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AN AUTECOLOGICAL STUDY OF SOME LIMNOPHYTES AND HELOPHYTES IN THE AREA OF THE LARGE RIVERS

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"Im Wasser hängt die gesammte Ökologie mit der Bewegung zusammen. Sie ist die treibende und gestaltende Kraft; sie ordnet die Bestände und weist ihnen die Wohnplätze an, bestimmt die Zusammensetzung und Beschaffenheit des Grundes, den Einfluss der Pflanzenwelt, die chemische Zusammensetzung und das physikalische und mechanische Verhalten des Wassers..." (GEYER, 1927).

CONTENTS

I. INTRODUCTION

The field data used in this essay were assembled during the botanical inventory of old river-beds by a number of colleagues from the "Stichting tot Onderzoek van Levensgemeenschappen" (Foundation for Biocenological Research), namely Mrs. A. J. Quené-Boterenbrood (1954), Mrs. W. A. E. van Donselaar-ten Bokkel Huinink (1955), Mr. P. J. Schroevers (1954), Mr. J. van Donselaar (1955 and 1956), Mr. L. G. Kop (1956) and E. E. van der Voo (1954–1956). The observations were obtained from 125 old riverbeds of the Maas, Rhine, Waal and the Guelders IJssel (see survey list page 257).

On the basis of this investigation the degree of frequency of the plant species was examined in order to select those species which proved to be sufficiently frequent to be correlated with certain environmental factors. This led to the provisional choice of twelve species. Five among those were waterplants: *Nymphoides peltata* (Gmel.) O. Kuntze, *Nuphar luteum* (L.) Sm., *Polygonum amphibium* L. fo. *natans*, *Potamogeton natans* L., and *P. lucens* L. Six river-bank plants were also chosen, namely *Typha angustifolia* L., *T. latifolia* L., *Equisetum fluviatile* L., *Ranunculus lingua* L., *Glyceria maxima* (Hartm.) Holmb. and *Phragmites communis* Trin. Later, a few more species were added, e.g. *Stratiotes aloides* L., *Sparganium erectum* L., and *Oenanthe aquatica* (L.) Poir, because these proved to be important environmental indicators as well. In addition, one or two of secondary importance are also discussed.

The waterplants were considered together as "limnophytes" according to the definition of Iversen (1936) and the river bank plants as "helophytes" according to Raunkiaer (1934). The degrees of presence and dominance of the species were related to a number of environmental factors — water movement, depth of water, the bottom, the acidity and the chlorine content of the old river bed where the plants were growing. From this it appeared that the movement of the water must be considered as the master factor. The old riverbeds which in this view were ecologically similar, were typified as an "ecotope" following the definition of Mörzer Bruijns (1947). In this way three ecotopes were distinguished. The soil of the old river-beds in two of these ecotopes consists in general of river-clay sediments while the third incorporates various soil types. The three ecotopes are:

Ecotope with tidal inundation (Et) with 13 waters, subjected to tidal movements.

Ecotope with episodical inundation (Ee) — 66 waters, flooded in the winter (water-meadows on river forelands), 14 of which are in permanent connection with the river.

Ecotope with stagnant water (Es) with 46 stretches of still-standing water, rarely or never flooded, divided into 25 with a river-clay bottom, 10 with a river "loam" bottom and 11 with various types.

The ecotope Ee had our major attention, because the majority of waters belong to this category. Moreover they constituted a rather homogeneous ecological unit as they presented a similar bottom type. The number of stretches of water of type Et was too small for a statistical survey, while the ecotope denoted above by Es was less homogeneous by reason of the different types of bottom found in it.

In order to be certain that the differences found in presence degree were significant, a hypergeometrical method was employed, for which method we have to thank Mr. Bezem from Utrecht. Since other workers might like to make use of this method, we have given a fully worked example in the discussion of *Nymphoides peltata*. The ecology of this species is given a more expanded treatment than that of the other ones.

After the discussion of the separate species the relation between presence degree (also the degree of dominance) and the depth of water will be considered (the concepts of presence and dominance are used in the sense of BRAUN-BLANQUET (1928, 1932, 1951)). This investigation was made more difficult because it was not possible to measure the depth in every case, estimates then being used. Another adverse factor was that the waterlevels were subjected to seasonal changes. In 1956, for example, the waterlevel in the river areas was abnormally high.

By setting up an ecological affinity diagram, according to IVERSEN (1936), it was possible to establish the rate of mutual coincidence of all separate limnophytes and of all helophytes, as well as the rate of coincidence of some limnophytes with some helophytes. In this comparison use was made of their degree of presence and dominance in the ecotopes with stagnant and temporarily moving water (Es and Ee). The topographical situation was considered as well, to take into account differences in occurrence corresponding to differences in the areas of the four large rivers named above.

II. LIMNOPHYTES

According to IVERSEN (1936) limnophytes are water plants which show reductions in the vegetative as well as the reproductive shoots, over their terrestrial forms. This group falls approximately under the life form category "hydrophytes" of RAUNKIAER. A species such as *Stratiotes aloides* however does not strictly belong to the hydrophytes according to RAUNKIAER's definition, although it is certainly a limnophyte. The latter group and those of the telmatophytes and amphiphytes of IVERSEN's system, which will be dealt with in a later chapter (Helophytes), have been studied in the Netherlands by WESTHOFF (1947) and ZONNEVELD (1960). Plants referred to as limnophytes in this study belong to the subgroups Nymphaeids and Elodeids following DU RIETZ (1930), that is, plants which either root in the river bottom and whose leaves in general float on the surface of the water (for example *Potamogeton natans*), or, respectively, plants who root in the bottom and whose stems and leaves habitually stretch out through the whole depth of water, as in *Potamogeton lucens*.

We have restricted ourselves to discussing six species of limnophytes because these appear to give satisfactory data from which to draw reliable conclusions. These are: *Nymphoides peltata* (Gmel.) O. Kuntze, *Potamogeton lucens* L., *Nuphar luteum* (L.) Sm., *Nymphaea alba* L., *Potamogeton natans* L. and *Polygonum amphibium* L. fo. *natans*.

1. DISCUSSION OF THE SEPARATE SPECIES

1. 1. NYMPHOIDES PELTATA (GMEL.) O. KUNTZE

1. 1. 1. Distribution

Nymphoides peltata is found in the waters of the low-lying areas of South, West and Middle Europe and in temperate Asia. In Europe, its northern limit coincides with the 16° July isotherm. To the North, its closed areas goes up to the Netherlands, the Baltic and Russia. In Denmark, South Sweden (as far as 60° N) and in Lithuania there are localised occurrences (HULTÉN, 1950). It is not found in Switzerland (HEGI, 1935). According to CLAPHAM, TUTIN and WARBURG (1952) the plant may be found in central and East England in ponds and slowly flowing rivers. It is also reported from France (ROUY and FOUCAUD 1908). It seems to want however in the upper river areas in mountainous regions, for example the Alps, Pyrenees, Scotland and Ireland. The distribution of the plant for the Netherlands is given on one of the plant maps published by the I.V.O.N. (Institute for the Survey of Vegetation in the Netherlands) (1951). From this it appears that in Limburg and Brabant, along the Maas, the plant is to be found in only six localities. In contrast to this, to the North and West of Cuyk, the plant has a continuous distribution in the area of the Maas, Waal, Rhine and Guelders IJssel. However, in the tidal area of the large rivers to the South of the Old Maas and to the West of a line from Willemstad to Barendrecht, the plant is known from only a very few places. Our own observations are almost entirely in agreement with these statements. Upriver from Wychen, the plant was not observed in any of the 14 riverbeds visited, as was also the case with 8 old riverbeds on the South Holland Islands. In one of the following chapters it will appear that the failure of the plant to appear in the areas mentioned above is connected with certain extreme environmental factors. In the remaining old riverbeds, the plant was found fairly regularly in the Maas area and nearly everywhere in the Rhine, Waal and Guelders IJssel areas.

1. 1. 2. Habitat

Nymphoides peltata belongs, according to the definition of DU RIETZ (1930), to the Nymphaeids. These are limnophytes which root in the bottom and whose leaves float on the upper surface of the water.

According to foreign literature, *Nymphoides peltata* is a plant of stagnant or slowly streaming water. HEGI (1935) indicated its preference for old riverbeds ("Altwasser") in lowlying areas and for "Haffen" (brackish water) and river-mouths in Northern Germany. OBERDORFER (1949) states that the plant occurs rarely, but locally dominant in floating plant communities. The environment is, according to him — "nährstoffreiche, flache sommerwarme Gewässer über humos-schlammige Tonböden, Teiche und Altwässer."—TANSLEY (1949) reported *Nymphoides peltata* from the river-basin of the Thames above Oxford. The river flowed here fairly hard and had a sandy bottom with a thin layer of silt, while in a silted-up bay *Nymphoides peltata* was mentioned as the subdominant in a zone of waterplants with *Nuphar luteum* as the dominant. A similar observation published DE WEVER (1917–1918), who found the plant in bends of the Maas in Dutch Limburg.

HEUKELS and VAN OOSTSTROOM (1956) gave the habitats as ditches, canals, waterways and "break-through" pools of dykes, mostly where clay is present. From this the impression is gained that apart from the "break-through" pools, the plant is restricted to more or less artificially formed bodies of water. This is true inasmuch as the digging out of bodies of water which a clay bottom aids the spreading of the species, just as in waterways and ditches that are cleared out annually; even in a swimming-bath (near Barendrecht) an extensive vegetation was observed. But we come far short of the true situation if we do not recognise that the handsome and striking vegetation which grows in natural habitats in the old riverbeds and forelands of the large rivers (especially in the Waal area), is also part of this plant's distribution.

The plant's appearance in "break-through" pools along the coast of the former Zuyder Sea has been accounted for by VAN DIJK and WESTHOFF (1955) as follows: "It is possible to find more or less densely growing vegetation of *Nymphoides peltata*, whenever, as a result of the break-throughs, the bottom came to consist entirely or partly of clay" (translated from the original). According to VLIEGER in VAN ZINDEREN BAKKER (1942) in the lake of Naarden the plant prefers habitats with a clay bottom.

1. 1. 3. Environmental factors

1. 1. 3. 1. *Temperature*

According to OBERDORFER (1949) *Nymphoides peltata* is "wärmeliebend" (thermophilous); MEUSEL (1943) joins it with *Trapa natans* in a (thermophilous) distribution type named "Trapa-Typ". MÜLLER-STOLL and KRAUSCH (1959) have remarked, however, that, at least in Central, South and South-East Europe, *Nymphoides peltata* behaves like a "subatlantic", or, more exactly, a "suboceanic" species. Its major occurrence there is in the upper course of the larger rivers near the sea, whereas *Trapa natans* and *Salvinia natans* — comparable to *Trapa* — show a subcontinental distribution. MÜLLER-STOLL and KRAUSCH are concluding that *Nymphoides peltata* is not so much thermophilous in the sense of needing warm summers, but indeed in not supporting cold winters. In fact, in North Germany and Poland the plant mainly occurs in the mouth of large rivers (HEGI 1935). On the Baltic coast, it even goes down right to the sea coast, e.g. in the "Haffs" (HEGI 1935, JESCHKE 1959), whereas on the German North Sea coast it is not found in the estuaries of the Ems and the Weser

(MEYER and VAN DIEKEN 1947), nor in that of the Elbe (CHRISTIANSEN 1953). This difference may be explained 1° by the insignificance of tidal movement on the Baltic coast, 2° by the low salt content of the Baltic compared to that of the North Sea.

It is remarkable, however, that *Nymphoides peltata*, in the lower course of the Elbe, although lacking in the very estuary, does not evade the interior tidal area, neither the fresh nor the brackish one (CHRISTIANSEN 1953, MÜLLER-STOLL and KRAUSCH 1959); it is thriving there in old river-beds, minor affluents and sheltered crooks and inlets.

Comparing this situation to that in Western Europe, *Nymphoides peltata* appears to behave here in an other way: it evades the waters with tidal movements and is retiring more inland, as well in the Netherlands as in Britain and atlantic France (see above). We get the impression, therefore, that, in the cooler summers of the atlantic region, summer temperature in shallow and relatively quiet waters probably satisfies the warmth requirements of the species in its vegetation period; however, this may be not the case in deeper waters subjected to ebb and flow. The critical minimum summer temperature may not be reached in the atlantic tidal areas. In fact, the isoamplitude of 15° C in Europe coincides with the Western limit of occurrence of *Nymphoides peltata* in tidal waters.

1. 1. 3. 2. *Water movement and bottom*

Field observation led to the impression that *Nymphoides peltata* occurred less frequently in the stagnant waters than in places with winter flooding. To testify this impression a survey was made in which the areas visited were grouped according to the type of water-movements (Table 1):

After this, a subdivision was employed according to the physical constitution of the water bottom, by means of which group I must be divided into 9 subgroups. It is directly obvious from the table, that *Nymphoides peltata* occurs most of all in the river forelands with a clay bottom, and which are subjected to winter flooding. This does not imply however, that the plant prefers permanently flowing water. During the vegetation period, in fact, the foreland-waters are simply stagnant water, even though a number of them have an open connection with the river. They are flooded only in the winter months and then are "flowed through" temporarily in many cases as well.

We will now examine the behaviour of *Nymphoides peltata* in each of the areas mentioned above.

1. 1. 3. 2. 1. *Ecotope with stagnant waters, rarely or never flooded* (Es)

By examining Table 1 (column 1) it appears that *Nymphoides peltata* hardly occurs in the never or rarely flooded forelands (area of the Maas) and in old river-beds which have no connection with a river and receive water only from the vicinity and as a result of rainfall. If the vicinity consisted of sand, river "loam", estuary silt-, salty peat-,

Table 1

Survey concerning the occurrence of various plant species in open water (Potamion) in connection with water movements and nature of the soil in the surroundings.

Water movement	I. Ecotope with stagnant water — rarely or never flooded (Maas) ↓										II. Ecotope with at times water movement in connection with the river		III. Ecotope with tidal movements	
Nature of the soil in the surroundings	sand	sand	sandy clay	"loam"	clay	clay	clay	peat with clay	sea clay	total stagnant water	clay	clay	clay	
	most sandy soils	inland dune sand	river levée soils	river "loam" soils	river foreland clay soils	Zuyder Sea coastal clay soils	estuary silt soils	salty peat soils	marsh silt soils		river foreland clay soils	river foreland clay soils	river foreland clay soils and estuary silt soils	
number of areas	1	1	15	10	10	1	3	2	3	46	52	14	13	
occurrence of the plant	p a	p a	p a	p a	p a	p a	p a	p a	p a	p a	p a	p a	p a	p = present a = absent
Nymphoides peltata	0 1	0 1	9 6	0 10	5 5	1 0	0 3	0 2	0 3	15 31	*39 13*	*14 0*	4 9	Faithful species of the *Limnanthemo-Potametum pectinati*
Potamogeton perfoliatus	0 1	1 0	3 12	0 10	1 9	1 0	0 3	0 2	0 3	6 40	3 49	4 10	6 7	
Potamogeton pectinatus	0 1	0 1	1 14	0 10	0 10	0 1	0 3	1 1	2 1	4 42	9 43	7 7	4 9	
Nymphaea alba	1 0	1 0	8 7	9 1	6 4	0 1	0 3	0 2	0 3	25 21	23 29	6 8	1 12	Faithful species of the *Myriophylleto-Nupharetum*
Potamogeton lucens	1 0	1 0	6 9	1 9	2 8	0 1	0 3	0 2	0 3	11 35	*40 12*	*12 2*	2 11	
Myriophyllum spicatum	0 1	0 1	5 10	0 10	3 7	1 0	0 3	0 2	0 3	9 37	10 42	4 10	1 12	
Nuphar luteum	0 1	1 0	11 4	6 4	6 4	1 0	0 3	0 2	0 3	25 21	*42 10*	*13 1*	5 8	Faithful species of the *Potamion eurosibiricum*
Polygonum amphibium	0 1	1 0	1 14	0 10	2 8	0 1	0 3	0 2	0 3	4 42	23 29	*11 3*	1 12	
Potamogeton natans	1 0	0 1	3 12	9 1	4 6	1 0	0 3	0 2	0 3	18 28	23 29	6 8	1 12	

or marsh silt soils (terminology of EDELMAN 1950), then the plant was never found at all. Only in stagnant waters over sandy-clayey river levée soils or river foreland clay soils it was found in 56 % of the areas examined. This result suggests some preference for fresh-water clay. The question arises as to why the plant is not found in the other 44 %. Under-mentioned survey is an attempt to answer this question. (Table 2).

From the description in this table of the nature of the old riverbeds, it appears that the plant's absence (except in M. 17, and the "break-through" pools of R. 27 and W. 48) is due to one of the following factors: the bodies of water in question are too small and shallow, are filled up with marsh-plants, or are overshadowed.

The fairly large pool near Hout-Blerick (M. 17) lies, it is true, in Holocene river-clay deposits, but the bottom is covered with a thick layer of peat, and in addition, this water is to a great extent over-grown with *Nymphaea alba*. Thus the absence of *Nymphoides peltata* here can be accounted for equally well by the peaty ground or the competition, but it is supposed that the first factor is the primary one.

The two open water channels near Maasbracht (M. 19) are also situated on holocene river-clay deposits, but we can account for the absence of *Nymphoides peltata* here by its geographical distribution in the first place. It has already been stated above that the plant was not seen in any of the old riverbeds visited upstream from Wychen; a fact not to wonder at, for the bottoms of nearly all these are covered with a layer of peat. Thus, although the habitat near Maasbracht is exceptionally suited, the cause for the absence of *Nymphoides* can be put down to a factor of inaccessibility. Why the plant was absent from one or two "break-through" pools near Lienden (R. 27) and in "the Wiel" near Tuil (W. 48) — no satisfactory explanation could be found.

We remember that *Nymphoides peltata* does occur in the remaining 56 % of the areas with stagnant water and a similar bottom-type, i.e., river-clay. This concerns stretches of water in five forelands of the Maas between Megen and Poederoyen and in nine river levée-areas of the Maas, Waal and Guelders IJssel. The plant was noticed here only in small groups. Only in the Maas forelands near Empel (M. 22) and Poederoyen (M. 26), in the area of a small dyke-burst of an old riverbed in the river levée soil of the Doornwaard near Heusden (M. 16), and in the Hoendernesterbeek near Zutphen (G. 84), a large abundancy was observed. The plant appeared again only sparsely in the Noorderdiep (G. 117), which is a long, broad and

Supplement to Table 1.

I. Areas with stagnant water, rarely or never flooded, and therefore normally not even in temporary connection with the river (Es).

II. Areas with, at times (episodical), water movements (Ee).
  IIa. Areas with winter flooding.
  IIb. Areas with winter flooding, and, in addition, in open connection with the river.

III. Areas with tidal (periodical) water movements (Et).

TABLE 2

Eleven areas with stagnant water, in rarely (or never) flooded foreland clay soils (f.c.s.) of the Maas and never flooded levée soils (l.s.) along the Maas, Rhine and Guelders IJssel, where *Nymphoides peltata* was absent.

no.	Waters	Bottom	pH	Cl	Depth	Type of river-bed
M. 17	Water South of Houtblerick	f.c.s.	6.2		shallow	relatively large pool with peat-bottom
M. 18	Wood South of Obbicht	f.c.s.	6.8			filled-in and grown over by wood
M. 19	Gulleys in "Grote Beemd" near Maasbracht	f.c.s.	7.2		<1.50 m	4 long, narrow gulleys, two filled in by Glyceria maxima
M. 20	Old riverbed near Reuver	f.c.s.	7.2		1.00 m	with Glyceria maxima filling the water
M. 25	Gully near "Zandplaat" and "Esmeer"	f.c.s.	7.5	110		marsh with two small waters
M. 14	"Balgoise meer"	l.s.	6.7[1]	40	0.40 m	narrow, very shallow watercourse
R. 27	Meander of the Rhine at Lienden	l.s.	7.5	60		narrow, shallow ditch, some shallow sheltered pools and deeps
R. 28	The Old Rhine between Aalst and Kesteren	l.s.	7.7	40		narrow, shallow ditch
R. 29	Old riverbed West of "Oude Haven" near Wageningen	l.s.				no open water
R. 30	The Strang at Opheusden	l.s.				no open water
W. 48	The "Wiel" at Tuil	l.s.	7.3	41	1.50 m	relatively large sheltered water

[1]) The levée-soil here is not calcareous.

relatively deep water course, once an estuary on the Zuyder Sea coast. This coastal clay soil type is poorer in calcium and more sandy than the river-clay. The plant was absent in an isolated water in the far South-West end of the Noorderdiep. For further details, see undermentioned Table 3.

This table only intends to suggest that *Nymphoides peltata* is not frequent in stagnant waters which are not in connection with the river, in contrast to its frequency in the areas with winter flooding, which are to be considered in the following section. If in the former habitat *Nymphoides peltata* occurs, than it is only on clay-bottom.

1. 1. 3. 2. 2. *Ecotope with stagnant waters, episodically flooded in winter and which in a number of cases are also in open connection with the river* (Ee).

From the examination of table 1 (column II) it appears that *Nymphoides peltata* was observed in 39 of the 52 river foreland areas subject to winter-flooding and in all 14 of similar areas which are moreover in permanent connection with the river, a total of 80 % of the cases. The bottom-type, river-clay, was the same in each case.

In the under mentioned Table 4 this situation in 39 waters is given in detail. If we compare the manner of occurrence according to these two tables with that given in Table 3, then *Nymphoides peltata* is not only frequent, but usually dominant, in areas subjected at times to water-movement. It appears that the interplay of environmental factors in such a habitat is optimal for the plant. We will return to such areas in a later chapter, and for the moment will only draw attention to the stretches of water given in column II of Table 1, where *Nymphoides peltata* was missing. Of these, seven were waters completely overgrown with a helophyte (*Glyceria maxima*), and two in addition were covered entirely with *Stratiotes aloides* and *Potamogeton* species. (The two waters were, more precisely, an old water-course North of Eck and Wiel and another in the Bovenpolder near Amerongen, both in the area of the Rhine).

In the remaining six cases it is doubtful whether the waters may really be considered to be part of the flood area of the related rivers. In some of them, for example, a layer of peat was found on the clay bottom, which might indicate the cessation of erosion by flowing water. (These areas were as follows: old riverbeds near Lexmond, Groot Ammers, Zuilinchem and an isolated water near Wilsum).

1. 1. 3. 2. 3. *Ecotope with tidal movements* (Et)

If Table 1, column III is examined, it appears that in 9 of the 13 examined areas, *Nymphoides peltata* was missing, which indicates a decreasing frequency. It did occur in the remnant of a meander near Hedel (M. 106), in the Krook near Slijkwel (M. 107), in a creek near Veen (M. 108) and in a smaller number in a creek near Poederoyen (M. 109). The rise and fall of the water here is on the average some 40 cm, so it is quite small. In this connection we must remark that

Table 3

Fourteen areas with stagnant water, in the rarely (or never) flooded foreland clay soils (f.c.s.) of the *Nymphoides peltata* occurs.

No.	Area	Bottom type	pH	Cl.
M. 21	Old Maas at Megen . . . . Surface 1000 × 100–150 sm	f.c.s.	7.1	22
M. 22	Remains of an ancient Maasmeander near Hedel . . . . . . (Easterly- and Westerly water)	f.c.s.	7.1	44
M. 23	"Hedikse Maas" near Haarsteeg . . . . Surface 1500 × 100 sm	f.c.s.	7.0	40
M. 24	Old creek in the Banwaard and Wijkswaard near Veen . . . Surface 200 × 40 sm	f.c.s.	7.2	72
M. 26	Water in the "Waarden" near Poederoyen . . . . Surface 200 × 25 sm	f.c.s.	7.0 7.2	44
M. 11	The Lake of Wychen near Wychen . . . . Surface 3000 × 100 sm	l.s.	7.0	44
M. 15	The Lake of Oss near Megen . . . . Surface 1000 × 80 sm	l.s.	7.2	70
M. 16	Gully in the "Doornwaard" near Heusden . . . . Surface 600 × 50 sm	l.s.	6.9	30
W. 47	"Ooyse Graaf" near Erlecom pool and ditch	l.s.	7.6	—
G. 78	"Barlose kolken" and Meander in the "Olsterwaard" near Olst Surface II: 1000 × 100 sm	l.s.	7.3	29
G. 79	"Schellerwade" near Oldeneel . . . . Surface 1000 × 100 sm	l.s.	7.3	33
G. 80	Old IJssel, along the Western edge of the "Oudendijkse polder" near Kampen . . . . Surface 160 × 60 sm	l.s.	7.2	60
G. 84	Old IJssel and "Hoendernesterbeek" near Zutphen	l.s.	7.0	28
M. 113	Old "Maasje" near Drongelen	l.s.	7.1	42

Maas and the never flooded levée soils (l.s.) along the Maas, Waal and Guelders IJssel, where

Depth	Type of area	Occurrence
1.30 m	large water; E-W, little open water, fairly sheltered from Western winds, peat-mud bottom	rare in South-East end In open water with Nymphaea
± 1.50 m in the middle fairly deep	largish Easterly water, 500 × 75 sm; in flow and outflow of water possible via a ditch, 1 m broad; fairly sheltered, E-W.	150 sm
	largish Western water, can join with Easterly water at high water, sheltered	occasionally
bank 1.50–2.50 m	large water, N.E.-S.W., in connection to the river via a ditch (a few km long). Unsheltered peat-bottom	few degree of coverage 1
shallow	water recently dammed from a creek, little open water; unsheltered	small groups
shallow	small water, E-W, open centre, unsheltered, clay-bottom	2 to 3 m broad strip at a depth of 1.50 m In centre Nymphaea
middle ± 2.00 m bank 1.20 m	very large stretch of water, temporary currents may occur, unsheltered	occasionally (water is cleaned at times)
1.00–1.50 m	largish water, N.E.-S.W., temporary currents possible, unsheltered, levée soil more clayey	a few small clusters
shallow near banks 0.50–1.20 m	largish water, N.W.-S.E., in the middle a dyke break-through water. Sheltered. Sandy clay-bottom.	regularly in vegetation of Polygonum amphibium at a depth <1.00 m (vegetative). In dyke breakthrough water abundant (flowering)
10 m	dyke break-through water	Sparsely, near bank at 1.20 m, degree of coverage 2
1 m	ditch, unsheltered	at one place at 0,45 m, degree of coverage 2
fairly deep (in S.W. shallow)	large water, S.W.-N.O., fairly sheltered, sand-bottom	rare, in S.W.
shallow	large water, S.E.-N.W., fairly sheltered, locally peat-bottom	sparsely in N.W.
shallow	small water, N.N.E.-S.S.W., covered with floating plants, sheltered	occasionally
shallow	small water, 100 s. metres, formerly dug out, now shut in swamp plants, sheltered	dominant (with Nymphaea)
shallow	irrigation canal, fairly sheltered	scattered, observed at depth >1.00 m, coverage 2.
deep	3 km long and 25 m wide stream, E.-W., unsheltered	sparsely

TABLE 4

Thirty-nine areas with stagnant water in

No.	Area	pH	Cl.
R. 33	The two old "Rijnstrangen" near Pannerden (Herwen and Aerdt) Northern strang	6.9/7.0	
R. 34	Southern strang	7.3	
R. 36	The "Strang" at Huissen	7.3	60
R. 37	Old riverbed near the "Looveer" near Huissen	7.3	76
R. 38	Old riverbed near the "Renkumseveer" (Heteren)		
R. 44	The "Kil and Kilsloot" near Amerongen	7.3	48
R. 45	The "Roodvoet" near Rijswijk (Maurik)	7.4 7.5	
W. 49	Old Waal near Kekerdom (Ubbergen)	7.3	
W. 51	The "Strang" in "Sophia's Kamp" near Ooy	7.1	32
W. 52	The Old Waal at Nijmegen	7.1	56
W. 53	The "Zeumke" at Nijmegen	7.0	88
W. 54	The "Strang" at Bemmel	7.5	44
W. 55	The "Zandkolk" at Oosterhout (Valkenburg)	7.2	
W. 56	The "Strang" in the "Loenense buitenpolder" (Valburg)	7.2	96
W. 58	The "Strang" and the "Weversgat" near Turksweerd (Druten)	7.5	40
W. 59	The Old Waal East of Ochten (Echteld)	7.1	88
W. 60	The Hoek of the "Lange Krib" near Ochten (Echteld)	7.1	104
W. 61	The "Strang" and the "Bovenstrang" near Hien (Dodewaard)	7.3	80
W. 62	The "Kil" at Ooy (Echteld)		
W. 63	Old riverbed South-West of Tiel		
W. 64	The "Kil" of Tiel	7.3	52
W. 65	Old riverbed South-West of Wamel	7.1	76
W. 66	The "Kil" of Hurwenen (Hurwenen and Zaltbommel)	7.5	41
W. 67	The "Kil" of Waardenburg (Waardenburg)	7.3	41
G. 81	"Vreekolk" and surroundings (Steenderen)	7.3	40
G. 83	The "Lamme IJssel" (Angerlo and Doesburg)	7.3	36

river forelands subject to flooding in winter

Depth in m	Bottom	Occurrence
1.00–1.50	fine clayey, often somewhat peaty	alternately dominant with Nuphar
1.00–1.50	ditto	
± 3.00	centre very muddy, at the sides stiff clay	in Sparganium zone
shallow	soft mud to stiff clay	common
shallow	stiff clay on the sides	present
2.00 or more	ditto	dominant
shallow	muddy sand. Wind exposed	fairly large amount
shallow	clayey-sandy	dominant over large stretches
?	clay	present in little open water
1.00–1.50	on the bottom thin mud, in places soft muddy clay, sticky in dry places	locally dominant
1.40	in the middle very muddy clay	abundant, with Nuphar dominant
1.00–2.00	sticky clay, sandy patches	abundant (Nuphar dominant)
1.75	very soft muddy clay, firm on sides	fairly frequent
>1.30	sides of clay	aspect-determining, abundant
>2.00	clay in Weversgat	present
4.25–1.65	soft muddy clay, banks firmer, one sandy patch	dominant
?	oily clay	dominant
centre 3.00–3.50 bank 1.00–1.25	stiff clay, locally very hard; very soft in the middle	fairly common
?	clay	present (cleaned)
max. 1.00 m	clay	dominant in a narrow strip of plants
2.00–2.50	stiff clayey	dominant in shallower zone
?	sandy clayey	dominant in 5 m broad zone
centre 6.00 m	clayey-sandy banks	locally common
± 1.00	clayey-sandy	fairly common
?	clay, begin of peat	present
fairly deep	clay, little sand	present at only one place

TABLE 4

No.	Area	pH	Cl.
G. 85	The "Blanke Hank" and other waters near the castle Nijenbeek (Voorst)	7.0	39
G. 88	"Strang" near Herkelo (Zwollerkerspel)	7.5	37
G. 95	Old riverbeds in the "Hengvorden- and Olsterwaarden" (Olst) . . .	7.5	42
G. 94	"Munnikenhank" (Diepenveen)	7.0	44
G. 82	"Rhedense Laak" (Rheden)	7.3	24
G. 86	"Hank" at Welsum (Olst)	7.2	72
G. 87	"Scherpenzeelse Hank" (Wijhe and Olst) . . . . Ditto, small water	7.5	50
G. 89	"Hank" near Zalk (IJsselmuiden)	7.2	56
G. 91	Old riverbed in the "Spankerense weilanden" South-West of the castle "the Gelderse toren" (Rheden)	7.2	38
G. 92	Waters in the "Waarden" near Wilp	7.4	44
G. 93	Old riverbed in the "Ossenwaard" (Deventer)	7.2	62
G. 96	"Barlose kolken" and meander in the "Olsterwaard" (Olst)	7.3	70
G. 97	"Hank" near Veessen (Heerde)	7.6	38

the absence of the plant further West is not a result of the horizontal and vertical movement of the water alone. Other environmental factors also under the influence of tidal movements may play a part here; the water is generally colder there, which is itself an unfavourable circumstance for a thermophile species, and the chlorine content of the water may also be a factor of importance in the lower tidal areas (see page 189).

1. 1. 3. 3. *Statistical control of the results obtained*

From the observations above we have obtained a provisional picture of the behaviour of *Nymphoides peltata* with respect to the two habitat factors water-movement and bottom-type. The impression is gained, that this plant prefers areas of water with a river-clay bottom, which are, as a result of inundation in the winter, subject to movement of the water, or which, in some cases, stand in open connection with the river. This may be thus explained that, outside the vegetation

(*continued*)

Depth in m	Bottom	Occurrence
?	oily clay	present
1.50	clay with peat	present
?	clay with sand	in shallower zone around the centre; otherwise mainly in the extreme ends
shallow	sandy-clayey	in one of the extremities (10 sm)
?	clay, locally sand	locally, at the landside from Sparganium-vegetations; fairly regularly in open water
?	clay	in the less-sheltered Grote Hank more common than in the Kleine Hank
?	clay	especially in extreme ends
?	clay	8 × 20 sm dominant
1.20–1.50	clay with a little sand	sparsely
?	oily clay	fairly common on South-East bank and landside of zone of Glyceria maxima
1.00	clay	locally a few fields
?	clay	after Nuphar the most frequent
± 1.00	sandy clay	present in open water
?	clay	present; dominant in some places

period, the water in these old riverbeds is replenished with consequent erosion of the bottom, while in some cases a permanent replenishment of the water is possible, due to the connection with the river, within the vegetation period as well. In the latter case, *Nymphoides peltata* occurred in the greatest abundancy (see page 184, "open water and abundance").

In the above chapter we have also given percentages concerning the occurrence of this limnophyte in areas with a difference in water-movement. Thus, in one ecotope (Es), consisting of stagnant waters over river levée soils and river foreland clay soils, the occurrence was 56 %, while in another ecotope (Ee), consisting of waters subjected to winter-flooding on river foreland clay soils, the occurrence was 80 %. The percentage differences are not always so obvious and very often an uneven number of areas are compared, for example 25 areas in the first ecotope and 66 in the second.

To prevent any doubts as to the exactitude of the differences, we have used the test of contingency. An example follows, using the situation mentioned above.

	Ecotope Es 25 stagnant waters on a river-clay bottom	Ecotope Ee 66 waters, at times subjected to water movement on a river-clay bottom	Totals number of waters
number of times species present	$x = 14$ (56 %)	53 (80 %)	$a = 24$
number of times species absent	11	13	$n{-}a = 24$
total number of bodies of water	$n_1 = 25$	$n_2 = 66$	$n = 91$

Explanation of the symbols used above, which will also be employed directly in formulae:

n – total number of bodies of water in both ecotopes: 91
a – total number of times *present* in both ecotopes: 67
n–a – total number of times absent in both ecotopes: 24
n_1 – number of bodies of water in ecotope Es: 25
n_2 – number of bodies of water in ecotope Ee: 11
x – number of times present in Es: 14

The formulae used are:

$$\mu = \frac{an_1}{n} \qquad \sigma = \sqrt{\frac{a(n-a)\,n_1 n_2}{n^2(n-1)}} \qquad Z = \frac{|x-\mu|-0{,}5}{\sigma}$$

In the last equation, only the absolute value of (x—μ) is calculated, which means that a negative result is finally reckoned as a positive.

$$\mu = \frac{an_1}{n} = \frac{67{,}25}{91} = 18{,}41. \qquad \sigma = \sqrt{\frac{a(n-a)\,n_1 n_2}{n^2(n-1)}} = \sqrt{\frac{67.24.25.66}{91.91.90}} =$$

$$= \sqrt{3{,}5560} = 1{,}89$$

$$Z = \frac{|x-\mu|-0{,}5}{\sigma} = \frac{|14-18{,}41|-0{,}5}{1{,}89} = \frac{3{,}91}{1{,}89} = 2{,}07.$$

The value of P when $Z = 2{,}07$ is then looked up in a table (probability-integral I and bilateral exceedence of chance P, for the normal distribution $\mu = 0$ and $\sigma^2 = 1$).

If P is now $\leqslant 0{,}05$, as is here the case, there is a significant difference, that is, in the survey given above *Nymphoides peltata* is indeed showing preference for ecotope II.

If $P > 0{,}05$, we may not draw conclusions that a difference is being shown. This value ($P > 0.05$) was in fact obtained, when we compared the occurrence of the plant in the river-clay areas of ecotope Es (56 %) with that in the river-clay areas in a part of ecotope Ee (75 %), where the waters in open connection with the river were not taken into account. In this case, P had a value of 0.159, thus larger than the value mentioned above — 0,05. This proved the necessity for the use of the hypergeometric distribution, because one would expect to be allowed to draw conclusions from the percentages 56 and 75.

There is no sense in using the equation, if the totals involved are the results of a small number of observations, and for this reason it is not possible to compare the occurrence of *Nymphoides peltata* in the ecotope with stagnant waters with respect to the different types of bottom. It was possible, on the other hand, to compare the 25 areas with river-clay bottom from this ecotope with 13 areas having another bottom type (omitting the areas with estuarine or sea-clay types). The hypergeometric distribution gave a value for P in this case of 0.012, i.e. less than the value of 0.05. From this the preference of *Nymphoides peltata* for clay ground appeared once more. Other factors, however, must not be forgotten; geographical distribution was given as the cause for the absence of *Nymphoides peltata* on silty bottoms, for example.

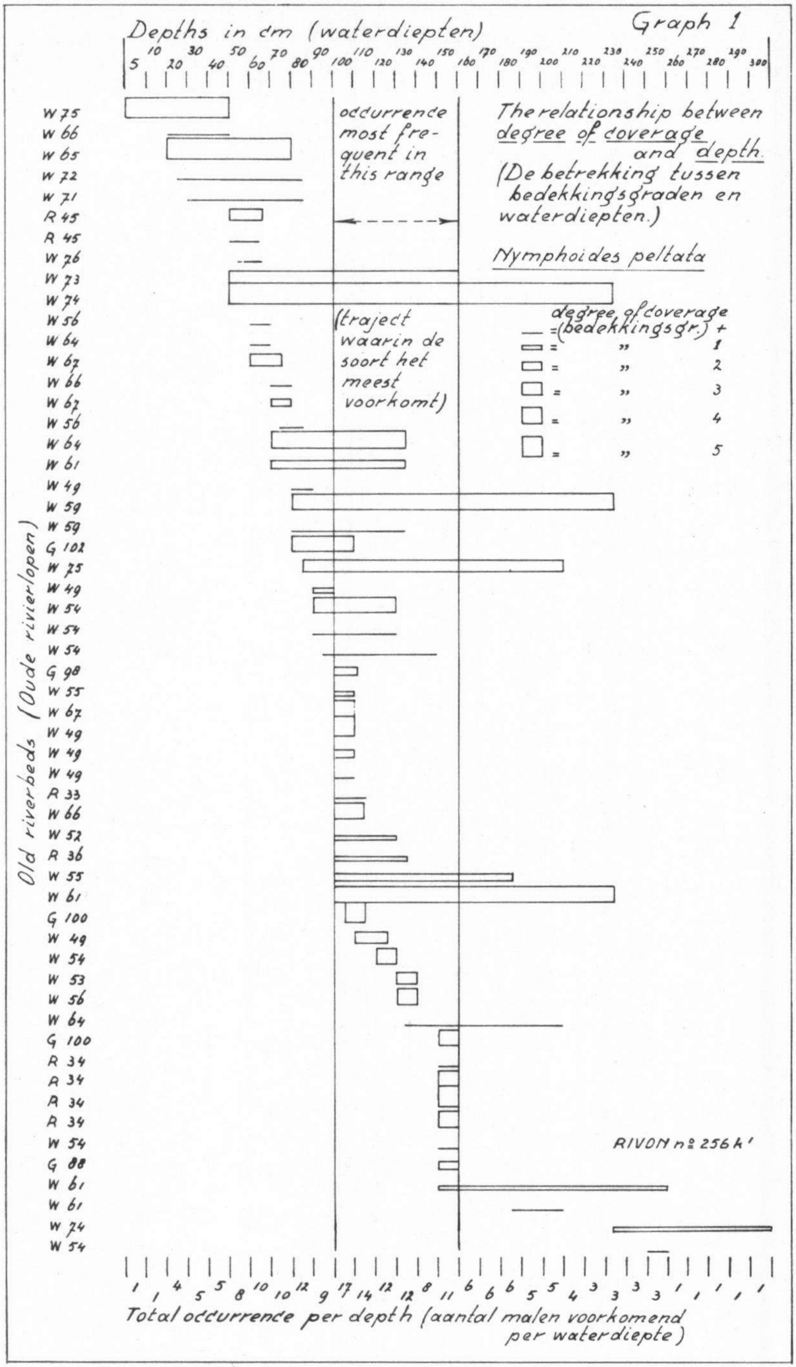
The test of contingency has been used in the following study of the autecology of the other limnophytes, and conclusions have been drawn in the same manner as to the difference in behaviour in relation to environmental factors.

1. 1. 3. 4. *Depth of water and degree of coverage* (see graphs 1 and 2)

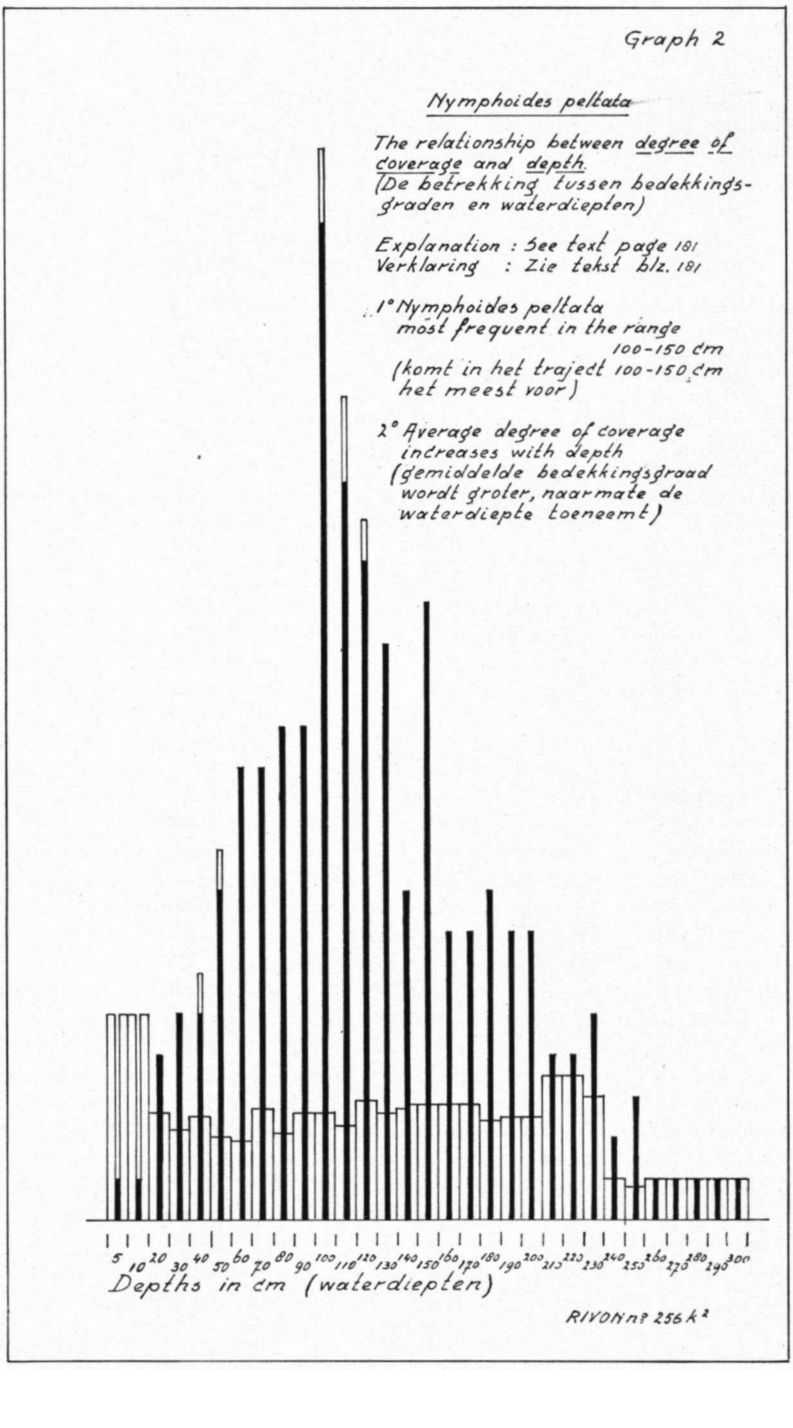
Whenever possible, a number of vegetation records (using the method of Braun-Blanquet) of the different areas were made in open water. The abnormally high water-level in the summer of 1956 was a handicap in this work, as was the difficulty in many cases of arranging for boats. In graph no. 1, the degrees of coverage are plotted against the depth of water, and from this appears that *Nymphoides peltata* is most frequent in water between 1.00 and 1.50 m deep, although a high degree of coverage can also occur in both deeper and shallower waters. Under 3.00 m deep no investigation was put out. According to MEYER and VAN DIEKEN (1947) the plant occurs in water to a depth of 1.50 m.

In graph 2 the data have been treated in another way — here every depth of water has three columns. That in the middle gives the number of times that the plant occurred with a given depth of water. The two outer columns both give the number obtained by the sum of the cover degrees in the survey of a given depth of water, divided by the number of times that the plant occurred at this depth (average cover degree).

By this representation it appeared not only that *Nymphoides peltata* occurred most in depths of water from 1.00–1.50 m deep, but also that the average cover degree becomes larger as the depth of water increases.



Depths in dm (waterdiepten)
Graph 1
5 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230 240 250 260 270 280 290 300
occurrence most frequent in this range
(traject waarin de soort het meest voorkomt)
The relationship between degree of coverage and depth.
(De betrekking tussen bedekkingsgraden en waterdiepten.)
Nymphoides peltata
degree of coverage =(bedekkingsgr.) +
= " 1
= " 2
= " 3
= " 4
= " 5
Old riverbeds (Oude rivierlopen)
W 75
W 66
W 65
W 72
W 71
R 45
R 45
W 76
W 73
W 74
W 56
W 64
W 67
W 66
W 67
W 56
W 64
W 61
W 49
W 59
W 59
G 102
W 75
W 49
W 54
W 54
W 54
G 98
W 55
W 67
W 49
W 49
W 49
R 33
W 66
W 52
R 36
W 55
W 61
G 100
W 49
W 54
W 53
W 56
W 64
G 100
R 34
R 34
R 34
R 34
W 54
G 88
W 61
W 61
W 74
W 54
RIVON nº 256 k'
1 1 4 5 5 8 10 10 12 9 17 7 14 12 12 8 11 6 6 6 5 5 4 3 3 3 3 1 1 1 1 1
Total occurrence per depth (aantal malen voorkomend per waterdiepte)


Graph 2
Nymphoides peltata
The relationship between degree of coverage and depth.
(De betrekking tussen bedekkingsgraden en waterdiepten)
Explanation : See text page 181
Verklaring : Zie tekst blz. 181
1° Nymphoides peltata most frequent in the range 100-150 cm
(komt in het traject 100-150 cm het meest voor)
2° Average degree of coverage increases with depth
(gemiddelde bedekkingsgraad wordt groter, naarmate de waterdiepte toeneemt)
5 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230 240 250 260 270 280 290 300
Depths in cm (waterdiepten)
RIVON nº 256 k²

1. 1. 3. 5. *Open water and abundance*

Since in *Potamion*-vegetation only a limited number of "relevés" (quantitative sample plot records) could be made, the circumstantial descriptions from the field investigation were used to obtain a corroboration of the above. A valuation number was given as a measure of the size of the bodies of water without dense vegetation, or at most, submerged vegetation, where *Nymphoides peltata* occurred in the areas subjected to episodic movement of the water. These valuation numbers, between 0 and 5, were specified as follows:

Mostly open water:	5
Much open water in the middle:	4
Less open water in the middle:	3
Little open water in the middle:	2
Generally little open water:	1
No open water, because surface of the water was grown over by floating vegetation:	0

Independently from these, the occurrence of *Nymphoides peltata* in these areas was also given values from 0–5 specified as follows:

Dominant and conspicuous — usually as a long broad fringing zone around the centre:	5 or 4
In the fringe zone around the centre locally dominant:	3
Smaller groups, still regularly occurring:	2
Occasional or infrequent:	1
Absent:	0

The two values were then compared and written next to each other per area. They appeared in 78 % of the cases to agree quite well. As a yardstick for this "quite well" the values must not differ more than by one unit. In other cases, the values differed by two or more, as given in the under-mentioned table 5 in which the conditions are indicated which may contribute to an interpretation of the difference. Four areas with a weak tidal movement, lower down in the table, are worth considering more closely.

If we compare the pool in the Hedelsewaard (M. 106) with that in Slijkwel (M. 107) and Poederoyen (M. 109) which all have much open water, then we see that the abundance of *Nymphoides peltata* falls off in the direction of the lower river course. It is reasonable that the conditions in this direction should become less favourable (deeper and cooler water with less mud). But the condition in the Kreek of the Banwaard near Veen (M. 108) conflicts with these three cases. It may still be possible to explain this, however, as the blind furthest end of the creek where *Nymphoides peltata* covers 50 % of the water surface has very likely been dug out recently. In addition, the horizontal movement of the already weak tide is further lessened by a dense growth of *Phragmition*-vegetation. Since the vertical water movement is small too, the deposition of mud is favoured with the turn of the tide. Finally, it can be expected that the temperature of the water in this creek, because of its shallowness, sheltered position and weak current,

TABLE 5

Interpretation of cases in which the rate of occurrence of Nymphoides peltata did not coincide with the rate of density of submersed vegetation.

No.	Area	Value for degree of openness of the water	Value of occurrence for Nymphoides peltata	Circumstances which may aid in interpreting the difference
	Flooded in winter and not *in open connection with the river.*			
R. 36	The "Strang" at Huissen	4	1	Nymphaea alba dominant
W. 51	The "Strang" in "Sophia's kamp" at Ooy	1	3	uncertain
W. 58	"Weversgat" at Turksweerd	4	2	much Nuphar
	"Strang" at Turksweerd	4	0	narrow and probably too shallow (1.00 m)
W. 62	The "Kil" at Ooy (Echteld)	4	1	Potamogeton natans dominant
G. 83	The "Lamme IJssel" (Angerlo and Doesburg)	4	1	too shallow?
G. 95	Old riverbeds in the "Hengvorden" I	3	1	much Potamogeton lucens in the middle
	and "Olsterwaarden" (Olst) IV	4	2	much Nuphar; Nymphoides only in the ends of the water
G. 94	"Munnikenhank" (Diepenveen)	4	1	cleaned for fishing?
G. 86	"Hank" at Welsum (Olst)			at one place between Scirpeto-Phragmitetum and Nuphar, with Nymphaea
G. 92	Waters in the river-forelands at Wilp	1	3	between Scirpeto-Phragmitetum and bank; in middle Nuphar
G. 96	"Barlose kolken" and a meander in the "Olsterwaard" (Olst)	4	1	in open water nearly no waterplants; too deep?
	Flooded in winter and in open connection with the river.			
G. 98	"Dierense Hank" (Dieren and Angerlo)	4	1	Nymphaea, Nuphar, Potamogeton species, all unfrequent; too deep?
G. 99	Hank at Veessen (Heerde)	1	4	little Nuphar
M. 106	Remains of an old Maasmeander at Empel and Hedel	5	3	weak tidal-movement
M. 107	Krook at Slijkwel	5	2	ditto
M. 108	Old creek in the "Banwaard" and Gully near "Wijksewaard"	1	4	ditto
M. 109	Gully near "Wijksewaard", the "Zandplaat" and "Esmeer" (Poederoyen)	5	1	ditto

is higher than in the other three cases, where these conditions are not so in force.

It appears further that *Nymphoides peltata* in many cases is dominant or aspect-determining in areas with a depth of 2 m and more in the centre, which is apparently more than in N.W. Germany (MEYER and VAN DIEKEN 1947). Possibly therefore, the limiting environmental factor is the depth and not the water movement. It is probable however that the greater depth is a result of stronger water movements, which is then an indirect environmental factor. Under these conditions the plant forms a broad fringe around the open water. This was the case in the following former riverbeds in the forelands of the Waal: Strang near Bemmel (W. 54), Zandkolk near Oosterhout (W. 55), the Weversgat near Turksweerd in the community of Druten (W. 58), Bovenstrang near Hien (W. 61), Old Waal East of Ochten and the Hoek of the Lange Krib near Ochten (W. 59 and 60) and the Kil near Ophemert (W. 74). This agrees with the conclusions drawn from graph 2, showing that the degree of coverage increases with the depth of water, which means, in addition, that the plant presents an optimum growth in *open* water *about 2 m deep.* In river forelands with winter flooding (table 1, column IIa) the plant was given a value of 4 or 5 in 25 % of these areas and the same values were given in 55 % of the cases where the river forelands had winter flooding and stood in open connection with the river (table 1, column IIb). Following the result obtained by the method explained above (test of contingency) the percentages given do in fact indicate a difference. The species has thus a preference for areas standing in *open* connection with the river which are flowed through episodically and which possess, as a result of erosion, a depth of 2 m or more. Such conditions appeared most frequently in the Waal area, which explains why *Nymphoides peltata* occurred there in such a striking way.

pH / Bottom-types	6.9	7.0	7.1	7.2	7.3	7.4	7.5	7.6
I. river levée soil	1	2	1	2	2			
river foreland clay soil . . .		1	2	2				
Zuyder Sea costal clay soil					1			
IIa. river foreland clay soil . . .	1	3	5	6	12	2	6	1
IIb. ditto . . .	1	4	3	2	2		1	
IIc. ditto . . .			2	1	1			
Number of times .	3	10	13	13	18	2	7	1 (total 67)

1. 1. 3. 6. *Other environmental factors*

1. 1. 3. 6. 1. *Acidity*

The question arises whether the acidity of the water has any influence on the distribution of *Nymphoides peltata*. The survey above indicates *the number of times that Nymphoides peltata occurred at a given pH*, distributed over areas with or without water movements and various bottom-types.

Within these 67 observations, the plant occurs most frequently at pH values of 7.0–7.3, with a culmination at 7.3.

The following survey indicates *a given pH value as it occurred in one of the areas* without water-movements and with a given bottom type.

Bottom-type / pH	6.9	7.0	7.1	7.2	7.3	7.4	7.5	7.6
I. river levée soil . . .	1	1						
river foreland clay soil			1	1				
Zuyder Sea coastal clay soil								
IIa. river foreland clay soil	1	1	4	4	8	2	3	1
IIb. ditto	1	3	3	2	1	–	1	–
IIc. ditto			2	1				
Number of times	3	5	*10*	*8*	*9*	2	4	1

From this it appears that the pH values of 7.1–7.3 occur mostly in river foreland clay soils (river-clay areas). Since a connection between the bottom-type and the pH is obvious, it is no longer necessary to see the relations "occurrence of plant–bottom type" and "occurrence of plant–pH" as separate ones. The environmental factors of bottom-type and acidity are correlated.

So far we have considered only the relation between pH and the presence of *Nymphoides peltata*. An investigation was made therefore to see how far the cover degree of the plant showed an optimum in a given pH range.

It appeared from the records that the degrees of coverage 3, 4 and 5 occur as follows: (p. 188).

It will be seen that the rate of dominance shows a definite peak at a pH of 7.3. The impression is, then, that the ecological amplitude refered to the pH factor is smaller by "abundant" to "dominant" occurrence than is if considering arbitrary quantitative records. However, this number of 18 suitable observations is much smaller than the 67 observations on page 186 concerning the occurrence of the plant in arbitrary quantities. So this smaller amplitude is perhaps not significant. This may be examined as follows:

pH	number of times
7.6	0
7.5	2
7.45	1
7.4	0
7.3	$\boxed{6}$
7.2	2
7.1	3
7.0	3
6.9	6
	18

From the descriptions of the areas where a value was given to the species on the base of a rough quantitative estimation only (see page 184) the following was found for the values 3–5:

pH	number of times with value 3–5
7.6	1
7.5	3
7.45	1
7.4	1
7.3	$\boxed{7}$
7.2	$\boxed{5}$
7.1	$\boxed{8}$
7.0	4
6.9	1
	31

By this way the number of cases (31) to deal with is larger than in the case of considering the very sample plot records only. By the former way the pH optimum appears to be extended over a range of 7.1–7.3, which is rather similar to the dates obtained in considering the occurrence arbitrarily.

The impression is gained here that the connection between occurrence and this pH range (in the "abundant" to "dominant" classes) is stronger than in the case of arbitrary values; but the latter is concerned with more than twice as many cases (67). If we use the test of contingency (see page 180) this stronger connection appears to be not significant. With this data it is not possible to state with certainty whether *Nymphoides peltata* is, in connection with pH, a "presence-indicator" or a "frequency indicator", using both terms in the sense employed by D. M. DE VRIES (1953). Another question is whether from the preference of the plant for the pH range 7.0–7.3 a preference for areas of certain river-beds can also be inferred. In the survey below, the occurrence of a given pH is given numerically per river-area:

pH / River	6.9	7.0	7.1	7.2	7.3	7.4	7.5	7.6	7.0–7.3
Maas	2	3	4	4					11
Waal		2	8	5	6	0	3	1	21
Guelders IJssel .	2	5	0	6	7	3	5		18
Rhine.		1	0	3	6	3	0		10

We see that the values 7.0–7.3 occurred in the Maas, Waal, Guelders IJssel and Rhine areas 11, 21, 18 and 10 times respectively. Seemingly these totals indicate differences, particularly if one compares the totals of the pH values 7.0–7.3 from the Maas and Rhine (21) with those from the Waal and Guelders IJssel (39). Yet the test of contingency shows no real difference. In this way therefore no preference can be shown for *Nymphoides peltata* for the Waal and Guelders IJssel areas where the plant seems to occur most frequently.

We note here that the pH may vary through the year as a result of the developing vegetation in the water and effects from the surroundings (fertilizers, pasturing) which may cause differences of 0.1 or 0.2.

Furthermore the pH is a factor which works almost entirely indirectly — indeed, fairly high or low values are not toxic for the plant. Whenever the occurrence or absence of a species appears to be correlated with a given pH then it is possible to look for a cause-and-effect relationship in several directions, e.g. where two competing species, both with a large pH range overlap; the absence of one from a given sector of the range may be due to competition and not to the pH value as such (see Olsen 1923, Goedewaagen 1934 (erroneously published under the name of O. de Vries), D. M. de Vries 1940, Ellenberg 1953, 1954, 1956 and Knapp 1954). Care is therefore necessary in drawing conclusions in this matter.

1. 1. 3. 6. 2. *Chlorinity*

According to Heukels and Van Ooststroom (1956)*Nymphoides peltata* is salt-avoiding. In our own chloride measurements it was not possible to establish at which level of chlorinity the abundance fell off, or at which level the plant disappeared.

One must remember that, in the former riverbeds concerned, not only the chloride content increases and may thus have a limiting effect, but also other environmental factors such as water movement, depth and temperature — all of which may control development of the plant. "Salt-avoiding" is an elastic term and there is, rather, a combination of environmental factors to be considered, which hinder the occurrence of *Nymphoides peltata.*

How far the plant was present (or was absent) in 18 areas with a chlorinity of > 90 mg per l is to be seen in the following survey, which will not be further considered.

No.	Area	Watermovement	Cl, mg/l	Occurrence
M. 25	Gully near the "Zandplaat" and "Esmeer" (Poederoyen)	stagnant water	110	absent in small waters
R. 46	The "Kleine Lek" near Vianen	winter-flooding	96	absent in small waters, 1 metre deep
W. 56	The "Strang" in the "Loenense buitenpolder" (Valburg)	ditto	96	aspect-determining
W. 60	The "Hoek of the Lange Krib" near Ochten	ditto	104	dominant
G. 90	"Hank" at Wilsum (IJsselmuiden)	ditto	114	absent in 2 isolated waters, 1.00–1.20 m deep
W. 73	The "Kil" at Dreumel	ditto	96	vegetation-forming
W. 75	Old riverbed near Heerewaarden	ditto	96	occasionally dominant
W. 76	The "Weiwaardsgat" near Heerewaarden	ditto	92	locally dominant
G. 100	"Spoolderhank" (Zwollerkerspel)	winterflooding +open connection	106	locally dominant
G. 101	The "Koeluchtergat" (IJsselmuiden)	ditto	92	quite frequent
G. 102	"Hank" at Wilsum (IJsselmuiden)	ditto	112	aspect-determining
L. 104	"Binnen-Lek" along the island the "Bol" (Lopik)	weak tidal movement	110	absent, by ebb depth 1.00 m
M. 108	Old creek in the "Banwaard" and "Wijksewaard" near Veen	ditto	100	covering great surface
M. 109	Gully near the "Zandplaat" and "Esmeer" (Poederoyen)	ditto	102	little, along the banks
W. 111	"Bloemstrang" (Brakel)	tidal movements	113	absent, land drying on the ebb
W. 112	"Avelingerdiep" (Gorinchem-Hardinxveld)	ditto	124	not in deep water and not in 0.50 m deep ditch too
W. 116	The "Kooigat" and surroundings (Poortugal)	ditto	122	absent; as M. 115

1.1.4. Summary (1.1.1.–1.1.3.)

The limnophyte Nymphoides peltata is found not only in ditches, moats, canals and "break-through" pools, but *also in former riverbeds*. It occurs mainly whenever these riverbeds are also river-forelands which are flooded in winter, or better still, which are in open connection with the river (e.g. the Waal area). This means that the species is most frequent in *clay*, for erosion by water during the flooding ("running through") prevents the formation of peat. *Nymphoides peltata* occurs therefore least in stagnant waters without winter flooding and where the bottom is covered with peat or where the amount of nutrition decreases (river-"loam" areas of the Maas). It is less common as the influence of tide increases. The unfavourable factors here are probably the horizontal and vertical water-movements, the lower temperature of the water, the greater depth of water and perhaps also an increase in the salt-content, although the latter must be doubted somewhat in connection with the small number of observations that were carried out in the brackish areas. It is possible that in Western Europe there is a *smaller ecological amplitude with respect to the tidal movement* than in Middle Europe which might be, than, the reason why HEUKELS and VAN OOSTSTROOM (1956) called the plant "salt-avoiding". However, this may be due not so much to the factor of salt content than to the critical minimum summer temperature in atlantic tidal waters. A wider investigation on the lower reaches of the large rivers together with breeding and seeding experiments would probably give a decisive answer.

1.1.5. Relations to some companion species

Nymphoides peltata has been regarded as a faithful species of the *Limnanthemo-Potametum pectinati* (ALLORGE 1922). The other faithful taxa would be *Potamogeton perfoliatus* and *P. pectinatus* fo. *vulgaris*. It is outside the limits of this study to consider whether this association is present in the studied area; we will restrict ourselves to indicate how often the three mentioned taxa occur together.

From the examination of table 1, concerning the areas where the three taxa mentioned above were seen together or alone, it follows that in areas with winter flooding and open connection with the river — and also in the areas with a weak tidal effect — there was the greatest chance of finding the three taxa together. In nearly 59 % of the 82 areas concerned, *Nymphoides peltata* was found *without* the other two. In the remaining areas the plant was observed 7 times with *P. perfoliatus*, 9 times with *P. pectinatus* and 8 times with both. The latter occurred in the Roodvoet near Maurik (R. 45) along the Rhine in the Old Waal East of Ochten (W. 59), the Goldmine near Druten (W. 70), the Kil of Ophemert (W. 74), the old riverbed at Heerewaarden (W. 75) — all along the Waal and, in addition, the Strang at Herkelo (G. 80), along the Guelders IJssel and, finally, in the Krook at Slijkwel (M. 107) and in a creek at Poederoyen (M. 109), both on the Heusdens Maas. It is striking that six of the eight cases of combined occurrence were in the Waal area, where *Nymphoides peltata* occurs in such a high abundance in so many waters. From the sample plot records, it appears that *Nymphoides peltata, P. perfoliatus* and *P. pectinatus* appeared only together in the Roodvoet at Maurik in the Rhine area. In most cases both *Potamogeton* taxa were observed scattered over the various bodies of water.

A plant that was found regularly with *Nymphoides peltata* was *Nuphar luteum*. This plant too occurs mostly at a depth of about 1–1½ m.

If both plants are present, then competition or priority will arise. *Nuphar luteum* appears first and blooms in May, whereas *Nymphoides* appears later and blooms in July.

Now it is a striking fact that the optimal degree of coverage of *Nuphar luteum* lies at a water depth of 1.70 m. At a greater depth, the degree of coverage gradually decreases (graphs 5). In the case of *Nymphoides peltata*, however, the degree of coverage increases by a small amplitude at a depth below 2 m. From this, the conclusion can be drawn at this depth *Nymphoides peltata* is less disfavoured by competition and can therefore be *abundant in the deeper section of the water.*

1. 2. POTAMOGETON LUCENS L.

1. 2. 1. Distribution

The distribution of *Potamogeton lucens* covers nearly the whole of Europe. In Denmark, Lithuania it is less common, in the other Baltic countries fairly common; in South Sweden and further North to the 67th parallel it is to be found only locally (HULTÉN 1950). It is entirely absent in North-Scandinavia (HEGI 1935). In the Netherlands it is common (HEUKELS and VAN OOSTSTROOM 1956).

1. 2. 2. Habitat

Potamogeton lucens belongs to the Elodeids according to DU RIETZ (1930). These are limnophytes which root in the bottom and whose vegetative growth remains below water surface. *Potamogeton lucens* occurs in rivers, ponds and ditches (HEGI 1935), in canals (CLAPHAM, TUTIN and WARBURG 1952) and in large waterways and open bodies of water (HEUKELS and VAN OOSTSTROOM 1956). OBERDORFER (1949) reported the plant from stagnant or slowly streaming water, one to three or more m deep with high nutrition content and a mud bottom. It appears in company with *Nuphar luteum* also in old river-beds, according to the same author, especially in "den tiefen Schlammbuchten der Seen". In the latter biotope the plant is a faithful species of the *Potametum lucentis*, says Oberdorfer, and here it forms thick vegetative growths with other pond-weeds. HEGI (1935) and PASCHER (1936) found the plant as deep as 6 m in the Lake of Constanz, where it also formed extensive and thick growth. This great depth is, according to Pascher, a rarity, however. He states that the plant grows in water from 50 to 200 cm deep and seldom, as in the old riverbeds of the Rhine, from 300 to 400 cm deep. CLAPHAM, TUTIN and WARBURG (1952) further state that *P. lucens* grows on a basic mineral substrate, usually in hard water. TANSLEY (1949) found the plant in a moderately flowing section of the Thames above Oxford, where the sandy bottom is covered by a thin clay layer in the middle of the river. The submersed dominants in this plant community were *Sagittaria sagittifolia* f. *vallisneriifolia* and *Potamogeton perfoliatus*, while *P. lucens* was sub-dominant. Here *Nuphar luteum* presented submerged blades only. In the moderately to weakly flowing river above Cambridge, *P. lucens* was found with a large number of other submerged water plants — but it was, in fact, rarely abundant. In the "pond-like" river Lark where the flowing was about nihil and the bottom of mud, the plant was dominant, in company with *Nuphar luteum*, *P. natans* and *P. crispus*, all frequent. The plant was also found as dominant at another place in the Thames, with *P. pectinatus* as sub-dominant, and some other water plants as well.

Potamogeton lucens prefers a freshwater habitat. In comparing a number of Dutch broads and waters with different salt contents WESTHOFF (1959) stated that it was limited to fresh and oligohalinic waters (up to 1000 mg Cl per l). VLIEGER, in VAN ZINDEREN BAKKER (1942) states that the species occurs in the open water of the Naarderlake, especially at depths of 105 to 145 cm, and that it penetrates the open broads further inwards than *Nuphar luteum* and *Nymphaea alba* do.

1.2.3. Environmental factors

1.2.3.1. *Water movement and bottom*

In 46 areas with stagnant water, distributed over the bottom types of the region, *P. lucens* was observed occasionally in 11 waters only, and in only one case it was dominant — as can be seen from table 1, column 1. Furthermore, the plant was seen in only two of the 13 river-clay areas subjected to ebb and flow movements (see column II) and these were really habitats where the horizontal water movements were minimal, due to local circumstances.

The species was frequent and often abundant in 66 areas with stagnant water, given in the same survey in column II, which may be flowed through or temporarily inundated and which in a number of cases present an open connection with the river; all of them were situated on river clay, sometimes mixed up with sand. It occurred in 79 % of the 66 areas and was abundant in 56 % of the cases.

By using the same statistical method as in the case of *Nymphoides peltata* in the previous chapter, we have worked out whether the difference in percentage could lead to a definite conclusion. This was indeed the case, for *P. lucens* appears — just as *Nymphoides peltata* — to have a significant preference for an environment influenced by only temporary or weak water movements. This preference appeared in about the same degree (79 %) as in the case of *Nymphoides peltata* (80 %).

The plant's occurrence in the ecotope with stagnant waters (32 %) and in that with tidal movement (15 %), on a similar bottom type, was, in comparison to *Nymphoides peltata* in the same ecotope, somewhat lower (respectively 56 % and 30 %).

The following table summarises these percentages: (p. 194).

This suggests that *P. lucens* has a smaller ecological amplitude than *Nymphoides peltata*, as far as water movement is concerned, in that it is much less frequent in stagnant and tidal waters.

Ecotope / Species	Es 38 stagnant water (except in South Holland)	Es 25 stagnant water river clay only	Ee 66 episodical or weak water movements river clay only	Et 13 ebb and flow (tidal movements) river clay only
Potamogeton lucens	29 %	32 %	79 %	15 %
Nymphoides peltata	39 %	56 %	80 %	30 %

1.2.3.2. *Depth of water* (graphs 3 and 4)

According to the sample plot records, *P. lucens* was seen most in water between 100 and 110 cm deep and fairly frequently at depths of 50–140 cm. The depth of water, according to these data, varies between 10 and 300 cm, but it should be mentioned that no observations were made at greater depths. At depths between 40 and 300 cm the cover degree ranged from 3 to 5 and at depths from 80–300 cm the degree was 5. The greatest cover degrees (3–5) from the records appeared most frequently at a depth of 1 m. These records were from 5, 4, 2 and 8 localities in the Waal, Rhine, Maas and Guelders IJssel areas. The average cover degree however was highest at 150 cm.

The cover degree increased again between 210 and 300 cm. This is due to the fact that, at this depth, the larger floating plants are absent and competition is not so severe. From this and other facts it would appear that the species still develops well at depths greater than 3 m and perhaps even occurs optimally there (see description of habitat).

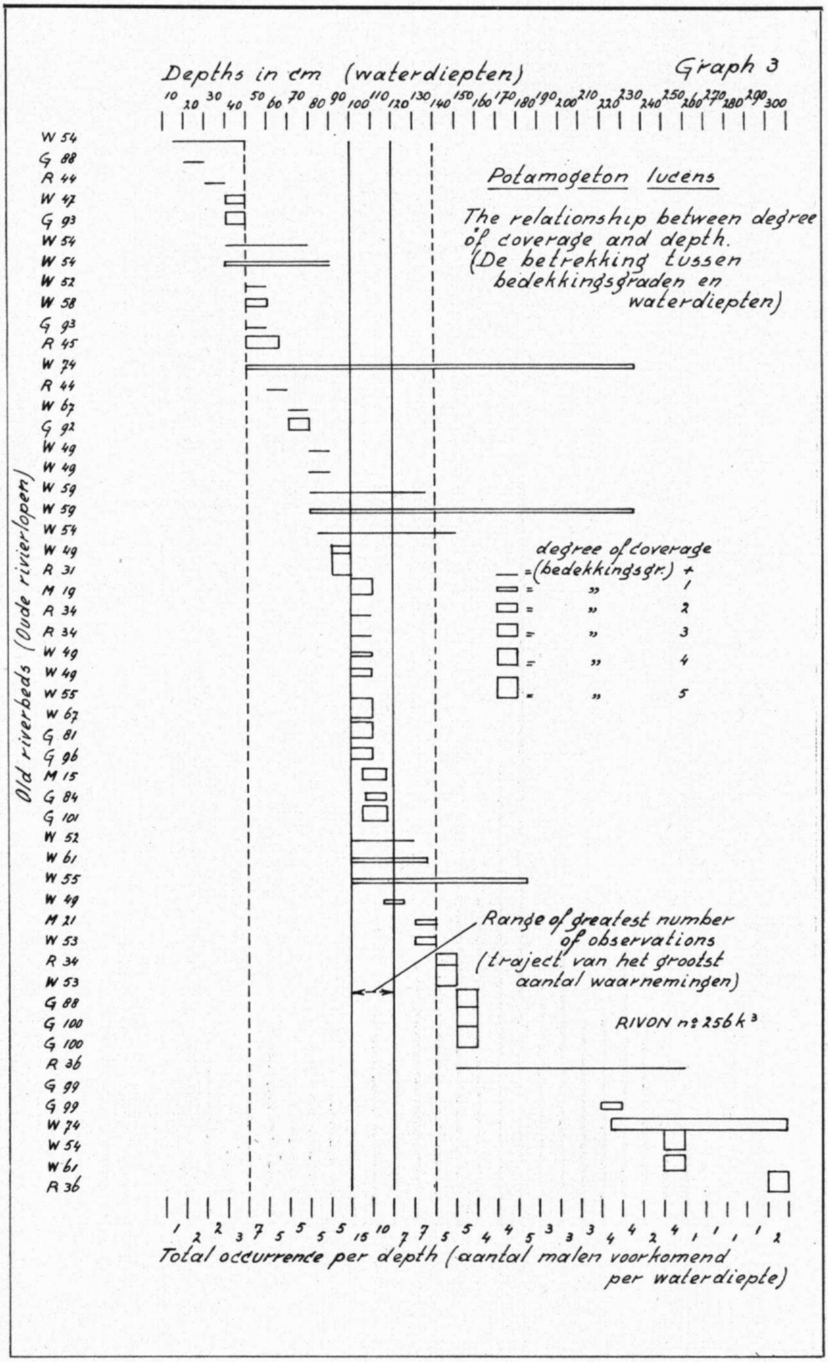
1.2.3.3. *Other environmental factors*

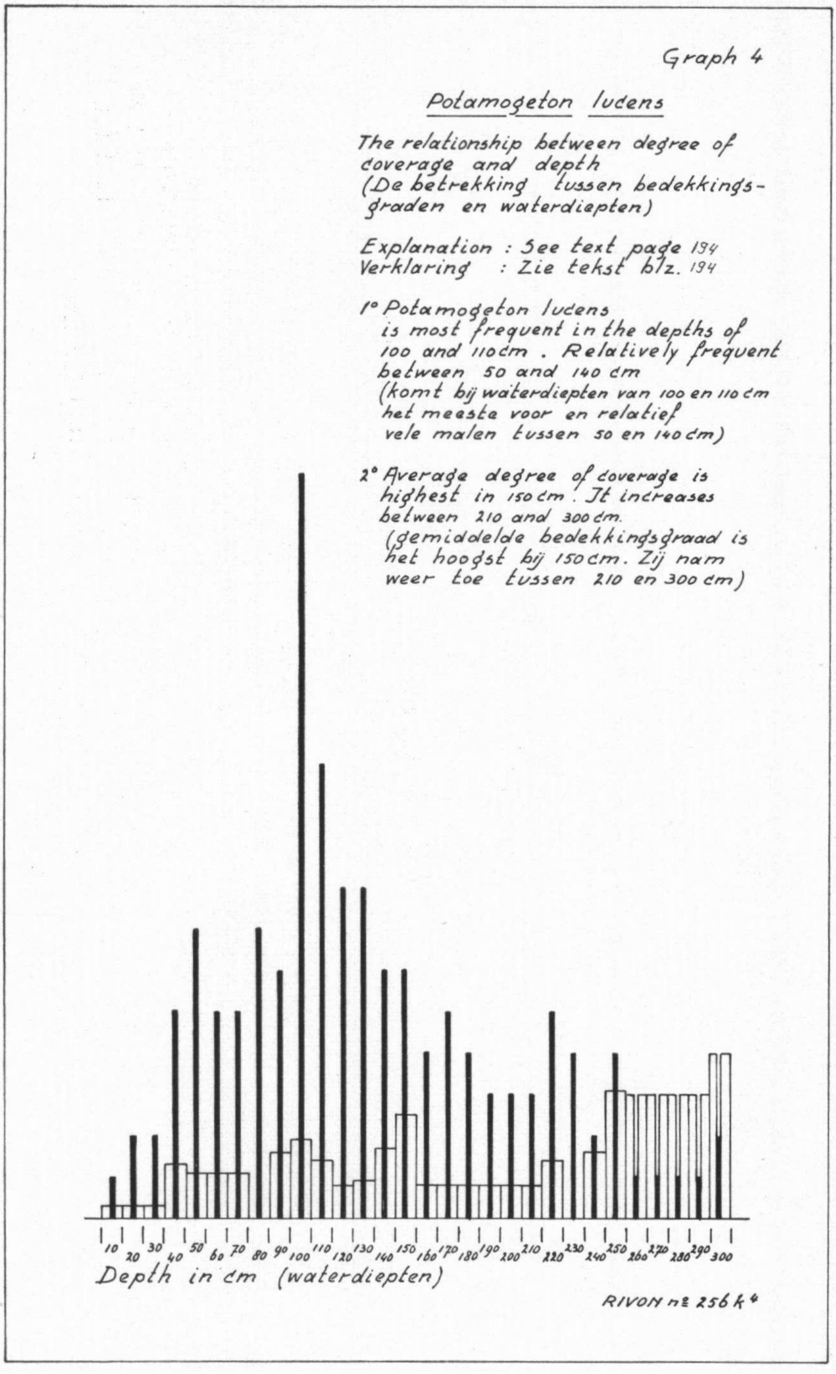
Potamogeton lucens behaved in the same way as *Nymphoides peltata* in relation to acidity. In the 18 areas mentioned in the chapter on *Nymphoides peltata* (page 190), *Potamogeton lucens* presented a lower abundance than *Nymphoides peltata* if the chloride content was higher than 90 mg/l. This observation might suggest that *Potamogeton lucens* has a lower tolerance of salt. There was an exception, however, in two areas in the Guelders IJssel, namely in the Spoolderhank (G. 100), with a chloride of 106 mg/l and in the Koeluchtergat (G. 101) with a content of 92 mg/l where the plant was still abundant at these concentrations.

1.3. Nuphar luteum (L.) Sm.

1.3.1. Distribution

Nuphar luteum has a distribution which stretches from North-Africa in the south to the 69th parallel in the North (Hegi 1935). In England the plant is common, less so in Scotland (Clapham, Tutin and War-


Depths in cm (waterdiepten)
Graph 3
Potamogeton lucens
The relationship between degree of coverage and depth.
(De betrekking tussen bedekkingsgraden en waterdiepten)
degree of coverage =(bedekkingsgr.)
Range of greatest number of observations (traject van het grootst aantal waarnemingen)
RIVON nº 256k³
Old riverbeds (Oude rivierlopen)
Total occurrence per depth (aantal malen voorkomend per waterdiepte)


Graph 4
Potamogeton lucens
The relationship between degree of coverage and depth
(De betrekking tussen bedekkingsgraden en waterdiepten)
Explanation : See text page 194
Verklaring : Zie tekst blz. 194
1° Potamogeton lucens is most frequent in the depths of 100 and 110 cm. Relatively frequent between 50 and 140 cm
(komt bij waterdiepten van 100 en 110 cm het meeste voor en relatief vele malen tussen 50 en 140 cm)
2° Average degree of coverage is highest in 150 cm. It increases between 210 and 300 cm.
(gemiddelde bedekkingsgraad is het hoogst bij 150 cm. Zij nam weer toe tussen 210 en 300 cm)
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230 240 250 260 270 280 290 300
Depth in cm (waterdiepten)
RIVON no 256 k4

BURG 1952), while in Norway and North-Scandinavia there are scattered habitats known (HULTÉN 1950). The plant is common in the Netherlands, although it is absent from the West-Frisian Islands and in North Holland North of the North Sea Canal. It is rare in Zeeland and the South Holland Islands (HEUKELS and VAN OOSTSTROOM 1956). Our own observations agree with those of the last two authors.

1.3.2. Habitat

Nuphar luteum belongs to the Nymphaeids, defined as by DU RIETZ (1930). These are limnophytes which root in the bottom and whose leaves float on the upper surface of the water. According to HEGI (1935), PASCHER (1936) and SCHMEIL-FITSCHEN (1951) this limnophyte occurs frequently in stilstanding or slowly flowing waters, in ponds, pools, marshes and old river-beds. CLAPHAM, TUTIN and WARBURG (1952) indicate the same habitats, which are also valid for Belgium. ROBIJNS (1955) adds to these bodies of water as deep as 5 m, while, according to him, *N. luteum* prefers a non-chalky bottom. OBERDORFER (1949) states that the plant occurs in rich (preferably deep) cool water where a mud bottom is found, but also in water poor in lime. TANSLEY (1949) found *Nuphar luteum* in the Thames above Oxford in moderately flowing water. The river bottom was of sand, covered with a thin mud layer. The plant grew there with submerged leaves in a mass of water-weeds, in obviously unfavourable circumstances for growth, but, in a bend of the same river with a thick mud bottom and a depth of 60 cm, the plant was dominant. Competition here was with *Nymphoides peltata*. *Nuphar luteum* was also found in slowly flowing water, although here it was not so abundant. In very slowly flowing — or nearly stagnant — water over a muddy bottom, the plant was frequent again. In the Netherlands the species is found in ponds, ditches and open water bodies (HEUKELS and VAN OOSTSTROOM 1956). It maintains for a long time after the succession from open water to closed vegetation, for example in areas of dense *Sphagnum* (VLIEGER in VAN ZINDEREN BAKKER 1942).

1.3.3. Environmental factors

1.3.3.1. *Water movement and bottom*

In 8 pools of stagnant water (Table 1, column I) in areas visited in South Holland islands, no trace of *Nuphar luteum* was seen, agreeing with the statements given above under distribution.

In 38 areas of stagnant water (table 1, column I) the plant was common independent on the differences in the bottom, appearing in 66 % of the areas. This is an importantly higher percentage than that of *Nymphoides peltata* (39 %) and *Potamogeton lucens* (29 %).

In the 66 areas of stagnant water, flooded in the winter (or flowed through) and in a number of cases in permanent open connection with the river (table 1, column II) this limnophyte appeared in 83 %

of the areas, which is a slightly higher percentage than that for *Nymphoides peltata* (80 %) and *Potamogeton lucens* (79 %).

Using the test of contingency, *no* preference in presence could be shown for either stagnant or episodical moving waters, whereas the statistical difference in abundance is significant indeed. *Nuphar luteum* proved to be abundant or dominant in 50 % of the river foreland waters flooded in winter, but in only 10 % of the examined stagnant waters.

In the 13 areas with tidal movements (Table 1, column III), *Nuphar luteum* was found five times and the abundance was low, except in the Old Creek of the Banwaard at Veen (M. 108). The horizontal and vertical water movements were weak here, however, so that the unfavourable conditions that are due to tidal movements were not marked (note the agreeing case of *Nymphoides peltata* on the same locality). Summarizing *Nuphar luteum* presents a wide ecological amplitude, even though its preference is for the same ecotope with occasional water movements, for which *Nymphoides peltata* and *Potamogeton lucens* showed a great affinity. However, in this ecotope *Nuphar luteum* is more frequent in that waters which are less exposed to water movements, such as the Rhine and the Guelders IJssel. This will be shown in a following chapter.

1.3.3.2. *Depth of water* (graphs 5 and 6)

The species amplitude of water depth extends from 0 to 300 cm. According to the sample plot records the species had its greatest frequency at depths of 100 and 110 cm, and it was fairly frequent between 40 and 150 cm. In water from 80 to 200 cm deep, *Nuphar luteum* was found to have a cover degree of 3 (and once only in water of 150 cm depth, a value of 4), no higher value being found anywhere. The values of 3 and 4 appeared in 7, 2 and 2 waters in the Waal, Rhine and Guelders IJssel areas respectively. The plant was most frequently recorded as dominant at depths of between 100 and 120 cm. According to VLIEGER in VAN ZINDEREN BAKKER (1942) the species grows by preference in the Naardermeer at depths of 100 to 160 cm. From graph 6 there appears a gradual decrease in the average cover degree in areas where the depth increased from 170 to 300 cm.

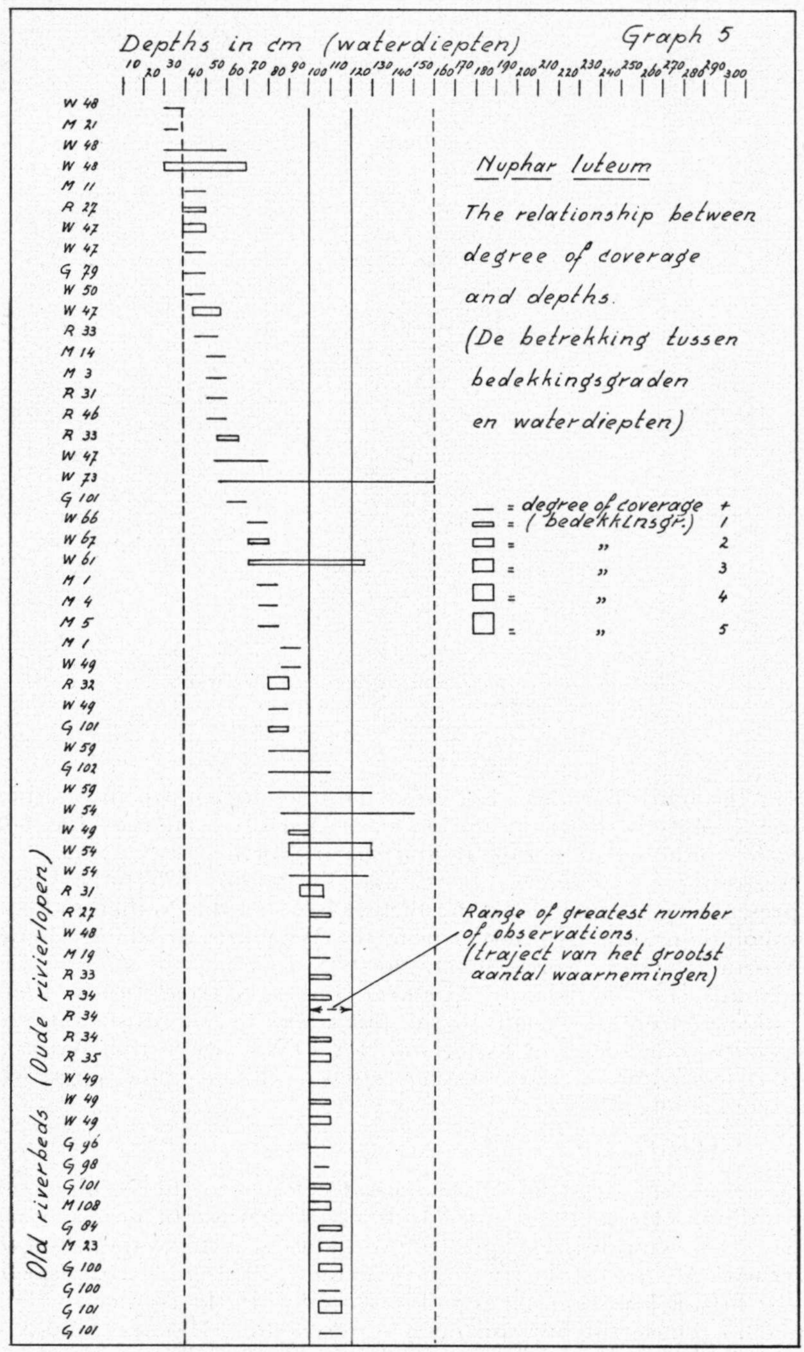
1.3.3.3. *Other environmental factors*

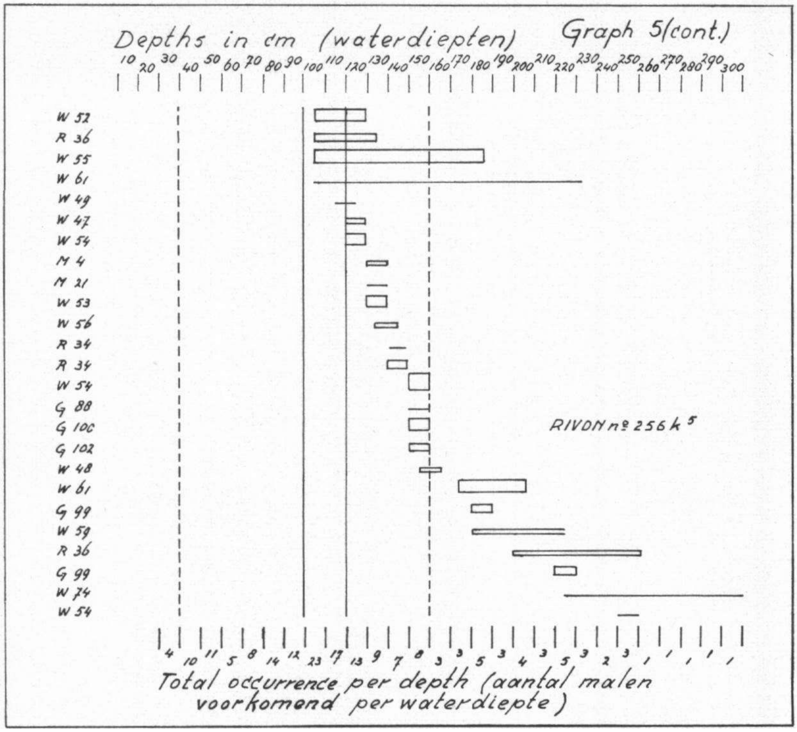
The behaviour of *Nuphar luteum* at a given level of acidity or in increasing chlorinity is very much the same as that of *Nymphoides peltata*. The former also was still able to dominate at a chloride level of 100 mg per l.

1.4. NYMPHAEA ALBA L.

1.4.1. Distribution

Nymphaea alba appears nearly everywhere in Europe (HEGI 1935) although, according to HULTÉN (1950) it is less common in Denmark, in the far South of Sweden, the Baltic and in Southern Finland (as


Depths in cm (waterdiepten)
Graph 5
Nuphar luteum
The relationship between degree of coverage and depths.
(De betrekking tussen bedekkingsgraden en waterdiepten)
= degree of coverage +
= (bedekkingsgr.) 1
Range of greatest number of observations.
(traject van het grootst aantal waarnemingen)
Old riverbeds (Oude rivierlopen)

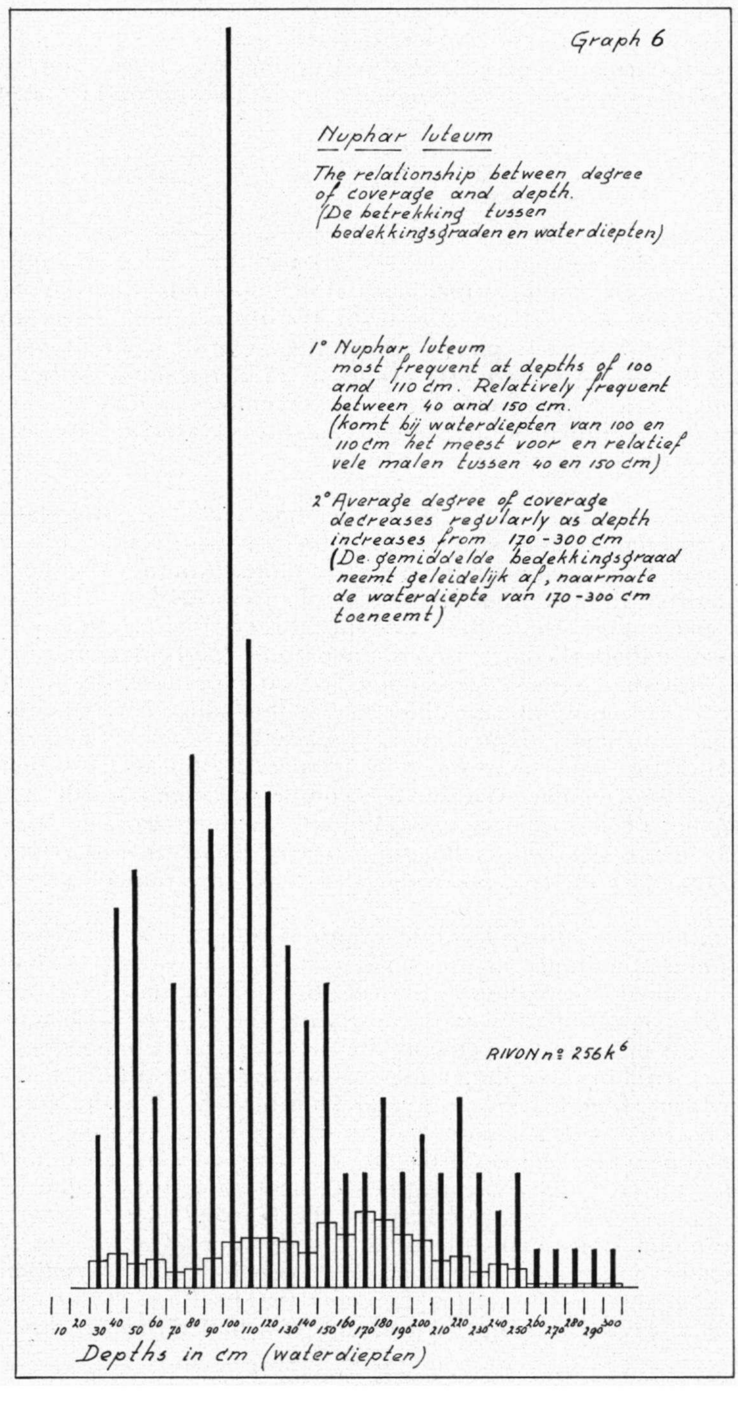


far as the 63rd. parallel). Localised habitats are known in Southern Norway and Sweden, on the coast of Norway as far as the 68th parallel, although it is rare inland so far North.

According to CLAPHAM, TUTIN and WARBURG (1952) the species is present over the whole of the British Isles. In the Netherlands it is also common, although absent from the West Frisian Islands, is rare in North Holland (North of the North Sea Canal), in Zeeland and the South Holland Islands (HEUKELS and VAN OOSTSTROOM 1956). It appears from the plant maps published by the Instituut voor Vegetatie-onderzoek van Nederland (I.V.O.N.) (1951) that *Nymphaea alba* is less common than *Nuphar luteum*, and our data agree with this completely.

1.4.2. Habitat

Nymphaea alba, just as *Nuphar luteum* belongs to the Nymphaeids. According to HEGI (1935) and PASCHER (1936) it is a plant of stagnant or slowly-flowing waters, appearing in pools, ponds, swamps and old riverbeds. CLAPHAM, TUTIN and WARBURG (1952) report the species in the British Isles from lakes and ponds only. In the Netherlands it is found in ponds, ditches and open water bodies (HEUKELS and VAN OOSTSTROOM, 1956). OBERDORFER (1949) gives the plant's biotope as


Graph 6
Nuphar luteum
The relationship between degree of coverage and depth.
(De betrekking tussen bedekkingsgraden en waterdiepten)
1° Nuphar luteum most frequent at depths of 100 and 110 cm. Relatively frequent between 40 and 150 cm.
(komt bij waterdiepten van 100 en 110 cm het meest voor en relatief vele malen tussen 40 en 150 cm)
2° Average degree of coverage decreases regularly as depth increases from 170 - 300 cm
(De gemiddelde bedekkingsgraad neemt geleidelijk af, naarmate de waterdiepte van 170 - 300 cm toeneemt)
RIVON nº 256k⁶
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230 240 250 260 270 280 290 300
Depths in cm (waterdiepten)

in summer warm waters, rich in nutrition, with a mud bottom — but less frequent also in colder and less rich waters.

Observations in the literature concerning depth of water where *Nymphaea alba* occurs will be returned to under the appropriate heading.

1. 4. 3. Environmental factors

1. 4. 3. 1. *Water movement*

According to Table 1, column I, there are 46 areas with stagnant waters without temporary connections with the river. Included in these are 8 large waters in the South Holland islands, where *Nymphaea alba* was not seen — agreeing with the distribution given above. Leaving aside these 8 pools (where the chloride content was the limiting factor), *Nymphaea alba* occurs in 25 of the other 38 bodies of stagnant water — i.e., in 66 % — a percentage as high as that for *Nuphar luteum*. Both species seem to have a greater affinity for this ecotope with stagnant water than *Nymphoides peltata* or *Potamogeton lucens*.

In stagnant waters in the river forelands, which are inundated or flowed through in the winter, and which may in some cases be in permanent connection with the river (see table 1, column II), *Nymphaea alba* occurred in only 29 of the 66 possible areas (44 %). This last is a lower percentage than that for the three previous limnophytes. However, statistical comparison of the presence percentage in stagnant water with the presence percentage in water occasionally in movement, showed no significant difference at this point. Nevertheless will be shown in a later chapter, that *Nymphaea alba* does, in fact, show a preference for water movement, but especially for water subject to only *slight* movements. Within the ecotope with temporarily moving water, the species appears to occur only in those parts of it which are least exposed to winter flooding. It even occurs in waters in open connection with the river, provided that these are situated in sheltered areas.

Examining only those localities where *Nymphaea alba* occurred with a maximal abundance or a cover degree of at least 5 % (value 2 of the combined estimation scala of Braun-Blanquet), the species occurred in 9 of the 29 waters constituing the ecotope with stagnant waters and no water movements due to temporary connections with the river. In 3 of those the greater part of the water surface had been grown over (Meerlo, Wansum and Houtblerick). On the contrary, in the ecotope with stagnant waters affected by temporary flooding, the localities where this cover degree was observed were less numerous, whereas the average cover degree in these cases was higher. 81 % of these cases were old riverbeds in the Guelders IJssel area.

Examining statistically the plant's preference of either the Waal or Guelders IJssel areas, we are able to conclude that *Nymphaea alba* shows a distinct preference for the Guelders IJssel, i.e., for an ecotope with relatively weak water movement. We shall return to this point later.

In 13 areas with tidal movement (Table 1, column III) *Nymphaea alba* was seen only once: in the Krook at Slijkwel, where a small growth of the limnophyte was to be found at the blind end of the creek, which is several kilometres long, resulting in only slight horizontal and vertical water movements.

1.4.3.2. *Depth of water* (graph 7 and 8)

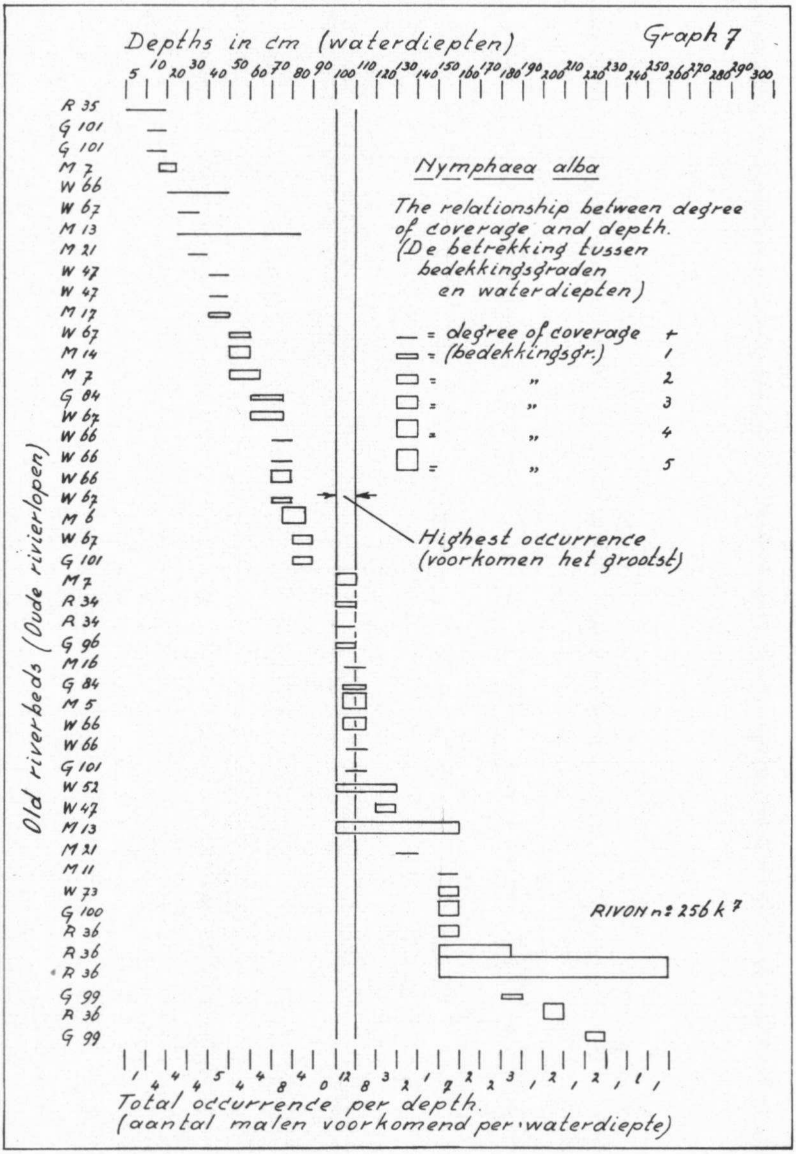
The depth amplitude for *Nymphaea alba* extends from 5 to 250 cm. The sample plot records show that the greatest occurrence was at a depth of 100 cm. Secondary optima were found at depths of 70, 110 and 150 cm (graph 8). The greatest cover degree was at depths of between 70 and 250 cm. The following survey gives the greatest cover degrees:

depths of water (cm)	cover degrees
70	3, 4
100	3, 3, 3, 4
110	3, 3, 4
120	3
130	3
140	3
150	3, 3, 3, 4, 5
160–180	3, 5
190	5
200	5, 5
210–250	5

From this it seems to appear that the plant was dominant most frequently at a depth of 150 cm. It should be noted however, that deeper waters were not so often considered in the survey. It is probable that the depth was about 150 cm in the three waters mentioned above in Limburg (Meerlo, Wansum, Houtblerick), but a lack of a boat prevented any observations of the depth being carried out here.

It can be seen, in addition, from graph 8, that the average cover degree increases with the depth of water, but that above a depth of 180 cm, the increase stops. On the basis of these facts we can probably conclude that *Nymphaea alba* has its optimum at a depth of 150 cm or more, but the data are too small to allow a statistical treatment. In the literature, depths are given from 50–250 cm, rarely 300–500 cm (PASCHER 1936), 200–250 cm in Esthwaite Water (TANSLEY 1949), and to 200 cm, rare.y more (ROBIJNS 1955) — the latter adding that *Nymphaea alba* prefers shallower and more sheltered places. From our experience we can say that *Nymphaea alba* is, on the contrary, optimal in deeper waters than *Nuphar luteum*, but indeed in more sheltered places than the latter. Water where this situation occurred was found at Veessen (G. 27) ,the Spoolderhank (G. 100), the Hank at Wilsum (G. 90) and the Kil of Tiel (W. 64). We give below the results (graphs 6 and 8) of comparing water depths for these two nymphaeids:

	Depths of water in cm	
	Nuphar luteum	Nymphaea alba
range	0–300	5–250(?)
most frequent	100–110	100
relatively frequent	40–150	70, 110, 150
high cover degree (3 and more) –	80–200	70–250
greatest frequency of cover degrees 4–5	100–120	150
average cover degree	170→300 (decreasing)	150→180 (increasing)



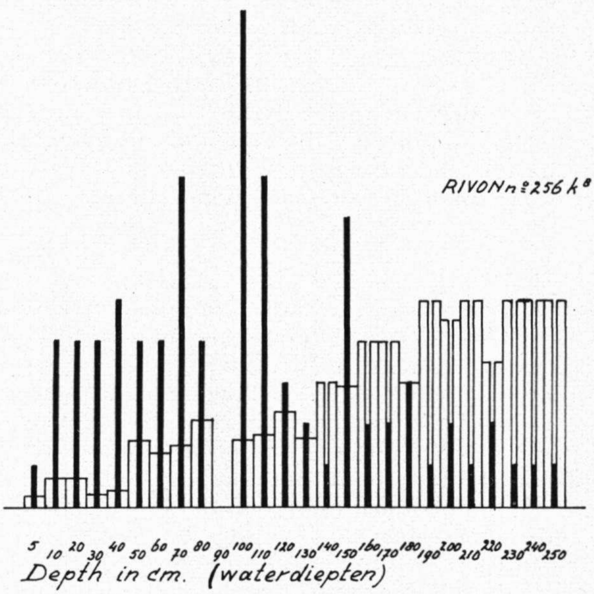
Graph 8

Nymphaea alba

1° Nymphaea alba is observed most frequently at a depth of 100 cm. Secundary optima at 70, 110 and 150 cm.
(is bij een waterdiepte van 100 cm het meest aangetroffen, secundaire optima lagen bij 70, 110 en 150 cm)

2° The average degree of coverage inceases with the depth.
(de gemiddelde bedekkingsgraad wordt hoger, naarmate de waterdiepte toeneemt)

3° The optimum is probably at 150 cm deep.
(wellicht heeft Nymphaea alba bij 150 cm haar optimum)



1. 4. 3. 3. *Other environmental factors*

Apart from the areas with tidal movements *Nymphaea alba* was found in only 9 of the 29 waters which had a chlorinity of 70 mg/l or more. In comparison with *Nuphar luteum*, *Nymphaea alba* was less frequent in this biotope, but this difference is not due to salinity but to another factor — the influence of water movement. This may be concluded from the fact that *Nymphaea alba* occurred in this biotope in quiet waters with the highest chloride content observed (114, 112, 106 mg/l), and occurred there in fact abundantly. The plant was absent, nevertheless, in the waters of the South-Holland islands: here the chloride-content was 200 mg/l or more.

The pH range, where *Nymphaea alba* was found, was the same as that for *Nuphar luteum*, although its abundance was larger at a pH between 6.1 and 6.9, than that of the latter. It was also frequent in poorer waters. It avoids an organic substratum less than *Nuphar luteum* and has in this respect a greater ecological amplitude — which is shown, in fact, by the plant's occurrence in pools with a mesotrophic and even oligotrophic environment.

1. 5. Potamogeton natans L.

1. 5. 1. Distribution

Potamogeton natans is a species with a widespread area stretching over the temperature and subtropical zones of both hemispheres (Hegi 1935). It is, according to Hultén (1950) common in Denmark, on the coast of Southern Norway, in Southern Sweden, in the South-East of Central Sweden, in the Baltic and in Finland (to the 64th parallel). Further to the North-West and the North its occurrence drops off sharply and above the 70th parallel it is absent. In the Netherlands the plant is very common (Heukels and Van Ooststroom 1956).

1. 5. 2. Habitat

Potamogeton natans belongs to the Nymphaeids as defined by Du Rietz (1930). Oberdorfer (1949) states that in S.W. Germany this species is fairly frequent in floating plant-communities in poor, moderately acid stagnant or slowly flowing waters, especially in tarns and in bog-areas. This preference for meso- to oligotrophic water does not hold true for N.W. Europe, the species there being common both in eutrophic and mesotrophic habitat.

Hegi (1935) reports the species from sheltered places (also from ditches) and indicates the shallow depths of these habitats. On the contrary Pascher (1936) found the species in a depth of 250–500 cm. Clapham, Tutin and Warburg (1952) give as habitats: lakes, ponds, rivers, ditches and especially spots where the bottom has a highly developed organic structure, commonly by a depth less than 1 m. Tansley (1949) described two habitats for *Potamogeton natans*. In the first place this was a bay of the moderate flowing Thames above

Oxford. Across the mouth of the bay there was a strip of *Scirpus lacustris* growing in a depth of 1.20–1.80 m. Between this strip and a reed fringe on the landside there was only 60 cm of water over a thick mud layer and the water surface was covered here with a layer of floating water plants. In this, *Nuphar luteum* was dominant and *Nymphoides peltata* subdominant. In the same community, *Potamogeton natans* was frequent, together with *Polygonum amphibium* fo. *natans* — to be dealt with later — and *Callitriche stagnalis*. In the second place, Tansley records an observation from Butcher (1933) in the river Lark with nearly stagnant water and a mud bottom — a biotope approaching that of a "pond". Here *Potamogeton lucens* and *Potamogeton pectinatus* were respectively dominant and sub-dominant, while *Sparganium simplex* was very common. In this same community *Potamogeton natans*, *P. crispus* and *Nuphar luteum* were frequent in the Netherlands. Heukels and Van Ooststroom (1956) give freshwater as habitat, also valleys in dunes, pools and outside the water in peat bogs.

1.5.3. Environmental factors

1.5.3.1. *Water movement and bottom*

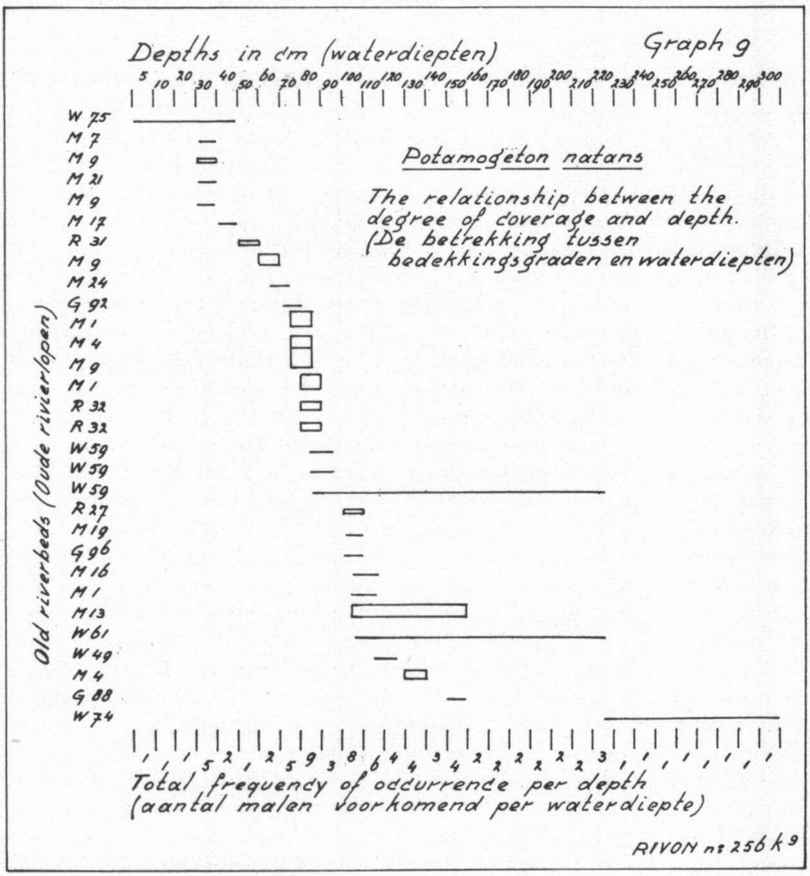
In 8 old river-beds with stagnant waters in the South-Holland islands, no trace of *Potamogeton natans* was found. In 38 old river-beds elsewhere, also with stagnant waters, the plant was present 47 % — these being mostly in the Maas area, where there was a river "loam" bottom. Just as *Potamogeton lucens* and contrary to *Nymphoides peltata*, *Nuphar luteum* and *Nymphaea alba*, *P. natans* was less frequent in the waters with clay bottom belonging to the ecotope with stagnant water and without temporary connection with the river than it was on other bottom types of the same ecotope. This preference was confirmed by the statistical method given above. Since in the old riverbed area waters with peat bottom are poorer in nutrients than clay bottom pools, a preference of *Potamogeton natans* for waters relatively poor in nutrients might be concluded from the statement above. Such a conclusion would be wrong, however; we have only to do with a local coincidence. In fact, it is more probable that its relative avoidance of clay bottom is correlated with its preference for sheltered habitat with quiet water. Nor is it allowed to consider *Potamogeton lucens* a species with a preference for water poor in nutrients, *Potamogeton lucens* having its very optimum in large broads on peat bottom where the water is rich in nutrients and is strongly moved by wind.

In 66 river-forelands, flooded in winter and, in several cases, in permanent open connection with the river (table 1, column II), the plant was present in the same degree as *Nymphaea alba* — i.e. 44 %. There is no significant preference for either stagnant or weakly moving waters. But it is argued in a later chapter that *Potamogeton natans* (just as *Nymphaea alba*) seeks places less exposed to the winter floods. If we examine the abundance of *Potamogeton natans* then it appears that the number of waters where the species was abundant was small — 7 out of 38 stagnant waters and 9 out of the 66 areas subject to winter flooding. These 16 areas all had a sheltered situation.

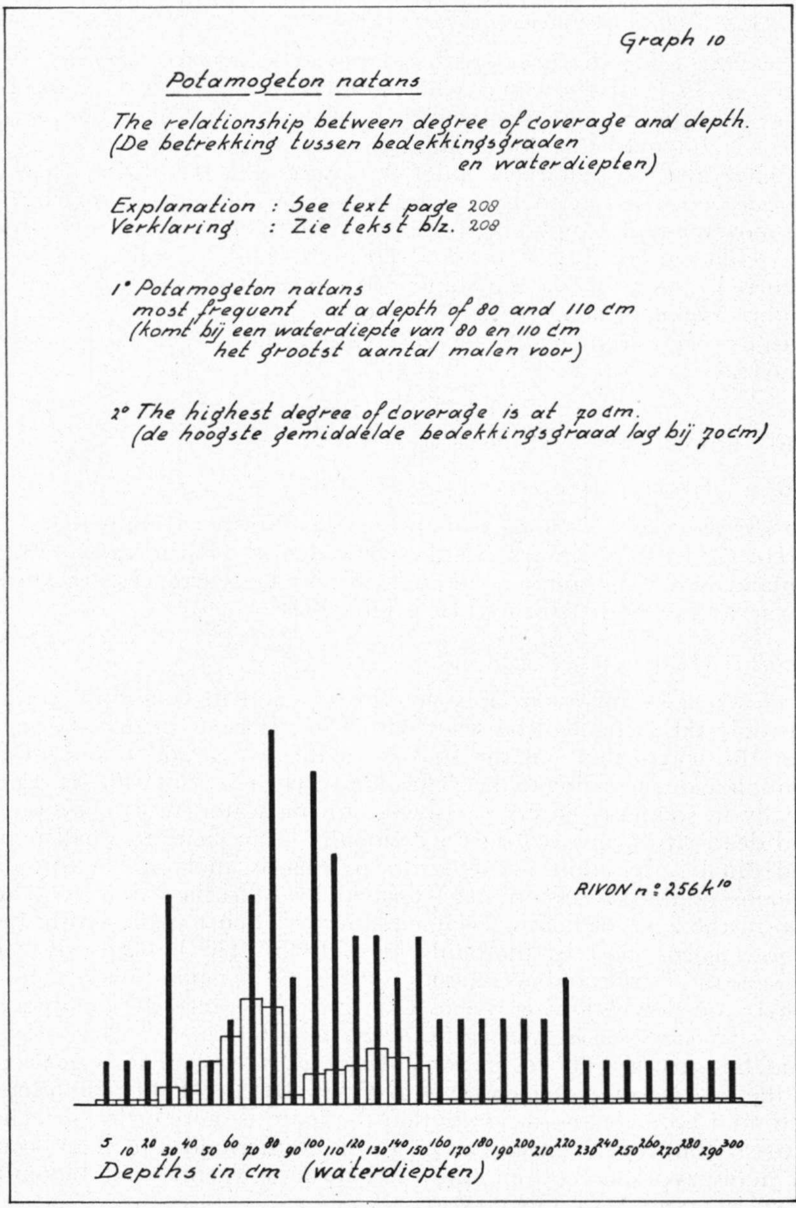
In the 13 areas subjected to tidal movements (table 1, column III), *P. natans* was observed only once and then in a narrow sidestream of the Avelingerdiep at Gorinchem (W. 112) where the horizontal and vertical movement of the water was weak.

1.5.3.2. *Depth of water* (graphs 9 and 10)

The range of depth where *Potamogeton natans* occurs runs from 0–300 cm. The vegetation records show that the species was most frequent between 80 and 100 cm. The highest cover degrees were, however, at depths of 60, 70 and 80 cm, in five old riverbeds with stagnant water and a river "loam" bottom in the Maas area. Only in one case — in the Galgenwiel near Loon op Zand — was there a high cover degree in a depth of 100–150 cm. This presence optimum can only strengthen the conclusion arrived at above, that *Potamogeton natans* chooses a sheltered habitat. The highest average degree of coverage



was calculated at a depth of 70 cm, agreeing with the observations of CLAPHAM, TUTIN and WARBURG (1952) that the plant usually grows in less than 100 cm of water and in a strongly organic bottom. The observation of TANSLEY at Oxford (1949) also agrees with this. On the contrary, the highest cover degree ever observed by us was



in a pool near Winterswijk (Guelderland), where tertiary clay had been dug out, and which was more than 3 m deep. Here *Potamogeton natans* presented a cover degree 4 (MELTZER and WESTHOFF, 1942, photograph nr 11). This observation corresponds with the statement of PASCHER (see above).

1. 5. 3. 3. *Other environmental factors*

Leaving aside the areas with tidal waters, *Potamogeton natans* was found in 35 % of the waters where the chloride level was 70 mg/l or more. This percentage is somewhat higher than that of *Nymphaea alba* (26 %) and markedly lower than that of *Nuphar luteum* (66 %). As we have already remarked under *Nymphaea alba*, this difference with *Nuphar luteum* is not to be attributed to the chloride factor, but to the movement of water. The species was still to be found as a dominant at a chloride level of 76 mg and 80 mg/l, while it still sporadically occurred as far as 104 mg/l and even once at a value of 124 mg/l in the Avelingerdiep.

In its reactions to acidity the observations agree with those relating to *Nymphaea alba*.

1. 6. POLYGONUM AMPHIBIUM L.

1. 6. 1. Distribution

Polygonum amphibium is a plant of the Northern temperate zone (HEGI 1935). In Denmark, Southern Sweden, the Baltic and Southern Finland is it less common although localised occurrences are known as far as the 70th parallel (HULTÉN 1950).

1. 6. 2. Habitat

This species grows on land (fo. *terrestre*) and in water (fo. *natans*), but only the latter will be dealt with here. It roots in the bottom so that the leaves float on the surface of the water and is one of the Nymphaeids according to the definition of DU RIETZ (1930). It occurs locally in stagnant waters, or slowly moving water, in ditches, ponds and dead riverarms. It forms occasionally large facies in small ponds and ditches. In addition, it occurs frequently in lakes, broads and streams in the succession stage formed by bulrushes and reed, and also in the zone of floating water plants — often together with *Potamogeton natans*, close by the bank (HEGI 1935). The habitats given by CLAPHAM, TUTIN and WARBURG (1952) for England were: pools, canals and slowly flowing rivers. TANSLEY (1949) records one observation of *Potamogeton amphibium* fo. *natans* in a 60 cm deep bay with a mud bottom (see above, under *Potamogeton natans*). The water form of the species grows, according to OBERDORFER (1949), in humus-rich mud bottoms and he states that the plant is more or less attached to areas of nitrogen concentration. In the Netherlands the plant occurs on many types of bottom, the land form frequently not blooming (HEUKELS and VAN OOSTSTROOM 1956).

1.6.3. Environmental factors

1.6.3.1. *Water movement and bottom*

Polygonum amphibium was nowhere to be found in the 8 stagnant waters in the South Holland islands (table 1, column I). In 38 stagnant waters without a connection to the river (table 1, column II), the plant was present in only 11 %. In comparison to the other 5 limnophytes described above, this is a very low percentage.

In the 66 stagnant waters, flooded in the winter and, in a number of cases, in permanent open connection with the river (table 1, column II), the plant was present in 52 % of those cases. After using the test of contingency described above, it appeared that the percentage did, in fact, indicate a choice and that *Polygonum amphibium* fo. *natans* prefers an ecotope with, at times, moving water. This preference becomes obvious when we examine in which sections of the biotope the plant was most common. This was the Waal area, where the winter flooding has its greatest effect and as a result of the erosion, organic sediments are removed. (This will be returned to later). Thus, *Polygonum amphibium* may prefer a mineral bottom, a fact that will also be discussed later.

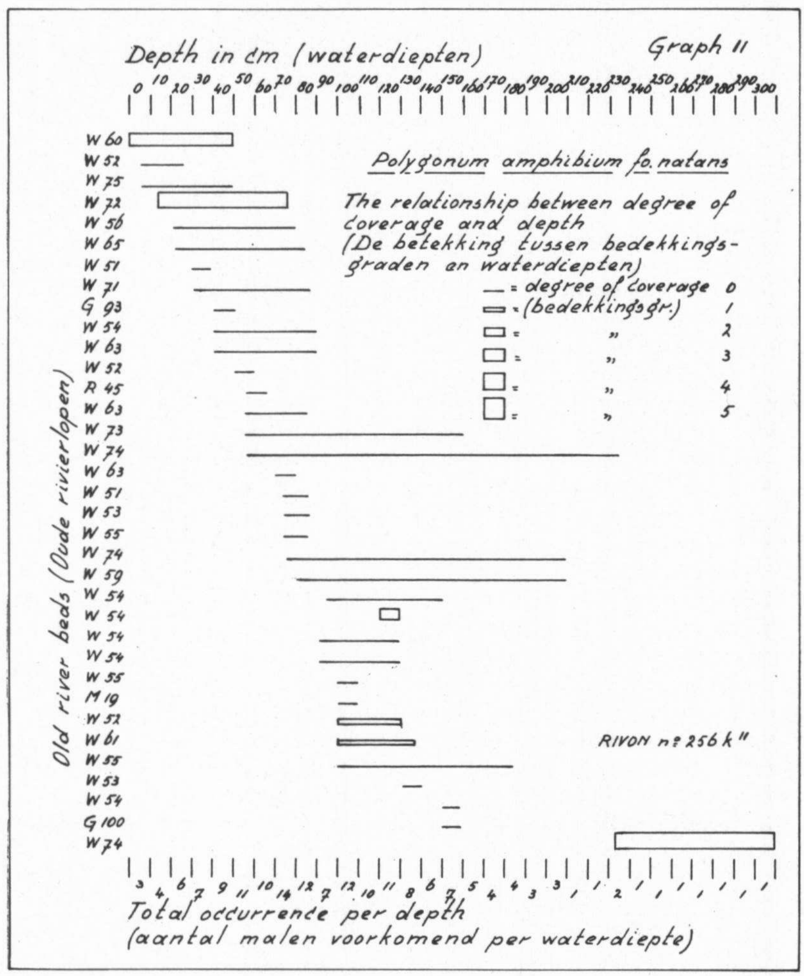
If we examine the abundance of this species then it appears that in the ecotope with temporarily moving water, it was found to be abundant in 38 % of the 34 waters where it occurred at all. This was also the case, however, in 3 of the 4 waters from the ecotope with stagnant water where the plant has been observed. We have the impression that whenever *Polygonum amphibium* fo. *natans* occurs anywhere, it is mostly dominant. In the 13 areas with tidal movements (table 1, column III), the species was seen once — in a narrow outlet of the Avelingerdiep near Gorinchem (W. 112) where the horizontal and vertical movements of the water was weak Here also *Potagometon natans* occurred, which agrees with the statement of HEGI (1935), that both species frequently occur together.

1.6.3.2. *Depth of water* (graphs 11 and 12)

The depth range for *Polygonum amphibium* fo. *natans* runs from 0–300 cm. The sample plot records show that the frequency was highest at a depth of 70 cm; a minor frequency range runned from 40–120 cm. The average cover degree was highest at 0–40 cm; the highest degrees (3 and 4) were found at depths of 0–70 and 120 cm and only once at a depth of 225–300 cm. The latter case was in the Kil at Ophemert (W. 74), in the zone of water plants against the open centre; *Polygonum amphibium* fo. *natans* was dominant in the deeper section, while *Nymphoides peltata* became dominant in the shallower water.

1.6.3.3. *Other environmental factors*

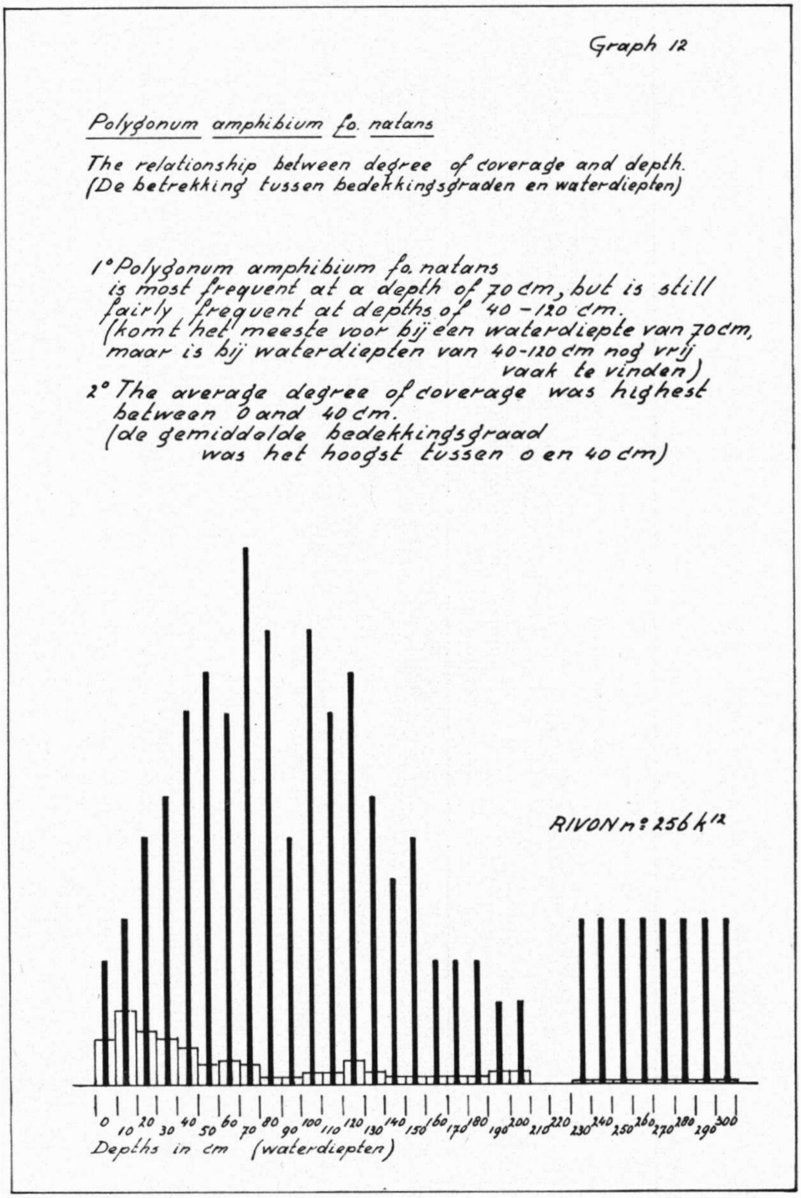
Leaving aside the areas subjected to tidal water movements, *Polygonum amphibium* fo. *natans* was present in 49 % of the pools where the chloride content was 70 mg/l or more. This is a higher percentage



than for *Potamogeton natans* (35 %) and *Nymphaea alba* (26 %), but lower than that for *Nuphar luteum* (66 %). The plant was still abundant at levels of 80–104 mg/l. It was observed once in an old riverbed at a level of 124 mg/l; a single specimen occurred in the "Binnenbedijkte Maas" at Westmaas where the chloride content was 200 mg/l.

The pH range lay between 6.5 and 7.6; the range of dominance was somewhat smaller, 6.7–7.5. This preference for a neutral to basic environment agrees with the described preference (see above) for a mineral bottom — acidity and bottom type being in fact coupled together (see chapter on *Nymphoides peltata*).

Finally it is not impossible that this species is nitrophilous (OBERDORFER 1949). It was noticeable, for example, that *Polygonum amphibium* fo. *natans* bloomed luxuriously in a strip some 100 m long and 2 m



wide on a mud bottom a few metres out from the Northern bank of the old riverbed of the Doornwaard in the district of Heusden (M. 16). Because the bottom was sandy right to the high and steep bank, cows were able to drink there and it is thus explicate that a high nitrogen content could be expected in the water.

Survey of the percentage concerning *the presence-degree* of the six limnophyted discusses, in connection with the *water movement* and *bottom type*.

Ecotope / Limnophytes	38 stagnant waters (except in South-Holland islands) Ecotope Es all bottom-types	13 stagnant waters Ecotope Es different bottom-types, except clay	25 stagnant waters Ecotope Es river clay bottom	66 episodical- or weak moving waters Ecotope Ee river clay bottom	13 tidal waters Ecotope Et river clay bottom
Nymphoides peltata	39%	8% ←	→ 56% ←	→ 80%	30%
Potamogeton lucens	29%	11%	32% ←	→ 79%	15%
Nuphar luteum	66%	61%	68%	83%	38%
Nymphaea alba	66%	85%	56%	44%	8%
Potamogeton natans	47%	85% ←	→ 28%	44%	8%
Polygonum amphibium fo. natans	11%	8%	12% ←	→ 52%	8%

The percentage figures in the 2nd, 3rd and 4th vertical columns were mutually compared by the test of contingency. Significant differences are connected by arrows.

Survey of the connection between *the range of occurrence* of the six limnophytes discussed and *the water depth* in cm. (graphs 2, 4, 6, 8, 10 and 12)

Range of water depth / Limnophytes	Occurrence	Most frequent	Relatively frequent	Highest cover degrees	Highest number of times dominant	Average cover degree
Nymphoides peltata	5–230	100–150	60–150	5–230	100	from 200 increasing
Potamogeton lucens	10–300 and more?	100–110	50–150	90–300	100	first top at 150, 210–300 increasing
Nuphar luteum	0–300	100–110	40–150	80–200	100–120	first top at 170, to 300 decreasing
Nymphaea alba	5–250 and more?	100	70, 110, 150	70–250	150	150–180 increasing
Potamogeton natans	0–300	80–100	30, 70, 110	60, 70, 80, 100–150	80	—
Polygonum amphibium fo. natans	0–300	70	40–120	0–70, 120, 225–300	—	—

The figures obtained concerning the occurrence of the 6 limnophytes considered, in connection with water movement, bottom type and depth of water as described in the chapters above have been brought together in the foregoing two tables, to give a broader picture:

1. 7. Two surveys of the presence of limnophytes related to movement of water, bottom and the depth of water

See pages 214 and 215.

2. THE CONNECTION BETWEEN THE DEPTH OF WATER AND THE OCCURRENCE AND RATE OF DOMINANCE OF THE 6 LIMNOPHYTES

The connection between the depth of water and:

a) the occurrence,

b) the rate of appearance of the 6 limnophytes already separately described, is brought together in the following synopsis. The details can be obtained from graphs 1 to 12 in the foregoing chapters. In the synopsis below is given:
   a) in how many river-beds the species occurred at a given depth;
   b) in how many river-beds the species covered more than 25 % of the water surface at a given depth (rate of dominance).

The connection between the depth of water and a) the

species \ depth in cm		0	10	20	30	40	50	60	70	80	90	100	110
Nuphar luteum	a				8	10	11	5	8	14	12	33	17
	b				1	33	2	1	0	1	2	11	7
Nymphoides peltata	a	1	1	3	5	5	9	12	12	12	12	24	18
	b	1	1	2	2	2	4	5	7	7	8	16	11
Potamogeton lucens	a		1	2	2	3	7	5	5	5	5	15	10
	b					2	2	1	1	0	2	8	2
Nymphaea alba.	a	1	4	4	4	5	4	4	8	4	0	12	8
	b		1	1	0	0	2	1	3	3	0	5	4
Potamogeton natans	a	1	1	1	5	2	1	2	5	9	3	8	6
	b							1	3	6	0	1	1
Polygonum amphibium fo. natans .	a	3	4	6	7	9	11	10	14	12	7	12	10
	b	1	2	2	2	2	1	1	1	0	0	0	0

☐ largest number of river-beds; for further explanation, see text.

The limit of 25 % was chosen on the basis of the observation technique employed, this limit separating the estimation values +, 1, 2 from the values 3, 4, 5.

We remember a fact mentioned in the chapter on *Nymphoides peltata* (page 181) namely, that the depth could not be measured accurately everywhere. Often it was only estimated. When this depth was about one metre, the method is open to criticism — namely that when one is accustomed to the decimal system, a value of 10 dm will be noted more frequently than 9 dm or 11 dm. From this it follows that should an optimal depth occur at 10 dm, not the slightest value can be placed in it — it being only an apparent value. A real value, however, can be attributed in finding a depth range stretching over several dm, including the value of 10 dm. It should also be mentioned that the yearly differences in the amount of inundation and precipitation are unfavourable factors in the data. In the synopsis given above, figures under a) are underlined when they indicate that the species occurred in 5 % or more at different depths. In some parts of the range this line is dotted, which indicates that in this case the real value of this figure may be doubted. To give an example: when *Nymphaea alba* occurs at a depth of 100 cm and 70 cm, one wonders why the plant occurs much less at 80 cm and not at all at 90 cm. A factor of

occurrence and b) the rate of dominance of the 6 limnophytes.

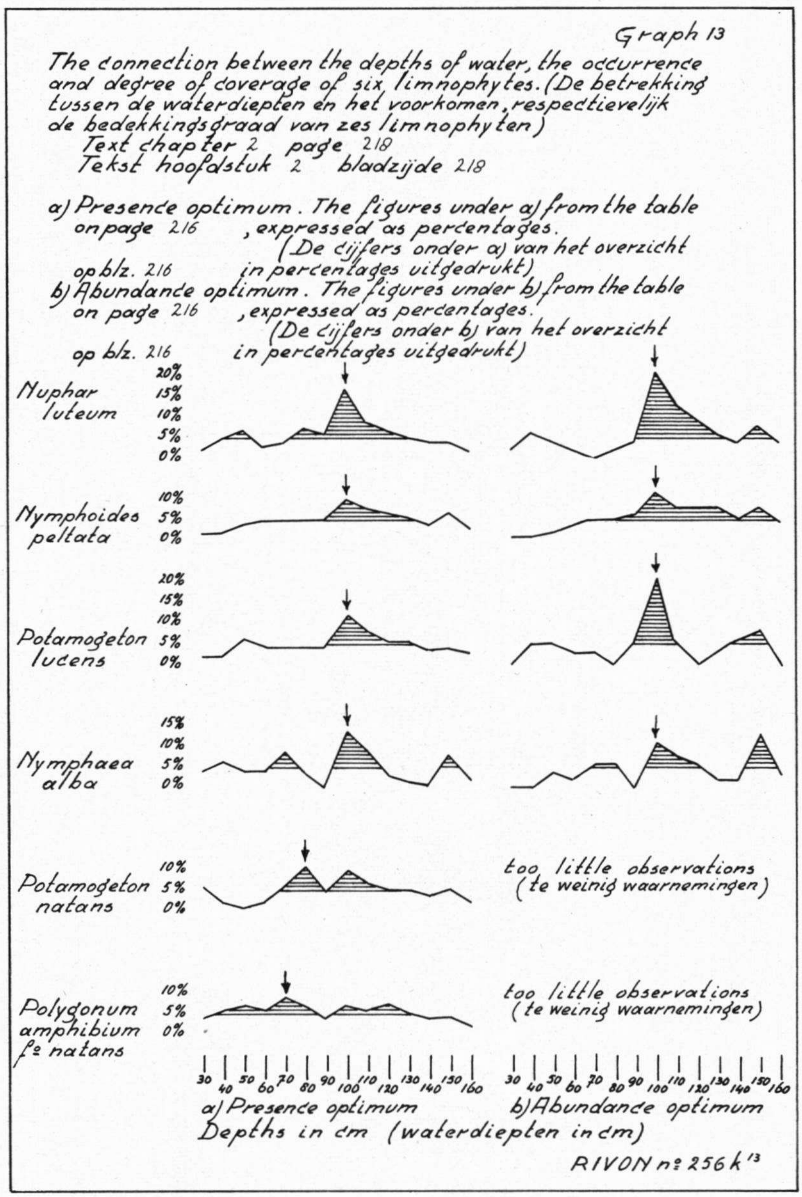
120	130	140	150	160	170	180	190	200	210	220	230	240	250	260	270	280	290	300	Total of figures
13	9	7	8	3	3	5	3	4	3	5	3	2	3	1	1	1	1	1	190
5	3	2	4	2	2	3	1	1	0	1									52
16	14	8	15	7	7	8	7	7	4	4	5	2	3	1	1	1	1	1	226
11	10	6	10	5	5	4	4	4	3	3	3								134
7	7	5	5	4	4	5	3	3	3	4	4	2	4	1	1	1	1	2	126
0	1	2	3	0	0	0	0	0	0	2	1	1	3	1	1	1	1	2	37
3	2	1	7	2	2	3	1	2	1	2	1	1	1						87
3	1	1	6	2	2	2	1	2	1	2	1	1	1						46
4	4	3	4	2	2	2	2	2	2	3	1	1	1	1	1	1	1	1	82
1	2	1	1																17
11	8	6	7	4	4	4	3	3	1	1	2	1	1	1	1	1	1	1	164
1																			13

competition might be presumed, but when we compare this phenomenon with that of *Nuphar luteum*, *Nymphoides peltata* and *Potamogeton lucens*, then the same feature appears. We must, therefore, consider such figures to be an "apparent value" mentioned above.

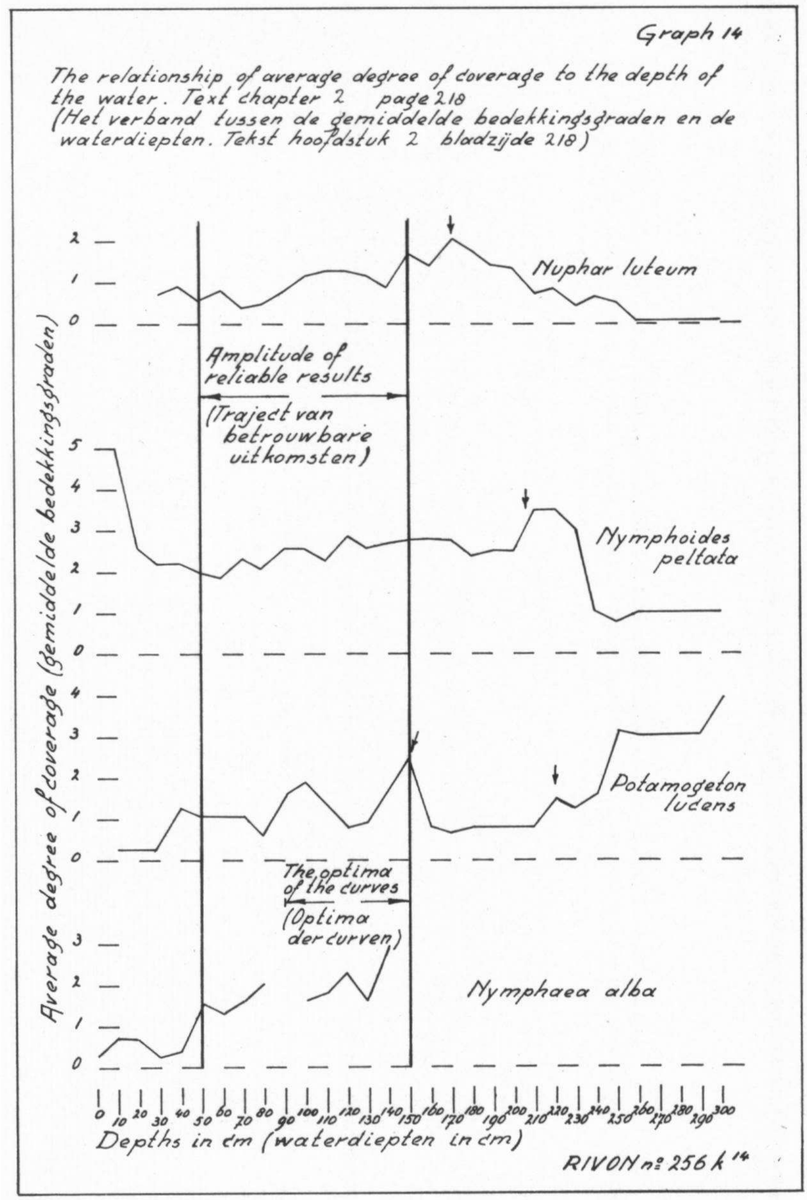
From the synopsis it can be seen that the amplitude of water depth runs from 30–160 cm, within which one or more of the limnophytes is present in 5 % or more of the considered waters. In addition, there is a narrower amplitude from 60–120 cm within which all six species are present in at least 5 % of the cases. This is an environment where the species may compete. The question then arises as to in what mass the species occur there and it is then necessary to consider the cover degree. In section b) therefore, it is given in how many biotopes a species covers more than 25 % of the surface in the sample plot records (cover degree 3–5). These figures are given in graph 13 as two curves, after being expressed as percentages.

From these one might conclude that the optimal presence (curves a) and optimal abundance (curves b) indicate a preference of *Nuphar luteum*, *Nymphoides peltata*, *Potamogeton lucens* and *Nymphaea alba* for a depth of 100 cm, while *Potamogeton natans* and *Polygonum amphibium* fo. *natans* prefer 80 and 70 cm respectively. It is unlikely, however, that a species would show a quantitative maximum at only one depth, considering the differences in water-level mentioned above. We have, therefore, given (in graph 14) a curve for 4 limnophytes, showing the relation between the average cover degrees and the depth of water. The averages are calculated by summing all the degrees of coverage and dividing by the number of observations (see the graphs concerned in the treatment of the separate species). Such a calculation is trustworthy, of course, only when a sufficient number of observations have been made. If, for example, at a given depth only one observation was made, and the cover degree chanced to be high there, then the curve will show a high peak, which is in no way comparable with a peak arising from a number of observations. In graph 14, therefore, there is only one reliable section — that from 50–150 cm. The curve for waterlevels more than 150 cm can be seen as only an indication of a possible connection between the average degree of coverage and the corresponding depth of water. From graph 14 it appears then, that the optimum of the curve for the four limnophytes is not, as in graph 13, at a depth of 100 cm, but is to be found in the range 90–150 cm. It will depend on circumstances, e.g. competition, as to whether a species will prefer an even smaller range of depth. This synecological problem will not be considered here.

In graph 14 it appears further that the cover degree increases, in general, with increasing depth. Although the reliability of the curve decreases beyond the depth of 150 cm, we would like to point out some peculiarities in this section. The average cover degree of *Nuphar luteum* gradually falls off, having reached an optimum at 170 cm, while that of *Nymphoides peltata* increases at 200 cm. The average cover degree of the submerged *Potamogeton lucens* reaches an optimum at a depth of 150 cm, falls off after that only to increase again at 210 cm.



In some river-beds this statistical approach could be tested by direct observation, through the dominance of the species concerned in different zones — e.g., in the Zandkolk near Oosterhout (W. 55). In the middle of the approximately 2 m deep water, where there were no floating waterplants and where *Potamogeton lucens* was abundant,



Nymphoides peltata formed, as dominant species, a broad, distinct strip. But in other cases these species were concentrated in the middle of an old riverbed, as in the Koeluchtergat (G. 101) and in the Spoolderhank (G. 100). In that case, the species are competing with each other and we are invading the territory of the synecologist.

3. THE MUTUAL RELATIONSHIP OF THE SIX LIMNOPHYTES, IN CONNECTION WITH THEIR OCCURRENCE IN STAGNANT WATERS AND IN WATERS SUBJECT TO EPISODIC MOVEMENTS (ECOTOPE Ee)

To determine the mutual relationship of the six limnophytes an ecotope was chosen consisting of a number of old river-beds in which the environmental factors differed as little as possible. We shall not consider areas with stagnant water on different bottom types, nor water subject to tidal movements. There remain over for this special ecotope Ee some 66 waters in river forelands on clay soil along the big rivers. The water movement here was confined to flooding in the winter months, with or without being directly flowed through. This means that the river forelands come not only under water, but that they (and the old river beds in them) are at times flowed through by the river. Fourteen of the 66 waters stood, in addition, in permanent open connection with the river. In some places the riverclay was sandy, but not in the last mentioned 14 waters. In some of those not subjected to actual flowing, peat-formation had started, due to their more sheltered positions. The pH was measured nearly everywhere and the water was neutral or weakly basic. The most frequent pH value was 7.2 or 7.3, as shown below (see also section on *Nymphoides peltata* under "acidity").

pH	Number of times measured in the ecotope above
6.9	2
6.9–7.0	1
7.0	7
7.1	8
7.2	13
7.3	16
7.4	6
7.5	6
7.6	1
7.7	1
7.8	–
7.9	1
not measured	8

The various habitat types to be distinguished within this ecotope (see below) were examined as to their floristic assemblage of limnophytes. There were 31 species, and from these *Nuphar luteum* was present in 84 %, *Potamogeton lucens* in 80 %, *Nymphoides peltata* 79 %, *Lemna minor* in 69 % and *Lemna trisulca* in 63 % of the waters considered as belonging to this ecotope. These plants furnished reliable data. Other species that were less frequent — but still of importance — were used in the investigation when their frequency was not much less than 50 % of the frequency shown by *Nuphar luteum*. These other plants were: *Hydrocharis morsus-ranae*, *Ceratophyllum demersum*, *Polygonum amphi-*

bium fo. *natans*, *Spirodela polyrhiza*, *Nymphaea alba*, *Elodea canadensis* and *Potamogeton natans*. Although *Stratiotes aloides* appeared in only 28 % of the waters, it was also considered in the group, because it is an important indicator of sheltered conditions.

For each of the plants mentioned above, a percentage was calculated, showing the number of times that it was present in the pools of the ecotope, while another of the plants was present alike. This percentage, named Q, was calculated by the formula

$$Q = b/a \times 100\ \%$$

where a = the number of waters in which a plant occurred, from the possible 66 waters, and b = the total number of times that the given plant was observed together with another species in the same water. The results showing the amount of affinity of the species for one another, expressed as Q, were then tabulated. This gives us an "ecological affinity diagram" (Table 6) — in the sense used by IVERSEN (1936).

From the species given in the above diagram, those which root in the bottom will be able to withstand the winter flooding and currents and thus remain better in the habitats. Floating or submerged plants which are not rooting (e.g. the *Lemna* species) may be swept away by currents; this means that such plants will not occur so frequently in places exposed to the river. With this factor of water movement in mind, the comparison of the affinity-percentages (Q) of the species must be considered with care; to draw conclusions from the diagram, six species are the most reliable — of which three occurred the most. These six species are placed above in the diagram. In addition, *Stratiotes aloïdes* and *Hydrocharis morsus-ranae* were also used. The question now raised on the basis of the affinity diagram is, whether an optimal development of some of these 8 species — as it was concluded from the presence and dominance data in the vegetation records — coincided with a great mutual affinity of these species. From this greater or smaller mutual affinity a preference would appear for a special section (habitat type) of the ecotope, in which the environmental factors are optimal for any combination of these 8 species. Any possible competition was left out of consideration, this factor being a synecological problem not dealt with in this study.

To begin with, average of the percentages was calculated from the affinity-diagram. It had a value of 57. This figure we will use as a yardstick to draw a ficticious boundary, so that we can speak of "higher" or "lower" percentages. Thus, when an affinity of one species for another is 57 or more, then we can refer to this as "a high affinity" and vice-versa.

From the affinity-diagram it appears then that from the eight underlined species, *Potamogeton lucens*, *Nymphoides peltata* and *Nuphar luteum* show a higher affinity with respect to all of the other species, that can occur in the ecotope. This is a consequence of the high presence degree and the regular distribution of the former species all over the ecotope. Moreover, the mutual affinities of these three

Table 6

Occurrence in 66 waters of Ecotope Ee	*Ecological affinity diagram* concerning 13 *limnophytes* Reason for italicizing: see text	Potamogeton lucens	Nymphoides peltata	Nuphar luteum	Nymphaea alba	Potamogeton natans	Polygonum amphibium fo. natans	Elodea canadensis	Stratiotes aloides	Hydrocharis morsus-ranae	Spirodela polyrhiza	Lemna minor	Ceratophyllum demersum	Lemna trisulca
80 %	*Potamogeton lucens*	—	83	83	75	93	73	75	86	82	77	83	84	85
79 %	*Nymphoides peltata*	82	—	79	81	70	97	85	67	68	83	79	95	74
84 %	*Nuphar luteum*	87	85	—	84	83	76	85	95	89	87	87	84	87
	Nymphaea alba	40	44	43	—	27	37	33	*67*	42	37	38	49	32
	Potamogeton natans	47	36	40	25	—	34	45	43	47	33	44	33	49
	Polygonum amphibium fo. natans	47	*63*	46	44	43	—	45	19	26	43	42	*59*	40
	Elodea canadensis	42	47	44	34	50	39	—	43	45	*57*	48	54	49
28 %	*Stratiotes aloides*	30	24	30	44	30	10	27	—	42	30	36	30	40
	Hydrocharis morsus-ranae	52	44	54	*59*	*60*	26	51	90	—	*70*	*65*	49	68
	Spirodela polyrhiza	38	42	41	34	33	34	51	43	55	—	54	43	53
69 %	Lemna minor	*72*	*69*	*71*	*62*	*77*	*58*	*75*	*90*	*89*	*93*	—	*67*	*92*
	Ceratophyllum demersum	55	*63*	52	*59*	43	*60*	*64*	*57*	42	*57*	50	—	51
63 %	Lemna trisulca	*67*	*59*	*65*	47	*77*	50	*70*	*90*	*84*	*83*	*83*	*61*	—

plants are expressed in high percentages. They thus occur very frequently together in the same pools.

If one examines the presence of these three limnophytes according to the percentage of their occurrence, by splitting it over the forelands of the three rivers — taken in couples — then the following results are obtained:

Rivers	Rhine	Waal	Guelders IJssel
Number of waters	16	29	30
Nuphar luteum + Nymphoides pèltata	43 %	70 %	74 %
Potamogeton lucens + Nymphoides peltata	50 %	73 %	63 %
Potamogeton lucens + Nuphar luteum	$\boxed{79\ \%}$	63 %	74 %

By use of the test of contingency it was found that the apparent difference between the combination of *Nymphoides peltata* with the other two species in the Rhine area and this same combination in the Waal or Guelders IJssel was not significant. On the contrary, the higher occurrence of the combination *Potamogeton lucens-Nuphar luteum* in the Rhine area, compared to the occurrence of the two other combinations, proved to be significant indeed (79 % as against 43 % and 50 %). Before considering this fact we would like to consider some other species. The other plants from this group of eight species show a high affinity for one species only, or — in any case — for a smaller number of species. Their high affinity for one given species is limited therefore: *Nymphaea alba* shows a high affinity (indeed the highest affinity at all) for *Stratiotes aloides*, while *Polygonum amphibium* fo. *natans* shows a high affinity for *Nymphoides peltata* and *Ceratophyllum demersum* only. It is known that *Stratiotes aloides* is a plant of calmer waters, which might indicate that *Nymphaea alba* may also prefer such waters, but this will be returned to later. The high mutual affinity of *Polygonum amphibium* fo. *natans* and *Nymphoides peltata* indicates that they both prefer an environment where the winter flooding has a major influence. This agrees with the statements in the previous chapters concerning the individual species.

Stratiotes aloides shows, according to the affinity diagram, a low affinity for *Nuphar luteum* (30 %), *Potamogeton lucens* (30 %) and *Nymphoides peltata* (24 %). This appears to contradict the fact that *Hydrocharis morsus-ranae* and the *Lemnaceae* have a high affinity for these species, although they are restricted to calm water even more than *Stratiotes aloides* is. This apparent contradiction is to be explained, however, by the special ecology of all latter species. Whereas *Stratiotes aloides* prefers calm open water, *Hydrocharis morsus-ranae* and the *Lemnaceae* also occur between already dense-growing helophytes in bank vegetation, such as reed-zones and floating swamps. Such communities also occur commonly on the banks of flowing, or otherwise moving open water — a less favourable environment for *Stratiotes aloides*. That does not mean, that *Nuphar luteum*, *Potamogeton lucens* and *Nymphoides peltata* occur in the same vegetation type as *Hydrocharis morsus-ranae* and the *Lemnaceae* do. The apparent contradiction refered to above is thus a result of the fact that we are comparing bodies of water as a whole, while there are, in fact, different vegetation types within each of them.

We now want to try to demonstrate these vegetation types from the affinity diagram. For this purpose, we choose from the eight species already selected, the less frequent four — i.e. *Nymphaea alba*, *Potamogeton natans*, *Polygonum amphibium* fo. *natans* and *Stratiotes aloides*.

Table drawn from the *affinity-diagram* on page 223	Polygonum amphibium fo. natans	Nymphaea alba	Potamogeton natans	Stratiotes aloides
Polygonum amphibium fo. natans . .	—	44	43	$\boxed{19}$
Nymphaea alba	37	—	27	67
Potamogeton natans	34	25	—	43
Stratiotes aloides	$\boxed{10}$	44	30	—

The mutual affinity of *Stratiotes aloides* and *Polygonum amphibium* fo. *natans* is thus very small. On the basis of our observations above, this small affinity is due to the existence of two different biotopes within our ecotope, namely that with the least, and that with the most water-movements. *Nymphaea alba*, and less obviously *Potamogeton natans* — two species with an equal mutual affinity — show a higher affinity for *Stratiotes aloides* than for *Polygonum amphibium* fo. *natans*. This indicates a definite preference for extremely calm water. To investigate this result more closely the occurrence-percentage was calculated for *Polygonum amphibium* fo. *natans*, *Nymphaea alba* and *Stratiotes aloides*, in the waters found in the river forelands of the Rhine, Waal and Guelders IJssel, which belong to the ecotope in question.

In the first place, these percentages were calculated by means of the usual statistical method. Not all the mutual differences proved

Old riverbeds / Limnophytes	Guelders IJssel 21 areas	Rhine 16 areas	Waal 29 areas
Stratiotes aloides	29 %	50 %	21 %
Nymphaea alba	81 %	38 %	21 %
Polygonum amphibium fo. natans . .	48 %	13 %	79 %

to be significant. The arrows in the table above indicate those percentages which are, in fact, reliable. The following conclusions can be drawn:

Stratiotes aloides has an apparent greater affinity for the Rhine areas than for those of the Waal. This species occurs in all three areas, whenever the old riverbed is as little exposed as possible to the river, a situation which occurred frequently in the Rhine area.

Nymphaea alba has a greater affinity for the Guelders IJssel areas than for those of the Waal, probably because the intensity of flooding is less in the former than in the latter.

Polygonum amphibium fo. *natans* has a greater affinity for the Waal areas, with intensive flooding, than for the Rhine areas, where it is less intensive.

Furthermore, it appears that *Nymphaea alba*, which also prefers calmer water according to the observations above, in the Guelders IJssel area, is to be found in another vegetation type than that in which *Stratiotes aloides* is at an optimum. There appear to be, therefore, three biotopes (vegetation types) within the main ecotope, in each of which one of the three limnophytes mentioned above always plays a major role.

We will now discuss the common floating limnophytes which prefer even more sheltered habitats than *Stratiotes aloides*, and one of these in particular, *Hydrocharis morsus-ranae*. According to the affinity diagram, its highest affinity percentage is for *Stratiotes aloides* (90 %) and in addition it shows a high affinity for *Nymphaea alba* (59 %) and *Potamogeton natans* (60 %), while it has a much lower affinity for *Polygonum amphibium* fo. *natans* (26 %). This indicates a triple affinity, which in each separate case agrees with the affinity of each of those species for a given environment in the ecotope. The master factor (although it operates outside the season of vegetation development) is the water movement, especially the intensity of the winter flooding. When we resolve this factor into horizontal and vertical components, we can differentiate three biotopes within the ecotope:

a) *The biotope Mi* (*minor inundation*) whereby the vertical component dominates — thus flooding in winter, but without continuous flowing through by the river. This type occurred everywhere, whenever the old river-bed, or even a section of it, was hardly exposed to the river. (This was rare in the Waal area).

b) *The biotope Me* (*medium inundation*) whereby both components are acting, but still with a weak horizontal component. During the winter flooding there is also, at times, a moderate flow on to the river forelands — a strong current being stopped by trees, bushes and other obstacles, which all tend to decrease the power of the current, or because the current water spreads over vast river forelands, losing much of its speed then. This type was most common in the area of the Guelders IJssel, but it also occurred in the Rhine area, although it was common in the Waal area.

c) *The biotope Ma* (*major inundation*) whereby both components are acting and with a powerful horizontal component, with, as a result, intensive flow through the old river-bed in the river forelands — the water frequently scouring the banks of the winter dykes. This type appeared most commonly in the Waal area.

These biotopes correlated with the optimum-presence of certain limnophytes. In biotope Mi *Stratiotes aloides* was the predominant species; in biotope *Me, Nymphaea alba;* in biotope Ma, *Polygonum amphibium* fo. *natans.*

We now return to three limnophytes mentioned earlier — *Nymphoides peltata, Nuphar luteum* and *Potamogeton lucens.* The question was raised at the beginning of this chapter as to why *Potamogeton lucens* and *Nuphar luteum* occurred together in the Rhine area in many more (79 %) pools than either of this species with *Nymphoides peltata* (50 % and 43 %). Below we give the percentages concerning the affinity of these three limnophytes for the 3 species which indicate a certain type of biotope.

Type of biotope / Limnophyte with high presence all over the ecotope	Mi characterised by Stratiotes aloides	Me characterised by Nymphaea alba	Ma characterised by Polygonum amphibium fo. natans
Nymphoides peltata	67	81	97
Nuphar luteum	95	84	76
Potamogeton lucens	86	75	73

Nymphoides peltata, Nuphar luteum and *Potamogeton lucens* have all three a high affinity for the three species which show an optimum presence in one type of the main ecotope. *Nymphoides peltata* has, nevertheless, a preference for biotope Ma, while *Nuphar luteum* and *Potamogeton lucens* show a somewhat weaker preference for biotope Mi. This agrees with the above statement that the latter two species formed an obvious combination in the Rhine area.

The affinity of these three limnophytes for the biotope Me shows a smaller mutual difference than that in the biotopes Mi and Ma. This would suggest a preference for a "mean" biotope, between Mi and Ma. This is also the case with regard to water movements.

From the above we can conclude that it is possible to use the affinity diagram in which the correlation of the occurrence in limnophytes in a given biotope is expressed, to examine if a certain environmental factor — in this case water movement — can influence the rates of occurrence and of coincidence of these limnophytes.

To reverse the process, it is possible to draw the conclusion that the occurrence and frequency of certain limnophytes can be used to indicate the nature of water movement in a given area.

The movement of water is, however, generally not a direct factor, as it does not occur, for the most part, during the active growth season of the plants. It prepares in most places the environment in which the plants renew their life-cycles every year. In the present case, water movement (flooding) acts as an indirect factor ensuring that the environment remains more or less rich in nutrients and oxygen, while keeping the formation of peat down. The intensity of the water movements is determined by the nature of the substrate which is flooded in winter.

These ecologically obtained results have been verified hydrographically during a discussion with Ir. J. W. Tops (Research Department of the Ministry of Public Works). Our conclusions about the intensity of water movements in the old river-beds of the Rhine, Waal and Guelders IJssel agreed entirely with the evaluation of Ir. Tops, based on hydrographic data.

We will consider once more the ecological data on the separate river-beds, to illustrate the results obtained concerning the divisions of the ecotope under consideration. We begin with the area of the Guelders IJssel. The river foreland waters examined are arranged in Table 7 in the topographical order in which they are situated between Rheden in the South and Kampen in the North. From the above it will be seen that *Potamogeton lucens*, *Nuphar luteum* and *Nymphoides peltata* occur in most places and that their rate of occurrence increases, in general, in the downstream direction. The abundance of *Nymphoides peltata* was lower here than in the Waal area. The waters 1 to 6 lie on the stretch of the Guelders IJssel between Rheden and Wilp where the current is probably more powerful than it is downstreams, although it is weakened by flowing over the wide river forelands and becomes, therefore, weaker than that of the Waal. *Nymphaea alba* (representative of biotope Me) occurs here and at once more than in the Waal, but its abundance is low. *Stratiotes aloides* (representative of biotope Mi) is nowhere to be found. The waters 7 to 11 lie on a section between Wilp and Olst with narrow river forelands and a slightly meandering river which allows an increase in the speed of the current, the forelands probably being flowed through with a greater force. It is striking that *Polygonum amphibium* fo. *natans*, which shows an optimum presence in biotope Ma (see Waal areas, below) was regularly and abundantly present while *Nymphaea alba* was much less in evidence. That the latter species occurs in the Hengvordenwaarden and the Hank at Welsum in this middle section, against tentative expectation, is due to local circumstances. In both cases there was shelter against a powerful current, caused by a factory and trees. Accordingly *Nymphaea alba* occurred much more in the calmer Southern section. Just the opposite is true for *Nymphoides peltata*. — The last downstream section containing waters 12 to 21 between Olst and Kampen begins with a large meander near Fortmond, followed by a series of weaker bends, while at Zalk more, large, meanders appear. In this downstream section, where the river probably once more loses much current speed and where the river forelands are locally wider, *Nymphaea alba* occurs abundantly and constantly. In addition, we find in this section (although only locally in small waters and ditches) *Stratiotes aloides* — representative of the biotope Mi. This limnophyte was very locally dominant in only two of the river-beds situated extremely downstream.

Polygonum amphibium fo. *natans* was seen only once in the downstream

Table 7

		Old riverbeds of Guelders IJssel		a: Stratiotes aloides	b: Nymphaea alba	b: Potamogeton lucens	b: Nuphar luteum	c: Nymphoides peltata *)	c: Polygonum amphibium fo. natans	Environmental type per riverbed
1	G. 82	Rhedense Laak	upstream section		·			·	○	cb
2	G. 83	De Lamme IJsel				·	·	·		b
3	G. 98	Dierense Hank			·	·	·	·	·	bc
4	G. 91	Old riverbed near Gelderse Toren			○	·	·	·		b
5	G. 81	Vreekolk and vicinity				·	·	·	·	b
6	G. 85	Blanke Hank			·	·	●	·		b
		and other waters near Nijenbeek			●	●	·	○	○	bc
7	G. 92	Waters in "Waarden" near Wilp	middle section			●	●	●	●	cb
		ditto, less exposed				○	●	·	·	b
8	G. 93	Old riverbed in Ossenwaard				●	●	○	·	b
9	G. 94	Munnikenhank			·	·	·	·	●	cb
10	G. 95	Old riverbed in Hengvorden		○	·	·	·			a
		and Olsterwaarden			●	●	●	○	○	bc
11	G. 86	Hank near Welsum			·	·	·	·	·	bc
		and Kleine Hank			●	●		·		b
12	G. 96	Old riverbed Olsterwaard	down-stream section	○	○	·	·	○		b
13	G. 97	Hank near Veessen IV			●	·	●	●	·	ba
		ditto II			·	·	·	·	·	b
14	G. 99	ditto I					○	●		bc
15	G. 87	Scherpenzeelse Hank			●	○	●	·	○	bc
16	G. 88	Strang near Herkeloo		●		·	·	·		a
17	G. 100	Spoolderhank		·	●	●	●	○	·	b
18	G. 89	Hank near Zalk		●	○	·	●	·		ba
19	G. 101	The Koeluchtergat		○	○	○	●	○		ba
20	G. 90	Hank near Wilsum		●	○		○			a
21	G. 102	Hank near Wilsum			○		●	●		b

This survey is taken from the general survey of the entire ecotope (see page 257)

· = present

○ = fairly common

● = very common

*) = Nymphoides peltata was less frequently dominant in the area of the Guelders IJssel than in the Waal-area

section of this series with a fairly high abundance — in the Scherpenzeelse Hank, just in the most Northern outside bend of the meander around Fortmond. It was sporadic in the Spoolderhank, situated much further North.

From the above we see that the biotope Me (characterised by *Nymphaea alba*) dominates in the area of the Guelders IJssel. In the median section of this type, there is a change over to biotope Ma (characterised by *Polygonum amphibium* fo. *natans*). In the downstream section there are various changeovers to the biotope Mi (characterised by *Stratiotes aloides*). This subdividing is only of a general nature; local circumstances may cause exceptions.

In the Waal area, the manner in which these limnophytes occurred was quite different. *Stratiotes aloides* and *Nymphaea alba* were rarely present; exceptions were the pools of the Old Waal at Nijmegen (W. 52), the Western riverbed of the Kil at Tiel (W. 64), the Eastern section of the Kil at Hurwenen (W. 66) and the Kil at Waardenburg (W. 67). These four old river-beds are, however, the most sheltered from the river, and although certainly flooded, the current does not pass directly through them. As far as *Stratiotes aloides* is concerned, this was also the case in the Strang near Hien (W. 61). The behaviour of *Nymphoides peltata* and *Polygonum amphibium* fo. *natans* was very striking, both species being abundant in 16 of the 27 old river-beds of the Waal, which percentage was very much smaller in both other areas — i.e. that of the Rhine and Guelders IJssel. These 16 areas we consider as being part of biotope Ma.

In the Rhine area only twelve old river-beds could be compared for the differentiation of types. Although the river-beds near Lexmond (R. 31) and Groot Ammers (R. 32) represented the calmer type of biotope Mi, and the Strang near Huissen (R. 36) resembled that of biotope Me strongly, it is not possible to place the remaining river-beds of the Rhine in a definite biotope — they were, in fact, mixed biotopes, which appeared along the Waal and Guelders IJssel as well. The difference between the biotopes becomes clear whenever one considers a number of objects, in which obvious environments can be differentiated. As soon as one goes into details, it is possible to find two biotopes in the same area. This occurs, for example, when an old river-bed consists of several waters each having a different situation from the river.

A good example of this is the area of the Blanke Hank and other waters near the Castle of Nijenbeek in the district of Voorst (G. 85). The Blanke Hank itself lies far from the river and the current is weak here, due, according to our observations, to the fact that the main dyke (Voorster Kleidijk) at this point runs back rather far and a few smaller dykes give some shelter. Floating swamps in this water indicate that very little erosion takes place. The surface of the water is covered with a little *Nymphoides peltata*, some fields of *Nymphaea alba*, but especially by *Nuphar luteum*. One might expect *Stratiotes aloides*, but a helophyte, *Typha latifolia*, indicates the calm nature of the surroundings here. In pools that are nearer to the river, *Polygonum* *amphibium* fo. *natans* occurs and *Nymphoides peltata* has an even greater abundancy — indicating biotope Ma.

The phenomenon of mixed biotopes may also have this aspect, that in one single pool separate sections can be differentiated, the one section being more exposed to the winter flooding than the other. In the old river-bed at Amerongen (R. 44) *Potamogeton natans* dominated in the Southern shallow half (Kilsloot), while *Nymphoides peltata* was the most obvious species in the Northern and deeper half (Kil). In the Old Waal, South-West of Ochten (W. 72), the Eastern section was, to a large extent, overgrown with *Potagometon natans*, while in the Western part, *Polygonum amphibium* fo. *natans* and *Nymphoides peltata* dominated. In the first example the limiting factor is probably the depth of water. In the second case, the limiting factor is probably the difference in exposure to the river.

Finally, some remarks will be made on *Potamogeton natans* and *Hydrocharis morsus-ranae.*

In some waters the first mentioned limnophyte covers great areas, and these are strongly reminiscent of biotope Me. Probably these waters are too shallow for *Nymphaea alba.* Examples are the Old Loop at Elst (R. 41), the river-bed in the Waterschap Bovenpolder at Amerongen (R. 34) and the Kilsloot at Amerongen (R. 44) mentioned above.

Hydrocharis morsus-ranae is a regularly occurring species in the sheltered helophyte zone of the Guelders IJssel area. One can consider this species as an indicator of the extremely calm environmental type, if it forms a community at the centre of the water with, for example, *Stratiotes aloides*, and is then abundant. This was observed in a small water against the dyke in the area of the Hank near Veessen (G. 99) in the Northern section of the Guelders IJssel, where *Typha latifolia* occurred as well, in the small water of the Hank near Zalk (G. 89) and in an isolated water of the Hank near Wilsum (G. 90), all areas in the most Northern IJssel section. The same phenomenon was seen in an isolated water from the gully of the Kersbergsrak near Lexmond (R. 31) and, less obviously, in an isolated water in an old river-bed of the Lek near Groot Ammers (R. 32). *Hydrocharis morsus-ranae* was, therefore, co-characteristic of the biotope Mi in the ecotope concerned.

4. CONCLUSIONS CONCERNING THE SPECIES OF LIMNOPHYTES SEPARATELY

1) *Nymphoides peltata* (Gmel.) O. Kuntze was only observed in the Maas, Waal and Rhine areas downstream from Wychen to nearby Drongelen (Oude Maas), Poederoyen (Heusdense Maas), Zaltbommel (Waal), Maurik (Rhine) and nearby everywhere in the Guelders IJssel area as far as Kampen. The plant grows there in waters of the old river-beds, that are mostly situated in river forelands. These pools are stagnant, shallow, eutrophic waters, sometimes in still open connection with the river; in the winter months they are flooded or flowed through. In the waters of the Waal forelands with a clay

bottom, where the erosion of the river is the most powerful, and the depth is, in general, considerable, we find *Nymphoides peltata* most frequently. It occurs a great deal in depths between one and one and a half metres and competes in these places with *Nuphar luteum*. It reaches its maximum vitality at a depth of about 2 m, probably because competition with *Nuphar luteum* then no longer takes place. Unfavourable environmental factors for the plant are the absence of water movements or, on the other hand, the presence of tidal movements (resulting into low temperature, greater depths and perhaps also increasing salinity). In the Roodvoet at Maurik, *Nymphoides peltata* was observed together with *Potamogeton perfoliatus* and *Potamogeton pectinatus*. This was the only case approaching a full *Limnanthemo-Potametum pectinati*, as defined by ALLORGE (1922). The question whether this association occurs in the Netherlands at all is examined in the study by J. VAN DONSELAAR: "Former riverbeds and their vegetation in the Netherlands" (1961). In 41 % of the areas the plant was observed with one of the mentioned *Potamogeton* species, mostly in the Waal forelands, where *Nymphoides peltata* showed a high abundance in so many waters. In 59 % of the areas *Nymphoides peltata* occurred without the two *Potamogeton* species. In many Waal forelands *Polygonum amphibium* fo. *natans* was one of the plants found in the same biotope as *Nymphoides peltata* (see conclusions concerning *Polygonum amphibium* fo. *natans*).

2) *Potamogeton lucens* L.

This plant grows frequently and often abundantly in the waters of former river-beds, most of all in those flooded in winter. On the other hand it was seldom found in stagnant waters that are rarely or never inundated or in the tidal areas. The greatest abundance was at depths of 100 cm and 110 cm and to a lesser extent in 50–150 cm water. Over a wide depth amplitude from 40–300 cm (and probably even deeper) the plant may dominate. The average degree of coverage increases between depths of 210 and 300 cm, which is probably a result of the absence of competing floating water plants at this depth.

Unfavourable environmental factors for the plant are the absence of water movement and the presence of tidal movements. In waters with a chloride content of more than 90 mg/l, the abundance of *Potamogeton lucens* was lower than that of *Nymphoides peltata*, which suggests that it prefers fresher water.

3) *Nuphar luteum* (L.) Sm.

This plant was found frequently in the waters of the old river-beds, showing a preference for waters in the river forelands which are flooded in the winter. This was also shown in its abundance or dominance in these places.

The plant was rarely seen in areas subject to tidal influence and then only in places where the horizontal and vertical movements were small. It occurred the most at depths between 100 and 110 cm and frequently at depths between 40 and 150 cm. At depths of 80–200 cm the plant was able to dominate and at 100 cm and 120 cm it was the most frequently seen as dominant. The average degree of coverage gradually decreased as the depth increased from 170 to 300 cm.

The behaviour of *Nuphar luteum* towards acidity and increasing chlorinity was nearly the same as that of *Nymphoides peltata.*

4) *Nymphaea alba* L.

This plant was less commonly found in the waters of the old river-beds. It showed a preference for the areas with stagnant water, seldom or never flooded, especially in those waters on river-"loam" soils. In such stagnant waters the plant occurred nearly as much as *Nuphar luteum.* In the areas with winter flooding, the species was present only one half as much as *Nuphar luteum* and then almost entirely in waters not directly in the current. It was seen only once in tidal areas. As far as abundance is concerned *Nymphaea alba* was locally conspicuous in stagnant waters seldom or never flooded; in the three old river-beds in the river-"loam" areas, the plant covered the greater part of the water surface. In various waters not directly affected by current, in the forelands of the Guelders IJssel, the species was abundant.

At depths of 100 cm the plant was frequent, less so at depths of 70, 110 and 150 cm. The greatest cover degrees were observed at depths from 70 to 250 cm; at a depth of 150 cm it occurred most frequently as a dominant. With increasing depth, the average degree of coverage also increased down to 180 cm. *Nymphaea alba* is thus optimal at a greater depth than *Nuphar luteum,* provided that the situation is sheltered. Its optimum presence was correlated with a certain type of the old river-beds — that in which the horizontal component of the flood water is not intensive —, a type which was frequent in the valley of the Guelders IJssel. The species proved to be insensitive to increasing salinity up to a level of 112 mg/l chloride.

5) *Potamogeton natans* L.

This plant was uncommon in the waters of the old river-beds. In stagnant waters without winter flooding it occurred much less frequently than *Nymphaea alba,* although it was found everywhere together with *Nymphaea alba* in waters with a bottom of "river-loam". In the river forelands with winter flooding it was as common as *Nymphaea alba.* The abundancy was low in waters subject to direct current. It was seen only once in areas with tidal movements and then in a place where the effect of the water movement was low.

The plant was found most frequently at depths of 80 and 100 cm, less frequently at 30, 70 and 100 cm. This agrees with results published by other authors, where it is stated that the plant usually occurs less in water below 100 cm deep. The higher degrees of coverage were recorded at a depth of 60, 70, and 100 to 150 cm, with a maximum at a depth of 80 cm — when the plant was most frequently dominant too. The species was intensive for chlorinity up to a value of 104 mg/l.

6) *Polygonum amphibium* L. fo. *natans*

This plant was infrequent in stagnant waters not flooded and totally absent in very calm waters. In foreland waters flooded in winter it was observed somewhat more than *Nymphaea alba* and *Potamogeton natans*. It showed a great affinity for the waters where *Nymphoides peltata* was found. In the areas subject to tidal movements the plant was observed only once and then in a place where the influence of the water movement was little.

The plant was observed most frequently at a depth of 70 cm, but was also rather frequent in depths between 40 and 120 cm. The highest degrees of coverage were recorded in depths between 0 and 70 cm, at 120 cm, and between 240 and 300 cm. The three peaked optimum is peculiar and is probably the result of insufficient data.

III. HELOPHYTES

1. INTRODUCTION

Apart from the limnophytes some species will be dealt with here which are no waterplants in a proper sense; according to their life from they are regarded as helophytes by RAUNKIAER (1934). This definition implies plant species with over-wintering buds in water or in the submerged bottom, but which differentiate themselves from the limnophytes in that their vegetative organs are, under normal circumstances, partially raised above water level. Precise definitions within this group were given by IVERSEN (1936) who did not regard the place of the winterbuds as crucial, but the adaptation of the plant to the factor water. As far as we are concerned here, Iversen's different types are:

Telmatophytes: species with assimilative branches adapted to the atmosphere outside water and possessing a tissue rich in air-spaces (*Typha* spp., *Equisetum fluviatile*, *Glyceria maxima* and *Phragmites communis*).

Amphipytes: species which as well as being emergent and adapted to living above water, form definite hydromorphic branches or habitat modifications. In the water forms, in contrast to the land forms, the vegetative parts are larger, while the blooming shoots are reduced (*Scirpus lacustris*, *Ranunculus lingua*).

These groups, as well as the limnophytes in the sense given by Iversen, have been studied in the Netherlands by WESTHOFF (1947) and ZONNEVELD (1960).

We have restricted ourselves to a choice of six species in our discussion of the above groupings, because from these species a preliminary calculation indicates that reliable results are obtainable. Thesewere five species of telmatophytes — *Typha angustifolia* L., *T. latifolia* L., *Equisetum fluviatile* L., *Glyceria maxima* (Hartm.) Holmb., and *Phragmites communis* Trin., while the sixth species, *Ranunculus lingua* L. was considered to belong to the amphiphytes, because the winter leaves, formed in water, differ in structure to the summer leaves formed later in the air.

Both *Typha* species possess an exceptionally developed system of air-cavities, developed by the tearing of cells (rhexigen tissue). Both *Glyceria maxima* and the *Typha* species possess an aerenchymous tissue in the lowest sections of the stems and roots. They are thus equiped to take in oxygen from the air above the water, and to conduct this to a part which is exposed to an environment poor in oxygen or polluted.

2. DISCUSSION OF THE HELOPHYTES SEPARATELY (DISTRIBUTION AND HABITAT)

2. 1. TYPHA ANGUSTIFOLIA

2. 1. 1. Distribution

Europe (not Greece), West Asia and North America. It is less common in Denmark, South Sweden and the Baltics to about 60° N, but occurs further to the North (to 63° N) in scattered localities (HULTÉN 1956).

2. 1. 2. Habitat

In and along rivers, "boezems", canals, ditches, pools, lakes and millponds (Münsterland), also marshes, reedswamps, dune valleys, heath pools and peat holes.

The plant is to be found in stagnant or slowly moving water and on sheltered spots, with an organic substrate consisting of a thick layer of sandy mud above a hard sand layer, or of softish dead remains, both plant and animal. The plant also forms a floating strip on the free water side of reed belts along banks, frequently as a facies of overwhelming vegetative plants. In *Sphagnum*-rich areas it occurs higher up the banks with a lessened vitality (VLIEGER, in VAN ZINDEREN BAKKER 1942). At a depth of 200 cm, vital tussocks are still formed, but sterility increases with depth. The species likes warmth, and tolerates salinity. OBERDORFER (1949) calls this, incorrectly, "etwas salzliebend", but the species occurs in water with a very low chloride content in equal numbers and with equal vitality as in mesohaline water.

2. 2. TYPHA LATIFOLIA L.

2. 2. 1. Distribution

In the North temperate zone of Europe, North-Africa, Northern Asia, North-America and in the tropics, also in Australia and Polynesia, but absent in central and Southern Africa. In the North its area resembles that of Typha angustifolia, but it is to be found in Finland and in the Gulf of Bothnia as far as 66° N, although on isolated localities.

2.2.2. Habitat

In and along ditches, canals, rivers, lakes, broads, swamps, reed-marshes, dune valleys. Avoids large bodies of water, but is plentiful in borrow-pits near tile works (MEYER and VAN DIEKEN 1947). It is restricted to sheltered corners and bends. According to VLIEGER in VAN ZINDEREN BAKKER (1942) in the lake of Naarden optimal in swamp areas completely filled in by succession and in habitat rich in *Sphagnum*. WESTHOFF (1948) and MEYER and DE WIT (1955) recorded the species in the vegetation analyses of Botshol, resp. Kortenhoef, on the contrary, not in *Sphagnum* growths, but in less acid water. Since the Naardermeer is intermediate to Botshol and Kortenhoef as far as chlorinity is concerned, difference in chloride content cannot be sought as the origin of this contradiction.

The species can pioneer in both damp places and water habitats (depth 0–2 m) (ALLORGE 1922). According to BOER (1942) the species prefers sand poor in phosphate in contrast to *Typha angustifolia;* according to CLAPHAM, TUTIN and WARBURG (1952) the plant grows especially on an inorganic substrate or in an environment where sedimentation and the rapid disposal of organic material take place. This agrees with our experience in the Netherlands. BLAAUW (1917) states that *Typha latifolia* probably formed floating swamps in the 17th and 18th centuries in an old — in 1220 shut-off — sea-arm near Rockanje. Later, this "Meertje van Rockanje" developed into a large reedswamp in which *Typha latifolia* was still to be found locally in 1956. On the Eastern side of the Berenplaat (an little island shut in by the Old Maas, the Spui and the Berengat in the community of Oud Beyerland) there is a sheltered spot between two jetties, where the water inundates the thick mud only at the highest tide. In summer this habitat is sweltering hot. In this spot *Typha latifolia* grows over a surface of about 200 square metres, not as a facies, but distributed between the 2½ m high stems of *Phragmites communis* var. *latifolia.* Probably, *Typha latifolia* arrived there first and the species is gradually disappearing, as is the case at Rockanje. In both cases an environment is involved, where sedimentation takes place (or took place).

It was also striking that, in the so-called Great Pond originally dug for hunting purposes in the mesotrophic basin bog of the nature reserve "The Korenburger Veen" at Winterswijk, where *Typha latifolia* used to occur frequently but not abundantly, the plant suddenly became absolutely dominant when the "pond" fell completely dry in the exceptionally dry summer of 1947 and the layer of organic mud on the bottom began to oxidise rapidly (WESTHOFF and VAN DIJK 1952). The same phenomenon was observed during the systematic survey of Dutch non-eutrophic pools in 1957. In the community of Zundert, the pool "Oude Zoek" in the middle of the reclaimed meadows was visited. This had almost run dry and nearly half of the pool was found to be overgrown with an luxurious and vast vegetation of *Typha latifolia* (VAN DER VOO 1957).

In N.W. Europe, this species appears to have more preference for meso- or oligotrophic habitats than *Typha angustifolia*, although OBERDORFER (1949) recorded it in Southern Germany as a pioneer in stagnant waters rich in nutrients. It is possible that this difference is connected with the warmer summer climate in the continental area last mentioned.

Typha latifolia was found in the "Meertje" at Rockanje, at a chlorine level of 2006 mg/l chloride. On the outside of the "Berenplaat", the value was 122 mg/l chloride (observations 1956).

2. 3. EQUISETUM FLUVIATILE L.

2. 3. 1. Distribution

Europe (but rare in the Mediterranean region, in some areas even absent; until above 2400 metres in the Alps and above the 68th parallel); Northern Asia and North-America. The plant is fairly common in the Netherlands, throughout the whole country — according to VAN OOSTSTROOM (1948), less common in the Haf district and on the South-Holland and Zeeuws islands. In our experience this statement over the Haf district is true only for cultivated landscape; in the extensive fens and swamps of the provinces Holland and Utrecht and North-West Overijssel — being the most characteristic part of the Haf district —, *Equisetum fluviatile* occurs in large quantities indeed.

2. 3. 2. Habitat

In and on ditches and on moist stations, also in ponds, dam-breakthrough pools, heath pools, peat-diggings, along the banks of old river-beds, canals, lakes and broads.

In stagnant or hardly moving water to a depth of 2 m, rarely in flowing water. It occurs in waters both rich and poor in nutrients (eutrophic to oligotrophic). When pioneering in shallow waters it may form large vegetations. It can also form floating swamps (HEGI 1935) by means of which the entire surface of the water may become covered. In mountain areas, the plant tends to be vicarious of the reed swamp community. According to BOER (1942), the species encroaches from water, in some cases being found with *Menyanthes trifoliata* in the outermost fringe, into the *Scirpeto-Phragmitetum*, also into the large reed swamps (transitions from *Phragmition* to *Magnocaricion*) and even often into the degenerated (more acid) reed swamps as well, although in the last case with a lessened vitality. It shows therefore a great ecological variation. Its ecology has been examined by KUIPER (1958) in N.W. Overijssel, who regarded vegetations with dominant *Equisetum fluviatile* as a stage in one of the three chief land forming seres in the area — that characterised by *Carex diandra*. The difference between these seres is controlled by the depth and extent of the open water where the succession begins. See also VAN DER VOO (1957) in a description of the Kameriks Nessen in the Oude Miland.

2.4. Glyceria maxima (Hartm.) Holmb.

2.4.1. Distribution

Nearly over entire Europe (absent in the most Northern area of Scandinavia and Russia). It is less common in Denmark and the Baltic countries, but is known locally North to the 65th parallel (Hultén 1950).

2.4.2. Habitat

Along rivers, canals, ditches, broads, lakes, ponds, dam-breakthrough pools, in reed-swamps and sedge-fen, in wet, fertilised and open grasslands, strikingly common in pastures used for geese and the flood areas of brooks.

In wet places with eutrophic, stagnant or hardly moving water, also in the mud on the banks of large waters, lakes and ditches. Thermophilous; prefers calcareous habitat. In the large mesotrophic swamp area in the lake of Naarden, for instance, it has been observed only in few localities, probably because it prefers moving water richer in oxygen than this area presents (Vlieger in Van Zinderen Bakker 1942). According to Boer (1942) *Glyceria maxima* is strongly facies-forming, frequently making bands along reedbanks and *Typha* vegetations in ditches and at the entrance of fen broads partially filled up by succession and with nearly stagnant water, such as in the Zuideindiger-, Belter- and Beulakerwijde. The species finds an optimal environment in the ditches containing very rich water and filled with deep, centuries old mud, in the polder-water reservoirs fen of the "Vlaardinger Vlietlanden", where a concentrated mixture of finely divided organic material and fine silt is suspended in the water. According to Tansley (1949), the development of the species depends more on the presence of the humus layer formed by itself than on the mud deposition of the river. The mat of rhizomes and rotting parts of this species is more resistant to erosion than the vegetative parts of species such as *Sparganium erectum.*

2.5. Phragmites communis Trin.

2.5.1. Distribution

Belongs to the most widespread cosmopolitan plants. Distributed over Europe, Asia, America, Africa, Australia (appears to be absent in New-Zealand), Polynesia. It is to be found in Iceland (Bittmann 1953) and in Finland as far as the 70th parallel, but just as much in moist, low-lying tropical areas, while it reaches a height of 3000 m in Tibet.

2.5.2. Habitat

Along and in ditches, canals, rivers, old river-beds, waters, lakes, broads, pools and ponds, marshes, peat-holes, in wet grit-diggings, in fens and stream marshes, also in marshy woodlands and moist to wet grasslands, in moist to wet dune valleys, in reclaimed land (*en masse* in the N.O. Polder) and lands artificially covered by sand or mud; frequently long standing when its habitat is drying up or has been blown over by sand; also on brackish or salt ground. As a result of increasing water pollution it is gradually spreading in pools and fens, where it was absent until a short time ago.

Not in water extreme poor in nutrients (raised bogs and oligo-dystrophic heath pools). In stagnant or hardly moving fresh waters, in fresh and brackish tidal waters, but also in salt steppes and on saltmarshes, while it is to be found on clay and sand as much as peat bottoms. The presence of calcium in the soil is not necessary. Nitrogen compounds appear to influence the growth of reed more than any other nutrients (BITTMANN 1953). The size and the density of growth in this species show a maximum in warm and tropical areas, and a minimum in cold zones. At sea-level, it shows a great vitality while this decreases with increasing height, reducing to a minimum in the mountains. According to BOER (1942) the species grows in water to a depth of 120 cm; SCHRÖTER and MAGNIN (acc. GADECEAU 1909) recorded a maximum depth of 2.00 m. JANSEN (1951) states that it occurs down to a depth of about 2½ metres. HAVINGA (1956) recorded a depth of 10 to 30 cm as an ideal condition for reed cultivation.

2.6. RANUNCULUS LINGUA L.

2.6.1. Distribution

Europe and Asia, but not in the far North; HULTÉN (1950) states that in Denmark, South-Sweden and Finland it is known from scattered localities as far as the 65th parallel, but that further North it is very rare. It is found in the Alps not higher than 600 m alt.

2.6.2. Habitat

This marsh plant occurs on the edges of the water in broads, lakes, ditches, in swamps with a peaty bottom, in peat holes in wet fen and also in floating swamps, as soon as these have gained a firmer constitution.

In stagnant or hardly moving shallow water with a substrate rich in humus and nutrients, mostly calcareous. Thermophilous and halophobous.

3. THE RELATIONSHIP BETWEEN THE DEPTH OF WATER AND THE OCCURRENCE AND RATE OF DOMINANCE OF THE SIX HELOPHYTES

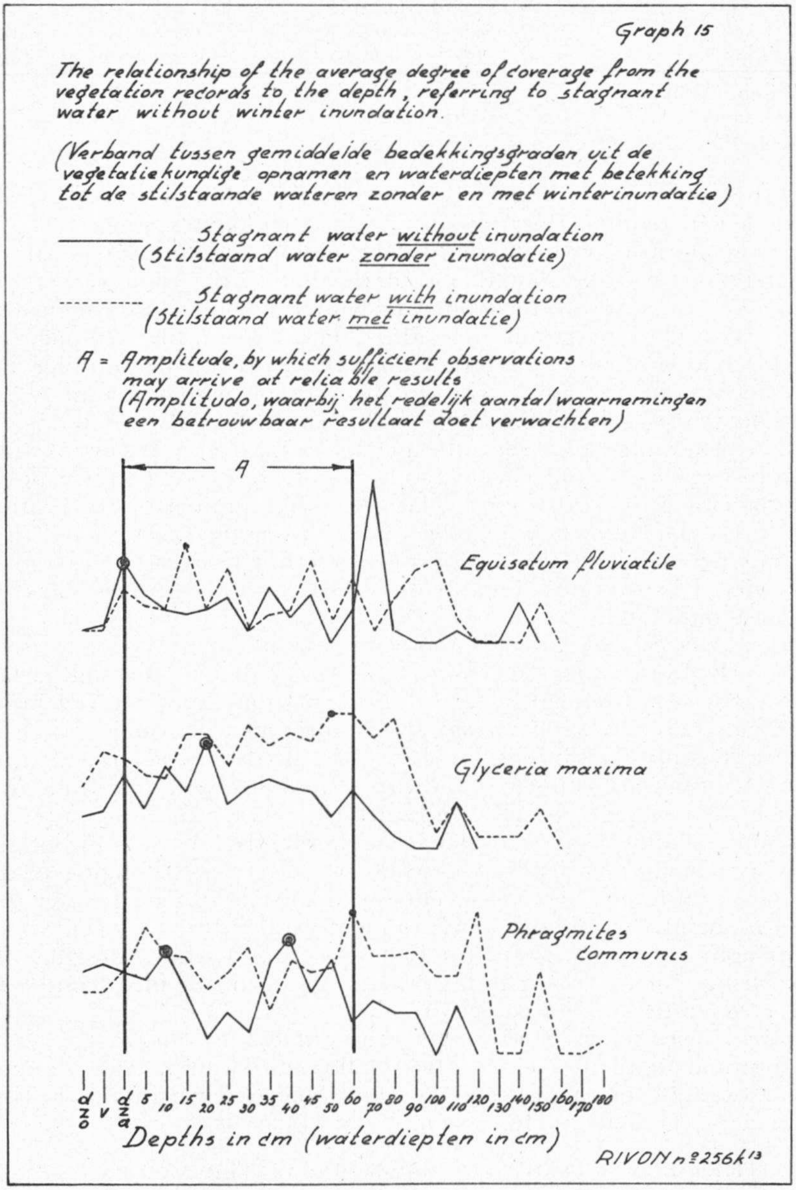
In accordance with the manner by which the presence and average cover degrees at various depths based on the sample plot records were considered for the limnophytes, the six helophytes (*Typha angustifolia, Typha latifolia, Equisetum fluviatile, Phragmites communis, Ranunculus lingua* and *Glyceria maxima*) will also be discussed. The conclusions are shown in the following table:

Species	flooding	Presence optimum at depth (in cm) of:	Amplitude of depth in cm	Cover degrees 3, 4 or 5 at depths (in cm) of:	Maximum of the average cover degree at depth (in cm) of:
Typha angustifolia . . .	●	50, 90, 100	*d*–150	10, 60, 75–140, *f.f.*	100, 110
	○	20	*m*–120	35, 40, 50–60, 100 *f.f.*	40, 60
Typha latifolia	●	80	0–80	*f.s.*	35, *f.s.*
	○	*m*, *f.s.*	*d*–100	f.s., t.s.	*sw*, *f.s.*
Equisetum fluviatile . . .	●	25	*d*–150	*sw*, 10–50, 80	15
	○	*sw*, *f.s.*	*d*–140	*sw*, *t.s.*, *f.s.*, 3, 20–40, 60	70
Phragmites communis [1]) .	●	5	*d*–180	*d*, *m*, *sw*, 0–150	60, 120
	○	m	*d*–110	*d*, *m*, *sw*, *f.f.*, 0–70	40
Ranunculus lingua . . .	●	45, *f.s.*	*m*–80	10	45
	○	*sw*, 25	*m*–110	—	5, 60
Glyceria maxima	●	25	*d*–150	*d*, *sw*, 0–100	50
	○	25	*d*–120		20

Explanation of abbreviations:
● = waters inundated in winter flooding
○ = waters without winter flooding
d = damp
m = moist
sw = swampy
t.s. = trembling swamp
f.s. = floating swamp
f.f. = floating fringe

[1]) See page 239 concerning the habitat of *Phragmites communis*.

From the six helophytes under consideration *Equisetum fluviatile*, *Glyceria maxima* and *Phragmites communis* were recorded most frequently in the sample plot analyses. In graph 15 we have given the relationship between the average cover degrees of these three species and the depth of water, as for stagnant waters without winter flooding as well as stagnant waters with winter flooding. In examining the three curves, the total number of observations per depth must be considered, because a single observation with a high degree of coverage will lead to a rise, giving a false picture (see, for example, *Equisetum fluviatile* in 70 cm of water). In graph 15, therefore, that very depth amplitude has been represented over which reliable results can be obtained as sufficient observations have been made. This amplitude stretched between 0 and 60 cm. From this the following results were obtained, which are in some ways different to those given in the above table.


Graph 15
The relationship of the average degree of coverage from the vegetation records to the depth, referring to stagnant water without winter inundation.
(Verband tussen gemiddelde bedekkingsgraden uit de vegetatiekundige opnamen en waterdiepten met betekking tot de stilstaande wateren zonder en met winterinundatie)
Stagnant water without inundation
(Stilstaand water zonder inundatie)
Stagnant water with inundation
(Stilstaand water met inundatie)
A = Amplitude, by which sufficient observations may arrive at reliable results
(Amplitudo, waarbij het redelijk aantal waarnemingen een betrouwbaar resultaat doet verwachten)
A
Equisetum fluviatile
Glyceria maxima
Phragmites communis
d Z O
V
d Z a
5 10 15 20 25 30 35 40 45 50 60 70 80 90 100 110 120 130 140 150 160 170 180
Depths in dm (waterdiepten in dm)
RIVON nº 256k13

	Maxima of the average cover degree over the depth amplitude 0–60 cm	
	Ecotope Es stagnant waters without winter flooding at depth of	Ecotope Ee stagnant waters with winter flooding at depth of
Equisetum fluviatile . . .	0 cm (swampy)	15 cm
Glyceria maxima	20 cm	50 cm
Phragmites communis . .	10 and 40 cm	60 cm

From the course of the curves it might follow that in stagnant waters with winter flooding, these three helophytes reach a higher optimal cover degree in greater depths than in stagnant waters without winter flooding. We should note here, that in the ecotope Ee, with stagnant waters that are flooded in winter, the yearly differences in the size of the inundation affect the data unfavourably (see page 166 of the chapter on limnophytes). Therefore we restrict our consideration to the ecotope Es only — i.e. to the ecotope with stagnant waters without winter flooding.

The next table 8 represents the average cover degree at several water depths between 0 and 60 cm for the six helophytes in this ecotope. The averages derived from a relatively large number of observations are printed in italics, while the optima from these are boxed. The depths belonging to the boxed and underlined cover values can be considered as the most reliable ones. By these, the species show the highest or a high abundancy.

Equisetum fluviatile appears therefore, as indicated above, to occur optimally by a water level approximately equal to the soil surface and takes, very frequently, part in the formation of floating vegetation (see page 237). *Glyceria maxima* shows three nearly equal optima — i.e. in swampy conditions, in water 35 cm deep and as a floating fringe community. This may indicate a greater depth amplitude over which the coverage is really constant. This plant can also completely fill some shallow waters in the river forelands; an example of this was seen in the old arm of the Maas near Reuver, belonging to this ecotope. *Phragmites communis* occurs optimally in 10 cm of water, but also frequently in swampy environments and in 35 cm deep water. This agrees with the results of HAVINGA (1956) who states that the reed fringes in 10 to 30 cm deep waterways form the ideal conditions for reed cultivation (reed fen in N.W. Overijssel).

Typha angustifolia, *Typha latifolia* and *Ranunculus lingua* appear to be optimal in plant communities of floating swamp. An extremely good example of this is their combined occurrence in the Eastern section of the Kil at Hurwenen.

4. OTHER ENVIRONMENTAL FACTORS: WATER MOVEMENT AND BOTTOM

We have based our consideration of the six helophytes on the data given in the general survey (table 1). We have restricted our discussion of habitat factors to the influence of water movement, bottom type

Table 8

Depths of water in cm / Helophytes	0	5	10	15	20	25	30	35	40	45	50	60	f.s. [1]
Equisetum fluviatile	$\boxed{2.00}$	1.20	0.75	*0.70*	0.80	*1.10*	0.25	1.40	0.60	1.20	—	0.80	*1.60*
Glyceria maxima	$\boxed{1.80}$	1.00	2.00	*1.40*	2.60	*1.10*	1.50	$\boxed{1.70}$	1.50	*1.35*	0.75	1.40	*1.70*
Phragmites communis	*2.00*	*1.80*	$\boxed{2.50}$	*1.50*	0.40	*1.00*	0.50	*2.20*	2.75	*1.50*	2.30	0.80	*1.80*
Typha angustifolia	0.50	0.75	0.75	$\boxed{0.90}$	0.25	1.10	0.85	3.00	1.10	—	2.75	0.25	$\boxed{1.30}$
Typha latifolia	$\boxed{1.10}$	1.10	0.25	0.25	—	0.40	—	0.75	0.60	0.60	—	—	$\boxed{1.20}$
Ranunculus lingua	0.50	1.00	0.25	0.50	—	0.40	—	0.45	0.25	0.40	—	1.00	$\boxed{0.80}$

[1] Floating swamp with suspended mud below.

and water depth on the occurrence and abundance of each species. Just as with the limnophytes, attention is concentrated on the environment considered in the above chapter — consisting of waters in the river forelands subject to winter flooding which may or may not be in open connection with the river. We shall not consider stagnant waters without winter flooding which were situated on bottom types only seldom encountered.

In the general survey (Table 1) there is given for each of the six limnophytes, the number of times it occurred (or lacked) with a given water movement and bottom type. According to this, two groups can be differentiated:

a) 35 stagnant waters without winter flooding, on river-levée, river-"loam" or river foreland clay soils (see column I) belonging to ecotope Es.
b) 66 stagnant waters, which are flooded in winter, and which are, in a number of cases, in open connection with the river (column II), all on river foreland clay soil belonging to ecotope Ee.

The results obtained concerning the actual occurrence of the six helophytes in one of the two groups given above are expressed in percentages, as follows:

	Ecotope Es 35 stagnant waters table 1, column I		Ecotope Ee 66 stagnant waters with flooding in winter table 1, column II	
	Occurrence: number of observations	Occurrence: in %	Occurrence: number of observations	Occurrence: in %
Glyceria maxima	30	86	58	88
Phragmites communis . .	26	74	45	68
Equisetum fluviatile	28	80	38	58
Typha angustifolia . . .	14	40	27	41
Ranunculus lingua	16	46	14	21
Typha latifolia	24	68	12	18

The statistical reliability of the apparent differences bewteen occurrence in water with and water without winter flooding was tested by the use of the test of contingency as explained in the case of the limnophytes, see page 180. From this it appeared that only the differences in percentages in the case of *Equisetum fluviatile*, *Ranunculus lingua* and *Typha latifolia* were significant as a definite preference for stagnant water without winter flooding. This preference was particularly obvious for *Typha latifolia.* As far as the other species are concerned we must come to the conclusion that from the material available there is no obvious preference for one or other of the environments. We have calculated the percentage whereby these three helophytes occurred in the two types of water with the three bottom types present here.

bottomtype / helophytes	river levée soil	river "loam" soil	river foreland clay soil
Equisetum fluviatile	73 %	100 %	70 %
Ranunculus lingua.	53 %	50 %	30 %
Typha latifolia	47 %	100 %	70 %

Having used the statistical method on these figures, only the percentage difference in occurrence of *Typha latifolia* on river levée soil and river "loam" was real. This species thus seems to prefer areas with a "loam" bottom to those with river levée soils. This preference is, however, in the first place due to the circumstance, that in this case the waters with a "river loam" bottom coincide with the extremely calm environment of the old river-beds of the Maas. A layer of organic remains arose above the bottom here, as a result of the absence of erosion. In the sheltered, shallow pools with a soft peat bottom, *Typha latifolia* found just the environment that this species prefers.

As to the percentages concerning the ecotope Ee — i.e., stagnant waters with winter flooding — we have split the data once again; but not this time according to bottom types, for these were the same everywhere, but according to the areas of the Rhine, Guelders IJssel and the Waal respectively. This was done to find out just how much the helophytes occurred in each of these areas.

In the table below the percentages are given of the occurrence of the 6 helophytes in these three river areas. The reality of the percentage differences was examined by the usual statistical method. Significant differences have been connected in the table with an arrow: (p. 246).

From this table, the reality of some percentage difference is obvious. From our results in the treatment of the limnophytes, it might be expected that the presence of the helophytes in the different river areas should show significant differences in connection with the degree of intensity of the winter flooding. Both *Typha* species and *Ranunculus lingua* show a significant preference for the areas of the Guelders IJssel as against the Waal. In addition, *Typha angustifolia* and *Ranunculus lingua* show a real preference for the Guelders IJssel over the Rhine. This was also the case, by approximation, with *Typha latifolia. Equisetum fluviatile* shows, according to the percentage figures given below, a higher affinity for the Rhine area than for the other two areas. This preference proved, however, to be insignificant.

	66 stagnant waters with winter flooding (Ee) distributed over:		
	21 areas Guelders IJssel	16 areas Rhine	29 areas Waal
Glyceria maxima	100 %	81 %	79 %
Phragmites communis	81 %	63 %	55 %
Equisetum fluviatile	48 %	69 %	46 %
Typha angustifolia	62 % ←	→ 31 %	31 %
Ranunculus lingua	43 % ←	→ 13 %	10 %
Typha latifolia	33 %	26 %	7 %

Glyceria maxima and *Phragmites communis* showed no real preference for the relatively calm Guelders IJssel area over the Waal area with intensive flooding. Since the number of available data about these species permits reliable conclusions, we may conclude that these species are less sensitive to the occurrence of water movement than the other helophytes. We must remember when examining the percentages given above, just as with the limnophytes, that there is no sharp distinction between the characteristics of the three rivers. For example, in the area of each river there are pools which are more sheltered from the river than others. It is thus very likely that environmental types appear in the Waal area which are characteristic of the Guelders IJssel area. The opposite also occurs, namely, that an environmental type is represented in waters close near the Guelders IJssel which is reminiscent of a type characteristic for the Waal. In the following chapter, concerning the mutual relationships of the helophytes, this will be considered more closely.

5. THE MUTUAL RELATIONS OF THE HELOPHYTES

In the same way as for the limnophytes, an affinity-diagram was constructed for some of the helophytes, using Iversen's method. Apart from five of the helophytes dealt with above, two other species have been included from the submerged riparian zone. In this way the following species occur, arranged in their order of frequency: *Glyceria maxima*, *Scirpus lacustris*, *Phragmites communis*, *Sparganium erectum*, *Equisetum fluviatile*, *Typha angustifolia*, *Ranunculus lingua* and *Typha latifolia*. We restricted ourselves again to the specially chosen ecotope Ee; it consists of 66 waters in the forelands of the large rivers, which are flooded in winter.

The percentages given in the affinity-diagram (Table 9) were calculated by the formula

$$Q = a/b \times 100\ \%.$$

a = number of times one of the 8 helophytes occurred in the 66 waters of the special ecotope,
b = the number of times that one species was found with another in the same water.

The order of the helophytes is so arranged that the average percentage decreases from left to right. The highest and lowest percentages are shown then by *Glyceria maxima* and *Typha latifolia* respectively.

TABLE 9

Affinity diagram concerning helophytes	Glyceria maxima	Scirpus lacustris	Phragmites communis	Sparganium erectum	Equisetum fluviatile	Typha angustifolia	Ranunculus lingua	Typha latifolia
Glyceria maxima . .	—	93	74	71	64	45	22	19
Scirpus lacustris . . .	91	—	71	68	63	44	22	20
Phragmites communis.	95	93	—	75	67	54	29	24
Sparganium erectum .	98	95	81	—	76	55	31	28
Equisetum fluviatile .	99	97	79	84	—	61	29	29
Typha angustifolia . .	93	93	86	82	82	—	43	36
Ranunculus lingua . .	100	93	93	93	85	86	—	43
Typha latifolia . . .	85	92	85	92	85	77	46	—
Average percentage for the vertical columns	94	94	83	81	75	60	32	28

If we take the average of all the affinity percentages (68 %) as a yard stick we can speak about relative high or low affinity and it is then possible to differentiate 3 groups in the diagram.

1. The group *Glyceria maxima*, *Scirpus lacustris*, *Phragmites communis* and *Sparganium erectum*, all with affinity percentages above 68 %.
2. The group *Ranunculus lingua* and *Typha latifolia* with all percentages below 68 %.
3. The group *Equisetum fluviatile* and *Typha angustifolia* with affinity-percentages both above and below 68 %.

In the last case the diagram shows that the affinity of the first group is greater for *Equisetum fluviatile* than for *Typha angustifolia*. This may mean that *Equisetum fluviatile* has a greater ecological amplitude than *Typha angustifolia*, the more because also the species of the second group have a greater affinity for the first helophyte.

This leads to the question as to whether it is possible to differentiate biotopes within the ecotope Ee, as was done with the limnophytes in a previous chapter. We will now consider this.

All species show a definite low affinity for *Typha latifolia* and *Ranunculus lingua*. This indicates that the two latter species indicate a deviating environment. The mutual affinity between *Ranunculus lingua* and *Typha angustifolia* is not very great, but this is also true because they are unfrequent. Since in the above chapter it was shown that *Typha latifolia* has a habitat with a minimum of water movement, we can say that the environment of *Typha latifolia* must have a less exposed situation from the river. This biotope, indicated by A, corresponds to vegetation types of the following old river-beds: R. 31, gully of the Kersbergsrak at Lexmond; R. 32, river-bed filled up by succession in the Binnen-Nes of Groot-Ammers; W. 66, the Kil at Hurwenen (in the far East of the old river-bed); G. 81, Vreekolk and surroundings at Steenderen; G. 88, Strang at Herkeloo; G. 97, Hank at Veessen (waters on the dyk side); G. 101, Koeluchtergat at Zande. In five of these seven areas, *Stratiotes aloides* was also present, on the basis of which one could imagine a connection between the biotope A considered here, and that considered as biotope Mi in the limnophyte section. It is not so, however, that in all waters were *Typha latifolia* occurred, also *Stratiotes aloides* was present, or vice-versa. *Typha latifolia* was present in 15 waters, *Stratiotes aloides* in 20 waters, but together they occurred in only 6 waters. Before going into this more closely, we will first consider some of the other helophytes.

As mentioned above, *Glyceria maxima*, *Scirpus lacustris*, *Phragmites communis* and *Sparganium erectum* show an affinity, both above and below 68 %, with regard to *Equisetum fluviatile* and *Typha angustifolia*. This suggests that within the ecotope Ee there are two other biotopes to be differentiated, and in this connection attention must be paid to the behaviour of *Equisetum fluviatile* and *Typha angustifolia*. It was stated in the previous chapter that the latter species had no significant preference for the ecotope with stagnant water (Es) or for that with water which is in motion episodically (Ee), although there certainly appears to be an indication of a preference, within the latter biotope, for weakly moving water. A significant preference is shown by *Equisetum fluviatile* for the ecotope with stagnant water Es. This species appears to be more sensitive for the factor of water movement than *Typha angustifolia*, and can be better used to show the differentiation between stronger and weaker water movement within the ecotope discussed — that of water episodically in motion. We may assume therefore, that within our ecotope Ee there are two more biotopes — B and C; the former with weaker, the latter with stronger water movement; *Equisetum fluviatile* showing a higher presence in the former, a lower one in the latter. *Typha angustifolia* probably has a presence-optimum in one of these, as will be shown presently by means of an affinity-diagram.

In the discussion of the limnophytes two other biotopes (Me and Ma) were distinguished apart from the biotope Mi, within the ecotope considered. These two biotopes were characterised by the presence

IV. SURVEY-LIST of 125 old riverbeds of the Maas, Rhine, Waal and Guelders IJssel, visited by collaborators of the "Stichting tot Onderzoek van Levensgemeenschappen" in the years 1954–1956.

River	No. as used in text	Name of the area	Municipality	Type of watermovement and ecotope	Soil-type of the region	pH on date of visit	Chlorinity on date of visit	Date of visit
Maas	M. 1	Gully of the Maas at Horn ("Houter- and Klopven")	Horn			6.2	—	27.6.1955
	M. 2	Meander West of Boekend (Koelbroek)	Maasbree			6.2	—	29.6.1955
	M. 3	"Zwart Water" in the "Genooier heide"	Arcen-Velden-Venlo			5.9	—	28.6.1955
	M. 4	"Broekhuizerbroek" and "Lottumer Schuitwater"	Broekhuizen-Lottum			6.9	40	8.9.1954
	M. 5	Remains of an old Maas riverbed (Schuitwater)	Broekhuizen-Meerlo			6.8	—	29.6.1955
	M. 6	Water South-East of Meerlo	Meerlo			6.7	—	30.6.1955
	M. 7	Gullys along the North-East edge of the "Geysterender heide" ("Rozendaal")	Wansum		river "loam" soil	6.2	—	1.7.1955
	M. 8	The "Vilt"	Boxmeer	Free from inundation for very long time Es		6.5	30	26.8.1954
	M. 9	The "Lange Ven"	Bergen			6.2	—	10.6.1955
	M. 10	The Pool of Wychen	Wychen			6.5	32 22	2.6; 13.7.1955
	M. 11	The Lake of Wychen	Wychen			7.0	40	14 and 21.7.1955
	M. 12	The Lake of Hernen	Bergharen		non calcareous river levée soil	6.6	80	2.6; 20.7.1955
	M. 13	The "Galgenwiel"	Loon op Zand		inland dune sand	6.1	—	1.9.1955
	M. 14	The Lake of Balgoi	Overasselt		most sandy soils	6.7	40	1.6; 21.7.1955
	M. 15	The Lake of Oss	Megen, Haren and Macharen		non-calcareous river levée soil	7.2	70	11.8.1955
	M. 16	Gully in the "Doornwaard"	Heusden			6.9	30	25.7.1955
	M. 17	Water South of Houtblerick ("Tangkoelen")	Maasbree		calcareous river levée soil	6.2	—	27.6.1955
	M. 18	Wood South of Obbicht	Obbicht and Papenhoven			6.8	—	14.6.1955
	M. 19	Gullys in the "Grote Beemd"	Maasbracht			7.2	—	15.6.1955
	M. 20	Riverbed of the Maas at Reuver	Beesel-Reuver			7.2	—	17.6.1955
	M. 21	Old Maas near Megen	Megen	Recently become free from inundation Es		7.1	20	18.8.1954
	M. 22	Remains of an old Maasmeander near Empel and Hedel	Empel-Meerwijk		river foreland clay soil	7.1	40	25.5.1955
	M. 23	Hedikse Maas near Haarsteeg	Vlijmen-Hedikhuizen			7.0	40	23.8.1954
	M. 23	Old creek in the "Ban- and Wijksewaard"	Wijk and Aalburg			7.2	70	4.8.1955
	M. 25	Gully near the "Zandplaat" and "Esmeer" near Poederoyen	Brakel			7.5	110	11.5; 26.7.1955
	M. 26	Water in the "Waarden" near Poederoyen	Brakel			7.1	40	11.5; 26.7.1955
Rhine	R. 27	Meander of the Rhine at Lienden	Lienden			7.5	60	4 and 5.8.1954
	R. 28	The Old Rhine between Aalst and Kesteren	Kesteren	free from inundation stagnant Es		7.7	40	23.8.1955
	R. 29	Riverbed West of the "Oude Haven" near Wageningen	Wageningen		calcareous river levée soil	—	—	18.8.1955
	R. 30	The "Strang" at Opheusden	Kesteren			—	—	19.8.1955
	R. 31	Gully of the Kersbergsrak (River the "Lek")	Lexmond			7.2	80	17.7.1956
	R. 32	Riverbed in "Binnen Nes" (ditto)	Groot Ammers			7.4	100	3 and 4.7.1956
	R. 33					6.9	—	26.7–30.7.1954
	R. 34	Two "Strangs" of the Rhine near Pannerden	Herwen and Aerdt			7.3	—	
	R. 35	"Old Waal" and "Bijland" near Lobith	Herwen and Aerdt			7.4	—	
	R. 36	The "Strang" at Huissen	Huissen			7.3	60	16.8.1955
	R. 37	Old riverbed near "Looveer"	Huissen			7.3	80	16.8.1955
	R. 38	Old riverbed near "Renkumse veer"	Heteren			—	—	19.8.1955
	R. 39	Old riverbed near "Lexkesveer"	Heteren	inundation possible Ee	river foreland clay soil	—	—	19.8.1955
	R. 40	Meander of the Rhine at Lienden	Lienden			—	—	4 and 5.8.1954
	R. 41	Old riverbed at Elst	Rhenen			7.3	—	23.8.1955
	R. 42	Old riverbed North of Eck and Wiel	Maurik			7.4	40	12.9.1955
	R. 43	Old riverbed in the "Waterschap Bovenpolder"	Amerongen			—	—	31.8.1955
	R. 44	The "Kil and Kilsloot"	Amerongen			7.3	50	31.8.1955
	R. 45	The "Roodvoet" at Rijswijk	Maurik			7.2	—	5.8.1954
	R. 46	The "Kleine Lek"	Vianen			7.2	100	12.6.1956
Waal	W. 47	The "Ooyse Graaf" at Erlekom	Ubbergen	no inundation stagnant Es		7.6	—	3.8.1954
	W. 48	The "Wiel of Tuil"	Haaften		calcareous river levée soil	7.3	40	13.8.1954
	W. 49	Old Waal at Kekerdom	Ubbergen			7.3	—	2 and 3.8.1954
	W. 50					7.7	—	
	W. 51	The "Strang" in "Sophia's Kamp" at Ooy	Ubbergen			7.1	30	25.7.1955
	W. 52	The "Old Waal" near Nijmegen	Ubbergen			7.1	60	20 and 21.7.1955
	W. 53	The "Zeumke"	Nijmegen			7.0	90	21.7.1955
	W. 54	The "Strang" at Bemmel	Bemmel			7.5	40	14 and 15.7.1955
	W. 55	The "Zandkolk" at Oosterhout	Valburg			7.2	—	26.7.1955
	W. 56	The "Strang" in the "Loenense buitenpolder"	Valburg			7.2	100	24.8.1955
	W. 57	Old riverbed near Afferden	Druten			—	—	12.8.1955
	W. 58	The "Strang" and "Weversgat" at Turksweerd	Druten			7.3 7.5	50	11.8.1955
	W. 59	The "Old Waal" East of Ochten	Echteld			7.1	90	1 and 9.9.1955
	W. 60	The "Hoek of the Lange Krib" near Ochten (East)	Echteld	inundation Ee		7.1	110	9.9.1955
	W. 61	The "Strang" at Hien	Dodewaard			7.3	80	12 and 24.8.1956
	W. 62	The "Kil" at Ooy	Echteld			—	—	13.9.1955
	W. 63	Old riverbed South-West of Tiel	Tiel			—	—	25.8.1955
	W. 64	The "Kil" at Tiel	Tiel		river foreland clay soil	7.3	40	1 and 2.9.1955
	W. 65	Old riverbed South-West of Wamel	Wamel and Dreumel			7.1	80	5.9.1955
	W. 66	The "Kil" at Hurwenen	Hurwenen and Zaltbommel			7.5	40	9 and 11.8.1954
	W. 67	The "Kil" at Waardenburg	Waardenburg			7.3	40	11 and 12.8.1954
	W. 68	The "Kil" in the Breemwaard "Killeke"	Zuilinchem			7.2	70	23.5.1956
	W. 69	The "Strang" at Slijk-Ewijk	Valburg			7.1	—	26.7.1955
	W. 70	The "Goudmijn" at Druten	Druten			7.2	80	11.8.1955
	W. 71	The "Bovenstrang" at Hien	Dodewaard			—	—	12 and 24.8.1955
	W. 72	The Old Waal South-West of Ochten	Echteld and IJzendoorn	inundation, in addition open connection with the river Ee		7.0	80	13.9.1955
	W. 73	The "Kil" at Dreumel	Dreumel			7.2	100	26.8.1955
	W. 74	The "Kil" at Ophemert	Ophemert and Varik			7.1	50	25.8.1955
	W. 75	Old riverbed near Heerewaarden	Heerewaarden			7.0	100	5.9.1955
	W. 76	The "Weiwaardsgat" at Heerewaarden	Heerewaarden			7.1	90	29.8.1955
	W. 77	The "Hoek of the Lange Krib" near Ochten (West)	Echteld			7.3	70	9.9.1955
Guelders IJssel	G. 78	"Barlose kolken"	Olst			7.3	30	1.9.1954
	G. 79	Old riverbed near Oldeneel ("Schellerwaden")	Zwollerkerspel		calcareous river levée soil	7.3	30	2.9.1954
	G. 80	Old IJssel near Kampen	Kampen			7.2	60	18.7; 15.8.1956
	G. 81	"Vreekolk" and surroundings	Steenderen			7.3	40	27.6; 10.7.1956
	G. 82	"Rhedense Laak"	Rheden			7.3	20	26.6.1956
	G. 83	The Lamme IJssel	Angerlo and Doesburg			7.3	30	6.9.1954
	G. 84	Old IJssel and Hoendernesterbeek near Zutphen	Zutphen	no inundation stagnant Es		7.0	30	30.8.1954
	G. 85	"Blanke Hank" and other waters near the castle Nijenbeek	Voorst			7.0	40	30.5; 19.6.1956
	G. 86	"Hank" at Welsum	Olst			7.2	70	11.7.1956
	G. 87	"Scherpenzeelse Hank"	Wijhe and Olst			7.5	50	23 and 28.8.1956
	G. 88	"Strang" at Herkeloo	Zwolle			7.9 7.4	30	2.9.1954
	G. 89	"Hank" at Zalk	IJsselmuiden			7.2	60	14.8.1956
	G. 90	"Hank" at Wilsum	IJsselmuiden			6.9	110	1.6; 11.7.1956
	G. 91	Old riverbed in the "Spankerense weilanden" S.-W. of the castle "Gelderse toren"	Rheden			7.2	40	26.6.1956
	G. 92	Waters in the "Waarden" at Wilp	Voorst and Deventer		river foreland clay soil	7.4 7.2	40	20, 21 and 25.6.1956
	G. 93	Old riverbed in the "Osserwaard"	Deventer	inundation Ee		7.4	60	29.5.1956
	G. 94	Munnikenhank	Diepenveen			7.0	40	14.9.1956
	G. 95	Old riverbeds in "Hengvorden- and Olsterwaarden"	Olst			7.5	40	22 and 23.8.1956
	G. 96	Meander in the "Olsterwaard"	Olst			7.3	70	1.9.1954
	G. 97	Hank at Veessen II-IV	Heerde			7.6 7.2	40	11.7.1956
	G. 98	Dierense Hank	Dieren and Angerlo			7.3	40	6.9.1954
	G. 99	Hank at Veessen I	Heerde	inundation and in connection to the river Ee		7.5	70	8.8.1956
	G. 100	"Spoolderhank"	Zwollekerspel			6.9	110	11 and 13.7.1956
	G. 101	The "Koeluchtergat"	IJsselmuiden			7.0	90	12.7.1956
	G. 102	"Hank" at Wilsum (West)	IJsselmuiden			7.0	110	1.6; 11.7.1956
Lek	L. 103	Gully of the Kersbergsrak	Lexmond			7.0	80	17.7.1956
	L. 104	"Binnen Lek" along the island "Bol"	Lopik			7.0	110	19.7.1956
	L. 105	"Kil" along the island "Hoop"	Krimpen a. d. IJssel			7.2	90	20.7.1956
Maas	M. 106	Remains of an old Maasmeander near Empel and Hedel	Empel-Meerwijk, Hedel			7.1	80	25.5.1955
	M. 107	The "Krook" at Slijkwel	Ammerzoden			7.1	70	25.7.1955
	M. 108	Old creek in the "Ban- and Wijksewaard"	Wijk and Aalburg			7.2	100	25.7.1955
	M. 109	Gully near the "Zandplaat" and "Esmeer" near Poederoyen	Brakel	tidal movements Et		7.3	100	26.7.1955
	M. 110	The "Old Maasje" near Loevestein	Brakel		river foreland clay soil	7.3	90	27.7.1955
Merwede	W. 111	"Bloemstrang"	Brakel			7.1	110	16.8.1954
	W. 112	"Avelingerdiep"	Gorinchem-Hardinxveld			7.0	120	5.6; 27.6.1956
Maas	M. 113	Old Maas near Drongelen	Drongelen			7.1	40	24.8.1954
	M. 114	Old "Maasje" between Haagoord and Keizersveer	Capelle-Waspik			7.1	80	25.8.1954
	M. 115	"Buitenlanden" on the Old Maas near Heinenoord	Heinenoord			6.8	120	8.6.1956
	M. 116	The "Kooigat" and surroundings	Poortugaal			6.8	120	7.6; 26.6.1956
Guelders IJssel	G. 117	The "Noorderdiep"	Kampen		Zuiderzee coastal clay soil	7.5 7.3	100	3.9.1954
Maas and Waal a.o.	118	The "Voordevel"	Heerjansdam			7.5	70	17.8.1954
	119	Waal	Ridderkerk			7.2	90	31.8.1956
	120	"Binnenbedijkte Maas"	Westmaas		estuary silt soil	7.0	200	17.8.1956
	121	"Holle Mare"	Heenvliet	no inundation stagnant Es		7.5	670	31.7.1956
	122	"Vierambachtenboezem" ("Oostenrijk")	Geervliet		salty peat soil	7.2	690	14.6; 25.6.1956
	123	"Spui" near Brielle	Nieuwenhoven			7.5	250	25.7.1956
	124	"Grote Gat"	Zuid-Beveland			7.5	1100	26.7.1956
	125	The "Meertje of Rockanje" (Waal)	Rockanje		marsh silt soil	7.6	2008	6.8.1956

TABLE 10

Old riverbeds of the Guelders IJssel, Rhine and Waal.

Ecotope Ee. Stagnant waters, on river foreland clay soils, which are flooded in the winter and some of which are in open connection with the river.

No.	Riverbed G = Guelders IJssel R = Rhine W = Waal	Section of riverbed	Current [1]	Special features of the situations listed	Stratiotes aloides	Typha latifolia	Equisetum fluviatile	Nymphaea alba	Potamogeton natans	Typha angustifolia	Ranunculus lingua	Sparganium erectum	Nuphar luteum	Potamogeton lucens	Nymphoides peltata	Polygonum amphibium fo. natans	Oenanthe aquatica	Biotopes in the Ecotope Ee
G. 82	"Rhedense Laak" (Rheden)		r.t.	joins two meanders outside the bends			.	●	●	●		.			.	○	.	Me Ma
83	The "Lamme IJssel" (Angerlo-Doesburg)		slight	250–500 m West of the river		.	.			.			.	.	.			Me
98	"Dierense Hank" (Dieren, Angerlo)		r.t., o.c.				.	.	.			.	.	.	.	.	.	Me Ma
91	Old riverbed near "Guelders Toren" (Rheden)		r.t., o.c.	250 m West of the river				○				.	.	.	.		.	Me
81	"Vreekolk" and surroundings (Steenderen)		nil	plm 2 km East of the river		○	●			.	○	○	.	.	.	.	○	Mi Me
85	"Blanke Hank" and other waters	I	slight	500 m West of the river. Slight exposure		○	.	.	.			○	●	.	.		.	Mi Me
	near the castle "Nijenbeek" (Voorst)	II-VIII	r.t.	250–100 m West of the river			.	●	●			●	.	●	○	○	.	Me Ma
92	Waters in the forelands near Wilp	I-VII	moderate r.t.	riverside – 150 m West of the river					●			○	●	●	●	●	●	Me Ma
		VIII-XII	slight r.t.	dykeside – 500 m West of the river			●		.	○		.	●	○	.	.	●	Me
93	Old riverbed in the "Ossenwaard" near Deventer		r.t.	200 m West of the river					●			○	●	●	○	.	.	Me
94	"Munnikenhank" (Diepenveen)		r.t.	plm. 400 m East of the river				.		.	.	○	.	.	.	●	.	Me Ma
95	Old riverbeds in the "Hengvorden- and Olsterwaarden" (Olst)		slight	isolated and sheltered pool	○			.				.	.	.				Mi
			r.t.	dykeside, plm 400 m West of the river				●	.	○	.	○	●	●	○	○		Me Ma
86	"Hank" at Welsum (Olst)		r.t.	waters dug by riverside				.					.		●	●		Ma
	"Great Hank"		r.t.	plm. 100 m West of the river, dykseside				.		.			.	.	.	.		Me Ma
	"Little Hank"		slight r.t.	plm. 250 m West of the river, dykeside; sheltered			○	●	.			.		●	.			Me
96	Old riverbed in the "Olsterwaard" near Nul (Olst)		r.t.	plm. 150 m East of the river, halfway between river and dyke	○			○	.	○			.	. .	○			Me
97	"Hank" at Veessen (Heerde)	IV	r.t.	plm. 200 m West of the river, dykeside, beginning of outer bend		●		●	.		.	.	●	.	●	.		Mi Me
		II	r.t.	ditto, end of outer bend				.		●	.	.	.	.	.	.		Me
		I	o.c.	plm. 100 m West of the river, dykeside, end of outer bend				●					○		●			Me Ma
87	"Scherpenzeelse Hank" (Wijhe and Olst)		r.t.	plm. 400–100 m East of the river, dykeside, before outer bend			○	●		●	.	○	●	○	.	○		Me Ma
88	"Strang" at Herkeloo (Zwollerkerspel)		slight	plm. 400 m East of the river, dykeside; little exposure	●	○	●		.	○	○	○	.	.	.		.	Mi
100	"Spoolderhank" (Zwollerkerspel)		o.c.	plm. 100–0 m East of the river, between river and dyke	.		○	●		●			●	●	○	.	.	Me
89	"Hank" at Zalk (IJsselmuiden)		r.t.	(200 m West of the river, dykeside); 50 m West of river, riverside	(●)		○	○		○	○	.	●	.	.			Mi Me
101	The "Koeluchtergat" (IJsselmuiden)		o.c.	plm. 100 m West of the river	○	○	●	○	.	●	●	○	●	○	○			Mi Me
90	"Hank" at Wilsum (IJsselmuiden)	East	r.t.	plm. 400 m East of the river	●		.				.		.					Mi
102	"Hank" at Wilsum (IJsselmuiden)	West	r.t.	plm. 200 m East of the river				○		○			○					Me
102	"Hank" at Wilsum (IJsselmuiden)		o.c.	80–0 m East of the river			.	○		●		.	●		●			Me
R. 33	Two old "Strangs" of the Rhine near Pannerden (Herwen and Aerdt)			plm. 4 km North of the river	.		●	●				●	●	○	●		.	Mi Me
34					.		●	●				●	●	○	●		.	Mi Me
35	"Old Waal" and "Bijland" near Lobith			plm. 2 km North of the river		●	○	.		●		●	●			○	○	Me
36	The "Strang" at Huissen			on a dyke, 800 m West of the river, innerbend; flooded in the winter	●			●				●	○	.	.		●	Mi Me
37	Old riverbed near the "Looveer" (Huissen)			between the river and summer-quay, outerbend					●					.	●	●		Me Ma
38	Old riverbed near the "Renkumse Veer" (Heteren)		o.c.	250 m South of the river, between summer-quay and dyke; very sheltered				.					.	.	.		.	
39	Old riverbed near the "Lexkesveer" (Heteren)			500 m South of the river, dykeside, innerbend			.					.					.	
40	Meander of the Rhine near Lienden	West. section					.											
41	Old riverbed near Elst (Rhenen)			direct North of the river, after quay, innerbend; not flooded every winter			.		●			●		●				Me
42	Old riverbed North of Eck and Wiel (Maurik)	S.W.-section		200 m South of the river, between dyke and quay	●		.					○		●			.	Mi
43	Old riverbed in the Waterschap „Bovenpolder" (Amerongen)			300 m North of the river, between dyke and quay, outerbend; flooded winterly at times	.		.		●	●			.	●				Mi Me
44	The "Kil" and the "Kilsloot" near Amerongen			250 m North of the river, between dyke and quay, innerbend; flooded at times	○		.		●			. ●	. .	●	●		. .	Me Mi
45	The "Roodvoet" at Rijswijk (Maurik)			remains of a meander, 800 m South of the river		.						.		●	●	.	.	Me Ma
46	The "Little Lek" (Vianen)			400 m South of the river, near dyke			.			●	.	.	○	●		(.)	.	Me
31	Gully of the "Kersbergsrak" (Lexmond)			400 m South of the river, near dyke	. ●	●	●	. .	.	●		●	● .	● .			.	Mi
32	Old riverbed in the "Binnen-Nes" (Groot Ammers)			300 m South of the river, near dyke	●	.	●		●	.	.	.	●	.				Mi
W. 49	Old Waal at Kekerdom (Ubbergen)	West. section		1000 m South of the river, near dyke, outerbend; flooded in winter			○		.	○		.	○	●	●		○	Me
50		Eastern section				●	●			●		.					.	Mi
51	The "Strang" in "Sophia's Kamp" at Ooy (Ubbergen)			750 m South of the river, near dyke, innerbend; can be flooded				.					.	●	.	.	●	Me Ma
52	The "Old Waal" near Nijmegen (Ubbergen)			1000 m South of the river, near dyke; at least once flooded in winter	(●)		○	●		●	.	○	●	.	○	○	.	Mi Me
53	The "Zeumke" near Nijmegen			200 m South of the river, outerbend									●	●	●	●	●	Ma
54	The "Strang" at Bemmel			500 m North of the river, outer bend; flooded once in 3 winters			○			●		○	●	●	●	●	●	Me Ma
55	The "Zandkolk" at Oosterhout (Valburg)			100 m North of the river, between river and dyke; flooded every winter								.	●	○	●	○	●	Ma
69	The "Strang" at Slijk-Ewijk (Valburg)		o.c.	300 m North of the river, near dyke; flooded each winter					●				.	.	●	●	.	Ma
56	The "Strang" in the "Loenense buitenpolder" (Valburg)			250 m North of the river, dykeside; frequently flooded			.					●	○		●	.	●	Ma
61	The "Strang" at Hien (Dodewaard)			1000 m North of the river, near dyke; quay and cross-dyke; prevent flooding	●		○		.			●	●	●	●	.	.	Mi Me
71	The "Bovenstrang" at Hien (Dodewaard)		o.c.	incurrent; dykeside									.	.	●	.		Ma
57	Old riverbed near Afferden (Druten)			plm. 600 m South of the river, by dyke; flooded 2 out of 3 winters			.				.							
58	The "Strang" at Turksweerd (Druten)			200–700 m South of the river, between river and dyke; less exposed					●					.		.	●	Me Ma
	The "Weversgat" at Turksweerd (Druten)			700 m South of the river, near dyke; flooded 2 out of 3 winters								●	.	○	.		.	Me Ma
70	The "Goudmijn" near Druten		o.c.	400 m South of the river, between dyke and river; frequently flooded									.	.	●	●		Ma
59	The "Old Waal" East of Ochten (Echteld)			dykeside, with stagnation against the dyke at Ochten			.		.	●		●	○	●	●	○	●	Me Ma
60	The "Hoek" of the "Lange Krib" near Ochten	Eastern section	o.c.	200 m North of the river, between summerquay and river									.		●	●	.	Ma
77	The "Hoek" of the "Lange Krib" near Ochten	West. section													●	●		Ma
72	The "Old Waal" South-West of Ochten (Echteld and IJzendoorn)	Eastern section	r.t.	300 m North of the river, between dyke and river; flooded every year					●					○				
		West. section	o.c.									.	.	○	.	●	.	Ma
62	The "Kil" at Ooy (Echteld)			800 m North of the river, by dyke; flooded at least once per winter					●			○	.	.	.		○	Me Ma
64	The "Kil" at Tiel	Eastern section		200 m North of the river			.	●		●		●	●		●	.	.	Mi Me
		West. section		200 m North of the river; less exposed	●					.		.	.		.	.	.	Mi Me
65	Old riverbed South-West of Wamel			300 m South-East of the river near summer-quay; in North-East stagnation; flooded in winter									.		●	●	.	Ma
63	Old riverbed South-West of Tiel			300 m North-West of the river, between dyke and summer-quay; flooded in winter											●	●	○	Ma
73	The "Kil" at Dreumel		o.c.	300 m East of the river near dyke; nearly every winter subject to flooding				○					.	.	●	○		Me Ma
74	The "Kil" at Ophemert		o.c.	300 m North-West of the river; between dyke and summer-quay; usually flooded			.		○				.	●	●	●		Ma
75	Old riverbed near Heerewaarden		o.c.	150 m East of the river, between dyke and river; frequently flooded					○					○	●	○		Ma
76	The "Weiwaardsgat" near Heerewaarden	S.-W. section	o.c.	300 m East of the river, between dyke and river; flooded at least once in winter									.		●	.	.	Ma
66	The "Kil of Hurwenen" (near Zaltbommel)	East-section		2000 m South of the river, near dyke; flooded	.	●	●	●		●	○	●	●	●	●	.?	.	Me
67	The "Kil of Waardenburg"	East section		800 m North of the river, near dyke; flooded; much sheltered	○		.	●		●		●	○	●	●	.?	●	Mi Me
68	The "Kil in the Breemwaard" (Zuilinchem)			400 m South of the river, near dyke; flooded?	(.)		○			●		.	○	.			.	Me

Legend to Table 7.

1) Current r.t. = "running through"
o.c. = open connection

. = present
○ = fairly common
● = very common
( ) = local

Mi = Minor inundation
Me = Mediocre inundation
Ma = Major inundation

of *Nymphaea alba* in the areas with weak water movements and *Polygonum amphibium* fo. *natans* in the areas with a stronger water movement. We will now see if there is a connection between the supposed helophyte biotopes A, B and C the limnophyte biotopes Mi, Me and Ma. The affinity-diagram below serves to examine this. The mutual affinity-percentages of the helophytes for the supposed biotopes A, B and C and those of the limnophytes for the biotopes Mi, Me and Ma are given in it.

Affinity diagram concerning three helophytes (H) and three limnophytes (L)			A	B and C		Mi	Me	Ma
			Typha latifolia	Equisetum fluviatile	Typha angustifolia	Stratiotes aloides	Nymphaea alba	Polygonum amphibium fo. natans
H	Typha latifolia	A	—	—	—	45	40	$\boxed{20}$
H	Equisetum fluviatile	B and	—	—	—	45	41	$\boxed{32}$
H	Typha angustifolia	C	—	—	—	51	45	$\boxed{24}$
L	Stratiotes aloides	$\boxed{\text{Mi}}$	39	87	74	—	—	—
L	Nymphaea alba	$\boxed{\text{Me}}$	32	72	60	—	—	—
L	Polygonum amphibium fo. natans	$\boxed{\text{Ma}}$	12	41	24	—	—	—

It is obvious that *Typha latifolia* and *Polygonum amphibium* fo. *natans* have a low mutual affinity. This indicates the extreme contrast in the nature of their environments — the contrast between environments with the least and most water movement respectively. *Typha latifolia* shows the greatest affinity for *Stratiotes aloides*, a limnophyte characteristic of very calm environment. That the affinity for *Nymphaea alba* is a little lower than for *Stratiotes* is explainable in that the former occurs in less calm waters too.

Equisetum fluviatile behaves as *Typha latifolia* towards *Stratiotes aloides* and *Nymphaea alba*, but occurs more in the waters characterised by *Polygonum amphibium* fo. *natans* than *Typha latifolia* does. The helophyt *Typha angustifolia* has a slightly higher affinity for the three just mentioned limnophytes than *Typha latifolia* or *Equisetum fluviatile*, and, just as both latter ones, a lower affinity for *Polygonum amphibium* fo. *natans*. This may indicate that *Typha angustifolia* is less frequent in the waters with the most movement in our ecotope. It was stated above that this apparent difference is not significant, although there was certainly an indication of it. The affinity-diagram shows that *Typha angustifolia* is less frequent, as far as water movement is concerned, in the most exposed places and thus the preference for a biotope with weakly moving water within our special ecotope is probable.

If we now start from the limnophytes in the above affinity-diagram we see that *Stratiotes aloides* and *Nymphaea alba* have a lower affinity for *Typha latifolia* than for *Equisetum fluviatile* and *Typha angustifolia*. This suggests that *Typha latifolia* prefers still another environment than the two limnophytes, which would indicate that the limnophyte biotopes Mi and Me are different to the supposed helophyte biotope A. This becomes clear if we examine in which environments *Typha latifolia* shows its presence-optimum, which proves to be in another ecotope — that with stagnant waters. It is to be found there regularly in very calm places, in, for example, a small, isolated water, in the far ends of a more extended pool or in a bend, in a small bay or outlets of larger waters. Typical examples are to be found in the Zwart Water in the Genooierheide (community of Arcen and Velden) and in the Broekhuizerbroek (community of Broekhuizen), both old river-beds of the Maas. A "carr" thicket (swampy woodland) surrounded this stagnant water, about 1 m deep and boiling hot in summer. The large floating swamp vegetation (drifting mat) of *Typha latifolia*, growing in a soft, thick peat layer, testified to the exceptionally favourable environmental circumstances for *Typha latifolia* which were present here. On these grounds we shall consider *Typha latifolia* when it occurs in our ecotope Ee with episodically moving water, only as an indicator of a calmer form of the limnophyte biotopes Mi and Me and thus not as a characteristic species of a separate biotope. The supposed helophyte biotope A is therefore invalid. *Stratiotes aloides* was also found with a presence-optimum in the ecotope with stagnant waters, such as the Old Maas near Megen and in an old creek on the Wijksewaard near Veen. In the ecotope under consideration, Ee, the plant was found in the back-ends of elongated waters as a dominant or on small waters and ditches completely covering them in the least exposed places. One could only expect than a high affinity between this limnophyte and *Typha latifolia*. We have studied the reason why, in fact, this was not so.

In 54 old river-beds of the Maas, Rhine, Waal and Guelders IJssel, where either *Typha latifolia* or *Stratiotes aloides*, or both occurred, a differentiation was made between 28 stagnant and 26 temporarily moving waters, the latter — as a result of their less exposed situation — having weak water movements. In the 28 stagnant waters *Typha latifolia* was present as 86 % and *Stratiotes aloides* only as 46 %. In the 26 moving waters, *Typha latifolia* was present in 42 % and *Stratiotes aloides* in 69 %, which indicates a difference. With the help of the usual statistical method it could be shown that there was a real difference between the occurrence of *Typha latifolia* in stagnant and episodically-moving waters, which was that the species occurred much more in the former type. A similar difference could not be demonstrated for *Stratiotes aloides:* this species occurred in both environments. This explains why *Stratiotes aloides* and *Typha latifolia* occurred together in only a small number of waters. In addition, it appears that *Stratiotes aloides* can support some water movement. Apparently it has even a preference for very weak water movements, provided that a shelter is present against the wind. A typical example is the small roundy water outside the dyke in the Hank near Zalk (G. 89) in the community of IJsselmuiden. In this connection we would like to remark that also the two river-beds mentioned above, where *Stratiotes aloides* covered a great area of the centre of the water, were situated outside the dyke, while the winter dyke arose at a short distance South-West of the pool. The second author already stated before (WESTHOFF 1949) that *Stratiotes aloides* may occur and even dominate in water courses with temporary, even strong current, in this case in the oligo- to mesohalinic swamp area Botshol near Amsterdam. The preference-difference between *Typha latifolia* and *Stratiotes aloides*, in relation to the difference in water movement, indicates that *Typha latifolia* has its optimum in mesotrophic environment, while *Stratiotes aloides* has its optimum in eutrophic environment.

Whenever *Typha latifolia* occurs in the limnophyte biotopes Mi and Me, it indicates the beginning of a change in the environment.

We will now consider further the supposed helophyte biotopes B and C, which have not yet been discussed separately. From the affinity-diagram given above there appears a greater couple-affinity between *Equisetum fluviatile* + *Typha angustifolia* on the one hand and *Stratiotes aloides* + *Nymphaea alba* on the other, than between the first two species and *Polygonum amphibium* fo. *natans*. We come to the conclusion then that there is a difference between the supposed biotopes B and C. The cause of the difference — the weaker and stronger water movements respectively — is the same that was valid for the limnophyte biotopes Me and Ma. We conclude therefore that the biotopes B and C coincide with the limnophyte biotopes Me and Ma. In the limnophyte biotope Me, the helophytes *Equisetum fluviatile* and *Typha angustifolia* have a higher presence than in the limnophyte biotope Ma. From this an agreement in the behaviour of the two helophytes could be expected. But in the first helophyte affinity-diagram on page 247 of this chapter and, in addition, as appeared in the previous chapter, they behave differently, in fact.

The following table makes these differences clear:

Rivers / helophytes	Guelders IJssel, presence in 21 riverbeds	Rhine, presence in 16 riverbeds	Waal, presence in 29 riverbeds
Typha angustifolia	62%	31%	31%
Equisetum fluviatile	48%	69%	46%

Typha angustifolia shows a significant preference for the area of the Guelders IJssel, as shown above. Since in this river area the limnophyte biotope Me, of the ecotope Ee with episodically moving water was preponderant, this species would be expected to have the highest affinity for this biotope Me. Wherever this helophyte occurred in the Rhine or Waal areas, this was always in an old river-bed that was isolated or in which the current had been stagnated by various factors (e.g. a dyke or quay across the direction of flow).

Equisetum fluviatile showed no significant preference in presence for one of the three mentioned rivers. Therefore we tried to see whether the rate of abundance indicated a preference, which proved to be the case. In the Rhine area this helophyte was observed as a dominant in 3 old river-beds. Two of these river-beds had an isolated situation (gully of the Kersbergsrak at Lexmond and an old river-bed in the Binnen Nes near Groot Ammers). In the third river-bed (the two old Rijnstrangen at Pannerden) the current of the stream may have been decreased by the settlement of willows and by willow cultivation grounds. Next, the species was dominant in two old river-beds in the Waal area. One was an isolated claypit of the Oude Waal near Kekerdom and the other proved to be flooded only once in three years on the average (Strang near Bemmel). In the area of the Guelders IJssel the species was much more often dominant (8 times, in fact). In all these cases the old river-beds (or, in any case, their subdivisions where *Equisetum fluviatile* was dominant) had a sheltered situation, even though two of the eight waters were in open connection with the river. From this we see a preference for an environment which corresponds to our limnophyte biotope Mi and, to a lesser extent, biotope Me.

So far the preference of these two limnophytes in our ecotope are corresponding. But the presence of *Equisetum fluviatile* in the Waal was higher than that of *Typha angustifolia*. In the ebb-and-flow areas, a third ecotope, which is not studied in detail here (due to insufficient data), the same difference was obvious. If we consider further the ecotope with waters (Es), then we can show the different behaviour of the two helophytes as follows:

Equisetum fluviatile has a significant preference for the ecotope with stagnant waters called Es over that with episodically moving water (Ee), and occurs in the last case mostly in the limnophyte biotope Mi (characterised by *Stratiotes aloides*) or in transitions to the biotope Me (characterised by *Nymphaea alba*). *Typha angustifolia* has no significant preference for the ecotope with stagnant waters over that with episodically moving water, but it certainly does not have a significant preference for the biotopes Mi and Me in the last-mentioned ecotope, thus for a weak episodical movement. Its presence in the old river-beds of the Rhine and Waal is lower than that of *Equisetum fluviatile*, and it appears, in general, to be more sensitive to the influence of water movement than *Equisetum fluviatile*.

Ranunculus lingua had a significant preference for areas with stagnant waters and, within the areas with episodical water movement, for calmer waters. As there is little erosion in these waters, deposits of mud can be built up, and the waters remain shallow with the result that the bank vegetation penetrates sometimes far out into the open water, so that *Ranunculus lingua* may conspicuously spread in vegetations of *Equisetum fluviatile* and *Typha angustifolia*. This amphiphyte was abundant in a swamp where *Equisetum fluviatile* was dominant (Koelbroek near Maasbree in Limburg) and also in two bank vegetations in which *Equisetum fluviatile* was dominant and *Typha angustifolia* subdominant (Koeluchtergat near Zande in the area of the lower reaches of the Guelders IJssel and in the Ooyse Graaf inside the dyke near Erlecom in the Waal area). The plant, which has large yellow flowers, made a splendid effect against the green-brown *Equisetum* vegetation and the dark green *Typha* leaves. The species occurred occasionally in the bank vegetation of the sheltered old river-beds.

VAN DONSELAAR (1958) stated that the helophyte *Oenanthe aquatica*, from a synecological point of view, is a faithful species of a plant community in strongly moving water. After calculating the affinity percentage of this species for the indicators or our three biotopes, and after using the test of contingency explained previously, it was seen that *Oenanthe aquatica* did, in fact, have a significant preference for the biotope with intensive winter inundation, which strenghtens the synecological result. We have, therefore, added the helophyte *Oenanthe aquatica* to the two limnophytes characteristic of this type of biotope.

We would like now to consider the group of helophytes presenting high affinity percentages for all other species according to the affinity-diagram.

This group of helophytes consisted of the species mentioned in the following table:

	Percentages showing occurrence in:		
	21 areas of the Guelders IJssel	16 areas of the Rhine	29 areas of the Waal
Glyceria maxima	100%	81%	79%
Scirpus lacustris	100%	75%	83%
Phragmites communis . . .	81%	63%	55%
Sparganium erectum	81%	75%	48%

According to our calculations, only the presence difference of *Sparganium erectum* between the areas of the Guelders IJssel and Waal, is significant.

The affinity of this species for the Guelders IJssel area indicates a preference for an environment which contains both *Typha* spp., *Equisetum fluviatile* and *Ranunculus lingua* as important species.

We close this chapter with a summary over the limnophytes and helophytes that we have considered.

In the ecotope with stagnant water (Es) *Typha latifolia* and *Equisetum fluviatile* have a presence optimum, and *Stratiotes aloides* also, be it in a somewhat different habitat.

In the ecotope with episodically moving water (Ee) the three species just mentioned are not so common (in particular *Typha latifolia*); whenever they are observed, they occur in the limnophyte biotope Mi, which is to be found in the least exposed areas. In the other two limnophyte biotopes, the presence optimum is shown by *Nymphaea alba*, *Typha angustifolia* and *Sparganium erectum* in the biotope with moderate winter flooding, while *Polygonum amphibium* fo. *natans*, *Nymphoides peltata* and *Oenanthe aquatica* show theirs in the biotope with intensive winter flooding.

6. CONCLUSIONS

The question was posed as to whether a certain environmental factor, in this case the water movement, can influence the frequency of limnophytes and helophytes and the rate of their occurrence together. It proved possible to examine this by means of an affinity-diagram, in which the mutual relationship of the limnophytes from a special ecotope were shown. This ecotope was a group of 66 old river-beds, in river forelands which are flooded in winter and thus subjected to episodical water movement. A certain combination of limnophytes and helophytes, proved to be an indication for the differentiation of three biotopes within this special ecotope, in which the water movement was the deciding factor for the occurrence of the indicating species. These three biotopes within the ecotope were:

1. The biotope Mi (minor inundation) characterised by a weak winter flooding, without the area being continuously flooded. This could occur in all three river areas, if the waters were exposed as little as possible to the flooding. In the Waal area this biotope was observed only once, as against four times in the Rhine area and three times in that of the Guelders IJssel. The limnophyte and the helophyte which showed a presence optimum in this biotope were *Stratiotes aloides* and *Equisetum fluviatile*.

2. The biotope Me (medium inundation) characterised by a moderate winter flooding, with a regular but not intensive flow-through of river water. This biotope appeared most frequently in the Guelders IJssel area (23 times) compared to 9 times in the Rhine and 14 times in the Waal area. This biotope showed repeatedly areas transitional to the biotope Me or Ma. The plant species having a presence optimum here were the limnophyte *Nymphaea alba* and the helophytes *Typha angustifolia*, *Ranunculus lingua* and *Sparganium erectum*.

3. The biotope Ma (major inundation) characterised by intensive winter flooding with a regular and intensive flow-through of river water. This biotope was found most frequently in the Waal area (14 times) but was found only once in the Rhine and Guelders IJssel areas. The limnophytes showing a presence optimum here were *Polygonum amphibium* fo. *natans* and *Nymphoides peltata*, while the helophyte *Oenanthe aquatica* proved to be another characteristic species.

It is significant that biotope Me was most frequent in the old river-beds of the Guelders IJssel and the biotope Ma in those of the Waal. Because of this it is possible to typify each river. The usually broad, relatively high forelands of the Guelders IJssel, overgrown in a scattered way by stunted brushwood and willow-coppice, have a breaking effect on the current, while this is not the case in the narrower, "barer" forelands of the Waal. Although the current speed in the two rivers is equal, the intensity of flooding proved to be different — moderate to weak in the Guelders IJssel area and strong in the Waal area. In this respect the Rhine has a calm character, with various poorly-developed meanders, so that there is a relatively large number of inside bends, which give a better chance of calmly situated old river-beds than in the Waal forelands. This is expressed in the fact that the limnophyte *Stratiotes aloides* (optimal in very calm places) occurred, in proportion, just as much here as in the Guelders IJssel area. The biotope with weak inundations and the transitional type from weak to moderate inundation occurred — significantly — more frequently in the Rhine area than in the Guelders IJssel area.

Although we have specially considered the ecotope with episodical water movements (Ee), it was also necessary to pay attention to the ecotope with stagnant water (Es). From this it was shown that the latter ecotope occurred especially in the Maas area with rarely or never flooded river forelands, and that thus this river also showed a special character.

The autecological study of some limnophytes and helophytes made a closer examination of an ecotope possible, so that, within this ecotope, several special biotopes could be differentiated, each of them characterised by a more limited ecosystem than the ecotope as a whole presents. In addition this study lead to a definition of the different characters of the large rivers Maas, Rhine, Waal and Guelders IJssel.

In the general survey (table 10) of the ecotope with episodic water movements (Ee) these differentiated biotopes are given separately for each river-bed. We have compared the presence of the plant species given in the survey per river area. The result was a significant difference between the total presence of these species in the Guelders IJssel and the Waal, and between those in the Guelders IJssel and the Rhine. This difference was not significant between the Rhine and the Waal. The Guelders IJssel area proved to have the richest assortment of species. Here the environment with moderate water movement created, evidently, optimal conditions for the full development of the species combination which can live there.

This is so:

1. because by strong water currents erosion prevents or hinders the placing and (or) development of a number of species and (or) individuals (as in the Waal area);
2. because by stagnant water (no water movement, as in the Maas area especially):
   a. succession proceeds quicker, thus the stages follow one another

more rapidly and less time is available in each stage for the establishment of all species which may find a suitable habitat here; b. there is less supply of diaspores, so that the transport factor is unfavourable.

Weak to moderate inundation creates the best conditions of accessibility. This does not at all mean that the species living there have a preference for moderate water movement.

It has been further shown that from the relation between the average degree of coverage and the depth of water a preference could be found for a given depth. The average cover degree of *Nuphar luteum*, *Nymphoides peltata*, *Potamogeton lucens* and *Nymphaea alba* was highest at a depth of 90–150 cm. These depths appeared in those old river-beds where weak to moderate water movement allows the sedimentation of sand and silt, resulting into a soft mud bottom, or in those old river-beds where absence of water movement allowed peat formation. The average cover degree for *Nymphoides peltata* and *Potamogeton lucens* appeared to increase again, however, at depths of 200 and 210 cm. This was the case in old river-beds that are flowed through powerfully during the winter flooding and where sedimentation is prevented by erosion. The waters were here especially in the centre much deeper than those exposed to moderate or weak inundation. In the deeper old river-beds, the average cover degree of the competitor species *Nuphar luteum* decreased at a depth of 170 cm or more, so that *Nymphoides peltata* had the opportunity to dominate, while *Potamogeton lucens* can be dominant in even deeper places than *Nymphoides peltata*.

The knowledge of the divergent ecological amplitudes of these species may contribute to an explanation of the differences in structure of the plant communities occurring in the area being investigated. The study of autecology is thus a valuable tool enabling us to gain a more detailed view of the synecology of the vegetation formed by these species. The opposite is also true, synecological records providing irreplaceable data for both wider and deeper autecological results than could be obtained by habitat measurements and factor analysis only.

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