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# GERMINATION ECOLOGY OF SALICORNIA DOLICHOSTACHYA AND SALICORNIA BRACHYSTACHYA

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SUMMARY

A number of germination experiments was performed on seeds, collected from various populations of *Salicornia dolichostachya* and *Salicornia brachystachya.*

It appeared that the germination percentage of seeds from various populations of the same species did not differ, but a significant difference in the germination percentage between the two species existed. Both species germinated best at low salinity, while the optimum germination temperature decreased when salinity increased. The order of application was important when applying fluctuating salinities to the seeds: a low salinity level followed by a high salinity level slowed down or stopped the germination irreversibly, while the opposite order resulted in a higher total germination percentage. Soil moisture content that was undersaturated had no effect on the germination of *S. dolichostachya* but decreased the germination of *S. brachystachya* significantly. Fluctuating temperature regimes had no effect on the total germination percentage but did have an effect on the germination rate. Seeds buried under a layer of sediment of 1 cm or more did germinate but the seedlings were unable to emerge. A field experiment confirmed the findings in the laboratory. The results are discussed in relation to the distribution and size of the populations of both species.

## 1. INTRODUCTION

*Salicornia dolichostachya* Moss* is a tetraploid species growing on the lower marsh and the higher tidal flat, in other words below the Mean High Water line. *Salicornia brachystachya* (G. F. W. Meyer) König is a diploid species growing more often above the Mean High Water line and in non-tidal saline environments. The lower marsh and the higher tidal flat are flooded regularly which buffers extreme abiotic circumstances, e.g. soil salinity, soil moisture and soil temperature (HUISKES et al., unpubl.). These factors fluctuate considerably more in the higher parts of the marsh and in non-tidal situations.

As for many other halophytes the germination and seedling establishment are the most critical stages in the life cycle of *Salicornia* (UNGAR 1978). In this paper the germination of the two species will be compared both in the field and under controlled conditions. Although they live in a saline environment *Salicornia* species germinate best under freshwater conditions (UNGAR 1962,

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* The nomenclature follows VAN DER MEYDEN, R., E. J. WEEDA, F. A. C. B. ADEMA & G. J. DE JONCHEERE, (1983): Flora van Nederland, 20th ed., Wolters-Noordhoff, Groningen.

1978, CHAPMAN 1974) a quality shared by many other halophytes (UNGAR 1974, 1978, WAISEL 1972). UNGAR (1977) studied the germination of *S. europaea* from an inland saline area in North America and found a negative correlation between temperature and salinity; as salinity increases optimum germination occurs at lower temperatures. This agrees with the findings of RIVERS and WEBER (1971) on *S. bigolovii* and of LANGLOIS (1966) on a number of other annual *Salicornia* species. LANGLOIS (1966) experimented also with the influence of temperature fluctuations on germination but with inconclusive results. Light and a cold pre-treatment favours the germination of *S. stricta* (= *S. dolichostachya*) and *S. disarticulata* (LANGLOIS 1966) and of *S. emerici* (GROUZIS et al. 1976).

The flowers for most of the *Salicornia* species are grouped in clusters of three along the flowering axis. A bigger central flower is flanked by two smaller lateral flowers. The smaller lateral flowers produce also smaller seeds, which have a different germination behaviour (GROUZIS et al. 1976, KOUTSTAAL in prep.). For the experiments described in this paper the central and lateral seeds, were not separated.

## 2. MATERIALS AND METHODS

### 2.1 Field experiments

*S. dolichostachya* seeds were collected from plants in the transition zone between salt marsh and tidal flat south of Bergen op Zoom. *S. brachystachya* seeds were collected in open spots in the grassy vegetation of the higher marsh areas on the same location. The seeds were dried at room temperature and stored at 5 °C in the dark. For the experiment small sealed bags of plankton gauze (mesh size 300 $\mu$m) containing 50 seeds of *S. dolichostachya* or *S. brachystachya* were buried at a depth of 0.5 cm in different vegetation zones on the salt marsh south of Bergen op Zoom. These zones were (1) the transition zone between salt marsh and sand flat with a sparse vegetation of *Salicornia* plants and small *Spartina anglica* tussocks; (2) a zone dominated by *S. anglica* with *Aster tripolium* occurring frequently; (3) a zone with *Puccinellia maritima* accompanied by a number of other halophytes; (4) a zone with *Limonium vulgare, Plantago maritima* and *Triglochin maritima* also accompanied by a number of other halophytes. The seeds were buried on 14 December 1979. Pieces of wire were used to keep the bags in place. Every two to three weeks, beginning three weeks after burial, one bag with *S. dolichostachya* seeds and one with *S. brachystachya* seeds were retrieved from each zone. Seedlings, imbibed seeds and germinated seeds were counted. Imbibed seeds sometimes lose their seed coats but these seeds were regarded as germinated when the rootlet had started to elongate.

### 2.2 Incubator experiments

Unless otherwise stated the germination experiments under controlled conditions were done in petri dishes on wet filterpaper. 100 seeds were placed on the filterpaper, which was then moistened with 2 ml of the required NaCl-solution or demineralized water. Every other day the seeds were replaced on fresh

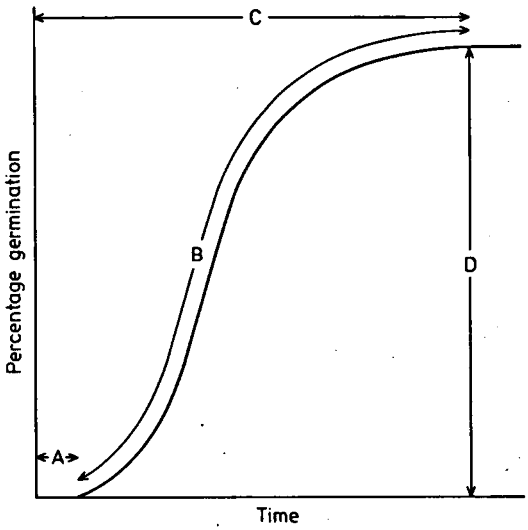


Fig. 1. Idealized germination curve to show derivation of constants used to describe germination. A = the delay between sowing and onset of the germination; B = the rate of germination between onset and finish in percent germination per day; C = the mean rate of germination between sowing and the attainment of maximum germination in percent germination per day; D = the maximum percentage germination (After WALTON 1977).

filter paper to prevent salt accumulation and excessive contamination with fungi. Unless otherwise stated the petri dishes were incubated at 25 °C in the dark as this was the temperature that gave maximal results in the first experiment, and received light only when handled.

For an experiment on the influence of soil moisture petri dishes were filled with a known amount of sand, dried and sieved with a 1 mm mesh size sieve. Demineralized water was added to this sand with an atomizer until it was completely saturated, *i.e.* a thin film of water appeared on the sand surface. The amount of water applied was measured by weighing. To establish various soil moisture levels, 25, 50, 75 or 100% of the measured amount of water was applied to the petri dishes.

The influence of burial on germination was studied by placing 100 seeds on a carefully leveled sand surface in beakers. The seeds were then covered with a layer of sand of known height. The sand was moistened with tap water. Burial depths studied this way were 0.5, 1, 2, 3, 4, 5, 7, 10, 12 cm. The depths were chosen according to the findings in the field where seeds of the species occur up to a depth of 12 cm. Most seeds however occur in the upper two cms of the soil. The beakers were wrapped in aluminium foil to prevent irradiation from the sides. All experiments were executed in duplicate.

### 2.3 Presentation of the results

"The presentation of large amounts of germination data in the form of graphs

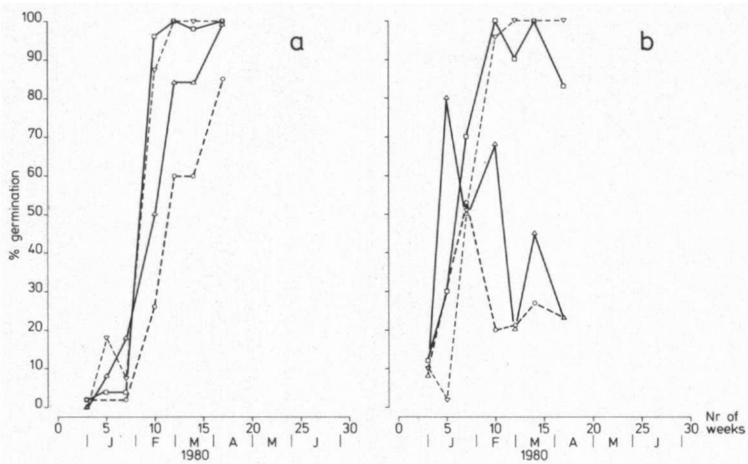


Fig. 2. Germination of seeds of *Salicornia brachystachya* (a) and *S. dolichostachya* (b) buried under 0.5 cm soil in different zones of the salt marsh. ○ = zone 1; □ = zone 2; △ = zone 3; ▽ = zone 4. For a description of the zones see section 2.1.

is costly in terms of space" (WALTON 1977). Various authors attempted to characterize germination by a set of constants from a mathematical equation (CZABATOR 1962, TIMSON 1965, POLLOCK & ROOS 1972, JANSSEN 1973 and WALTON 1977). Although nothing can compete with the graph as a form of presentation, the method used by Walton seems a rather successful substitute. He described germination by four characteristics (*fig. 1*). Constant A, expressed in days, is the delay between sowing and the onset of germination. B is the mean slope of the germination curve and describes the mean rate of germination between onset and finish. It is expressed in percent germination per day. Constant C is the mean rate of germination calculated from the time of sowing to the attainment of maximum germination; it is also expressed in percent germination per day. D is the maximum percentage germination achieved. In this model no estimate is provided for the variation in the rate of germination. JANSSEN (1973) did include in his model an estimate of the variation of the germination rate,

Table 1. Results of a factorial analysis of variance on the germination percentages of seeds of *Salicornia dolichostachya* and *S. brachystachya* incubated under different temperature and salinity regimes.

| | sum of squares | df | variance | F | P |
|---|---|---|---|---|---|
| species | 1360 | 1 | 1360 | 70.82 | <0.001 |
| temperature | 89000 | 7 | 12710 | 662.1 | <0.001 |
| chlorinity | 12320 | 5 | 2464 | 128.3 | <0.001 |
| spec. × temp. | 2805 | 7 | 400.7 | 20.87 | <0.001 |
| spec. × chlor. | 495.6 | 5 | 99.12 | 5.162 | <0.001 |
| temp. × chlor. | 2669 | 35 | 76.26 | 3.971 | <0.001 |
| spec. × temp. × chlor. | 2418 | 35 | 69.08 | 3.597 | <0.001 |
| rest | 1843 | 96 | 19.20 | | |

but did not include the delay between sowing and the onset of germination. Waltons method has the advantage over the method used by Janssen in that it is very simple to use without any sophisticated computation apparatus. The method of Walton was applied to a number of germination experiments.

## 3. Results

### 3.1 Field experiment

*Fig. 2* shows the number of germinated seeds in the buried bags on the successive sampling dates. Although the sampling went on till June, the results of the samplings in May and June are not shown, since most of the contents of the bags was no longer identifiable due to decomposition. *S. brachystachya* showed about the same germination response in all zones, with little germination in the very cold month of January. More *S. dolichostachya* seeds germinated in January.

### 3.2 Incubator experiments

Seeds collected at various places of different salt marshes were tested to establish differences in germination between local populations. A factoral analysis of variance applied to these results did not show a significant difference in germination between the various seed batches of one species ($F = 3.38$, $df1 = 4$, $df2 = 10$, $P < 0.05$) (*table 1*). *Fig. 3a* depicts the total germination percentages after 21 days under various temperature and salinity regimes. In *fig. 3b* is shown that both species germinate best at low salinities. The optimal germination temperature was not reached in this experiment. *S. brachystachya* has an optimum at 25°C but this is not significant (*fig. 3c*). *Fig. 3e* demonstrates the tendency of *S. brachystachya* to have maximal germination at lower temperatures as the salinity is higher: 25°C: at 8 and 12‰ $Cl^-$ (not significant) and 20–25°C at 14 ‰ $Cl^-$. This agrees with the findings of Langlois (1966), Rivers & Weber (1971) and Ungar (1977). *S. dolichostachya* however does not show this phenomenon (*fig. 3d*). Alternating temperatures have no significant effect on the seed germination of both species, but light results in a significant decrease in germination at high salinity levels (*fig. 3d, e*). The results of the factorial analysis of variance (*table 1*) show that there is a significant influence on the seed germination of both species by temperature and salinity and also – as already described before – a significant difference between the two species.

*Table 2* summarizes the results of a series of experiments with alternating temperatures, alternating chlorinity levels and different soil moisture levels. These figures are calculated using the method of Walton (*fig. 1*), but with a few alterations: (1) Germination of *Salicornia* starts very quickly, sometimes within one day. Constant A (*fig. 1*) is therefore not important in these experiments. (2) The germination of *Salicornia* usually has two phases: one phase up to the fifth to eighth day after the onset of germination with a high germination rate followed by a second phase whereby the remainder of the seeds germinate very slowly or not at all (*fig. 4*). It is not known whether these two phases in

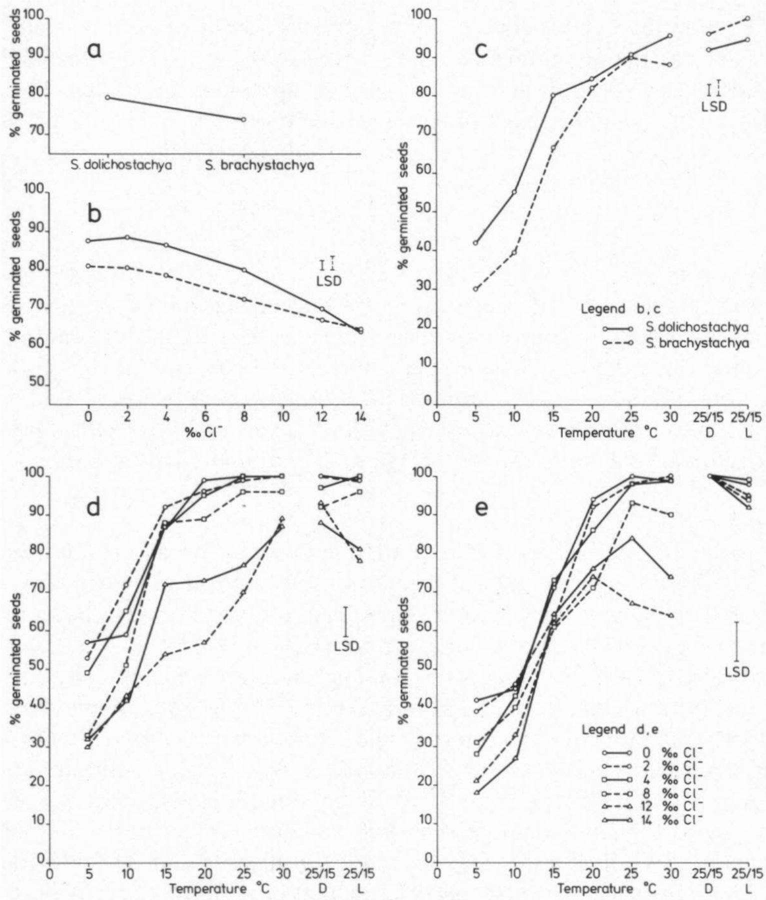


Fig. 3. Average percentages of geminated seeds of *Salicornia dolichostachya* and *S. brachystachya*, incubated under different temperature and salinity regimes.
Fig. 3a shows the difference between the overall percentages of *S. dolichostachya* and *S. brachystachya*; Fig. 3b shows the overall influence of salinity on the germination of *S. dolichostachya*, and *S. brachystachya*; Fig. 3c shows the overall influence of temperature on the germination of *S. dolichostachya* and *S. brachystachya*; Figs. 3 d and e show the influence of both temperature and salinity on the germination of *S. brachystachya* and *S. dolichostachya* respectively. The vertical bars represent the least significant differences (LSD).

germination are caused by the seed dimorphism in *Salicornia*. For the experiments described here the seeds of the top flower and the lateral flowers from the clusters of three flowers were not separated. To give a more realistic description of the rate of germination, the rate is given in two figures, one for each of the two phases. The experiments with the alternating temperatures once again show a significant difference in the total germination percentage between the two species but not in the germination rate. The temperature regime has however an influence on the germination rate; the higher the low temperature the greater

Table 2. Germination rates in percent per day and total germination percentages of seeds of *Salicornia dolichostachya* and *S. brachystachya* as influenced by temperature fluctuations, fluctuations in chlorinity and different soil moisture levels. Temperatures alternated 12 hourly. The chlorinity was changed every second day; the first figure gives the concentration applied first. The experiments were performed in duplo in the dark. The figures in this table are the average of the duplo values.

| Temperature | ‰ Cl⁻ | Soil moisture | Mean rate phase 1 | | Mean rate phase 2 | | Total % germination | |
|---|---|---|---|---|---|---|---|---|
| | | | S. dolich. | S. brach. | S. dolich. | S. brach. | S. dolich. | S. brach. |
| 10°–25°C | 0 | | 5.00 | 4.70 | 0.00 | 0.00 | 100.0 | 94.0 |
| 15°–25°C | 0 | | 8.25 | 8.63 | 0.00 | 0.00 | 99.0 | 95.0 |
| 25°C | 0–16 | | 19.60 | 11.70 | 0.15 | 0.70 | 100.0 | 67.5 |
| | 16– 0 | | 13.20 | 11.10 | 0.00 | 0.27 | 92.5 | 80.5 |
| | 0– 8 | | 19.40 | 13.40 | 0.00 | 0.70 | 97.0 | 76.0 |
| | 8– 0 | | 12.50 | 11.00 | 0.23 | 0.41 | 90.0 | 81.5 |
| | 8–16 | | 9.40 | 6.60 | 0.81 | 1.04 | 57.5 | 46.5 |
| | 16– 8 | | 10.71 | 6.00 | 0.27 | 0.86 | 78.0 | 52.0 |
| 25°C | 0 | saturated (= 100%) | 12.2 | 11.5 | 0.3 | 0.5 | 89.5 | 88.0 |
| | | 75% | 12.0 | 4.7 | 0.5 | 0.5 | 91.0 | 39.5 |
| | | 50% | 11.2 | 6.6 | 0.5 | 0.6 | 84.5 | 58.0 |
| | | 25% | 11.7 | 6.4 | 0.3 | 0.5 | 86.0 | 52.5 |

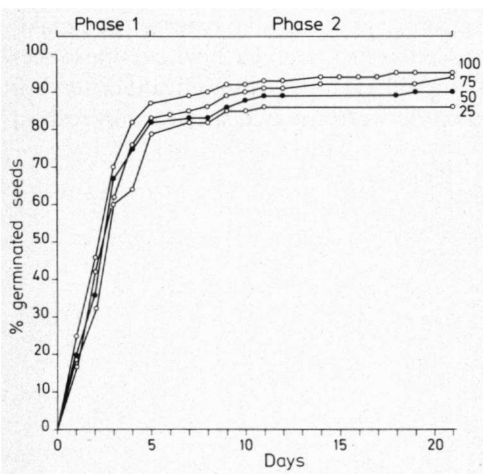


Fig. 4. Cumulative germination percentages of seeds of *Salicornia dolichostachya* which were incubated on sand with various moisture levels, to illustrate the two phases in the germination rate.

the germination rate. As was already shown in *fig. 3*, the germination of *S. brachystachya* is more affected by salt than that of *S. dolichostachya*. This can also be seen in *table 2*. Not only the applied concentrations but also the order of appliance is important: a low concentration to start with, in most cases results in a higher germination rate in both phases; probably during the period of low salt concentration the germination process has already started also in the slower germinating seeds, which not stopped by a subsequent period with high salinity.

A factorial analysis of variance and a calculation of the least significant difference (*table 3*) show that the germination rates in phase 1 decreased significantly when the applied salinities were higher, that there were significant differences between the two species, and that the order of salinity regime was not significant, but for the regimes 0–16/16–0‰ $Cl^-$ and 0–8/8–0‰ $Cl^-$ applied to *S. dolichostachya*. With respect to phase 2 the order of the salinity regime results in significant differences for *S. brachystachya* and in the case 8–16/16–8 ‰ $Cl^-$ for *S. dolichostachya*. In almost all cases is the germination rate of *S. brachystachya* in phase 2 significantly higher than that of *S. dolichostachya*. The total germination percentages in this experiment differed significantly between the species, the order of application of the salt in a number of cases also causes a significant difference.

Soil moisture does not affect the germination rate or percentage of *S. dolichostachya*. However it has a significant effect on the germination of *S. brachystachya*. On less than saturated soil the germination rate in phase 1 ($F = 16.2$, $df1 = 3, df2 = 81, P < 0.001$) drops significantly. Why lower values are obtained at 75% saturation than at 50% and 25% is not known. Burial of seeds has significant effects on their germination ($F = 12.2$, $df1 = 8$, $df2 = 18$, $P < 0.001$) and on seedling emergence (*fig. 5*). Only seedlings of superficially buried (0.5 cm) seeds stand a chance to reach the surface and emerge; seeds from deeper layers of soil may germinate but the seedlings are unable to emerge. The maximum burial depth of seeds that were able to emerge under field circumstances was observed to be 0.9 cm (Koutstaal, unpubl.). There is a significant difference – although not very big – in germination between the two species with respect

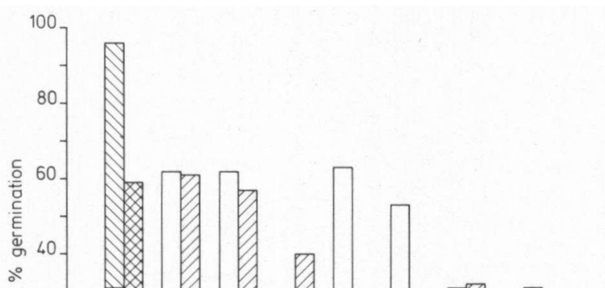


Fig. 5. Average germination percentages of seeds of *Salicornia dolichostachya* (open columns) and *S. brachystachya* (hatched columns) buried at various depths. The (double) hatched parts of the columns, representing the germination at 0.5 cm depth, shows the part of seeds of which the seedling emerged above the soil surface.

Table 3. Results of a factorial analysis of variance on the germination rates of seeds of *Salicornia dolichostachya* and *S. brachystachya* incubated under fluctuating salinity levels.

| | | Sum of Squares | dF | Variance | F | P | LSD |
|---|---|---|---|---|---|---|---|
| | salt | 276.04 | 9 | 30.67 | 11.78 | <0.001 | 2.38 |
| Germination rate | species | 93.94 | 1 | 93.94 | 36.09 | <0.001 | 1.06 |
| Phase 1 | salt × species | 60.49 | 9 | 6.72 | 2.58 | <0.05 | 3.37 |
| | rest | 52.07 | 20 | 2.60 | | | |
| | salt | 2.03 | 9 | 0.23 | 3.77 | <0.05 | 0.36 |
| Germination rate | species | 0.61 | 1 | 0.61 | 10.17 | <0.01 | 0.16 |
| Phase 2 | salt × species | 0.89 | 9 | 0.10 | 1.66 | n.s. | 0.51 |
| | rest | 1.19 | 20 | 0.06 | | | |
| | salt | 5236 | 9 | 581.78 | 11.40 | <0.001 | 10.5 |
| Total percentage | species | 2102.5 | 1 | 2102.50 | 41.19 | <0.001 | 4.7 |
| | salt × species | 1064.5 | 9 | 118.28 | 2.32 | n.s. | 14.9 |
| | rest | 1021 | 20 | 51.05 | | | |

to burial ($F = 8.09$, $dfl = 1$, $df2 = 18$, $P < 0.05$): *S. brachystachya* tends to be somewhat more susceptable to burial than *S. dolichostachya.*

## 4. DISCUSSION

The results of the field experiments show considerable differences in germination between the two *Salicornia* species in the different zones. These differences in germination are brought about by a combination of factors both natural and due to the experimental design which are hardly separable. The series of data for one zone are not subsequent observations of one batch of seeds but single observations on different seed batches, all being subject to slightly different environmental circumstances. An increase in sedimentation may affect the number of germinated seeds, while differences in soil moisture have a marked effect on the germination of *S. brachystachya* (*table 2*).

The results shown in *fig. 2* give no explanation for the fact that *S. brachystachya* is hardly found in the lower zones of the marsch and the upper regions of the tidal flat, as germination in these zones was found to be even higher than that of *S. dolichostachya.* Proposed explanations for this discrepancy are lack of seeds in these areas (Koutstaal and Markusse, unpublished) and greater mortality of seedlings and adult plants of *S. brachystachya* (Schat 1978, Paalvast 1980). What this experiment proved also is that very few seeds will stay viable after the germination period until the next. It may be concluded therefore that the two *Salicornia* species do not have a seedbank of any importance, which confirms the conclusions of Jefferies et al. (1981), although recent research by Koutstaal showed that under certain circumstances a seedbank can exist.

From the incubator experiments it is apparent that *S. dolichostachya* is the more versatile of the two species. It has a consistently higher germination percentage (*table 1*), and a higher germination rate during the first 5–7 days of the experiments (cf. *table 2*), but a lower rate afterwards which is advantageous in pioneer situations; just the opposite is shown for *S. brachystachya*. Germination of *S. dolichostachya* is less affected by higher salinities (*fig. 3*) and less affected by low soil moisture than *S. brachystachya* (*table 2*). *S. brachystachya* is normally found on the higher parts of the tidal salt marshes and it is mainly this *Salicornia* species that is found in the non-tidal saline areas in the S.W. Netherlands. These two habitats have in general a much greater fluctuation, but during the germination period (early spring) salinity is normally low and soil moisture high. BERGER et al. (1979) came to the same conclusion when comparing *S. emerici* and *S. brachystachya*. Higher salinites and low soil moisture mostly coincide: higher salinity which means a higher osmotic potential, results in difficulties to imbibe water, as is also true of a low soil moisture level. This agrees with the findings of UNGAR & CAPILUPO (1969), UNGAR & HIGAN (1970) and MACKE & UNGAR (1971), who show that for a number of halophytic species water potential rather than ionic toxicity influences the germination. WAISEL (1972) describes a number of cases whereby NaCl disturbs metabolic processes. A lower germination percentage and germination rate can not solely be ascribed to the unability of the seeds to imbibe water, the influence of the salt itself certainly plays an important role in the metabolic processes causing germination, which may be supported by the findings in the experiment with varying salinities (*table 2*). When started with a high salinity followed by a low salinity the total germination percentage was higher in the end than when the salinities were reversed. The metabolic processes, started under low salinity, seemed severely and – as observed – irreversibly interrupted by NaCl. The finding that light enhances germination especially under circumstances with high salinities (*figs. 3d* and *3e*) enables the two species to germinate in the open, saline areas of the salt marsh and the higher sand flat, where *S. brachystachya* and *S. dolichostachya* respectively are found. But this result is slightly obscured by the fact that the seeds germinating in the dark were handled in normal light which might have been enough to activate photomorphogenic responses.

The results, presented in this paper, suggest that both species can germinate under circumstances that may differ strongly in salinity, salinity fluctuation, soil moisture content, temperature and light regime. In nature, however, there is an apparent difference in occurrence of the two species as has been previously reported. *S. brachystachya* is found in the higher parts of the tidal salt marsh and in inland saline areas, which may vary strongly in salinity, soil temperature and soil moisture; *S. dolichostachya* is mainly found in the lower areas of the salt marsh and the higher areas of the sand flat, having a less fluctuating environment with respect to salinity, soil temperature and soil moisture. This may seem to demonstrate the incompatibility of laboratory experiments with the field situation. The field experiment however clearly showed that both species were able to germinate on the higher as well as on the lower parts of the salt marsh, which is in agreement with the laboratory experiment. From these findings the conclusion can be drawn that the proces of germination and some of the environmental factors influencing it do not or not alone determine the distribution and regulation of the populations of *S. brachystachya* and *S. dolichostachya*. In places however where heavy sedimentation buries the seeds to a depth fo ± 1 cm or more, germination and seedling emergence will be impaired.

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