

Comparative population ecology of dune slack species: the relation between population stability and germination behaviour in brackish environments*

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Abstract

Populations of short-lived pioneer species from brackish primary dune slacks and beach plains usually have to cope with unpredictably fluctuating abiotic conditions. Life history parameters play a major role in adaptation to temporal environmental heterogeneity. A population's susceptibility to fluctuating salinity levels may be largely determined by seed dormancy characteristics (e.g. seed variability, degree of enforced dormancy imposed by salinity) and juvenile salt resistance rather than by adult salt resistance.

Introduction

Pioneer species from primary dune slacks and beach plains usually have to cope with unpredictably fluctuating abiotic conditions. Populations of species from the *Centaurio-Saginetum moniliformis*, a common pioneer association from slightly saline wet slacks and beach plains in the coastal dune area of northwestern Europe (Freijssen, 1967) exhibit strong fluctuations in density, age structure and height zonation, mainly as a result of unpredictable fluctuations of some abiotic factors, such as the depth of the soil water table (drought, inundation) and the soil salinity level. The patterns of these population fluctuations are markedly species-specific (Freijssen, 1967; Schat, 1982; van Tooren *et al.*, 1983).

Comparative experimental studies on some species from this association revealed very pronounced interspecific differences in drought, inundation and salt tolerance during the established phase of the life cycle (Schat, 1982). However, interspecific differences in patterns of population fluctuation and height zonation could not be sufficiently ex-

plained in terms of specific tolerances of established individuals to the stress factors which check their populations. Specific dispersal characteristics and life history phenomena (e.g. seed dormancy, phenology, duration of the vegetative period, mode of reproduction) play a very important role too (During, 1980; Schat, 1982; van Tooren *et al.*, 1983). The latter authors showed that for short-lived species fairly subtle interspecific differences in the period of germination may produce zonation patterns which are inconsistent with expectations based on tolerance tests with established individuals. In addition, observations of Schat (1982) suggest that the effects of fluctuating salinity on populations of short-lived dune slack pioneers is determined by specific seed dormancy characteristics, rather than by salt toleration during the established phase.

The present study aims to provide some experimental evidence for the latter point of view. In a series of experiments the effects of temperature and salinity on the germination and the survival of seeds and seedlings of three species from the *Centaurio-Saginetum*, viz. *Plantago coronopus* (a paucennial), *Centaurium littorale* and *Samolus valerandi* (two more or less biennial species), are compared.

* Nomenclature follows Hegi (1966).

Two salt-sensitive species, viz. *Scrophularia nodosa* (perennial) and *Digitalis purpurea* (a biennial) have been used as a reference.

Materials and methods

Seeds of *Centaurium littorale*, *Samolus valerandi* and *Plantago coronopus* were collected from a beach plain on the Dutch island of Schiermonnikoog. Seeds of *Scrophularia nodosa* and *Digitalis purpurea* were collected from a forest clearing near Orsbach (western Germany). Prior to the experiments, the seeds had been dry-stored (20 °C) for about one year, apart from those of *Plantago coronopus*, which were stored for three years.

After three weeks of stratification at 4 °C, the seeds were placed on filter paper, saturated with solutions of 0, 62.5, 125 and 250 mmol NaCl/l (six replications of 50 seeds per concentration for *Centaurium littorale*, *Samolus valerandi* and *Plantago coronopus*, two for *Scrophularia nodosa* and *Digitalis purpurea*). The pieces of filter paper were placed on sponge, floating on a volume of the same solutions in translucent plastic trays of 10 × 10 × 10 cm. The lid of the trays was sealed with vaseline, in order to avoid evaporation. Two trays per species per concentration were placed in a germination cabinet with a daily light period of 14 hr (light intensity at plant level about 16 W/m²) and an alternating temperature regime of 15/25 °C (night

and day temperature, resp.). Two other trays were placed in a cabinet with the same light regime, but with a temperature regime of 5/15 °C. The remaining two trays were placed in a cabinet with a constant temperature of 4 °C and a daily light period of 8 hr (*Scrophularia nodosa* and *Digitalis purpurea* were only tested at 15/25 °C). Radicle protrusion, plumule protrusion and seedling mortality were recorded throughout the experiment. Complete necrosis of the radicle was used as a criterion for seedling mortality. After 40 days at 15/25 °C and after 50 days at 5/15 and 4/4 °C the seeds and seedlings were transferred to filter paper, saturated with demineralized water, and placed at 15/25 °C (14 hr light per day; 16 W/m²). Any additional germination and mortality was recorded. The experiment was terminated after two weeks without any additional germination.

Results

The percentage of germination (protrusion of the radicle is used as a criterion) after 40 days at 15/25 °C, or after 50 days at 5/15 °C is given in Figure 1 (upper row). The arithmetic mean germination day is given in Figure 2 (upper row). The reduction of germination by NaCl is higher for *Plantago coronopus* than for any of the other species. At 5/15 °C the percentage of germination is lower than at 15/25 °C, irrespective of the NaCl

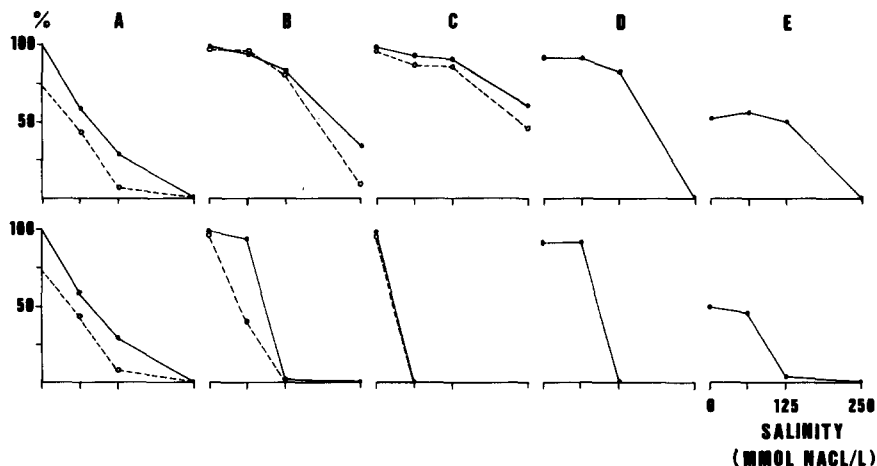


Fig. 1. Percentage of germination (upper row) and percentage of the seeds reaching the stage of plumule protrusion (lower row) after 40 days at 15/25 °C (solid lines), or 50 days at 5/15 °C (broken lines). A = *Plantago coronopus*; B = *Samolus valerandi*; C = *Centaurium littorale*; D = *Scrophularia nodosa*; E = *Digitalis purpurea*.

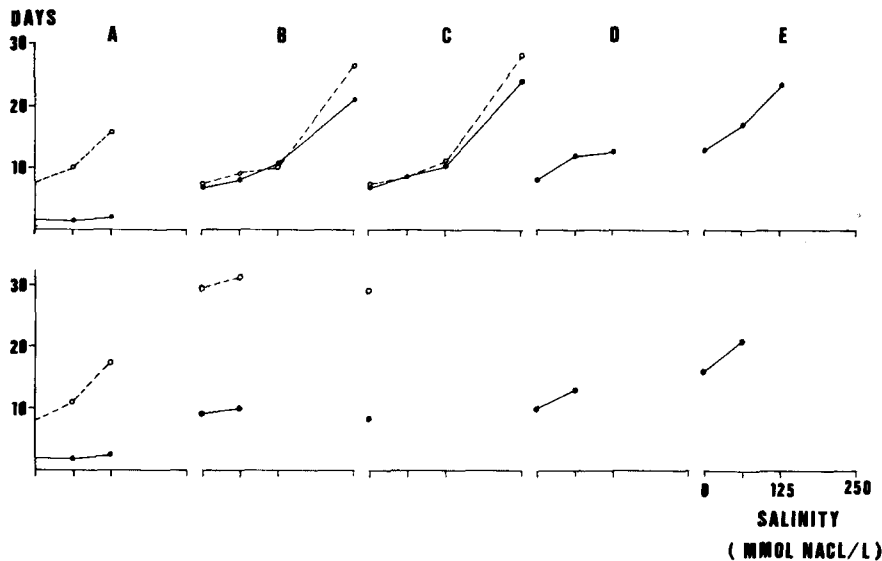


Fig. 2. Arithmetic mean day of germination (upper row) and plumule protrusion (lower row). Legends as in Figure 1.

concentration. The rate of germination is also higher at 15/25 °C. However, a considerable effect of NaCl on the rate of germination is only apparent at 5/15 °C. In *Samolus valerandi* and *Centaureum littorale* the percentage and rate of germination are hardly reduced by NaCl concentrations of 62.5 and 125 mmol/l; only at 250 mmol/l does a substantial reduction occur. The effects of temperature are much less pronounced than in *Plantago coronopus*: at 0, 62.5 and 125 mmol NaCl/l there is no effect at all; only at 250 mmol/l is the percentage as well as the rate of germination clearly lower at 5/15 °C than at 15/25 °C, suggesting that the effects of suboptimal temperature and salinity intensify each other. *Scrophularia nodosa* and *Digitalis purpurea*, like *Plantago coronopus*, exhibit no germination at all at 250 mmol/l, but at 62.5 and 125 mmol/l they germinate as completely as in demineralized water. However, of these two species especially *Digitalis purpurea* exhibits a strongly reduced rate of germination with increasing NaCl concentration.

Besides affecting germination, temperature and NaCl may also affect the further development after germination (Figs. 1 and 2, lower rows). In *Plantago coronopus* protrusion of the radicle is always rapidly followed by protrusion of the plumule, irrespective of temperature and salinity. In *Samolus valerandi* and *Centaureum littorale* a low temperature strongly delays the protrusion of the plumule (Fig. 2). NaCl does not seem to increase the

mean time span between germination and plumule protrusion, at least not at a concentration of 62.5 mmol/l; at concentrations of 125 mmol/l or higher it prevents the protrusion of the plumule for all species, except *Plantago coronopus*. In *Centaureum littorale*, even a concentration as low as 62.5 mmol/l is enough to produce such an effect.

During the experiment NaCl-induced seedling mortality occurred in each species, apart from *Plantago coronopus*. *Scrophularia nodosa* and *Digitalis purpurea* also exhibited some seedling mortality in the absence of NaCl, probably due to fungal attack. The mean period of survival after germination differs between species (increasing in the order: *Scrophularia*/*Digitalis*/*Centaureum*/*Samolus*/*Plantago*) and decreases with increasing NaCl concentration (Fig. 3).

Figure 4 summarizes the results of the experiments at 15/25 °C and at 5/15 °C. The figure shows that seeds which remain ungerminated after 40 days at 15/25 °C, or 50 days at 5/15 °C, do not always germinate after a transfer to demineralized water at 15/25 °C. The fraction which germinates after the transfer increases sharply with the NaCl concentration, to which they were exposed before their transfer, except for those of *Plantago coronopus* at 5/15 °C. The non-germinating fraction became overgrown with fungi, immediately after their transfer to demineralized water, suggesting that they were dead. At the moment of the transfer

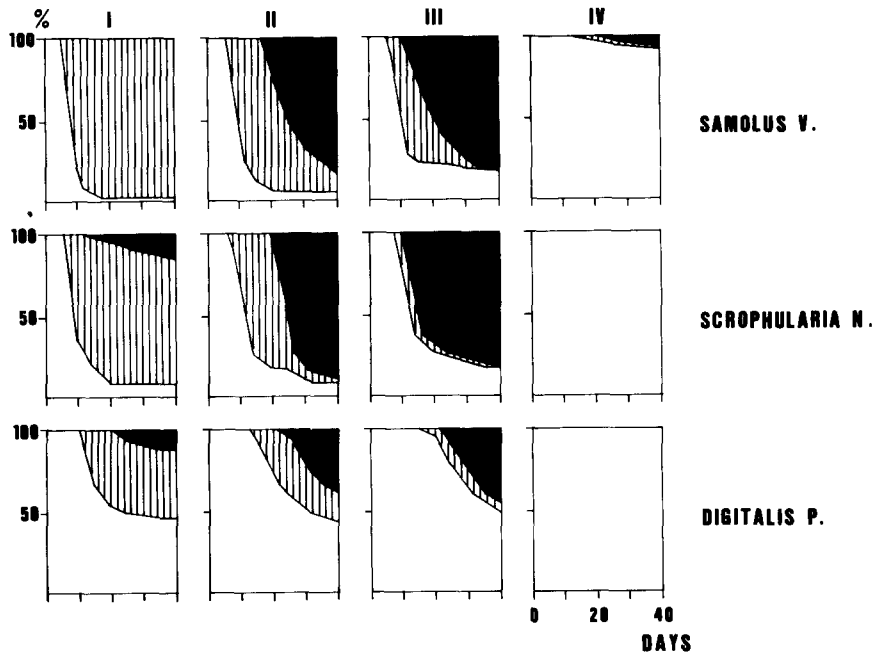


Fig. 3. Course of germination and seedling mortality at 15/25 °C, for *Samolus valerandi*, *Scrophularia nodosa* and *Digitalis purpurea* at salinity levels of 0 mmol/l (I), 62.5 mmol/l (II), 125 mmol/l (III) and 250 mmol/l (IV). The fraction of ungerminated seeds, living and dead seedlings are represented by open, hatched and black area's, resp.

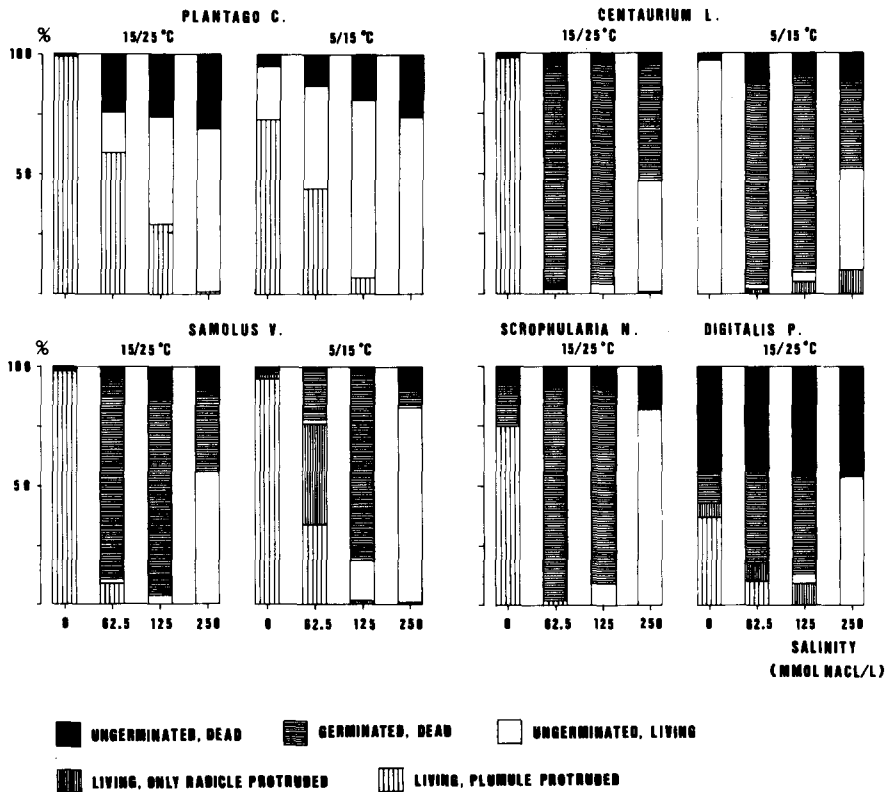


Fig. 4. Percentages of living seeds, dead seeds, living seedlings and dead seedlings after 40 days at 15/25 °C, or 50 days at 5/15 °C.

these seeds were already beginning to desintegrate, whereas the germinable seeds still had a hard and intact seed coat. The category of dead seeds, expressed as a fraction of the total number of seeds sown, increases with the NaCl concentration (*Plantago coronopus*), or is at least increased by the presence of NaCl (*Samolus valerandi*, *Centaurium littorale*), or remains more or less unaffected by NaCl (*Scrophularia nodosa*, *Digitalis purpurea*). In the case of the latter two species, there is no evidence for NaCl-induced seed mortality. In *Plantago coronopus* and *Samolus valerandi* the NaCl-induced seed mortality is clearly higher at 15/25 °C than at 5/15 °C; the opposite effect is shown by *Centaurium littorale*. At 4/4 °C NaCl fails to produce any effect on the germinability. After transfer to demineralized water at 15/25 °C the seeds of each species germinate rapidly and completely, like seeds that are immediately exposed to demineralized water at 15/25 °C.

The clear effect of temperature on the survival of seedlings of *Centaurium littorale* and especially *Samolus valerandi* (higher survival at 5/15 °C) is remarkable and not due to any effect of temperature on the rate of germination (Fig. 2). The potency to endure salinity obviously decreases with increasing temperature.

Discussion

Many studies, including the present one, suggest that adult salt resistance is not necessarily positively correlated with the tendency to germinate under saline conditions (Adriani, 1958; Ayers & Hayward, 1948; Chapman, 1960; Rozema, 1975; Ungar, 1978; Uphof, 1941; Waisel, 1958). The salt-sensitive germination of many halophytes should not be interpreted as poor adaptation. The superficial layers of saline soils often exhibit strong fluctuations in salinity, due to seasonal as well as unpredictable fluctuations of the precipitation/evaporation balance (Beefink, 1977; Chapman, 1960; Ranwell, 1972; Rozema, 1976; Schat, 1982; Tyler, 1971). Germination in periods of low salinity may be advantageous in such a situation, since even halophyte seedlings may be comparatively salt-sensitive (Baumeister & Schmidt, 1962; Waisel, 1972). Avoidance of germination at unfavourable salinity levels may be achieved by a sufficiently strong enforced dormancy,

either imposed by salinity itself, or by other factors which are sufficiently correlated with salinity. Strongly unpredictable and intense short-term fluctuations in salinity may favour strategies involving the maintenance of a reserve of dormant seeds, even under conditions favourable for germination and seedling survival (Cohen, 1966). Besides the fluctuation pattern of the salinity level, the degree and rate of development of salt resistance in newly germinated individuals will be decisive for the success of any given strategy. The above may help to explain the high diversity in the effects of salinity on the germination of halophytes. In addition, even when the germination strategy does not seem to be adjusted to the pattern of seedling mortality risk imposed by the fluctuation pattern of the salinity level in the natural habitat, it may be misleading to speak of poor adaptation, since salinity is only one out of many environmental factors that determine the patterns of mortality risk in halophyte seedlings. It is conceivable that an additional adjustment to the salinity pattern can only be realized at the expense of increased seedling mortality due to other factors. At any rate, the germination strategy may strongly determine a population's ability to cope with certain salinity regimes, irrespective of the nature of the selective factors which provoked its evolution.

Fresh seeds of *Plantago coronopus* exhibit a very pronounced polymorphism (Dowling, 1933; Schat, 1981), which leads to an extended period of germination (Schat, 1982). The unusually rapid and complete germination in the absence of NaCl at 15/25 °C (compare Schat, 1981) is probably due to the old age of the seeds (Blom, 1978). In the present experiment NaCl strongly reduced the percentage of germination. In a previous experiment, however, performed with fresh seeds at 5/25 °C, concentrations up to 125 mmol/l strongly reduced the rate of germination, but failed to reduce the final percentage (Schat, 1981). Anyway, NaCl concentrations as low as 60 mmol/l impose a strong enforced dormancy, at least for some time. The juvenile salt resistance of *Plantago coronopus* is comparatively high and rapidly acquired; salt-induced mortality seems to be confined to the earliest stages of the germination process, viz. the stages before the protrusion of the radicle (Fig. 4). Field studies at the beach plain of Schiermonnikoog have shown that these characteristics of the germination strategy

(seed variability, strong salt-imposed enforced dormancy, high juvenile salt resistance) sufficiently protect the annual rejuvenation from the potentially catastrophic effects of strong, unpredictable fluctuations in salinity (Schat, 1982).

Samolus valerandi and *Centaurium littorale*, on the other hand, exhibit a very explosive germination. Under almost any set of environmental conditions the germination is either rapid and complete, or almost completely inhibited, both in experimental and natural situations (Schat, 1982). Moderate NaCl concentrations fail to keep the seeds in a state of enforced dormancy, even at a day temperature of 15 °C, which is only slightly above the minimal day temperature at which germination takes place (Freijssen, 1967; Schat, 1982). Their juvenile salt resistance is remarkably low, in view of their preferential occurrence in brackish habitats (Freijssen, 1967; Hegi, 1966), and less rapidly acquired; even at NaCl concentrations which allow the seedlings of *Samolus valerandi* to develop up to an including the unfolding of the cotyledons, the mortality rate is very high (Fig. 3). Comparable mortality rates were established in previous experiments (Schat, 1982), even when the NaCl was dissolved in a full strength Hoagland's nutrient solution (Schat, unpubl.). However, seedlings of only two weeks old, germinated and grown under non-saline conditions, are able to survive a sudden increase in salinity up to 100 mmol NaCl/l (Schat, unpubl.). The presence of NaCl in fairly low concentrations during the earliest developmental stages apparently prevents the acquisition of salt resistance. Obviously, both species need a short period of non-saline conditions in order to establish themselves successfully. Due to the above-mentioned characteristics of the germination behaviour and the development of salt resistance, the annual rejuvenation of natural populations is extremely sensitive to unpredictably fluctuating salinity levels. Table 1 gives an example for *Centaurium littorale*. The results may be explained as follows: due to an exceptionally late storm flood in April and a subsequent dry period up to the third week of June, the salinity of the upper cm of the soil profile reached unusually high levels (150–270 mmol/l at 162 cm + NAP; 50–200 mmol/l at 170 cm + NAP and 50–150 mmol Cl/l at 190 cm + NAP). At 162 cm + NAP the salinity was high enough to keep a considerable fraction of the seeds in a state of enforced dormancy until June

15th, after which the salinity level dropped to less than 25 mmol/l and successful establishment was possible. At 170 and 190 cm + NAP the seed bank was nearly fully exhausted by germination (up to the stage of radicle protrusion) and subsequent mortality before the third week of June. Only at 190 cm + NAP some visible seedling emergence did occur before the June 15th. About 20% of these seedlings survived. Since *Centaurium littorale* is a fairly strict biennial and since the mortality risk sharply decreases with age, the following year's population of flowering plants clearly reflected the bipartite height zonation of the successfully established seedlings. The height zonation and density of populations of *Centaurium littorale* in brackish environment may thus be governed by the fluctuation patterns of the soil salinity and other abiotic factors (van Tooren *et al.*, 1983), even when the extreme levels of these factors permanently remain within the adult tolerance limits. This general conclusion probably applies to many other short-lived species from beach plain habitats as well (van Tooren *et al.*, 1983). The zonation patterns of long-lived perennials on the other hand, are more likely to be explained by their resistance in the adult phase to various kinds of stress and may be expected to reflect the average levels of stress factors over a long series of years, rather than any occasional short-term fluctuations (van Tooren *et al.*, 1983, for a detailed discussion). In any case, it is clear that a thorough understanding of the vegetation dynamics of beach plain requires a combination of intensive field studies (phenology, seed bank dynamics, establishment, mortality, dispersal, life history, frequent monitoring of abiotic conditions) and experimental approach.

Table 1. Seed bank density (number of seeds/100 cm²) and seedling emergence (number of seedlings emerged/100 cm²; only seedlings with unfolded cotyledons have been recorded) for *Centaurium littorale* at various heights along a dune slope at the beach plain of Schiermonnikoog.

Height ^a	Seed bank		Seedling emergence	
	April	August	Before June 15th	After June 15th
162	18 (±12)	0	0	4.7 (±3.1)
170	36 (±9)	0	0	0.1 (±0.1)
190	33 (±13)	0	2.3 (±1.5)	0.2 (±0.1)

^a Expressed in cm above NAP (Dutch Ordnance Level).

References

- Adriani, M. J., 1958. Halophyten. In: W. Ruhland (ed.), *Handbuch der Pflanzenphysiologie*, IV, pp. 709–736. Springer-Verlag, Berlin.
- Ayers, A. D. & Hayward, H. E., 1948. A method for measuring the effects of soil salinity on seed germination with observations on several crop plants. *Soil. Sci. Soc. Am. Proc.* 13: 224–226.
- Baumeister, W. & Schmidt, L., 1962. Über die Rolle des Natriums im pflanzlichen Stoffwechsel. *Flora* 152: 24–56.
- Beeftink, W. G., 1977. The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In: V. J. Chapman (ed.), *Wet Coastal Ecosystems*, pp. 109–155. Elsevier, Amsterdam.
- Blom, C. W. P. M., 1978. Germination, seedling emergence and establishment of some *Plantago* species under laboratory and field conditions. *Acta Bot. Neerl.* 27: 257–271.
- Chapman, V. J., 1960. *Salt Marshes and Salt Deserts of the World*. Hill, London.
- Cohen, D., 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* 12: 119–129.
- Dowling, R. E., 1933. The reproduction of *Plantago coronopus*: an example of morphological and biological seed dimorphism. *Ann. Bot.* 47: 861–872.
- During, H. J., 1980. Life forms and life strategies in *Nanocypereion* communities from the Netherlands Frisian Islands. *Acta Bot. Neerl.* 29: 483–496.
- Freijnsen, A. H. J., 1967. A field study on the ecology of *Centaurium vulgare*. Thesis, Utrecht.
- Hegi, G., 1966. *Illustrierte Flora von Mitteleuropa*. Carl Hanser Verlag, München.
- Ranwell, D. S., 1972. *Ecology of Salt Marshes and Sand Dunes*. Chapman and Hall, London.
- Rozema, J., 1975. The influence of salinity, inundation and temperature on the germination of some halophytes and non-halophytes. *Oecol. Plant.* 10: 341–353.
- Rozema, J., 1976. Vegetatiezonering op de strandvlakte van Schiermonnikoog. *Waddenbulletin* 3: 144–148.
- Schat, H., 1981. Seed polymorphism and germination ecology of *Plantago coronopus* L. *Acta Oecol. Oecol. Plant.* 2: 367–380.
- Schat, H., 1982. On the ecology of some Dutch dune slack plants. Thesis, Amsterdam.
- Tooren, B. F. van, Schat, H. & ter Borg, S. J., 1983. Succession and fluctuation in the vegetation of a Dutch beach plain. *Vegetatio* 53: 139–151.
- Tyler, G., 1971. Hydrology and salinity of Baltic seashore meadows. *Studies in the ecology of Baltic seashore meadows III*. *Oikos* 22: 1–20.
- Ungar, I. A., 1978. Halophyte seed germination. *Bot. Rev.* 44: 233–264.
- Uphof, J. C. T., 1941. Halophytes. *Bot. Rev.* 7: 1–58.
- Waisel, Y., 1958. Germination of some halophytes. *Bull. Res. Counc. Israel* 6: 187–189.
- Waisel, Y., 1972. *Biology of Halophytes*. Academic Press, New York.

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