Acta Bot. Neerl. 29(5/6), November 1980, p. 497–508.

# HAPAXANT SPECIES OF COASTAL BEACH PLAINS COLONIZING EMBANKED SAND FLATS

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SUMMARY

The article documents the colonization of sand flats exposed in a new polder by r-selected species of beach plain environments, i.e. *Sagina maritima, Juncus bufonius* ssp. *ambiguus, Centaurium pulchellum, C. littorale* and *Sagina nodosa* var. *moniliformis.* Species distribution along transects after eight years of succession in the polder and on the beach plain of the island of Schiermonnikoog were compared and related to combinations of the principal environmental factors: salinity, hydrology and % coverage of the vegetation. It is concluded that several hapaxant species of beach plain communities, and especially those belonging to the B2 life form (summer annuals exhibiting innate dormancy) are pre-destined to be successful colonizers of embanked flats, indicating temporary ecological similarity. The more even distribution of the species in the hapaxant life form spectrum of the polder susceptibly indicates the succession towards mesic communities.

## 1. INTRODUCTION

On the extended sandflats in the 1969 embanked Lauwerszeepolder (The Netherlands) a spontaneous vegetation succession occurs; the colonization of most plant species appears to be mainly determined by the velocity of the desalination process, in combination with their salt tolerance and reproductive and dispersal capacity (JOENJE 1978a, b). After the initial dominance by annual halophytes, succeeded by *consortia* of other salttolerants, several species increased which normally occur in wet and/or brackish slacks and beach plains e.g. on the nearby Wadden islands. From the third year onward *Juncus bufonius* ssp. *ambiguus, Sagina maritima* and from the fifth year *Sagina nodosa* var. *moniliformis, Centaurium pulchellum* and to a lesser extent *C. littorale* spreaded.

Their abundance is expected to be a temporary phenomenon due to the developments in soil and vegetation.

The species mentioned are characteristic of open, pioneer communities belonging to associations of the *Centaurio-Saginetum moniliformis* and the often neighbouring *Sagino maritimae- Cochlearietum danicae* (WESTHOFF & DEN HELD 1969). The occurrence of these beach-plain and dune-slack elements in desalinating embankments is documented by various authors e.g. BEEFTINK et al. (1971), DE VRIES (1961), BREHM & EGGERS (1974), JOENJE (1978a).

In this article the colonization history of all five species is summarized and their distribution after eight years is compared with the characteristic distribution patterns on the nearby beach plain of the island Schiermonnikoog.

## 2. MATERIALS AND METHODS

The data on the colonization history were collected during a long term study of the plant colonization and the primary succession (JOENJE 1978a); the data on vegetation and species distributions in the Lauwerszeepolder and on Schiermonnikoog were collected in 1976, the eighth year after embankment, along five selected transects mostly running from sandy and nearly fresh, down to siltier and brackish conditions (BRUINENBERG & WIERENGA 1977).

Soil salinities and moisture % were determined following the ABC-method (HOFSTEE & FIEN 1971); ground water tables were measured from tubes at irregular intervals.

Quantitative data on species abundance and reproductive output were derived from plants of various places in the polder and from the literature (SALISBURY 1942, FREYSEN 1967, JOENJE 1978a). The phytosociological relevés were made after LONDO (1975); names of phanerogams follow HEUKELS & VAN OOSTSTROOM (1979), those of syntaxa WESTHOFF & DEN HELD (1969).

## 3. OBSERVATIONS

### 3.1. Description of the environment

*The Lauwerszeepolder.* The four transects c.q. gradients studied, were situated on various sand flats, containing very little humus, silt or lime, although these components could be somewhat higher in the lower parts (*table 1*).

Local ground water regimes and hence the desalination are strongly dependent on texture and height level. In lower parts the brackish ground water remains in capillary contact with the superficial layers even in periods of prolongued drought, at a phreatic level of 60 cm below the soil surface. The higher parts of the flats with the coarsest sand fractions may present very dry conditions in which capillary rising water does not exceed a level of 50 to 75 cm below the surface at a phreatic level as low as -150 cm (1976) (*fig. 1*).

In wet periods and during most of the winter half of the year the flats are saturated with rainwater; the lowest parts are occasionally flooded with eutrophic fresh water from the bordering reservoir-lake.

Salinities in the upper cm often fluctuate: rain carries salt down the soil profile, evaporation again increases the concentrations (*table 1*), creating a hazardous milieu for germination. The gradual desalination of three plots along a soil- and height gradient (comparable to transect 1) in the first six years is depicted in the upper half of *fig. 3*.

*Schiermonnikoog.* The beach plain on the eastern part of the island of Schiermonnikoog has an elevation level of about 150 cm above Amsterdam ordnance datum (NAP). This sand flat with low elevations consists of sand, nearly devoid of silt and humus and low in calcium (*table 1*). In summer the phreatic level drops to 100–125 cm below the soil surface (*fig. 1*). As in the polder this creates a harsh environment with temporary desiccation and salting of the

Table 1. Environmental data of the five study areas. Salinity in g NaCl.$l^{-1}$ of soil moisture.

| | | height cm NAP* | Silt % (< 16mμ) | $CaCo_3$ % | June 1976 soil moisture % | | June 1976 salinity | | August 1976 soil moisture % | | August 1976 salinity | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| depth cm | | | 0–10 | 0–10 | 0–2 | 2–10 | 0–2 | 2–10 | 0–2 | 2–10 | 0–2 | 2–10 |
| transect I | | | | | | | | | | | | |
| plot | 1 | –43 | 7.5 | 4.0 | 5.2 | 6.7 | 151 | 20 | 6.0 | 7.5 | 52 | 31 |
| | 2 | –25 | – | – | 2.4 | 5.4 | 43 | 5 | 4.1 | 5.9 | 10 | 6 |
| | 3 | –15 | – | – | 1.9 | 5.0 | 32 | 4 | 3.9 | 5.4 | 12 | 5 |
| | 4 | –10 | 1.8 | 3.4 | .8 | 4.3 | 43 | 2 | 3.2 | 5.1 | 8 | 4 |
| | 6 | –4 | 4.1 | 3.4 | .9 | 2.8 | 17 | 3 | 4.3 | 3.9 | 3 | 4 |
| transect II | | | | | | | | | | | | |
| plot | 1 | –58 | 3.7 | 5.5 | 17.9 | 17.7 | 111 | 28 | 17.2 | 17.4 | 92 | 50 |
| | 3 | –60 | – | – | 22.4 | 17.6 | 15 | 6 | 27.7 | 17.8 | 44 | 20 |
| | 4 | –60 | 3.1 | 4.0 | 23.3 | 18.2 | 3 | 2 | 22.0 | 17.7 | 11 | 7 |
| transect III | | | | | | | | | | | | |
| plot | 1 | –62 | 4.0 | 3.9 | 20.2 | 18.3 | 78 | 16 | 21.2 | 19.1 | 54 | 37 |
| | 2 | –61 | 5.3 | 3.8 | 24.6 | 19.1 | 33 | 13 | 21.4 | 19.8 | 43 | 29 |
| | 3 | –30 | 9.3 | 6.1 | – | – | – | – | 9.5 | 11.1 | 6 | 4 |
| transect IV | | | | | | | | | | | | |
| plot | 1 | –35 | – | – | 20.4 | 18.6 | 1 | 0 | 19.6 | 20.1 | 3 | 1 |
| | 2 | –20 | – | – | 11.3 | 13.1 | 2 | 0 | 11.0 | 14.1 | 4 | 1 |
| Schiermonnikoog | | | | | | | | | | | | |
| plot | 1 | 150 | – | – | – | – | – | – | – | 35.9 | – | 1 |
| | 2 | – | – | – | – | – | – | – | 66.1 | 45.5 | 9 | 11 |
| | 3 | – | – | – | – | – | – | – | – | 5.8 | – | 2 |
| | 4 | – | 2.1 | 1.1 | 8.4 | 3.3 | 1 | 2 | 1.6 | 4.9 | 33 | 11 |
| | 5 | 180 | – | – | 9.9 | 6.5 | 4 | 4 | 1.3 | 2.5 | 9 | 2 |

*Amsterdam ordnance datum

upper layer.

In the winter half of the year the lower areas are saturated with rainwater, although some inundations with partially diluted seawater may occur.

## 3.2. Description of the vegetation

The species composition of the prevailing vegetation (*table 2*) reveals the resemblance between beach plain and polder; the difference is mainly caused by the absence of many species in the polder relevés. Here, on the lower rather saline parts of the flats, *Sagina maritima* and *Juncus bufonius* are accompanied by *Puccinellia capillaris*, *Spergularia marina* and *Aster tripolium* a.o., in communities of the *Puccinellietum retroflexae* and the *Puccinellietum distantis*, both

Table 2. Synoptical table of 21 phytosociological relevés ($m^2$) from the five study areas.

| Area | transect I | | | | | | transect II | | | | | transect III | | | IV | | Schiermonnikoog | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| relevé nr. | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 3 | 4 | 5 |
| coverage % | 40 | 80 | 90 | 70 | 75 | 70 | 30 | 35 | 60 | 85 | 95 | 10 | 45 | 55 | 85 | 60 | 70 | 75 | 95 | 50 | 35 |
| height cm | 2–5 | 2–10 | 2–10 | 3–10 | 3–10 | 2–10 | 3–10 | 3–8 | 2–10 | 15–30 | 5–30 | 2–70 | 2–20 | 2–25 | 1–15 | 1–15 | 1–12 | 3–20 | 25 | 5–15 | 5–40 |
| Species: | | | | | | | | | | | | | | | | | | | | | |
| Sagina maritima | m.2 | p.1 | | | | | m.2 | m.4 | m.1 | a.1 | | a.1 | m.4 | | p.1 | p.1 | | r.1 | | m.1 | p.1 |
| Juncus bufonius | a.1 | a.1 | | m.1 | | | m.1 | m.1 | m.1 | m.1 | m.1 | p.1 | m.1 | | a.1 | r.1 | 1 | m.2 | p.1 | | |
| Centaurium pulchellum | | a.1 | | | m.2 | r.1 | | m.1 | 1 | a.1 | p.1 | | | | m.4 | | m.2 | a.1 | | | |
| Sagina nodosa | p.1 | | a.2 | m.4 | 1 | 5 | | r.1 | r.1 | p.1 | p.1 | | | | m.4 | 1 | | | | a.2 | a.2 |
| Centaurium littorale | | | 1 | | | | | | | | | | | m.2 | | | a.1 | a.1 | a.1 | a.2 | m.2 |
| Salicornia europaea | a.1 | | | | | | m.1 | m.1 | a.1 | a.1 | a.1 | m.1 | m.1 | | | | | | | r.1 | |
| Spergularia marina | r.1 | p.1 | | | | | a.1 | m.1 | p.1 | p.1 | p.1 | m.1 | p.1 | | p.1 | | | p.1 | | r.1 | |
| Poa annua | p.1 | m.4 | m.4 | 1 | m.2 | a.2 | | r.1 | p.4 | m.4 | m.4 | | p.1 | 2 | a.2 | 1 | | a.2 | | | |
| P. trivialis | 1 | 1 | m.1 | 1 | m.1 | a.2 | | | r.1 | 1 | 4 | | | | | | | | | r.1 | |
| Festuca rubra | | | | | | | | r.1 | p.4 | 1 | m.4 | | | | | | | 2 | a.1 | m.4 | 1 |
| Agrostis stolonifera | | | | | | | p.2 | r.2 | r.1 | 3 | 3 | r.1 | 2 | 3 | 1 | r.1 | | 2 | a.1 | 1 | p.1 |
| Rumex crispus | | | | | | p.1 | | r.1 | r.1 | r.1 | a.1 | | p.1 | | | | r.1 | | | | |
| Sonchus arvensis | | | | p.2 | m.1 | | | | r.1 | | | | | a.1 | p.1 | p.1 | | | | | r.1 |
| Trifolium repens | | | | | | | | | | r.1 | r.1 | | | | | | r | a.2 | 1 | | |
| Odontites verna | | | | | | | | | | | | | | | | | | | | | |
| ssp. serotina | | | | | | | | | r.1 | | | | | p.1 | | | | | | m.2 | p.1 |
| Plantago coronopus | | | | | | | | | | | | | | | r.1 | m.1 | | | m.1 | p.2 | p.1 |
| Potentilla anserina | | | | | | | | | | | | | p.1 | | | | 3 | a.4 | 1 | 1 | p.1 |
| Triglochin maritima | | | | | | | | | | | | p.1 | | | | | | p.1 | | | |
| Leontodon autumnalis | | | | | | | | | | | | | | p.1 | | | | | | | p.1 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bryophyta | | 7 | 7 | 1 | 3 | | | m.2 | 2 | a.1 | m.1 | | | | 4 | 2 | m.1 | m.1 | a.2 | m.4 |
| Aster tripolium | m.2 | 1 | 1 | 2 | m.2 | m.4 | a.2 | 1 | 1 | a.4 | a.2 | 1 | 1 | p.1 | r.1 | p.1 | | | | |
| Puccinellia capillaris | 2 | r.1 | | | | | 2 | 2 | 1 | | | m.4 | a.2 | | | | | | | |
| Matricaria maritima | | | | p.2 | r.1 | | r.1 | p.1 | r.1 | a.1 | p.1 | | | p.1 | p.1 | p.1 | | | | |
| Suaeda maritima | p.1 | | | | | | r.1 | | r.1 | | | m.1 | p.1 | | | | | | | |
| Cerastium holosteoides | | | r.1 | m.4 | m.2 | m.2 | | | | r.1 | r.1 | | | | p.1 | | | | | |
| Epilobium parviflorum | | m.1 | a.2 | a.2 | p.4 | a.1 | | | r.1 | | | | | | m.2 | a.1 | | | | |
| E. tetragonum | | r.1 | r.1 | m.2 | p.1 | a.1 | | r.1 | a.1 | a.1 | | | | | a.1 | p.1 | | | | |
| Phragmites australis | | | | | a.4 | r.2 | | | | r.1 | a.4 | | | p.1 | p.2 | p.1 | | | | |
| Puccinellia distans | | | | | | | r.1 | r.1 | r.1 | | | p.1 | p.1 | | | | | | | |
| Taraxacum sp. | | | | a.2 | a.2 | p.1 | | | | | | | | a.1 | p.1 | a.2 | | | | |
| Epilobium hirsutum | | | | | p.2 | | | | | p.1 | 1 | | | | | | | | | |
| Ranunculus sceleratus | | | | r.1 | | | | | r.1 | | | | | | | | | | | |
| Lolium perenne | | | | | | | | | | p.1 | | | | | 3 | 3 | | | | |
| Cirsium arvense | | | | | | | | | | | p.1 | | | a.1 | | | | | | |

In addition the following species occurred in the relevés

Schiermonnikoog: Ammophila arenaria; Armeria maritima; Cardamine pratensis; Carex arenaria; Carex distans; Carex serotina; Cerastium semidecandrum; Eleocharis palustris pal.; Glaux maritima; Gnaphalium uliginosum; Halimione portulacoides; Hippophae rhamnoïdes; Holcus lanatus; Hydrocotyle vulgaris; Juncus articulatus; J. gerardii; J. maritimus; Leontodon nudicaulis; Linum catharticum; Lotus corniculatus; Luzula campestris; Lycopus europaeus; Myosotis caespitosa; Ophioglossum vulgatum; Parapholis strigosa; Parnassia palustris; Plantago maritima; Poa pratensis; Prunella vulgaris; Radiola linoïdes; Rubus caesius; Rumex acetosella; Sagina procumbens; Salix repens; Sedum acre; Senecio jacobaea; Sieglingia decumbens; Trifolium fragiferum.

Lauwerszeepolder: Alopecurus geniculatus; Arabidopsis thaliana; Atriplex hastata; Calamagrostis epigejos; Puccinellia maritima; Rumex acetosa; Senecio vulgaris; Spergularia media.

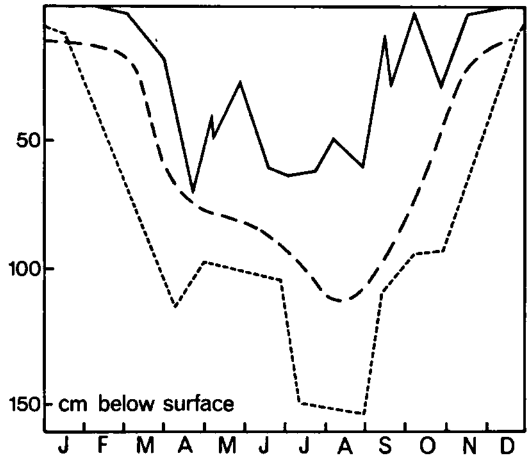


Fig. 1 Fluctuations of the ground water tables in 1976 in poldertransect 1 (...), transect 2 (——) and in the beach plain of Schiermonnikoog (---); levels in cm below the soil surface in the middle of the transect.

associations characteristic of beach plains and polders (WESTHOFF & DEN HELD 1969).

The communities with *Sagina maritima* and *Juncus bufonius* on Schiermonnikoog better match associations of *Saginion maritimae* and the *Centaurio-Saginetum moniliformis* association of the *Nano-Cyperion flavescentis*, all characteristic of slightly brackish belts along low sanddunes.

On moist and desalinated soils in the polder *Sagina maritima*, *Juncus bufonius*, *Centaurium pulchellum* and the other species mentioned, occur together with *Agrostis stolonifera*, *Festuca rubra*, *Poa annua* and *P. trivialis* and other species like *Matricaria maritima ssp. inodora*, *Epilobium tetragonum*, *E. parviflorum* and *Rumex crispus* a.o. which reveals affinities towards *Agropyro-Rumicion crispi*.

The communities of the drier and desalinated sands are already devoid of halophytes (-tolerants) and in addition to *Sagina nodosa*, *Aster tripolium*, *Poa annua*, *P. trivialis* and *Epilobium* spec. div., also *Taraxacum* sp., *Cerastium holosteoides*, *Sonchus* spp. and *Phragmites australis* are common.

The communities in the polder in which the five species under investigation participated, generally had a low % coverage: 10 to 40 % in saline areas and up to 80 % on desalinated drier places where Bryophytes accounted for up to 70 % of the cover. The five species were absent in the moist and nearly desalinated zones in between, where *Agrostis stolonifera* and/or *Alopecurus geniculatus* reached up to 100% coverage.

### 3.3. Occurrence and distribution of the five species

*Sagina maritima* was very abundant in the polder, in places varying from brackish to desalinated and from wet to dry, especially on scarcely vegetated areas. It formed massive mats in moist bare places such as prevailed in brackish conditions. On the beach plain the species occurs in wet or dry, generally bare and trodden places. In the polder it germinated in April, flowered in May and June and died; in September and October large numbers of seedlings were found.

*Juncus bufonius* gradually germinated in spring throughout the polder in both dry and moist open places; highest plant densities were found in wet, open places. The major part of the seedlings in drier places died because of increasing salinity in the prolongued drought. There may have been more than one generation. In the beach plain communities the species is confined to moist, open places.

*Centaurium pulchellum* in the polder germinated in May after a dormancy period and was abundant in the transition between brackish and desalinated soil; densities being higher in moist places and at lower coverage of surrounding grasses. On the beach plain of Schiermonnikoog the species was confined to very moist, almost completely desalinated places with a low coverage. The plants flowered in July and died, many plants, however, only partially: they recommenced growing and flowered again in September during the following wet period.

The three species mentioned above are annual. Their seeds are efficiently dispersed by water and wind action across the extended flats. This offers a marked contrast to the next two species which are more or less confined to drier conditions. *Centaurium littorale*, – a biennial of which only the flowering-phase was found in several places in the polder – occurred on nearly desalinated and dry soils with a low vegetation cover. The plants always occurred in 'seedling' – aggregates indicating a colonization process (JOENJE 1978a). This is in contrast with the distribution in the customary habitats of the beachplain where the species prefers the open, dry fringe along the low dunes (FREYSEN 1967). In one place in the polder a large aggregate of 350 m diameter of *Centaurium littorale* var. *iberoïdes* occurred. The plants in this patch had a decumbent, semi-spherical growth form producing relatively large numbers of capsules.

Rozettes of the first year stage were found more wide-spread, also in moist and lower places; they are expected not to survive the prolongued inundations in winter.*Sagina nodosa* was restricted in the polder to the almost completely desalinated drier places. Especially in dry, nutrient-poor sands this perennial species formed extended mats exerting dominance. These thick aggregates developed from branching and continuously growing stalks as well as from the sowing of "axillary buds" from September onward. In addition to these vegetative propagation seedling aggregates were found

The distribution of the five species along the transect no. 1, a characteristic soil and height gradient in the polder, was investigated on June 10, 1976 and is depicted in *fig. 2*. In the lower and brackish part of the gradient (left part of the figure) the subsequent drought increased the salinity up to 50 g NaCl per 1 soil moisture in the upper 2 cm layer in August, which caused a serious drop in % coverage, *e.g.* *Puccinellia capillaris* decreased from 30 to 10%. In the highest part of the transect the drought had killed most of the grasses *i.c.* *Poa annua* and *P. trivialis*; they probably were incapable of reaching the capillary zone.

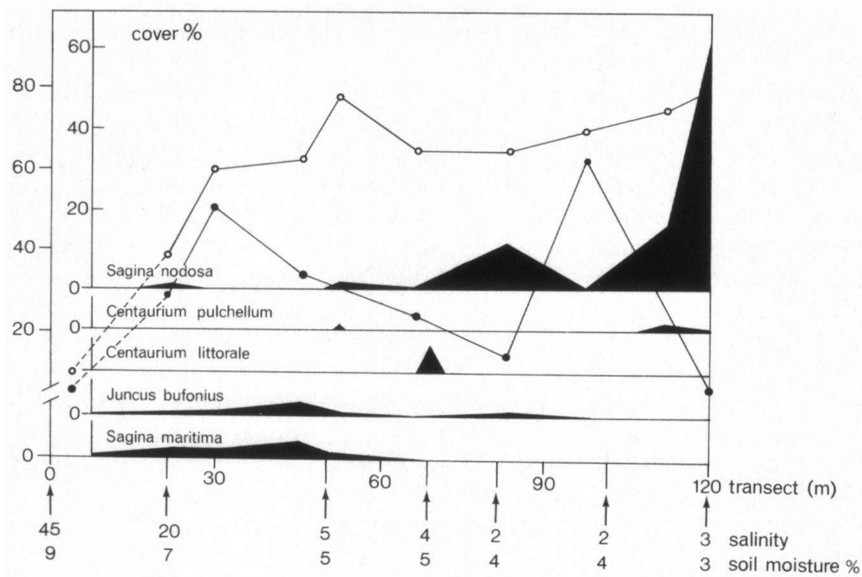


Fig. 2 Species distribution along transect 1, in June 1976, the height gradient running from left (–45 cm NAP) to right (–3 cm NAP). The coverage of each species is shown in black. On the abscissa the distance in m along the transect, the salinity (g NaCl $l^{-1}$ soil moisture) and soil moisture %, both of the 2–10 cm layer are given (sampled August 24th).
.——. cover % of the grases
O——O id. of the whole vegetation.

## 3.4. Colonization history of the five species in the polder

In *fig. 3* the colonization by the five species of three habitat-types of the sand flats is summarized.

*Sagina maritima* and *Juncus bufonius* spp. *ambiguus*, both annuals, up to 1969 occurred abundantly in and above the spray-zone along the former sea dike; seeds have most probably been present in various places in the polder at the time of the drainage. In the second year (1970) both species were found on superficially desalinated mussel heaps; succession rendered these places unsuitable, but after 5 years the species were frequent on sandy desalinated areas. In the 6th year aggregates of *Juncus bufonius* were found in fresh moist belts along the reservoir lake in the former tidal channels.

*Juncus bufonius* populations appeared to increase slightly faster than *Sagina maritima*. In the eighth year both species were abundant all over the area, their absence on the driest sands (transition, *fig. 3*) probably being determined by selection during ecesis, rather than migration.

The nearestby provenances of *Sagina nodosa*, *Centaurium pulchellum* and *C. littorale* were on the island of Schiermonnikoog. Drifting diaspores of many species were washed ashore along the enclosure dam and some have been blown into the polder. In the 4th year flowering plants of *Centaurium littorale* and in the

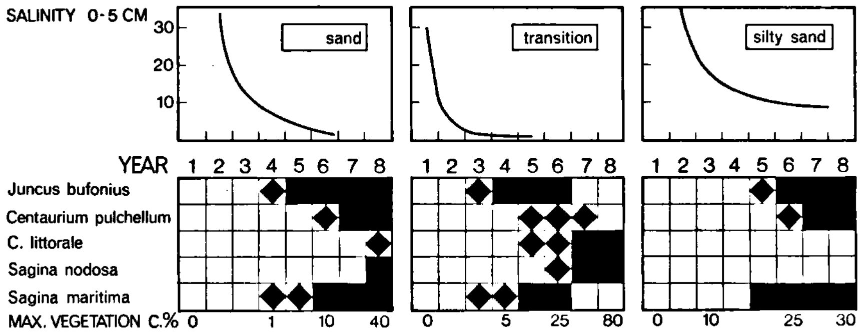


Fig. 3 Colonization of the three principal environments in the Lauwerszeepolder by the species studied in the first 8 years, as related to the desalination process (after data from JOENJE 1978a). Occurrence: ◆ occasional, ■ abundant

5th year numerous flowering plants of the other two species were found on a desalinated belt along the inner foot of the new dam. As judged from yearly harvests and study of permanent quadrats (JOENJE 1978a) population increases in the polder were not so quick, probably because of the low starting densities and the less efficient dissemination across the increasingly densely vegetated flats.

*Sagina nodosa* was found in various places in the polder in the sixth year, sometimes in seedling aggregates, all plants belonging to the var. *moniliformis*. In autumn the plants formed vegetative propagules (axillary buds) which were dispersed in large quantities (see ELLISTON WRIGHT 1953). A comparable dispersal of vegetative parts (gemmae) was found in *Bryum bicolor* and *Pottia heimii*, two highly succesfully colonizing bryophytes in this polder (JOENJE & DURING 1977).

The annual *Centaurium pulchellum* was found on various places on the sand flats in the 6th year and aggregates were found in the 7th year, with plants attaining heights of 1 to 12 cm. The species apparently prefers moist habitats.

The biennial *C. littorale* was not found (flowering) on the flats before the 6th year. In the 8th year several aggregates of flowering plants were present on dry and desalinated areas with an open vegetation; the plants reached a height of 5 to 20 cm. The markedly synchronous ("biennial") flowering was repeated in the 10th year all over the polder.

### 3.5. Densities and seed production of Centaurium spp.

A few data were collected pertaining to the reproductive capacity of the expanding populations of the two *Centaurium* species in the polder. Both species presented large flexibility in statue and hence in capsule production per plant; the correlations between log. -number of capsules (c) and the height (h) of each plant were $c = 1.15h-4.7$ and $c = h-0.5$, for *Centaurium littorale* and *C. pulchellum* respectively. In the centres of the (seedling) aggregates densities of over 600 flowering plants $m^{-2}$ (*C. littorale*) and over 3000 plants $m^{-2}$ (*C. pulchellum*) were found. In *table 3* some data on seed production are summarized.

## 4. DISCUSSION

### 4.1. Environmental factors and species distributions

In 1976, presenting an extremely dry growth season, the distribution of the five species studied has been greatly influenced by the salinity and moisture % of the soil and indirectly by the total coverage of the vegetation.

There existed a rather abrupt transition from brackish towards nearly completely desalinated soil. At increasing height and lower silt content the height of the capillary rise and the salt content per soil volume decrease. At a certain point the soil surface falls out of reach of the cappillary rise and from there the leaching-efficiency by precipitation greatly increases and shallowly rooting plants may experience desiccation.

It appears that all species occupy a wide range in salinity and soil moisture percentage. In all species the frequency of occurrence is correlated negatively with grass coverage together with either salinity or soil moisture (*table 3*). This conclusion is affirmed by the data of *fig. 2* and by additional field work summarized in *table 4*, which gives correlations between the frequencies of occurrence and the factors mentioned, based on 29 plots in the Lauwerszeepolder (BRUINENBERG & WIERENGA 1977). It holds for the polder and the beach plain equally; however the desalinating areas in the polder being colonized by grasses proceedingly, are only temporarily suitable to the five species. Their success underlines the dependence on open and changing environments such as found in association with nutrient-poor (sandy) and variable-salinity conditions, with a ground water regime primarily set by the precipitation-evaporation balance, and only slightly affected by winter inundations. The species need some salt tolerance, a large diaspore production, a short life cycle and euchorous dispersal. Such features of dispersal and life form, characteristic of "r-selected species" (MCARTHUR & WILSON 1966), will be discussed below.

Table 3. Seed production by *Centaurium pulchellum* and *C. littorale* in the Lauwerszeepolder in 1976.

| | capsule per plant | seeds per capsule | seeds $m^{-2}$ | seeds per plant |
|---|---|---|---|---|
| *Centaurium pulchellum* | | | | |
| centre of aggregate | 1 – 2 | 157 (80–220) | 768,000 | 225 |
| solitary plant | 12 (10–30;310) | do. | | 1,884 |
| *Centaurium littorale* | | | | |
| centre of aggregate | 7 (1–65) | 203 (150–283) | 889,140 | 1,421 |
| solitary plant | 107 (7–470) | do. | | 24,610 |

Table 4. Correlations between frequency of occurrence of the species and salinity (g NaCl.$l^{-1}$ soil moisture), soil moisture (g $H_2O$.100 $g^{-1}$ dry soil), both in the 2–10 cm soil layer, and the % coverage by grasses.

| | soil salinity | soil moisture | grass-coverage | salinity & grass-coverage | moisture & grass-coverage |
|---|---|---|---|---|---|
| Sagina maritima | . | * (+) | . | * | *** |
| S. nodosa | * (–) | . | . | ** | . |
| Centaurium pulchellum | . | * (+) | . | . | *** |
| Juncus bufonius | . | * (+) | . | . | ** |

* $0.025 < P < 0.005$
** $0.005 < P < 0.0005$
*** $P < 0.0005$

## 4.2. Dispersal, reproduction and life form

The occurrence in the polder of the five species studied over a widened range of ecological conditions reflects the result of reaching suitable places more efficiently than their usual neighbours (comp. *table 2*). Their early arrival on the new land and the subsequent spread (mostly "seedling" aggregates) demonstrates the efficient dispersal of either seeds or vegetative buds.

Production of propagules is known to be high in most of the species. We have indications that in the polder the reproductive outputs are well above levels normally encountered; e.g. the output of *Centaurium littorale* in the polder (*table 3*)889,140 seeds $m^{-2}$, as compared to 60.000 seeds $m^{-2}$ in natural conditions and with a number of seeds per capsule of over 200 against 150 seeds normally (FREYSEN 1967).

A general conclusion can be drawn from the descriptions above: the hapaxants studied (the perennial *Sagina nodosa* may be regarded as an "annual" in view of its peculiar vegetative reproduction) are known to be adapted to these hazardous environments associated with marine fore land (SALISBURY 1942, BAKKER 1966), which present such a characteristic combination of stress – and disturbance – environments (*sensu* GRIME 1979). The new polder appears to offer extended suitable areas, in the colonization of which the innate characters paid

Table 5. Life form spectra of hapaxants (after BAKKER 1966) in the communities of the polder and the beach plain as derived from *table 2*.
A. Ephemerals, B. Annuals, C. Biennials. The figures refer to specific combinations of life cycle characteristics, such as stage of development during the winter, dormancy, vernalization requirements and flowering time.

| life form | A1 | A2 | A3 | B1 | B2 | B3 | B4 | B5 | C1 | C2 | C3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| polder | 2 | 1 | 2 | 1 | 4 | 3 | 2 | 0 | 2 | 0 | 0 |
| beach plain | 1 | 0 | 3 | 1 | 6 | 1 | 1 | 0 | 1 | 0 | 0 |

off well. Especially the life form "summer annual with seeds exhibiting innate dormancy", class B2, according to the hapaxant life form system of BAKKER (1966), appears to be succesful (*table 5*).

In fact the successions in the polder communities towards more closed coverage and dominance by a few species, will increasingly restrict the species studied to habitats created by human disturbances, roads, tracks, recreational sites a.o. One aspect of the succession may be registered by comparing the life form spectra of the hapaxants from both areas studied, the beach plain and the polder (*table 5*). Hapaxants occurring in the polder are more evenly distributed over the life form classes.

## ACKNOWLEDGEMENTS

The authors are grateful to the Rijksdienst voor IJsselmeerpolders and to the Dienst der Domeinen for providing the access to the study areas, to Mr. E. Leeuwinga for preparing the figures and to Mrs. G. Joenje-Reuvekamp for typing the draft.

The guiding influence of the late Prof. D. Bakker on this and connected studies in colonizing plants species is thankfully memorized.

## REFERENCES

BAKKER, D. (1966: On the life forms of hapaxants in the Dutch flora. *Wentia* **15**: 13–24.

BEEFTINK, W. G., M. C. DAANE & W. DE MUNCK (1971): Tien jaar oecologische verkenningen langs het Veerse Meer. *Natuur en Landschap* **25**: 50–63.

BREHM, K & T. EGGERS (1974): Die Entwicklung der Vegetation in den Speicherbecken des Hauke-Haien-Kooges (Nord-Friesland) von 1959 bis 1974. *Schr. Naturw. Ver. Schlesw. Holst., Kiel* **44**: 27–36.

BRUINENBERG, J. & T. WIERENGA (1977): *Verspreiding en oecologie van enkele plantensoorten op tijdelijke zout-zoet gradienten in de Lauwerszeepolder.* Mimeographed report Lab. voor Plantenoecologie, Haren (Gn). 84 pp.

ELLISTON WRIGHT, F. R. (1953): Note on the dispersal of Sagina nodosa var. moniliformis Lange. *Watsonia* **2**: 369.

FREYSEN, A. H. J. (1967): *A field study on the ecology of Centaurium vulgare Rafn.* Thesis, Utrecht. 119 pp.

GRIME, J. P. (1979: *Plant strategies and vegetation processes.* London. 222 pp.

HEUKELS, H. & S. J. VAN OOSTSTROOM (1979): *Flora van Nederland,* 20th ed. Wolters-Noordhoff, Groningen. 909 pp.

HOFSTEE, J. & H. J. FIEǸ (1971): *Analysemethoden voor grond, gewas, water en bodemvocht.* Rijksdienst voor de IJsselmeerpolders, Lelystad.

JOENJE, W. (1978a): *Plant colonization and succession on embanked sandflats.* Thesis, Groningen. 160 pp.

– (1978b): Migration and colonization by vascular plants in a new polder. *Vegetatio* **38**: 95–102.

– & H. J. DURING (1977): Colonization of a desalinating Waddenpolders by bryophytes. *Vegetatio* **35**: 177–185.

LONDO, G. (1975): De decimale schaal voor vegetatiekundige opnamen van permanente quadraten *Gorteria* **7**: 101–106.

MCARTHUR, R. H. & E. O. WILSON (1967): *The theory of island biogeography.* Princeton, N.J. 203 pp.

SALISBURY, E. J. (1942): *The reproductive capacity of plants.* London. 244 pp.

VRIES, V. DE (1961): *Vegetatiestudie op de westpunt van Vlieland.* Gorinchem. 187 pp.

WESTHOFF, V & A. J. DEN HELD (1969): *Plantengemeenschappen in Nederland.* Zutphen. 324 pp.