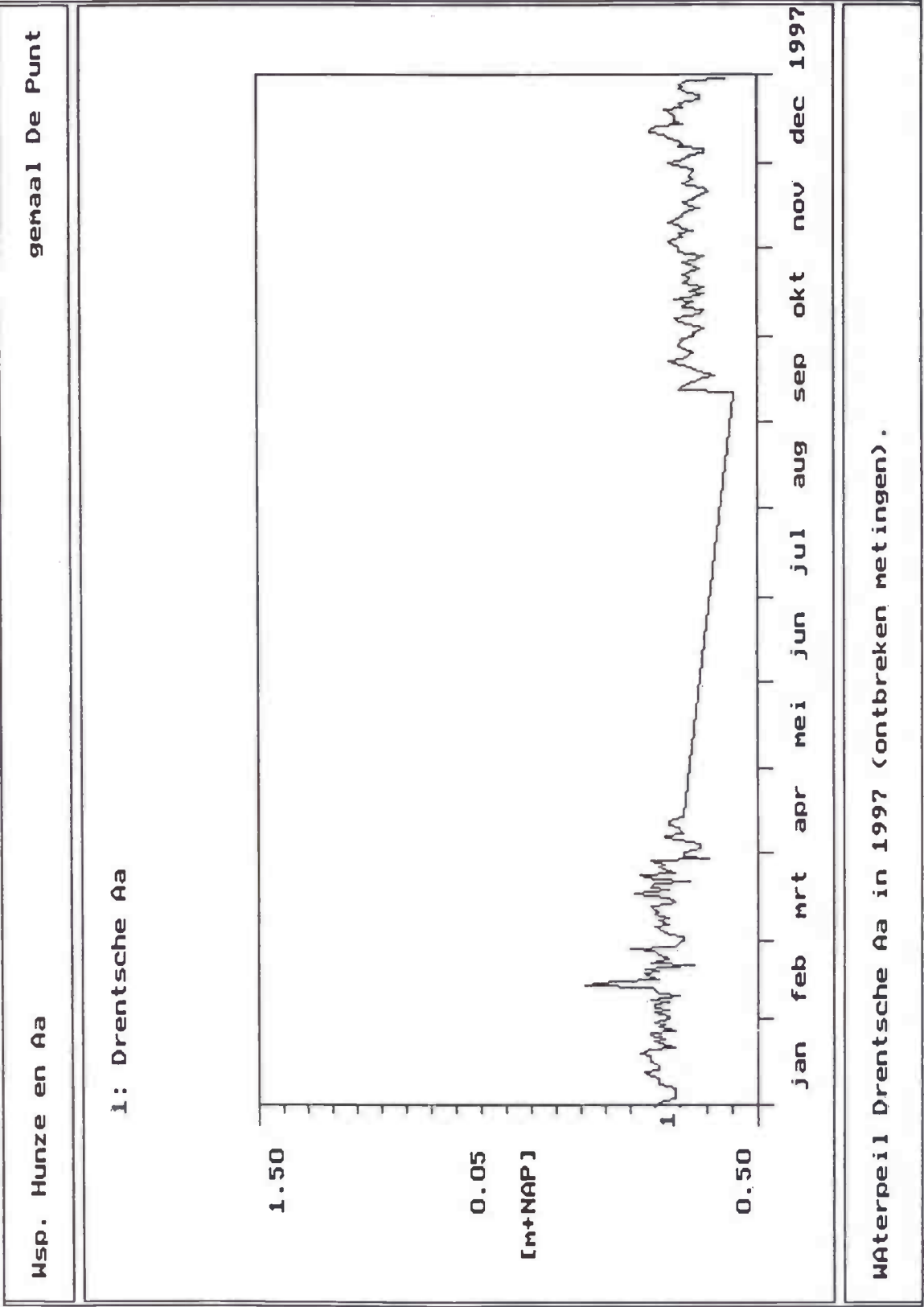
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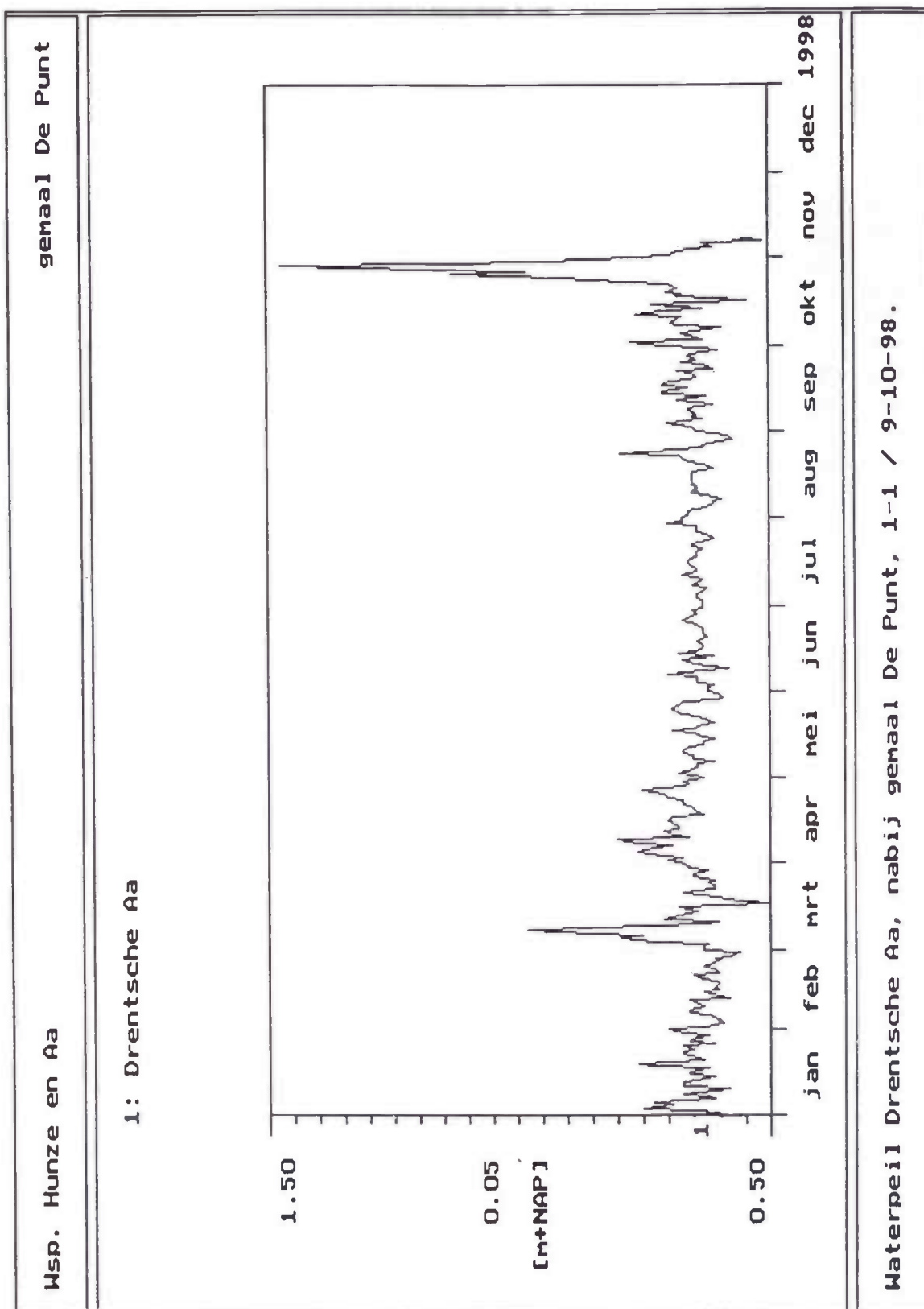
Appendix 1A: Water level fluctuation chart of the river Drentse Aa near the Kappersbult nature reserve for 1995.



Appendix 1B: Water level fluctuation chart of the river Drentse Aa near the Kappersbult nature reserve for 1996.

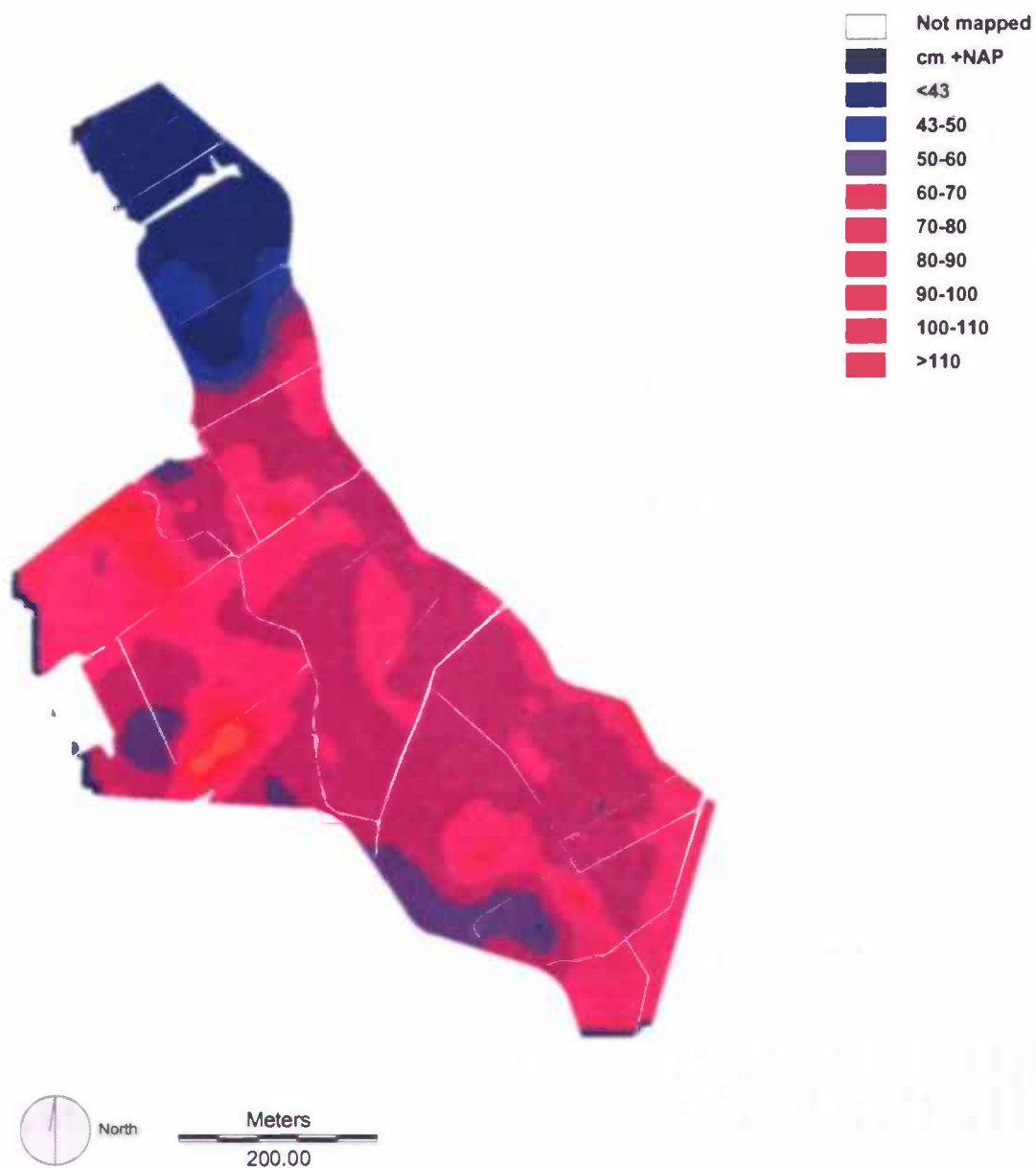


Appendix 1C: Water level fluctuation chart of the river Drentse Aa near the Kappersbult nature reserve for 1997 (missing data from April to September).



Appendix 1D: Water level fluctuation chart of the river Drentse Aa near the Kappersbult nature reserve for 1998 up to November.

Elevation map



Appendix 2: Elevation map of the Kappersbult nature reserve. Legend units are cm +NAP.

species	counted	#	large sedges			1-7-98			P. arundinacea					6-7-98		
			b	f	s	r	total	# diasp/m2	b	f	s	r	total	# diasp/m2		
Agrostis canina	seeds/plant	180	3	2			5	1,178	0	3	4	0	7	1,639		
Agrostis capillaris	seeds/plant	350					0	0					0	0		
Agrostis stolonifera	seeds/plant	200					0	0					0	0		
Alopecurus pratensis	seeds/plant	160					0	0			0		0	49		
Anthoxanthum odoratum	seeds/plant	58					0	0					0	0		
Calamagrostis canescens	seeds/plant	698		3	2		4	3,749	1	9	2	0	11	9,694		
Callitha palustris	seeds/flower	8					0	1					0	0		
Cardamine pratensis	seeds/plant	21					0	1					0	0		
Carex acuta	seeds/plant	175					0	0		0			0	27		
Carex aquatilis	seeds/plant	312			1		1	520			2		2	626		
Carex curia	seeds/plant	50					0	0					0	0		
Carex elata	seeds/plant	183			3		3	768					0	0		
Carex nigra	seeds/plant	135			2		2	292					0	0		
Carex panicea	seeds/plant	40					0	0					0	0		
Cirsium palustre	seeds/flower	52					0	0					0	0		
Deschampsia cespitosa	seeds/plant	658					0	0					0	0		
Eleocharis palustris	seeds/flower	25		1	5		6	184					0	0		
Eriophorum angustifolium	seeds/plant	12					0	0	0	1	1		2	28		
Festuca pratensis	seeds/plant	74					0	0					0	0		
Festuca rubra	seeds/plant	54					0	0					0	0		
Filipendula ulmaria	seeds/plant	1201					0	74					0	0		
Galium palustre	seeds/plant	2500	1	11			12	38,426	1	2		2	3	8,488		
Glyceria fluitans	seeds/plant	400					0	0		0	1		3	1,605		
Glyceria maxima	seeds/plant	620					0	0	0	1			1	1,052		
Holcus lanatus	seeds/plant	168					0	0					0	0		
Juncus acutiflons	seeds/plant	16300					0	3,019					0	0		
Juncus articulatus	seeds/plant	5900					0	0					0	0		
Juncus conglomeratus	seeds/plant	10000					0	0					0	0		
Juncus effusus	seeds/plant	10000					0	0			4		4	50,926		
Lychnis flos-cuculi	seeds/flower	50					0	0				2	2	131		
Mentha aquatica	seeds/plant	1320					0	0					0	0		
Myosotis laxa	seeds/plant	44		2	10	8	20	1,075			2	1	2	122		
Myosotis scorpioides	seeds/plant	44					0	0					0	0		
Pedicularis palustris	seeds/box	20				9	9	210					0	0		
Persicaria amphibia	seeds/plant	1000					0	0					0	0		
Phalaris arundinacea	seeds/plant	290					0	161			22		22	7,877		
Plantago lanceolata	seeds/plant	41					0	0					0	0		
Poa palustris	seeds/plant	100			1		1	123					0	0		
Poa trivialis	seeds/plant	106		1	1		1	137					0	0		
Potentilla palustris	seeds/flower	20					0	0					0	0		
Ranunculus acris	seeds/flower	36					0	0					0	0		
Ranunculus flammula	seeds/flower	23	2	2	3		8	226	6	6	10	3	25	699		
Ranunculus repens	seeds/flower	26					0	0					0	0		
Rhinantus angustifolius	seeds/flower	18					0	0					0	0		
Rumex acetosa	seeds/plant	30					0	0					0	0		
Stachys palustris	seeds/mullei	192			1		1	178					0	0		
Stellaria palustris	seeds/flower	7.7					0	1		5	4	0	9	88		
Succisa pratensis	seeds/flower	71					0	0					0	0		
Veronica scutellata	seeds/flower	2					1	1					0	0		

Appendix 3A: Species in a reproductive state found during the field survey in the large sedges and *Phalaris arundinacea* communities. The letters b, f, s and r respectively refer to plants with flower buds, flowers, seeds or released seeds per 0.81m².

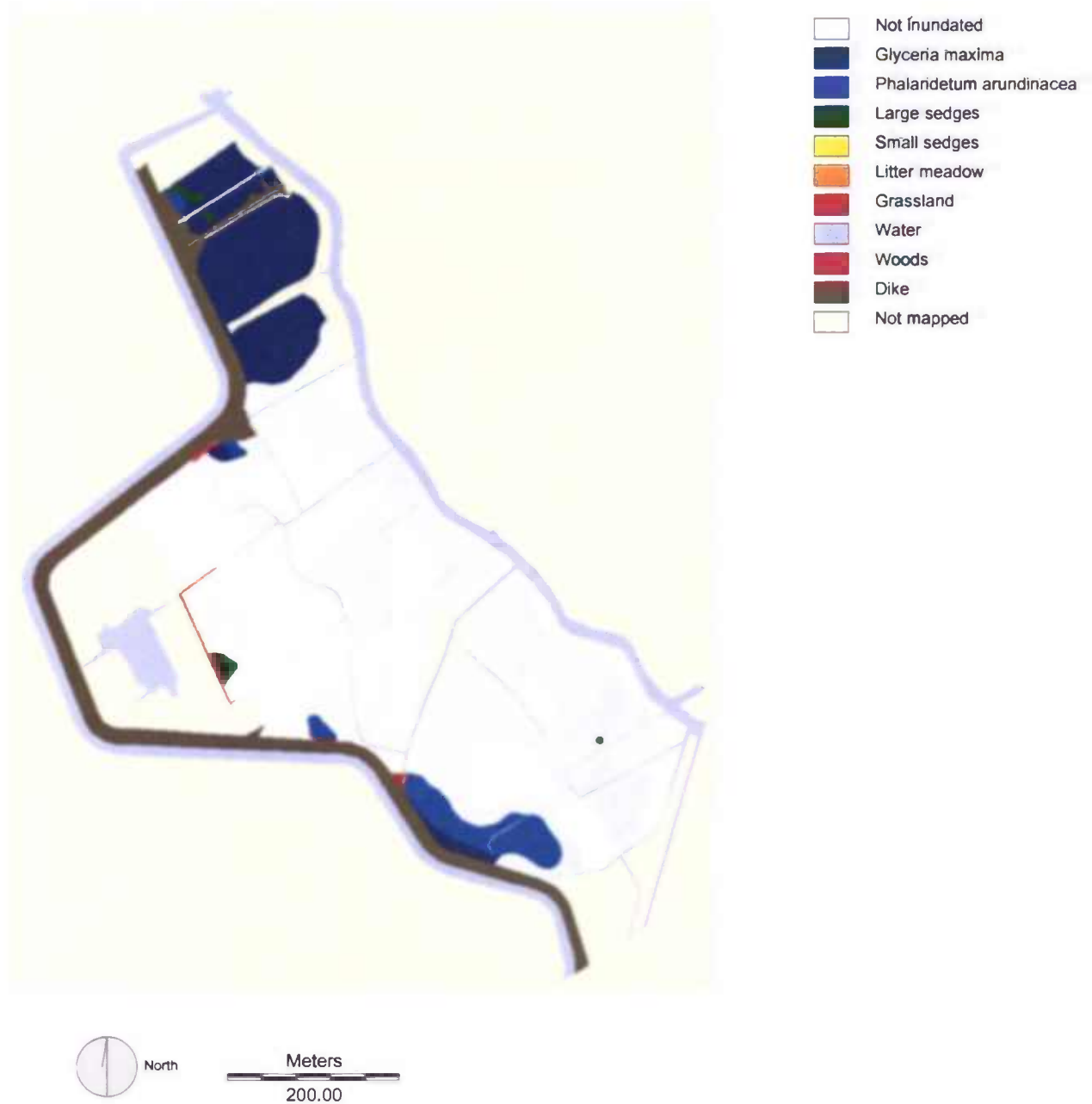
species	grassland					15-7-98					26-7-98				
	#	counted	b	f	s	r	total	#diasp/m ²	b	f	s	r	total	#diasp/m ²	
<i>Agrostis canina</i>	180	seeds/plant	2	1	1	1	4	778	14	2	26	0	42	9,267	
<i>Agrostis capillaris</i>	350	seeds/plant	6	19	2	2	27	11,451	0	0	0	0	0	86	
<i>Agrostis stolonifera</i>	200	seeds/plant					0	0					0	25	
<i>Alopecurus pratensis</i>	160	seeds/plant			1	2	3	514				0	0	0	
<i>Anthoxanthum odoratum</i>	58	seeds/plant			19	35	54	3,867					0	14	
<i>Calamagrostis canescens</i>	698	seeds/plant			0		0	172			0	0	0	172	
<i>Caltha palustris</i>	8	seeds/flower					0	0				0	0	1	
<i>Cardamine pratensis</i>	21	seeds/plant					0	0					0	0	
<i>Carex acuta</i>	175	seeds/plant					0	0					0	0	
<i>Carex aquatilis</i>	312	seeds/plant					0	0			1	0	1	347	
<i>Carex curta</i>	50	seeds/plant					0	0					0	6	
<i>Carex elata</i>	183	seeds/plant					0	0					0	0	
<i>Carex nigra</i>	135	seeds/plant			0	0	1	117			21	6	31	5,100	
<i>Carex panicea</i>	40	seeds/plant					0	0			0		0	10	
<i>Cirsium palustre</i>	52	seeds/flower	7	3	4		14	899					0	0	
<i>Deschampsia cespitosa</i>	658	seeds/plant		1			1	487					0	0	
<i>Eleocharis palustris</i>	25	seeds/plant					0	0			20	0	21	633	
<i>Eriophorum angustifolium</i>	12	seeds/flower					0	0	1	7	15	0	23	338	
<i>Festuca pratensis</i>	74	seeds/plant			2	2	3	292					0	0	
<i>Festuca rubra</i>	54	seeds/plant	0	3	2	8	13	853				2	2	140	
<i>Filipendula ulmaria</i>	1201	seeds/plant					0	0					0	0	
<i>Galium palustre</i>	2500	seeds/plant	1	0			1	3,086			1	2	3	9,568	
<i>Glyceria fluitans</i>	400	seeds/plant					0	0					0	0	
<i>Glyceria maxima</i>	620	seeds/plant					0	0					0	0	
<i>Holcus lanatus</i>	168	seeds/plant	4	1	22	57	83	17,298			0	1	1	124	
<i>Juncus acutifloris</i>	16300	seeds/plant	21				21	414,543					0	0	
<i>Juncus articulatus</i>	5900	seeds/plant			2		2	14,568					0	0	
<i>Juncus conglomeratus</i>	10000	seeds/plant		2	1		3	33,333					0	0	
<i>Juncus effusus</i>	10000	seeds/plant	3	0			3	40,741	0				0	2,469	
<i>Lychnis flos-cuculi</i>	50	seeds/flower					0	0					0	0	
<i>Mentha aquatica</i>	1320	seeds/plant					0	0					0	0	
<i>Myosotis laxa</i>	44	seeds/plant					0	0			0	1	1	60	
<i>Myosotis scorpioides</i>	44	seeds/plant					0	0					0	0	
<i>Pedicularis palustris</i>	20	seeds/box					0	0	1	1	1	18	21	521	
<i>Persicaria amphibia</i>	1000	seeds/plant					0	0					0	0	
<i>Phalaris arundinacea</i>	290	seeds/plant		1			1	215					0	0	
<i>Plantago lanceolata</i>	41	seeds/plant	1	1	13	7	22	1,109					0	0	
<i>Poa palustris</i>	100	seeds/plant					0	0					0	0	
<i>Poa trivialis</i>	106	seeds/plant					0	0					0	0	
<i>Potentilla palustris</i>	20	seeds/flower					0	0			0		0	2	
<i>Ranunculus acris</i>	36	seeds/flower	0	0	2	4	6	262					0	0	
<i>Ranunculus flammula</i>	23	seeds/flower	2	1	2	1	5	142	7	13	27	11	57	1,627	
<i>Ranunculus repens</i>	26	seeds/flower	0	0	2	10	12	385					0	0	
<i>Rhinanthus angustifolius</i>	18	seeds/flower	3	1	1	1	5	107					0	0	
<i>Rumex acetosa</i>	30	seeds/plant		0	1	12	13	493					0	0	
<i>Stachys palustris</i>	192	seeds/mullei					0	0					0	0	
<i>Stellaria palustris</i>	7.7	seeds/flower	0	0	1	4	6	59	0	1	6	4	11	102	
<i>Succisa pratensis</i>	71	seeds/flower					0	0					0	0	
<i>Veronica scutellata</i>	2	seeds/flower					0	0					0	0	

Appendix 3B: Species in a reproductive state found during the field survey in the grassland and small sedges communities. The letters b, f, s and r respectively refer to plants with flower buds, flowers, seeds or released seeds per 0.81m².

species	#	counted	G. maxima				6-8-98				litter meadow				15-8-98			
			b	f	s	r	total	# diasp/m2	b	f	s	r	total	# diasp/m2				
Agrostis canina	180	seeds/plant					0						37		37	8,311		
Agrostis capillaris	350	seeds/plant					0								0	0		
Agrostis stolonifera	200	seeds/plant					0								0	0		
Alopecurus pratensis	160	seeds/plant					0								0	0		
Anthoxanthum odoratum	58	seeds/plant					0					40		40	2,893			
Calamagrostis canescens	698	seeds/plant					0								0	0		
Caltha palustris	8	seeds/flower					0								0	0		
Cardamine pratensis	21	seeds/plant					0								0	0		
Carex acuta	175	seeds/plant					0								0	0		
Carex aquatilis	312	seeds/plant					0								0	0		
Carex curta	50	seeds/plant					0								0	0		
Carex elata	183	seeds/plant					0								0	0		
Carex nigra	135	seeds/plant					0					1		1	133			
Carex panicea	40	seeds/plant					0								0	0		
Cirsium palustre	52	seeds/flower					0					2	1	8	19	1,207		
Deschampsia cespitosa	658	seeds/plant					0							3	3	2,437		
Eleocharis palustris	25	seeds/plant					0								0	0		
Eriophorum angustifolium	12	seeds/flower					0					2		2	5	68		
Festuca pratensis	74	seeds/plant					0								0	0		
Festuca rubra	54	seeds/plant					0								0	0		
Filipendula ulmaria	1201	seeds/plant					0								0	0		
Galium palustre	2500	seeds/plant					0								0	0		
Glyceria fluitans	400	seeds/plant					0								0	0		
Glyceria maxima	620	seeds/plant			5	4	9	7,119							0	0		
Glyceria lanata	168	seeds/plant					0							23	23	4,729		
Juncus acutiflorus	16300	seeds/plant					0								0	0		
Juncus articulatus	5900	seeds/plant					0								0	0		
Juncus conglomeratus	10000	seeds/plant					0								0	4,938		
Juncus effusus	10000	seeds/plant					0							17	18	224,691		
Lychnis flos-cuculi	50	seeds/flower					0								0	0		
Mentha aquatica	1320	seeds/plant	1	9			10	16,296							0	0		
Myosotis laxa	44	seeds/plant					0								0	0		
Myosotis scorpioides	44	seeds/plant			1	0	3	152							0	0		
Pedicularis palustris	20	seeds/box					0								0	0		
Persicaria amphibia	1000	seeds/plant					0	247							0	0		
Phalaris arundinacea	290	seeds/plant					0	36							0	0		
Plantago lanceolata	41	seeds/plant			0		0	0					17	10	26	1,336		
Poa palustris	100	seeds/plant					0	0							0	0		
Poa trivialis	106	seeds/plant					0	0							0	0		
Potentilla palustris	20	seeds/flower					0	0							0	0		
Ranunculus acris	36	seeds/flower					0	0							0	0		
Ranunculus flammula	23	seeds/flower					0	0						4	6	11		
Ranunculus repens	26	seeds/flower					0	0					1	1	2	64		
Rhinanthus angustifolius	18	seeds/flower					0	0							0	0		
Rumex acetosa	30	seeds/plant					0	0					1	2	3	8		
Stachys palustris	192	seeds/mullei	0	0	2	0	3	759							0	0		
Stellaria palustris	7.7	seeds/flower					0	0							0	0		
Succisa pratensis	71	seeds/flower					0	0					6		6	561		
Veronica scutellata	2	seeds/flower					0	0							0	0		

Appendix 3C: Species in a reproductive state found during the field survey in the *Glyceria maxima* and litter meadow communities. The letters b, f, s and r respectively refer to plants with flower buds, flowers, seeds or released seeds per 0.81m².

Inundated at water level 50-60 cm +NAP



Appendix 4A: Flooding map of the Kappersbult nature reserve. Coloured areas, except for the dike, represent inundated plant communities at a river water level of 50-60 cm.

Inundated at water level 60-70 cm +NAP



- Not Inundated
- Glyceria maxima*
- Phalaridetum arundinacea*
- Large sedges
- Small sedges
- Litter meadow
- Grassland
- Water
- Woods
- Dike
- Not mapped



Appendix 4B: Flooding map of the Kappersbult nature reserve. Coloured areas, except for the dike, represent inundated plant communities at a river water level of 60-70 cm.

Inundated at water level 70-80 cm +NAP

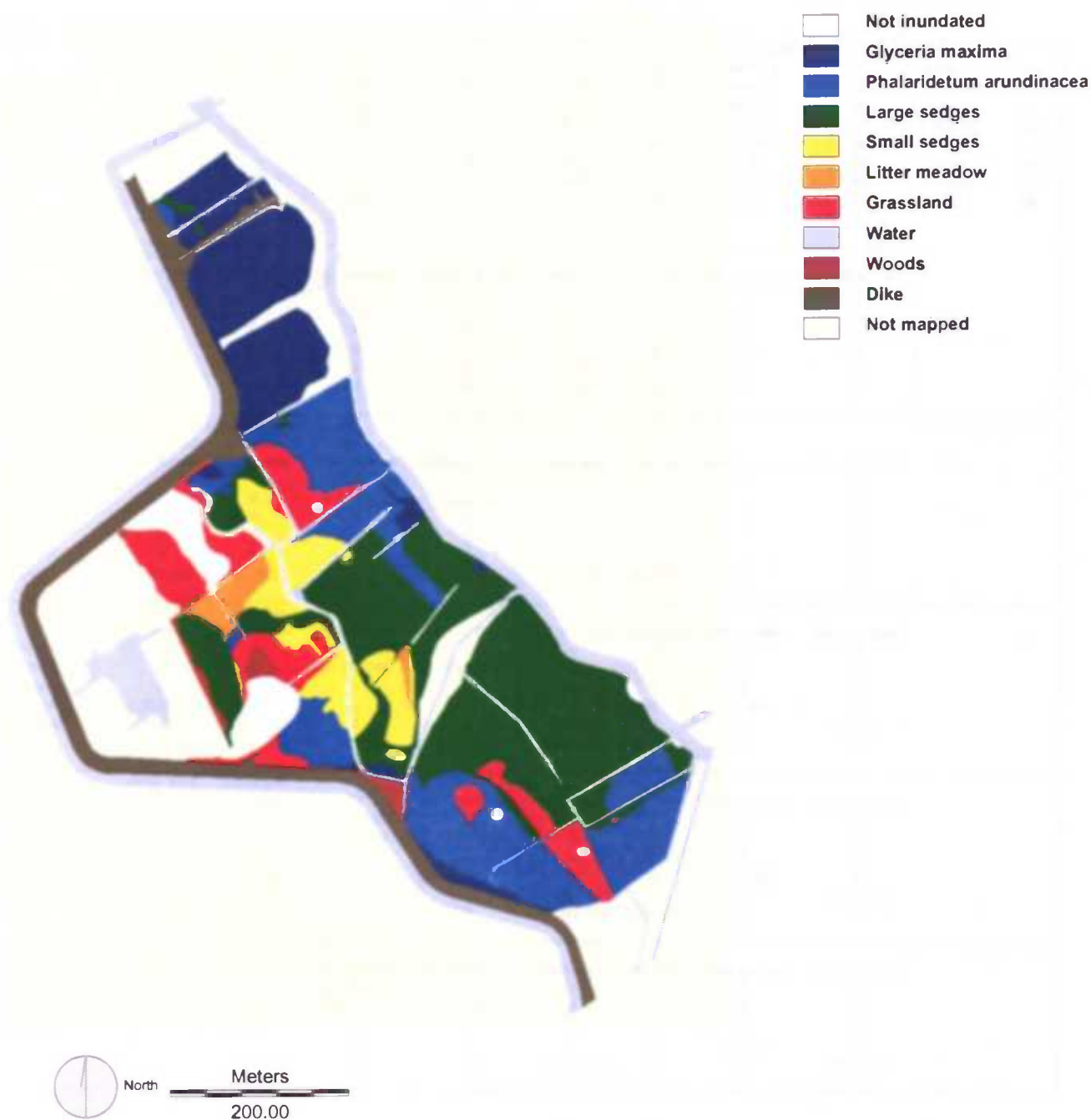


- Not inundated
- Glyceria maxima*
- Phalaridetum arundinacea*
- Large sedges
- Small sedges
- Litter meadow
- Grassland
- Water
- Woods
- Dike
- Not mapped



Appendix 4C: Flooding map of the Kappersbult nature reserve. Coloured areas, except for the dike, represent inundated plant communities at a river water level of 70-80 cm.

Inundated at water level 80-90 cm +NAP



Appendix 4D: Flooding map of the Kappersbult nature reserve. Coloured areas, except for the dike, represent inundated plant communities at a river water level of 80-90 cm.

	m2 veg	water level:	50-60 cm	%	60-70 cm	%	m2 inundated vegetation		80-90 cm	%
<i>G. maxima</i>	32,817		28,191	86	32,706	100	32,817	100	32,817	100
<i>P. arundinaceae</i>	48,342		8,286	17	33,419	69	46,052	95	47,996	99
large sedges	71,006		1,042	1	54,606	77	69,074	97	70,688	100
small sedges	16,495		0	0	9,729	59	16,212	98	16,436	100
poor meadow	3,768		0	0	257	7	2,782	74	3,768	100
Grassland	28,797		161	1	3,465	12	16,576	58	21,907	76
Woods	4,470		849	19	1,981	44	2,381	53	3,047	68

	# seeds/m2							
	Holc. lan	Anth. odor.	Glyceria max.	Lychnis fl. cuc.	Plant. lanc.	Fest. prat	Carex panicea	Succisa prat.
<i>G. maxima</i>	0	0	7,119	0	0	0	0	0
<i>P. arundinaceae</i>	0	0	1,052	131	0	0	0	0
large sedges	0	0	0	0	0	0	0	0
small sedges	124	14	0	0	0	0	10	0
poor meadow	4,729	2,893	0	0	1,336	0	0	561
Grassland	17,298	3,867	0	0	1,109	292	0	0

total # seeds at different elevation levels								
	water level	50-60 cm						
	Holc. lan	Anth. odor.	Glyceria max.	Lychnis fl. cuc.	Plant. lanc.	Fest. prat	Carex panicea	Succisa prat.
<i>G. maxima</i>	0	0	200,691,729	0	0	0	0	0
<i>P. arundinaceae</i>	0	0	8,716,872	1,085,466	0	0	0	0
large sedges	0	0	0	0	0	0	0	0
small sedges	0	0	0	0	0	0	0	0
poor meadow	0	0	0	0	0	0	0	0
Grassland	2,784,942	622,587	0	0	178,549	47,012	0	0

	water level	60-70 cm						
	Holc. lan	Anth. odor.	Glyceria max.	Lychnis fl. cuc.	Plant. lanc.	Fest. prat	Carex panicea	Succisa prat.
<i>G. maxima</i>	0	0	232,834,014	0	0	0	0	0
<i>P. arundinaceae</i>	0	0	35,156,788	4,377,889	0	0	0	0
large sedges	0	0	0	0	0	0	0	0
small sedges	1,206,396	136,206	0	0	0	0	97,290	0
poor meadow	1,215,353	743,501	0	0	343,352	0	0	144,177
Grassland	59,936,800	13,399,155	0	0	3,842,685	1,011,780	0	0

	water level	70-80 cm						
	Holc. lan	Anth. odor.	Glyceria max.	Lychnis fl. cuc.	Plant. lanc.	Fest. prat	Carex panicea	Succisa prat.
<i>G. maxima</i>	0	0	233,624,223	0	0	0	0	0
<i>P. arundinaceae</i>	0	0	48,446,704	6,032,812	0	0	0	0
large sedges	0	0	0	0	0	0	0	0
small sedges	2,010,288	226,968	0	0	0	0	162,120	0
poor meadow	13,156,078	8,048,326	0	0	3,716,752	0	0	1,560,702
Grassland	286,727,964	64,099,392	0	0	18,382,784	4,840,192	0	0

	water level	80-90 cm						
	Holc. lan	Anth. odor.	Glyceria max.	Lychnis fl. cuc.	Plant. lanc.	Fest. prat	Carex panicea	Succisa prat.
<i>G. maxima</i>	0	0	233,624,223	0	0	0	0	0
<i>P. arundinaceae</i>	0	0	50,491,792	6,287,476	0	0	0	0
large sedges	0	0	0	0	0	0	0	0
small sedges	2,038,064	230,104	0	0	0	0	164,360	0
poor meadow	17,818,872	10,900,824	0	0	5,034,048	0	0	2,113,848
Grassland	378,942,418	84,714,369	0	0	24,294,863	6,396,844	0	0

Appendix 5: Results of the flooding maps. The upper box deals with the inundated surface (m²) per community at different water levels. The second box lists the calculated number of seeds per m² of eight species in the different communities in the Kappersbult nature reserve. The lower four boxes present the calculated total number of seeds of eight species which are available in inundated communities at different water levels.

total # seeds in inundated community										this # seeds remains for flood at 1st of October									
Flood at the 10th of July										# seeds in river									
water level 50-60 cm										75									
Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.			Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.		
0	0	200,831,729	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G. maxima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. arundinaceae	0	8,716,872	1,085,466	0	0	0	0	0	0	0	0	1,085,466	0	0	0	0	0	0	0
large sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
small sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
poor meadow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
grassland	2,788,942	827,587	0	176,549	47,012	0	0	0	0	0	416,940	0	0	142,839	14,104	0	0	0	0
water level 60-70 cm										80									
Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.			Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.		
0	0	232,834,014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G. maxima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. arundinaceae	0	35,156,788	4,377,889	0	0	0	0	0	0	0	0	4,377,889	0	0	0	0	0	0	0
large sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
small sedges	1,206,396	135,206	0	0	0	0	0	0	0	0	102,155	0	0	0	0	0	0	0	0
poor meadow	1,215,353	743,501	0	0	0	0	0	0	0	0	527,836	0	0	274,682	0	0	0	0	0
grassland	59,936,800	13,399,155	0	3,842,885	1,011,780	0	0	0	0	0	10,049,366	0	0	3,074,148	303,534	0	0	0	0
water level 70-80 cm										90									
Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.			Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.		
0	0	233,624,223	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G. maxima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. arundinaceae	0	48,446,704	6,032,612	0	0	0	0	0	0	0	0	6,032,612	0	0	0	0	0	0	0
large sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
small sedges	2,010,268	276,948	0	0	0	0	0	0	0	0	170,226	0	0	0	0	0	0	0	0
poor meadow	13,158,078	8,048,326	0	0	0	0	0	0	0	0	6,036,245	0	0	2,973,402	0	0	0	0	0
grassland	286,727,864	64,059,392	0	18,369,784	4,840,192	0	0	0	0	0	48,074,544	0	0	14,706,237	1,452,056	0	0	0	0
water level 80-90 cm										100									
Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.			Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.		
0	0	233,624,223	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G. maxima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. arundinaceae	0	50,491,792	6,287,476	0	0	0	0	0	0	0	0	6,287,476	0	0	0	0	0	0	0
large sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
small sedges	2,038,064	230,104	0	0	0	0	0	0	0	0	172,578	0	0	0	0	0	0	0	0
poor meadow	17,818,872	10,900,824	0	0	0	0	0	0	0	0	8,175,618	0	0	4,027,238	0	0	0	0	0
grassland	376,842,418	84,714,369	0	24,264,653	6,396,844	0	0	0	0	0	63,535,777	0	0	19,435,890	1,919,053	0	0	0	0
water level 90-100 cm										110									
Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.			Holc. lan.	Anth. odor.	Gly. max.	Lych. fl. cuc.	Plant. lanc.	Fast. prat.	Carex pan.	Succ. prat.		
0	0	233,624,223	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G. maxima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. arundinaceae	0	50,491,792	6,287,476	0	0	0	0	0	0	0	0	6,287,476	0	0	0	0	0	0	0
large sedges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
small sedges	2,038,064	230,104	0	0	0	0	0	0	0	0	172,578	0	0	0	0	0	0	0	0
poor meadow	17,818,872	10,900,824	0	0	0	0	0	0	0	0	8,175,618	0	0	4,027,238	0	0	0	0	0
grassland	376,842,418	84,714,369	0	24,264,653	6,396,844	0	0	0	0	0	63,535,777	0	0	19,435,890	1,919,053	0	0	0	0

Appendix 6: Potential seed dispersal for eight species. The left box represents the total calculated number of seeds which are available in inundated communities at increasing water levels. The box in the middle presents the calculated number of seeds that can be transported by the river at the 10th of July at different water levels. The third box lists the calculated number of seeds that are not released yet and will be available for transport by a second flood. The water levels in the different boxes correspond to each other.

	wk25-26		wk28-29		wk30-31		wk32-33		wk34-35		total	
	n	z	n	z	n	z	n	z	n	z	n	z
<i>Agrostis canina</i>	0	0	0	0	69	0	319	0	0	0	388	0
<i>Agrostis capillaris</i>	0	0	0	0	0	104	0	38	0	0	0	142
<i>Agrostis stolonifera</i>	0	0	0	0	0	0	0	38	0	0	0	38
<i>Alopecurus geniculatus</i>	0	0	0	0	0	0	0	38	0	0	0	38
<i>Anthoxanthum odoratum</i>	0	0	0	0	0	52	0	0	0	0	0	52
<i>Berula erecta</i>	0	0	0	0	69	0	0	0	0	0	69	0
<i>Betula pubescens</i>	2883	1678	205	183	69	156	319	115	0	144	3475	2276
<i>Bidens cernua</i>	0	112	0	0	0	0	0	38	0	0	0	150
<i>Carex disticha</i>	0	0	0	0	0	0	106	38	0	0	106	38
<i>Carex nigra</i>	152	0	41	0	2474	0	0	0	0	0	2667	0
<i>Carex pseudocyperus</i>	0	0	41	0	687	0	479	0	128	0	1335	0
<i>Carex spec.</i>	455	0	164	31	0	0	319	38	320	0	1258	69
<i>Cicula virosa</i>	0	0	0	0	69	0	0	0	0	0	69	0
<i>Cirsium palustre</i>	0	0	0	61	0	52	53	77	0	0	53	190
<i>Conyza canadensis</i>	0	0	0	0	0	0	53	0	0	0	53	0
<i>Crataegus monogyna</i>	0	112	0	0	0	0	0	0	0	0	0	112
<i>Dactylis conglomerata</i>	0	0	0	0	0	0	0	64	0	0	64	0
<i>Epilobium ciliatum</i>	0	0	41	31	0	0	0	64	0	0	105	31
<i>Epilobium hirsutum</i>	0	112	0	0	206	52	160	38	448	96	814	298
<i>Epilobium tetragonum</i>	0	0	0	0	0	0	0	0	0	96	0	96
<i>Epilobium spec.</i>	303	0	123	92	0	156	1064	192	0	48	1490	487
<i>Festuca pratensis</i>	0	0	0	0	0	0	0	38	0	0	0	38
<i>Festuca rubra</i>	0	112	0	0	0	0	0	0	0	0	0	112
<i>Glyceria fluitans</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Glyceria maxima</i>	0	0	0	0	0	0	0	64	0	0	64	0
<i>Gnaphalium uliginosum</i>	0	0	0	0	0	0	0	64	0	0	64	0
<i>Holcus lanatus</i>	303	224	492	1708	275	311	0	77	0	0	1070	2320
<i>Hypochaeris radicata</i>	0	0	0	0	0	52	0	0	0	0	0	52
<i>Juncus bufonius</i>	0	0	0	0	0	0	0	64	0	0	64	0
<i>Juncus effusus</i>	152	112	0	92	69	363	372	231	576	480	1169	1277
<i>Lycopus europeus</i>	0	0	0	92	137	415	160	38	64	96	361	641
<i>Mentha aquatica</i>	0	0	0	0	69	0	0	0	64	0	133	0
<i>Myosotis laxa</i>	0	0	0	0	69	0	0	38	0	0	69	38
<i>Myosotis spec.</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Peucedanum palustre</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phalaris arundinacea</i>	0	0	0	0	412	0	0	0	0	0	412	0
<i>Poa trivialis</i>	910	2909	123	1861	206	1193	106	269	128	192	1474	6424
<i>Ranunculus repens</i>	0	0	41	92	0	0	53	0	0	0	94	92
<i>Ranunculus scleratus</i>	0	0	0	0	206	52	53	0	0	0	259	52
<i>Rorippa palustris</i>	0	0	0	0	0	156	0	0	0	48	0	204
<i>Rorippa spec.</i>	0	0	0	92	0	52	0	0	0	0	0	143
<i>Rorippa sylvestris</i>	0	0	41	0	0	208	106	0	0	144	147	352
<i>Rumex acetosella</i>	303	224	0	0	0	0	0	0	0	0	303	224
<i>Rumex hydrolapatum</i>	0	0	0	0	69	0	0	0	0	0	69	0
<i>Sagina procumbens</i>	152	0	0	0	0	0	0	0	0	0	152	0
<i>Salix spec.</i>	455	224	0	0	0	0	0	0	0	0	455	224
<i>Salvia pratensis</i>	0	0	0	0	69	0	0	0	0	0	69	0
<i>Stellaria aquatica</i>	0	0	0	0	0	0	53	0	0	0	53	0
<i>Stellaria spec.</i>	152	0	0	0	0	0	0	0	0	0	152	0
<i>Typha latifolia</i>	0	0	0	0	69	0	53	0	0	0	122	0
<i>Urtica spec.</i>	0	0	0	0	0	0	0	0	0	48	0	48
<i>Veronica beccabunga</i>	0	0	0	0	206	0	53	0	0	0	259	0
<i>Viola palustris</i>	0	0	0	31	0	0	0	0	0	0	0	31
Unknown 1	152	0	0	0	69	0	0	38	0	0	220	38
Unknown 2	303	0	0	0	0	0	0	0	0	384	303	384
total # seeds	6675	5817	1312	4362	5568	3373	3882	1384	2049	1777	19486	16712
total # species	13	10	10	12	20	15	18	17	12	11	total 55 spec.	

Appendix 7: Calculated numbers of seeds caught in the seed trapping experiment from mid-June to end-August 1998. 'Downstream' and 'upstream' refer to figure 2.