Salinity and seed germination patterns in coastal plants*

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Abstract

The seed germination behaviour of a number of coastal species suggests that they can be separated into three categories, whose response to salinity shows some correlation with habitat. All but two germinated well in fresh water. After immersion for several days in ½, full, and 1½ strength seawater all recover at least partly. Dune species are more adversely affected by salinity than those from shingle, driftline or salt marsh. Several species, mostly from salt marsh, exhibit 'salt stimulation'. The final germination on transfer to fresh water of these species is greater the higher the salinity during pretreatment.

Introduction

Coastal plants are exposed to varying amounts of salt, from complete immersion in seawater to occasional salt spray. Germination being a crucial stage in any plant's life history, we should expect coastal plants to exhibit some tolerance of salinity. From the time that Darwin (1855, 1857) investigated the effects of salt water on seed germination, few studies were made until the last thirty years, during which there has been a resurgence of interest. Comparability of the results is difficult because different workers used different experimental techniques. Ungar (1978) has reviewed the relevant literature.

Darwin was interested in the survival of seeds in seawater and their subsequent germination in soil. Of the many species he worked on only two were British coastal plants, *Crambe maritima* and *Beta vulgaris,* which germinated well after 37 and 100 days of immersion in seawater, respectively.

Boorman (1966, 1968) dealt mainly with *Limonium vulgare,* but on the basis of tests with several other species he distinguished three germination groups. He used too few species to establish whether these were the only three types of germination responses to salinity, but regarded osmotic effects as most important in affecting germination. He tested other factors, including oxygen tension, light and length of pretreatment. Others have investigated the possibility of specific ion toxicity, with rather inconclusive results, and of temperature. There is good evidence for synergistic interaction between temperature and salinity (e.g. Beadle, 1952; Springfield, 1966; Ungar, 1967). While in general halophytes are found to be more salt-tolerant than glycophytes, most of them germinate better in fresh than in salt water.

This study was aimed at screening a large number of coastal species, under similar laboratory conditions, varying only salinity. It was hoped to discern differences between germination responses of different species, and possibly to make some general

* Nomenclature follows Clapham, Tutin & Warburg (1983). Excursion Flora of the British Isles. Ed. 3.

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Table 1. Germination characteristics of coastal species. After the stated number of days in the solutions of the indicated salinities seeds were transferred to distilled water. Figures show percentage germination. Final germination figures are for the period of days in distilled water stated in the final column. F = fresh water; ½S = half strength seawater; S = seawater; 1½S = seawater × 3/2.

Species	Germination in seawater				Days	Germination in distilled water after transfer from				Days	Habitat
	F	½S	S	1½S		F	½S	S	1½S		
Type 1											
Ammophila arenaria	8	0	0	0	18	10	4	2	4	20	dune
Aster tripolium	78	58	24	2	25	80	67	80	54	20	marsh
Atriplex glabriuscula	17	1	5	0	18	18	4	11	5	20	driftline
A. laciniata	19	4	0	0	25	25	18	21	11	40	driftline
A. littoralis	2	0	0	0	25	5	3	5	3	30	driftline
Cakile maritima	10	3	0	0	18	13	11	10	8	24	driftline
Elymus arenarius	7	5	0	0	25	11	4	6	2	40	dune
E. farctus	53	18	5	0	25	76	53	47	28	40	dune
Lotus corniculatus	19	1	0	0	20	23	11	9	6	30	dune
Salsola kali	86	62	12	7	18	88	82	72	61	20	driftline
Suaeda maritima	6	2	1	0	18	9	3	2	1	25	driftline
Tripleurospermum maritimum	53	1	0	0	18	68	60	66	27	20	driftline
Type 2											
Armeria maritima (dune)	92	6	0	0	18	94	72	77	75	20	dune
Armeria maritima (marsh)	97	17	6	0	18	98	94	90	92	24	marsh
Carex arenaria	59	0	0	0	18	85	80	84	88	20	dune
Centaurium erythraea	96	4	0	0	20	97	91	95	91	25	dune
Limonium binervosum	99	19	4	0	18	99	99	98	99	20	shingle
Plantago coronopus	83	0	0	0	18	93	83	91	90	20	shingle
P. maritima	67	9	0	0	18	71	61	56	59	20	marsh
Rumex crispus (seeds only)	98	1	0	0	25	99	98	98	96	20	driftline
Silene maritima	91	4	0	0	18	92	83	87	84	20	shingle
Type 3											
Crambe maritima											
seeds only	9	0	0	0	25	14	14	21	23	35	driftline
whole fruits	10	0	0	0	25	4	1	3	6	35	driftline
Honkenya peploides	1	0	0	0	18	4	1	3	6	24	driftline
Juncus maritimus	84	27	1	0	18	84	29	47	74	20	marsh
Limonium bellidifolium	49	5	5	2	25	50	97	99	94	25	marsh/shingle
L. bellidifolium[a]	23	23	10	7	25	23	32	25	34	25	marsh/shingle
L. humile[a]	21	19	1	1	25	33	51	62	53	25	marsh
L. vulgare											
Missel Marsh	31	6	3	6	20	55	39	47	53	20	marsh
Upper Hut Marsh[a]	30	35	3	1	25	38	63	65	74	20	marsh
Plantago Marsh[a]	18	12	10	0	25	22	38	69	67	20	marsh
Upper Plover Marsh[a]	24	18	6	0	25	31	54	61	62	25	marsh
Rumex crispus fr.	77	0	0	0	25	79	93	93	92	25	driftline
Suaeda vera	7	2	1	0	20	11	8	18	23	100	marsh
Triglochin maritima	5	2	0	0	18	7	7	6	11	20	marsh

[a] Data from Boorman (1966).

observations concerning species of different habitats.

Materials and methods

Seeds or fruits were collected in the autumns of the years 1978–81, almost all from Scolt Head Island, Norfolk (G.R. 53:810465). They were sorted, cleaned and stored in paper bags in the laboratory, and used within a few weeks of collection. *Crambe maritima* was from Dungeness, Kent. Germination tests were carried out in 90 mm petri dishes, on Whatman's Grade 182 filter paper; 36 seeds were placed in each dish, in a 6×6 grid. 5 replicates were used for each treatment, except for *Armeria maritima,* where only 36 seeds were used. Each dish was watered with 5 ml of test solution. The solutions were:

1. Distilled water (0 mM NaCl).
2. ½ strength seawater (300 mM NaCl).
3. Full strength seawater (600 mM NaCl).
4. 1½ strength seawater (900 mM NaCl).

The seawater was from the North Sea, Skegness, Lincolnshire, with a salinity of 3.56% (600 mM NaCl).

Each dish was weighed and all were kept under plastic covers to reduce evaporation. Each time they were checked they were reweighed and made up to the original weight with distilled water, added beneath the edge of the paper to avoid fresh water flushing of the seeds. Titration has shown that this method maintains the solutions within 5% of the original salinity. The dishes were on a bench in a north-facing laboratory at $20 \pm 3\,^{\circ}$C. They were checked at two- or three-day intervals. Germination was defined as the emergence of healthy cotyledons or radicles. Germinated seeds were removed after checking.

After a period varying from 18–25 days the seeds were placed on new filter papers in clean dishes, each with 5 ml distilled water, and thereafter checked at intervals as before. Cumulative totals of all germinated seeds were kept. Some seeds were infected by fungi; these were removed to avoid the spread of infection. Experiments were continued until germination had completely or almost ceased. Usually a total of 50 days from the start of the experiment was more than sufficient, but a few species were kept going longer (Table 1).

Results

The results, summarized in Table 1, have been grouped into three types, corresponding well with Boorman's three groups. They are distinguished as follows:

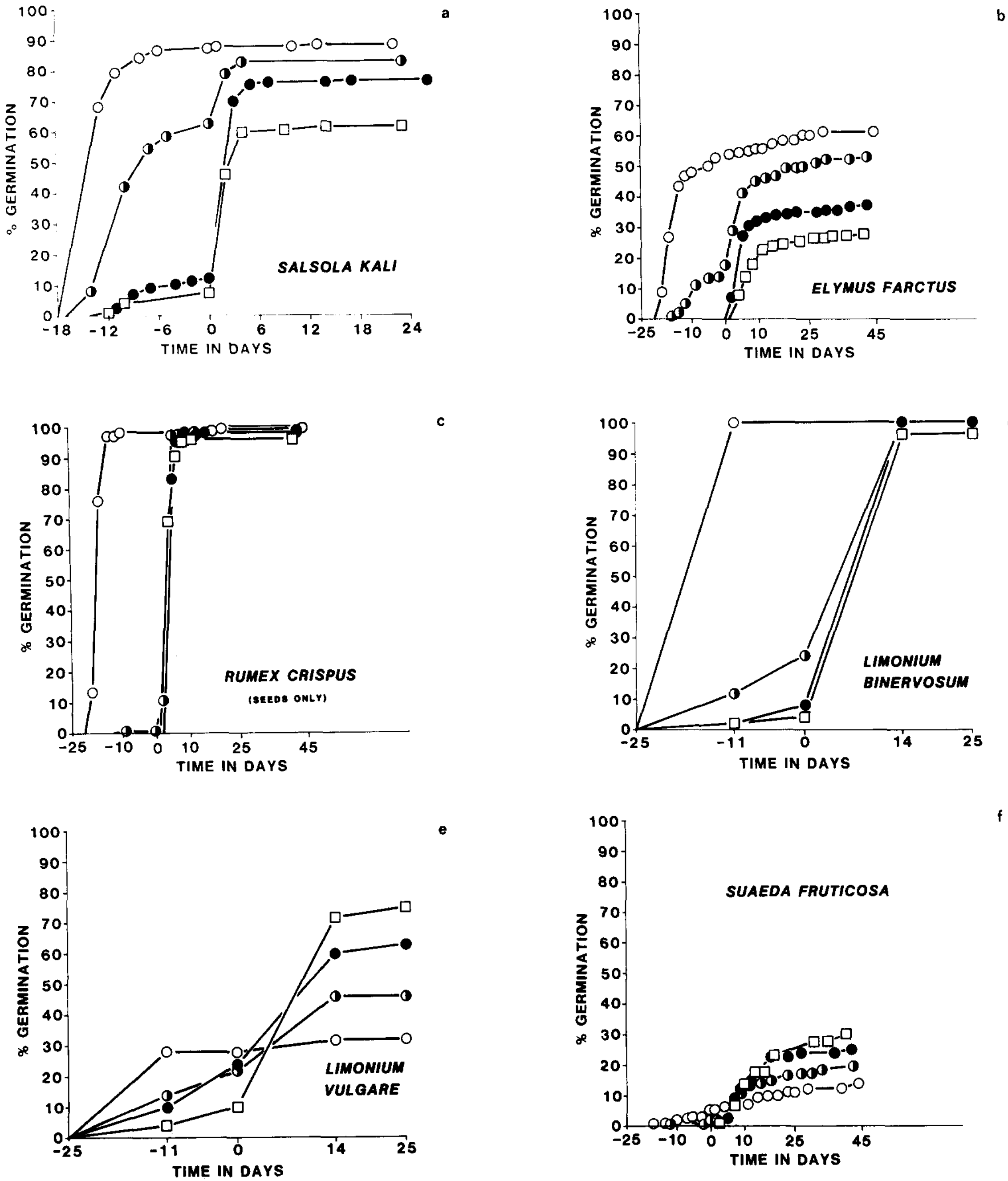
Type 1. If germination occurred at all it was inversely proportional to salinity. When transferred to fresh water, germination rose to quite high levels, but those seeds exposed to the highest salinity had lower final germination totals than those in ½ strength seawater, though all of the latter germinated less well than those in fresh water. It is noteworthy that six of these species, after exposure to salinity, germinated better after being in full strength seawater than in ½ or 1½ strength seawater

Type 2. Germination was strongly inhibited even by ½ strength seawater, but after transfer to fresh water all recovered to levels equal to or very little below those that had been in fresh water from the start. The exception was *Armeria maritima* from the dune habitat, in which though seeds recovered from every salinity level, only about 75% germinated finally compared with over 90% for those in fresh water. All seeds of *Armeria* from salt marsh recovered to almost the level in fresh water. It is arguable that dune *Armeria* should be classified as Type 1. The two species that Boorman classified as Group 2 fall into my Type 2.

Type 3. Germination was variable in salt water. Several species, all from salt marsh or marshy shingle, germinated in full strength seawater, and some in 1½ strength seawater. The remainder, all but one from non-salt-marsh habitats, did not germinate in any strength of seawater. All, when transferred to fresh water, exhibited the phenomenon of 'salt stimulation' i.e. an enhanced rate of germination after pretreatment in salt water. In most of these species the higher the salinity during pretreatment, the higher the eventual germination after transfer to fresh water.

Representative germination graphs are shown in Figure 1, to illustrate the three types in more detail.

In Table 1 are included some data from Boorman (1966). His results for *Limonium vulgare* and *L. bellidifolium* show together with mine that there is considerable variation within species, though the underlying pattern is the same. Boorman (1968) investigated intra- and inter-populational differen-



ces and was of the opinion that they were not very important at Scolt Head Island.

The species have been grouped into habitat types in Table 2. In Tables 1 and 2 marsh is defined as true salt marsh, inundated at least at every spring tide. Shingle refers to a type of stabilized shingle which occupies large areas of Scolt Head Island, and which is inundated at least during the equinoctial spring tides and also at some others. Driftline is the area where debris and seeds are deposited at the highest spring tides. The dune species are normally not inundated but some may be in exceptionally high tides. *Limonium bellidifolium* occupies a somewhat intermediate position at the very upper

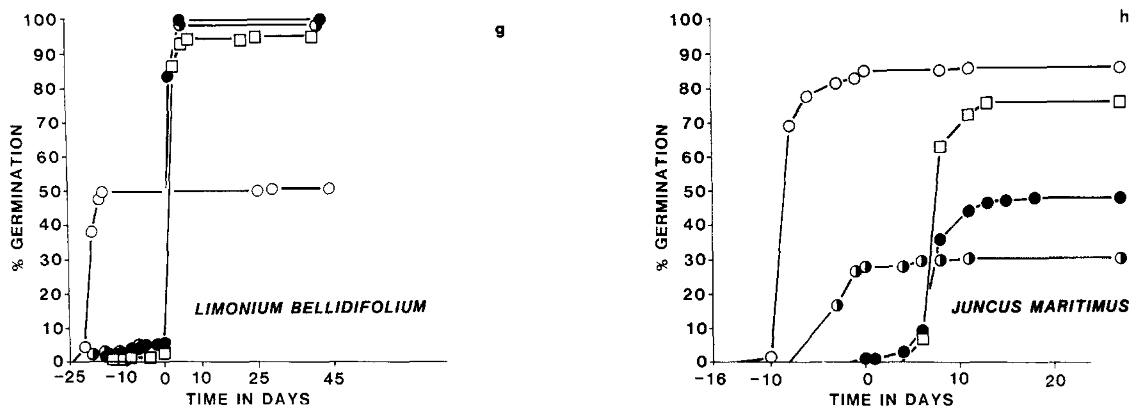


Fig. 1. Germination of eight species in relation to salinity. Graphs a and b, Type 1; c and d, Type 2; e and f, Type 3 species. Graph g, polymorphic response in *Limonium bellidifolium*. Graph h, *Juncus maritimus*, with best germination in fresh water, but Type 3 response after immersion in seawater. Day O is the day of transfer of seeds to fresh water, negative days are those before transfer. Open circles, fresh water; half-filled circles, ½ strength sewater; closed circles, full strength seawater; open squares, 1½ strength seawater. Data for Graph e from Boorman (1966).

edge of marsh where it merges into shingle, on a more muddy substrate than the other shingle species, and more often inundated.

In some species the total germination was small, and this must cast some doubt on the correctness of the allocation of these species to types. The consistency of the trends between replicates was distinct enough to enable a choice to be made without much difficulty. Two species, *Eryngium maritimum* and *Cynoglossum officinale* failed to germinate in the conditions we provided, in several successive years. *Euphorbia paralias* had too low a germination to allow its inclusion in these results.

Discussion

The seeds tested differ in their response to salinity and in their survival after exposure to salinity. None was totally killed by the period of immersion that was given nor even by a salinity of nearly 5.5% (940 mM NaCl). All, when changed to fresh water, recovered to give some germination. These results agree with others from experiments in which seeds have been subjected to salinity and then placed in fresh water (e.g. Ungar, 1962, 1978; Seneca & Cooper, 1971; Barbour, 1970; Macke & Ungar, 1971). The ability to survive immersion in seawater is consistent with findings of many investigators (e.g. Darwin, 1857; Boorman, 1968; Rozema, 1975). Darwin (1857) pointed out, and others have confirmed that species differ markedly in their ability to survive seawater.

The fact that plants of coastal habitats survive immersion in seawater is not surprising. The differences between them are worth further consideration. How does the germination behaviour of these different species relate to the conditions they face in their different habitats?

Type 1 species, apart from *Aster tripolium*, are all dune or driftline plants. The dune species tested all occur in early stages of the succession of coastal dune vegetation though some persist to later stages. Early dunes are subject to frequent salt spray but rarely inundated. Driftline plants are occasionally flooded, but the driftline is established by the March equinoctial spring tides and is unlikely to be inundated again until autumn, though salt spray

Table 2. The germination 'types' of coastal species in relation to habitat. *N.* = number of species in each type.

Type	N	Number of species from each habitat			
		Dune	Driftline	Shingle	Marsh
1	12	4	7	–	1
2	9[a]	3	1	3	2
3	9	–	3	1[b]	6[b]

[a] Includes *Armeria maritima* from dune and marsh.
[b] *Limonium bellidifolium* is included under each of these habitat types.

is frequent. Only during dispersal by flotation are these seeds likely to be subjected to as long an immersion as they were subjected to in my tests. The ability of some of these species to undergo limited germination in salt water may enhance their ability to become established after dispersal. In Western Europe it is likely that after immersion in seawater, they will soon be washed by rain, which will stimulate their germination.

Type 2 species are distinguished by their overall better germination, their very high initial germination in fresh water and by almost total survival at all levels of salinity in these tests. These are all useful attributes for seeds which may be inundated. At Scolt Head Island, the three dune species occur mainly, if not exclusively in dune hollows that are occasionally flooded by the sea, or, in the case of *Armeria maritima,* on frequently flooded dune fringes. The shingle species are flooded by most spring tides. The two marsh species are from the upper marsh which is flooded by spring tides. Thus all these plants are from habitats which are certain or likely to be flooded at some time by the sea, though the frequency of inundation will be less than that of Type 3 plants.

Type 3 species include six from salt marsh (one of which, *Limonium humile,* was studied by Boorman, but not in this investigation). The remainder are driftline plants. Both *Crambe maritima* and *Rumex crispus* are capable of long-term flotation (Guppy, 1917) and salt-stimulated germination may be an advantage to such species. The marsh plants will certainly be inundated more frequently and for longer periods than plants of Types 1 and 2. The ability to be stimulated to higher germination by immersion in seawater is likely to be of survival value. Boorman (1968) showed that the longer the immersion, the greater the 'salt stimulation' in *Limonium vulgare*, and that it was capable of surviving at least 21 weeks immersion in seawater. The ability of all these Type 3 species to germinate rapidly after return to fresh water confers upon them the potential for rapid establishment after dispersal by the sea, followed by rain, a likely combination of events in the autumn.

Two anomalies require comment. *Aster tripolium,* a salt marsh plant at Scolt Head Island, behaves as a Type 1 species. In this experiment it germinated much better than for Boorman (1968) or Chapman (1960). It grows in a much wider range of salinities in the wild than many salt marsh species, down to below 0.5% salinity (85 mM NaCl) in the Baltic Sea. A study of populations from a range of salinities would be instructive. *Limonium bellidifolium* germinated much better after immersion in any salinity than in fresh water for both Boorman and myself. The results of the present paper, with 50% germination in fresh water and nearly 100% after immersion in salt water, suggest that it may be polymorphic with respect to its susceptibility to seawater, with half the seeds requiring salt stimulation. Its habitat, on the marsh / shingle boundary, might favour such a polymorphism. Germination polymorphism has also been reported for other coastal species, (e.g. Schat, 1982).

The apparent more favourable response of some species, especially of Types 1 and 2, to full strength, than to ½ or 1½ strength seawater, requires more data to establish it as a certainty. If it is a real effect it might suggest a more precise adjustment to the actual salinity likely to be experienced than has been previously shown. The differences between dune and marsh populations of *Armeria maritima* also suggest a 'fine adjustment' of this sort, and the possible genetic isolation between these two populations discussed by Eisikowitch & Woodell (1975) could maintain such a difference. Again further work is needed.

The failure of *Cynoglossum officinale* to germinate, even if the nutlets' surface was abraded, may be related to the low nitrogen content of distilled water and the nitrogen effect of the germination of *Cynoglossum* reported by Freysen *et al.* (1980).

Conclusions

This study was planned as a simple screening of a number of species from one area to determine their germination response to one habitat factor only, salinity. Though many questions are left unanswered and more have been raised, the behaviour of the species can, at least partly, be related to their habitats at Scolt Head Island.

It would be unwise to generalize too freely from these results. Nevertheless the similarity of the germination types I found to those postulated by Boorman (1968) and to those which can be discerned from the rather wide range of experimental conditions of other workers (Ungar, 1978) encourage the view that plants which are exposed to seawater can be expected to show consistent germination responses, and that these responses may be related to the duration and intensity of their exposure to seawater in their natural habitats. It is clear, as Ungar (1978) pointed out, that none requires salt, but those which are most likely to be exposed to it are stimulated by it.

These experiments were deliberately kept simple. There is still a lot to be learned about the effects of seawater on seeds. Is it merely an osmotic effect or are specific ion effects important? What is the actual physiological mechanism involved? How precise *is* the adjustment of each species' germination response to the conditions which it experiences in the wild? How much do different populations of the same species differ in their responses to local conditions? How much do conditions from year to year affect germination performance? How important is polymorphism in coastal plant seed germination? There is plenty of scope yet for further fruitful investigation of these and other questions.

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