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PLANT-MIGRATION STUDIES NEAR THE FORMER ISLAND OF URK IN THE NETHERLANDS

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INTRODUCTION

Reclaimed in 1941 and 1942, the North-Eastern polder [1]) is the second reclamation district in the former Zuydersea, now being called IJssellake. Its formation added 48,000 ha of land to the Netherlands. The virgin soil of this polder mainly consists of sand and silty clay-loam and lies at about 0.5–4.0 m under mean sea-level. Upon these soils within just a few years an almost closed vegetation developed, in which predominated *Phragmites communis* Trin., *Scirpus maritimus* L., *Aster tripolium* L.,*Senecio tubicaulis* Mansf., *Polygonum nodosum* Pers., *Atriplex hastata* L., *Chenopodium rubrum* L. and species of the genus *Bidens*; all these species are pioneers on fertile, waterlogged unaerated soils. Locally saline soils occurred and on these *Puccinellia distans* Parl., *P. retroflexa* Holmb. and *Spergularia salina* J. et C. Presl flourished. With the exception of part of the seeds of *Phragmites*, *Aster* and *Senecio*, in this area propagules of all species mentioned above were distributed almost exclusively by water of the IJssellake from the coastal region, the mouths of the rivers or the islands of Urk and Schokland (Fig. 1). Prior to the reclamation of the polder propagules became deposited on the bottom of the lake, the submerged future polder. After being dispersed by wind into the IJssellake even a considerable number of seeds of typically wind-dispersed species was carried along further into the area of the future polder by means of water transport. Vegetation of *Aster* mainly arose from achenes sown by man during the first two years after reclamation and collected on salt marsh lands in the northern part of the Netherlands (FEEKES and BAKKER, 1954).

For the ecesis of the species mentioned above it is very important that their seeds, if kept under water, can maintain their germinative capacity for at least one year. Transport of rhizomes of *Phragmites* and *Scirpus* by water of the IJssellake occurred but very rarely and consequently in this publication this way of dispersal will not be considered.

Owing to the predominating influence of the water of the IJssellake as dispersing agent for the predominating species and also due to the great competitive power of these species, the North-Eastern polder as a

[1]) a "polder" is an area, reclaimed from the sea and protected against flooding by dikes.

whole proved to be a less favourable object for plant-migration studies than was initially expected (FEEKES and BAKKER, 1954). As a consequence of the competitive power within a couple of years an almost closed vegetation arose and species dispersed by other agents than water hardly got any opportunity to become established. However, in the extreme western part of the reclamation district, in the vicinity of the former island of Urk an area of about 800 ha, differed botanically and pedologically considerably from the main part of the polder. In this publication this area will be called Land of Urk. Pedologically it is characterized by an oftentimes very complex mixture of soil types and a higher location (at 0.5–2.5 m under mean sea-level) than the remaining part of the polder (at 2.0–4.0 m under mean sea-level). Its botanical pecularities were a rather open type of vegetation, very rich in species, and a large variation in plantcover over small distances, parallelled by sudden changes in soil conditions. From 1941, the year of reclamation, to 1951, the year of cultivation, this natural vegetation could develop undisturbedly. The isolated location of the district, the great variation in edaphic factors and the rather general absence of a closed vegetation with only few predominating species made this area extremely well suited to plant-migration studies, the results of which will be discussed in the following paragraphs.

THE PEDOGENESIS OF THE LAND OF URK

The geologically oldest deposits present at the surface are so-called pro-morainal sands, layed down prior to or simultaneously with Riss-morainal boulder clay. They were subject to a strong pushing influence of the icecaps, which deposited on top of them a cover of boulder clay, now lying at or very close to the surface. In the latter case it is covered by a thin layer of still younger deposits. During the Zuydersea period (1500–1932) a shallow water layer inundated the soils and they suffered heavily from wave action, resulting in the actual local presence at the surface of pure boulder clay.

A peat profile forms at present the topsoil in large areas east as well as south of the boulder clay region. Probably prior to 1000 A.D. fresh-water clay became deposited upon this peat. In the Zuydersea period again the sea encroached upon the area and previously off-shore lands were flooded, unless protected against this fate like on the island of Urk.

Another consequence of the rise in sea-level was the distribution of much sandy material by water. Originally this material was lying against or upon the hill of boulder clay or elsewhere it came to the surface through the eroding action of waves. Nowadays these Urk-sand deposits can be found in the peat area and all through the vicinity. Also the two sandy ridges, bordering the low-lying clay area of the island of Urk, are composed of this material as well as the "Tail of Urk". This Tail was a bank of very coarse gravelly and sandy material, projecting in north-eastern direction into the Zuydersea and after the reclamation arising in the landscape as a ridge. The subsoil of this bank was formed by fresh-water clay. In 1952 the material of the Tail was removed and utilized for building purposes.

Boulder clay, peat, Urk-sand and fresh-water clay form in a broad outline the pattern of soil types offered to the vegetation as habitat. For purposes of soil improvement during the construction period of the polder dikes large amounts of soil were deposited on the lake floor. This material originated from canals dredged out under water and is mainly of a light silty clay-loam character; the thickness of the layer is variable.

The natural vegetation of the Land of Urk

Based upon the soil characteristics mentioned in the previous chapter the authors distinguish the following six types of habitat:

1. Urk-sand and light silty clay-loam (dumped soil,) with a maximal thickness of 35 cm;
2. fresh-water clay and light silty clay-loam (dumped soil), in a layer heavier than 35 cm;
3. boulder clay;
4. Tail of Urk;
5. saline soils;
6. peat district.

Many times in types 2, 3 and 6 the soil type giving its name to the habitat does not occur at the surface but is covered by a thin layer of overlying sand. Frequently, however, this layer is so shallow or the influence of the subsoil upon the physical and/or chemical character of the profile so great that the pedological characterization of the habitat offers a good starting point to an ecological discussion.

During the first years after reclamation vegetation remained poor in species. Although usually in a little vital form, only those species occurred which were also predominating in the remainder of the North-Eastern polder. Consequently vegetation stayed open; particularly conspicuous were *Puccinellia*-species, propagules of which were supplied by the water of the IJssellake. Even in 1951 hardly any plant community could be distinguished although particularly after 1945 the total number of species present increased considerably. For a great part propagules of these species were wind-borne, a phenomenon to be returned to later on. First will be given a rough description of the vegetation of the 6 habitats as present during the years 1948–1950.

1. *Urk-sand and dumped soil with a maximum thickness of 35 cm*

In this region the all-predominating environmental factor was the water-economy. An almost completely closed vegetation could develop at some scattered low-lying spots at which the supply of water was guaranteed during the entire vegetation period. Usually, however, the habitat was less favourable due to the bad water-retaining capacity of the soil and the depth of the soil-water table. Particularly during the dry early summer periods vegetation here was very sparse and not before the more rainy summer months most plants came to flower. Consequently in this area the following seasonal vegetation aspects could be distinguished:

winter season: development of mosses and rosettes of winter annuals and perennials;

spring: development of mosses and flowering of some winter annuals (*Cerastium semidecandrum* L.) and perennials, *Taraxacum spec. div.*;
early summer: rather "dry" vegetation, flowering of some winter annuals, e.g. *Erigeron acer* L., *Bromus mollis* L.;
summer and late summer: flowering of many plants which overwinter with a rosette, e.g. *Epilobium spec. div.*, yellow flowering *Compositae.*

In this area species which usually occur under quite dry environmental conditions, strongly predominated. Higher plants covered 40–80 % of the soil surface.

2. *Fresh-water clay and dumped soil with a layer thicker than 35 cm*

In early spring these habitats were flooded for a shorter or longer period of time or they suffered from very high watertables. Many species preferring moist habitats occurred. The main part of the soil surface was occupied by species able to propagate very actively by means of subterraneous organs, e.g. *Phragmites communis* Trin., *Scirpus maritimus* L., *Tussilago farfara* L., *Cirsium arvense* Scop. The vegetation covered the area for about 80–100 %.

3. *Boulder clay*

On boulder clay like on other compact soils many plants suffer unsurpassable difficulties owing to the great resistance offered to the development of the root systems and due to the large swelling and shrinking characteristics of the soil material. Even in 1950 vegetation was still very sparse; the part of the soil covered by higher plants did not amount to more than 5–15 %, while 10–20 % was occupied by mosses.

As on peat soils the presence on the boulder clay of a shallow sandy layer appeared to promote the establishment of plants. Due to the imperviousness of the subjacent boulder clay such a sandy layer could keep its humidity rather long. Moreover, aeration of the sand was high and mechanical resistance very little. The major part of the species present were winter annuals, common on quite dry habitats, e.g. *Erigeron acer* L., *E. canadensis* L., *Crepis capillaris* Wallr.

4. *The Tail of Urk*

On the Tail the coarseness of the material increased with increasing elevation. However, even at the top of the ridge in early spring the phreatic level was not very low owing to the presence of the clayey subsoil. The striking coarseness of the topsoil permitted development of those species only, which are drought resistent or have during the wet season such a rapid root development that this feature enables them to reach the watertable very rapidly. Part of the species belonging to the latter type succumbed in the dry early-summer period before ever having flowered.

On top of the Tail the cover of higher plants did not amount to

more than 5 % of the total surface; mosses took in 10–30 %. The whole year through the xerophyte *Sedum acre* L. determined the aspect.

5. *Saline soils*

The area east and south-east of the island of Urk has received the name heterogeneous complex, indicating that patches of peat, sandy areas, fields of fresh-water clay and other young marine sediments are intermingled in a very irregular fashion. Also north-west of Urk and south of the boulder clay area regions of this character can be found. Locally environmental conditions occurred which could only be met by halophytes.

6. *Peat area*

Botanically the peat area was characterized by a very sparse vegetation (cover 0–20 %) and by the presence of narrow but rather densely vegetated bands, formed on clayey or mixed sand-clayey ridges, resulting from human activities in former ages. Compared to the other sparse vegetations on the boulder clay and the Tail, on account of the absence of even the slightest cover of mosses the peat area could be called the poorest vegetated part of the Land of Urk.

The peat area suffered from a very bad water-regime, owing to its location between the former island of Urk, the dike of the North-Eastern polder and the boulder clay region. Consequently chlorine, concentrated in the peat by diffusion during the saline Zuydersea period, could only be partly leached out. Through evaporation during summer months particularly at the surface layer of the peat locally very high salt contents could be reached.

In addition to these saline spots (salinity expressed as content in NaCl) the peat was characterized by a very high acidity. Formed in fresh water and very poor in mineral elements, after reclamation the acidifying influence of oxidative processes in the topsoil could not be neutralized. This resulted in the formation of hydrochloric acid because a large amount of chlorine ions occurred in the soil moisture in addition to sulfuric acid formed through oxidation of FeS.

On the saline peat halophytes rarely occurred, probably due to the low pH. All Dutch halophytes are base-frequent and of non-halophytic acid-frequent species only *Holcus lanatus* L. predominated.

The migration of plants to the Land of Urk

The ecesis of a plant at a specific habitat is the result of the action of a great number of factors, which can be separated into the two following groups:

1. the environmental factors;
2. the life-cycle of the plant.

As to the environmental factors, in a discussion of the migration of a plant species particularly the factor called accessibility (*sensu* Heimans, 1954) is of importance. Of the life-cycle characteristics the dispersal type has to be stressed.

Considering the accessibility of the Land of Urk two periods have to be clearly distinguished, viz. the period prior to and the period after the reclamation of the North-Eastern polder. Prior to reclamation propagules became deposited upon the lake bottom and after emergence of the land establishment of plants was possible. After reclamation only those plants could ecese which have propagules able to pass the distance between the area and the island of Urk or the much larger distance to the island of Schokland or to the still existing or former shore of the IJssellake (Fig. 1).

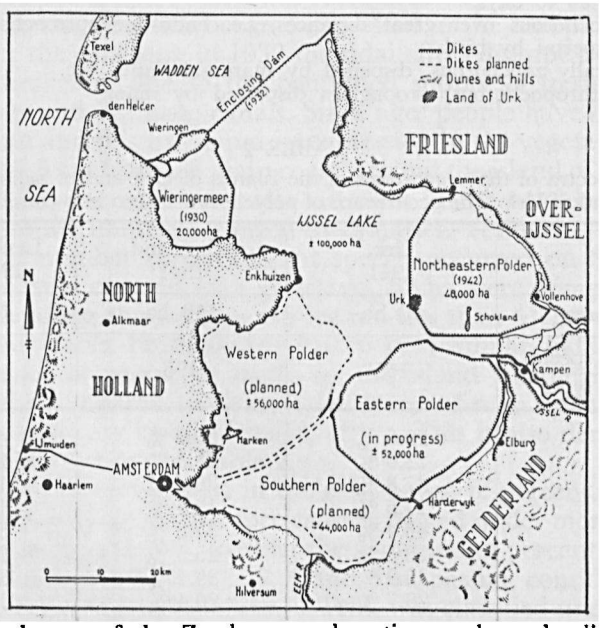

Fig. 1. Sketch-map of the Zuydersea reclamation works and adjacent areas.

In distinguishing several dispersal types use has been made of the principles followed by FEEKES (1936) and WESTHOFF (1947). As criterion for the distinction of dispersal types these authors used the effectiveness of the action of the distributing agent upon the propagule measured by the distance between mother plant and the spot that can be reached by the propagule. In our discussion the classification of Westhoff is followed (Table 1), differing only in minor details from the one used by Feekes.

WESTHOFF (1947) subclassifies these dispersal types respectively into euchorous or migration types (propagules of which can be dispersed over long distances) and dyschorous types where this is not the case. Of the types mentioned in Table 1, type A, *a*, H, Z and M are considered to be euchorous, type a, h and z dyschorous by Westhoff. From Table 2 it appears, that in the pioneer vegetation of the Land of Urk euchorous types were stronger represented than in the older vegetation of the islands of Urk and of Schokland.

TABLE 1

Dispersal-types according to WESTHOFF (1947)

A = anemochorous; propagules dispersed by wind over some to many kilometres.
a = anemochorous; propagules dispersed by wind over not more than some hundred metres to about one kilometre.
a = anemochorous; propagules dispersed by wind over at the most some tens of metres.
H = hydatochorous; propagules dispersed by water, remain floating for some weeks to years.
h = hydatochorous; propagules dispersed by water, remain floating for some hours to days.
Z = zoochorous over great distances, i.e. endo- or epizoochorous due to dispersal by birds.
z = locally zoochorous, dispersal by mammals, ants, etc.
M = anthropochorous, propagules dispersed by man.

TABLE 2

Dispersal spectra of the vegetations of the islands of Urk and of Schokland and of the Land of Urk. The occurrence of polychory is taken into consideration.

	Urk, 1941	Schokland, 1941	Land of Urk, 1942–1951
Total area	80 ha	119 ha	800 ha
Number of species / Dispersal types	165	196	182
A	20.6 %	23.0 %	40.2 %
a	23.0 %	25.5 %	26.9 %
a	27.8 %	28.6 %	17.0 %
H	17.5 %	19.4 %	18.6 %
h	45.4 %	57.6 %	53.8 %
Z	28.4 %	25.5 %	29.1 %
z	30.9 %	35.7 %	38.4 %
M	28.7 %	20.4 %	14.3 %
Sum of euchorous types	118.2 %	113.8 %	129.1 %

Migration proper was strongly influenced by all factors affecting germination of seeds. Due to this influence it is not known which propagules reached the area, neither in what degree they germinated. We only know which plants, whose propagules reached the area, passed through the entire ecesis stage, i.e. after the migration stage they came to germinate, development and reproduction.

It did not appear to be possible to follow along experimental lines the behaviour of different dispersal types in relation to the very remote location of the area, in other words the interaction between remote location and dispersal type. We could only proceed statistically in comparing the dispersal spectrum of the vegetation of the Land of Urk with the dispersal spectrum of the vegetation of the neighbouring island of Urk, which for our area will have been a source of propagules, and also of the island of Schokland. For this purpose species inventories of Urk and Schokland, taken by FEEKES (1942) in 1941 shortly

before the reclamation of the Land of Urk, were at our disposal [2]). Moreover we followed whether or not species present in the Land of Urk could originate from the mainland between Lemmer and Kampen, thoroughly floristically investigated during the years from 1929 to 1941 (FEEKES and BAKKER, 1954). Supply of propagules from habitats in the province of North-Holland could not be considered, because accurate species inventories of this region were not available. Almost exclusively supply by wind or by birds comes into consideration, considering the water barrier between the districts.

Until 1932 the island of Urk was surrounded by the brackish water of the Zuydersea, and this became expressed in the halophilous vegetation. After the enclosure in 1932 the tidal effect disappeared and the IJssellake freshened due to the continued supply of fresh water by several rivers and drainage canals. Since ages people have been living on this island and this has found its expression in the vegetation.

At about 5.5 km from the main coast, around the island of Schokland (about 119 ha) the water was less salt than in the neighbourhood of Urk owing to the influence exerted by estuaries. Yet during the brackish period a number of salttolerant species occurred on Schokland. Only 26 ha were covered with grassland, 52 ha were *Phragmites*-vegetation while along the western border not less than 41 ha were taken in by shallow pools. From about 1860 to 1941 human habitation and other presence of people or cattle on the island was negligible and consequently compared to Urk the influence of man upon the plant-cover remained very small (FEEKES, 1942). This is also demonstrated in the dispersal spectra of Table 2..

It has to be remarked that in the calculation of percentages of dispersal types represented most species were placed under more than one dispersal type (polychory), making the sum total of percentages in the different columns of Tables 2, 3, 4 and 6 surpassing considerably the figure 100. E.g., *Phragmites communis* Trin. was classified under type A, h and z, and *Trifolium repens* L. under H, Z and M.

RIDLEY (1930) and MOLINIER and MÜLLER (1938) pointed out that wind is the most important agent in the migration of species to open vegetations, while OSTERWALD (ULBRICH, 1928) demonstrated this phenomenon very clearly in the establishment of pioneer vegetations in a large sand-pit near Berlin and SALISBURY (1954) for the flora occurring on World War II bomb-sites in London. In agreement with these observations are the data of Table 2, from which we can conclude the tremendous importance of the wind factor for the formation of the pioneer vegetation of the Land of Urk, compared with the old established and almost closed vegetations of the islands of Urk and of Schokland. From Table 3 we can also draw the conclusion that the majority of the species of type A present in our area could not originate from the island Urk (although the Land of Urk was so closely adjacent to it) or from Schokland but came from the mainland. Moreover, only

[2]) The list of species could not be included in this publication. However the authors are willing to send interested persons a mimeographed list with indication of the dispersal types of all species found on and near Urk and on Schokland.

17.8 % of type A could have been dispersed over large distances by other agents than wind. Of these 17.8 % still 76.9 % was present on the island of Urk, making it highly probable that most species belonging to this type were borne by wind from Schokland, from the mainland between Lemmer and Kampen or from still further lying dispersal nuclei (Table 4). Only five species occurring in the Land of Urk were never found on the mainland between Lemmer and Kampen; of these 5 species 4 belong to type A (Table 5).

It is of no use to make a sub-classification of type A considering the rather small establishment of species in the Land of Urk. Mention can be made though of the occurrence of a great number of *Compositae*, "presenting" their fruits to the wind like *Taraxacum* does with a well-developed pappus.

In the Land of Urk, however, type *a* did not come more to the fore than on the two islands (Table 2); the majority of the representatives of this type also occurred on Urk and they may have originated from this island (Table 3). The dyschorous type a, however, was in the Land of Urk considerably less represented than on the two islands (Table 2). Probably thanks to the adjacent location of Urk this type was still able to attain a percentage of 17.0; the majority of the species was represented on Urk (Table 3) and those that were not did also belong to the euchorous types H, Z or M.

In the Land of Urk supply of propagules by lake water played a less predominating part than elsewhere in the North-Eastern polder. During the first few years after reclamation not one fourth of the total number of species present later on became established here. Probably this was due to the extreme drought conditions during summer, still permitting establishment of hydatochorous plants but not allowing development of a dense vegetation. That is to say, in the Land of Urk almost all species, predominating in the major part of the North-Eastern polder, became established immediately after reclamation. The percentage of typical hydatochorous plants (type H) did not differ noteworthy from that on the two islands (Table 2), so that this dispersal type is not characteristic for the pioneer vegetation under discussion. Moreover in 1941 81.1 % of the representatives of this type occurred on Urk and consequently a fast supply of propagules from far-removed dissemination nuclei cannot be proved, the more so as for 87.5 % of the type H species of the Land of Urk transport over large distances by other agents than water was possible (Table 4). Type h strongly predominated on the two islands and in the Land of Urk (Table 2) because many representatives of type A are also classified under "minor hydatochorous plants". Very probably, however, in the Land of Urk the majority among the h-group was not supplied by water of the IJssellake since many representatives of this type did not become established until several years after reclamation. It is striking that on the island of Schokland the percentage of species belonging to type h was higher than in the Land of Urk, although in the first region type A was considerably less represented than in the latter. However, also on Schokland many species occurred for which type h is one of the most impor-

tant ways of dispersal. Probably this was a result of its location at a rather short distance from the coast just in front of some rivermouths.

In the three regions under consideration quite a few typically zoochorous species (type Z) were found (Table 2). Yearly use of the islands as resting-places by many migratory birds may explain the quite frequent occurrence of type Z (TEN KATE *c.s.*, 1931, 1933). Feeding-experiments with ducks (EIKELBOOM, 1941, 1942) and with starlings (DE VRIES, 1939), as well as the results of investigation of crop and stomach contents carried out with ducks clearly demonstrate that seeds of many plant species can pass through the digestive tract of above mentioned birds without loosing their germinative capacity. In ducks digestion may take some 4–7 hours; within this time ducks can transport seeds over some hundreds of kilometres (EIKELBOOM, 1942). Epizoic dispersal may be very effective too when fruits and seeds stick with muddy soil to the legs or feathers of birds (RIDLEY, 1930). Particularly small fruits and seeds, and fruits and seeds carrying a pappus or wings come into consideration for this transport. However, it cannot

TABLE 3

Occurrence on the islands of Urk and of Schokland and on the mainland between Lemmer and Kampen of the 182 species represented in the Land of Urk. Species grouped according to dispersal type and polychory taken into consideration.

	Urk, 1941	Schokland, 1941	Mainland between Lemmer and Kampen, 1929–1941
Number of species / Dispersal types	102	110	177
A	39.7 %	47.9 %	94.6 %
a	75.0 %	69.4 %	97.6 %
a	66.7 %	72.7 %	100 %
H	81.1 %	72.5 %	100 %
h	60.0 %	38.9 %	96.6 %
Z	71.1 %	75.0 %	98.1 %
z	52.1 %	63.5 %	97.3 %
M	65.4 %	65.4 %	100 %

TABLE 4

Percentages of different euchorous dispersal types, present in the Land of Urk, belonging to more than one euchorous dispersal type and occurrence of these subgroups on the island of Urk in 1941.

Euchorous dispersal types	Belonging to more than one euchorous dispersal type	Occurrence on Urk in 1941
A	17.8 %	76.9 %
a	44.9 %	40.6 %
H	87.5 %	85.9 %
Z	76.9 %	75.0 %
M	38.6 %	90.0 %

always be ascertained whether transportation occurred epi- of endozoïcally, because some species can be distributed either way.

During fall and winter months the Land of Urk was covered by vast pools and continuously visited by water-fowl making supply of propagules by birds very probable. Presumably thanks to the favourable biotope for water-fowl and due to the proximity of the island of Urk (where 71.1 % of the typically zoochorous species present in the Land of Urk occurred, Table 3) about 1951 within a short period of time the percentage of type Z species increased tremendously. Although being very probable yet it cannot be said with certainty that zoochory has been of great importance in the Land of Urk because in this area 76.9 % of type Z species belonged to other euchorous dispersal types as well (Table 4).

Not including the salt-tolerant *Carex extensa* Good. all typically zoochorous species present in the Land of Urk were also found on the mainland between Lemmer and Kampen (Tables 3 and 5). The nearest growth sites of *Carex extensa* are at about 70 km from the island of Urk at the saline beaches of the Wadden Islands and supply of propagules by migratory birds is highly probable.

In the Land of Urk the percentage of locally zoochorous species (type z) was somewhat higher than on the two islands because several typically anemochorous species (type A) were also recorded under type z. This explains why only 52.1 % of type z present in the Land of Urk occurred on the island of Urk.

In the Land of Urk anthropochorous species (type M) played only a minor part. Yet 14.3 % of the species present belonged to this type, undoubtedly owing to the proximity of the island where 65.4 % of the species occurred. Another factor responsible for the rather high percentage of type M species is the sowing in 1947 on the Urk-sand of some small trial plots with pasture seed mixtures.

Species belonging to type A had a more conspicuous representation in the usually open vegetation of the Land of Urk than in the completely or almost completely closed vegetation of the two islands (Table 2). From this we see that a dispersal spectrum does not include all species which migrated to an area but only those species able to establish themselves after migration thanks to a suitable environment. Apparently in open vegetations conditions are more favourable to the establishment of representatives of type A. Usually pioneers do not form closed vegetations and consequently type A species will play an important part in them.

TABLE 5

Species present in the Land of Urk and not occurring on the islands of Urk and of Schokland and neither on the mainland between Lemmer and Kampen.

Species	Dispersal types
Carex extensa Good.	*a*, h, Z
Epilobium adenocaulon Hausskn.	A, z
Epilobium lanceolatum Seb. et Mauri	A, z
Gnaphalium luteo-album L.	A, h
Hieracium caespitosum Dum.	A, h

The vegetations on the six types of habitat mentioned previously developed almost simultaneously, only at the relatively elevated Tail some months earlier than elsewhere. There was not much difference either in location of the dispersal nuclei Urk, Schokland and the mainland between Lemmer and Kampen. Nevertheless it was of great importance that the six habitats differed greatly in extension, a factor which might have been of influence upon the supply of very rare migrants. This does not take away, however, that based upon the similar-

TABLE 6

Dispersal spectra of the vegetation of six habitats in the Land of Urk, polychory taken into consideration.

Habitat	Urk-sand and dumped soil < 35 cm	Fresh-water clay and dumped soil > 35 cm	Boulder clay	The Tail	Saline soils	Peat
Total area	350 ha	200 ha	50 ha	25 ha	50 ha	125 ha
% cover by vegetation	40–80 %	80–100 %	5–15 %	5–15 %	50–70 %	0–20 %
Number of species	170	74	63	76	40	47
Dispersal types						
A	41.7 %	29.7 %	50.8 %	50.0 %	30.0 %	44.7 %
a	27.1 %	32.4 %	29.0 %	23.6 %	35.0 %	27.6 %
a	17.1 %	22.9 %	14.3 %	14.4 %	20.0 %	23.4 %
H	17.1 %	31.1 %	19.0 %	18.4 %	55.0 %	31.9 %
h	53.5 %	54.1 %	60.3 %	53.9 %	42.5 %	53.2 %
Z	28.2 %	40.5 %	25.4 %	23.7 %	62.5 %	40.4 %
z	37.6 %	37.8 %	47.6 %	40.8 %	22.5 %	42.5 %
M	14.6 %	12.2 %	15.8 %	13.2 %	2.5 %	8.5 %

ity in location and period after emergence some conclusions can be drawn from a comparison of the dispersal spectra of the six habitats. The more so as the smallest region carried the greatest number of species per unit of area and the largest as well as the smallest region were taken in by open vegetations (Table 6).

It follows from Table 6 that not including the saline area, in all open vegetations type A was the most occurring euchorous dispersal type. At the saline habitats soil conditions had a very selective influence and ecesis of plants mainly occurred by salt-tolerant species, which are in the IJssellake region for a considerable part of typically hydatochorous and zoochorous character. Particularly in the very sparse vegetation on the boulder clay type A predominated, and also on the Tail and in lesser extent on the peat soils. Great humidity and locally occurring saline conditions caused that also on the peat a rather high percentage of typically hydato- and zoochorous species occurred. Type A also was of major importance in the quite dense vegetation of the Urk-sand and dumped soil regions. In the dense vegetation of the moist fresh-water clay area, however, typical anemochorous species decreased in importance, presumably due to the rapid establishment

of representatives of types H and Z. On the fresh-water clay only a limited number of species predominated, a phenomenon also expressed in the small number of species per unit of area.

Conclusions

From a comparison of the dispersal spectra of the Land of Urk and the islands of Urk and of Schokland it appears that in open vegetations typical anemochorous plants are predominant among the euchorous dispersal types, and we come to the same conclusion when comparing such spectra of six habitats, offering diverse environmental conditions. Pioneer vegetations usually not being closed, the most important agent in the supply of propagules will be mainly wind. Based upon our own investigations in the Land of Urk and upon experimental results and observations of Osterwald (Ulbrich, 1928) and Salisbury (1954) we conclude, that type A characteristics are important features in pioneers, at least in Western Europe. It could not be experimentally determined whether the open character of the vegetation plays a part during the migration phase of type A representatives, or that a partly vegetated habitat is of importance during the process of ecesis. It is very likely, however, that dense vegetations (particularly high forest) may hamper penetration of propagules borne by wind. Under very extreme edaphic conditions (in our case salinity) even in open vegetations typical anemochorous species were represented in a very low percentage. Salt-tolerant species of dispersal type A never occurred in great amount in the Zuydersea region and consequently their migration to the Land of Urk was only of limited importance. The investigations reported on here prove that environment has a great influence upon the composition of dispersal spectra, in other words in addition to edaphological factors accessibility can be of decisive importance.

SUMMARY

1. In the neighbourhood of the former island of Urk within the North-Eastern polder an area of about 800 ha, called Land of Urk, is distinguished from the remainder of the reclamation district by very peculiar soil conditions. Compared to plant establishment elsewhere in the polder also the development of a natural vegetation showed great differences. From 1941 until 1951, the development of natural vegetation proceeded almost undisturbedly.

2. Based upon differences in soil conditions in the Land of Urk six habitats were distinguished. Differences in soil conditions were strikingly parallelled by variation in vegetation.

3. The Land of Urk was extremely well suited to studies in the field of dispersal-biology. In our investigations use was made of dispersal types distinguished by Westhoff (1947), based upon the degree of interaction between the propagules and the various dispersal agents (Table 1). Only dispersal of fruits and seeds has been of importance.

4. From the euchorous dispersal types represented in the Land of Urk the highest percentage was taken in by species propagules of which can be wind-borne over many km (type A). However, in the dispersal spectra of the closed or almost closed vegetations of the adjacent islands of Urk and Schokland, type A was represented in a considerably smaller degree (Table 2).

5. In 1941 among the representatives of type A in the Land of Urk the major part did not occur on the island, whereas the other types for the most part were

found on Urk. In all probability the most important source of propagules of type A has been the island of Schokland and/or the mainland between Lemmer and Kampen (Fig. 1, Tables 3, 4 and 5).

6. A comparison of the dispersal spectra of the six types of habitat distinguished demonstrated that, excluding saline soils, in open vegetations type A was the most dominant euchorous dispersal type. The accessibility of a habitat appears to be of great influence upon the composition of the dispersal spectrum.

7. The authors propose the thesis that at least in Western Europe type A is the dispersal type par excellence for open vegetations and the characteristics of this type are important features of pioneers, pioneer vegetations usually being open.

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