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Species Specificity of Response to Fluctuations of Sea Water Salinity in Seeds of Coastal Plants

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Abstract—An analysis of seed germination pattern has revealed species-specific responses to water salinity (0, 25, 50, and 100% sea water vs. distilled water) in plants growing on sea coasts of the Russian Far East and in areas remote from the sea. The results show that coastal species are less sensitive to the adverse effect of sea water in the above concentrations, but only the seeds of halophytes from the family Chenopodiaceae are capable of germinating in 100% sea water. The relationship between the habitats of plant species and individual specificity of seed germination is discussed.

Key words: adaptation, sea coast species, seed germination, fluctuations of sea water salinity.

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Sea coasts in the Russian Far East (RFE) extend for 22000 km. Ecological–climatic conditions in these areas are fairly severe. They include poor skeletal soils, sandy and gravely substrate, salinization, high humidity in the warm period of the year, relatively low temperatures during the growing season, the absence of snow cover, parching winter winds, and deep substrate freezing. In extreme supralittoral habitats, plants are exposed to strong salt stress due to tidal phenomena, substrate salinity, and salt water impulverization. As a result, coastal vegetation is sparse and floristically poor, with its biological diversity being at high risk. Nevertheless, studies on the Far Eastern flora have shown that plant communities in the continent–ocean contact zone often have a mixed composition and include meadow, forest, and even steppe species as well as typical halophytes.

Sea coast plants have a variety of adaptations to their specific environment, but seed reproduction in some species is suppressed (Probatova and Seledets,1999; Voronkova et al., 2008). The formation of high-quality seeds capable of germination is a reliable indicator of successful adaptation in plants. In the coastal zone, soil salinity at the surface may be 100 times as high as that in deeper horizons; therefore, conditions for seeds are even more extreme, compared to conditions for maternal plants (Ungar, 1978). Since early stages of the plant life cycle are most sensitive to stress factors (Harper, 1977), studies on the processes of seed germination in sea coast plants are obviously relevant for evaluating their individual adaptation potentials. It is considered that adaptation at early stages of development is a key factor of plant fitness (Grime, 1979).

In the supralittoral zone, seeds germinate under unstable conditions, primarily because of changes in salinity. In a monsoon climate, substrates are periodically desalinized to some extent under the effect of pouring rains and river waters in deltas and estuaries (Shlyakhov and Kostenkov, 2000). An analysis of seed germination dynamics at decreasing concentrations of sea water salts may help reveal the effects of certain stress factors. The purpose of this study was to perform a comparative analysis of seed viability in plants expanding to the coastal zone in experiments on seed germination in different concentrations of sea water.

MATERIAL AND METHODS

Studies were performed in 2006 and 2007. Brief data on the distribution of species included in analysis and characteristics of their habitats are shown in Table 1. These data and the Latin names of plant species are given according to the monograph *Vascular Plants of the Russian Far East* (*Sosudistye...*, 1988, 1989, 1992, 1995, 1996).

The group of plants most typical of the supralittoral zone included six species of four families: *Salicornia europaea, Suaeda heteroptera, Salsola komarovii, Spergularia marina, Artemisia stelleriana*, and *Rumex stenophyllus*. Their seeds (for brevity, this term here also refers to achenes of *A. stelleriana*) were collected on sandy and boggy areas of thalassic salt flats in Sukhodol Bay, an inlet on the eastern coast of Ussuri Bay (Peter the Great Bay, the Sea of Japan). For com-

Table 1. Distribution of species studied and characteristics of their habitats

Species, family	Distribution	Habitats
Salicornia europaea L. (Chenopodiaceae)	RFE, Africa, America, and Eurasia: sea coasts (except in the north) and arid regions	Boggy or silty solonetzic soils on sea coasts
Salsola komarovii Iljin (Chenopodiaceae)	RFE, Japan, Korea, China	Pebble and sand beds on sea coasts
Suaeda heteroptera Kitag. (Chenopodiaceae)	RFE, Japan, Korea, China	Silty or boggy soils of coastal plains and sea coasts
Artemisia stelleriana Bess. (Asteraceae)	RFE and Japan	Sand and pebble beds on sea coasts, cliffs (rarely)
Spergularia marina (L.) Griseb. (Caryophyllaceae)	RFE, European Russia, the Caucasus, Siberia, Middle Asia, Mongolia, Japan, Korea, China	Sea terraces, lagoon coasts, river estuaries, salinized soils
Rumex stenophyllus Ledeb. (Polygonaceae)	RFE, European Russia, Ciscaucasia, Southern Siberia, Middle Asia, the Mediterranean, Mongolia, Japan, Korea, China	Moist, especially more or less solonetzic meadows, sand and pebble beds along rivers, populated areas, roadsides
Ermania parryoides Cham. ex Botsch. (Brassicaceae)	Endemic to northeastern RFE	Gravely and clayey mountain slopes, screes
Polemonium boreale Adams (Polemoniaceae)	RFE, European Russia, the Siberia, Mongolia, Northwest America	Cliffs, screes, lawns, dryad tundras, willow scrub

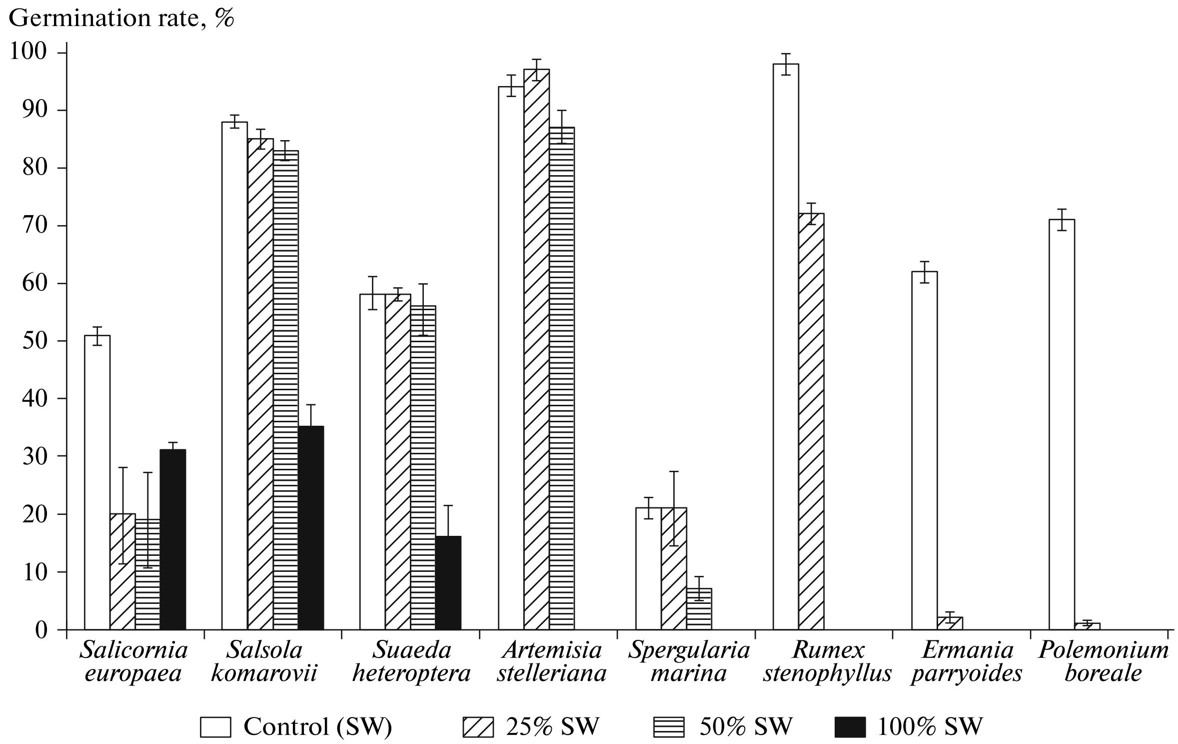
parison, we used the seeds of two species unadapted to saline soils (*Ermania parryoides* and *Polemonium boreale*), which were collected in high mountain areas.

Experiments on seed germination were performed with all species simultaneously. The seeds were placed in Petri dishes (50 seeds per dish, three replications) on filter paper underlain by a layer of cotton wool and soaked with 8 ml of sea water, undiluted or diluted two- or fourfold (100, 50, and 25%). In the control, distilled water was used. The dishes were kept under natural illumination at 23–25°C. To prevent excess salinization, the seeds were transferred every second day to new dishes with a fresh portion of sea water at the same concentration. As shown in preliminary experiments, the seeds of *Rumex stenophyllus, Spergularia marina*, and *Ermania parryoides* require cold stratification to stimulate germination. Therefore, Petri dishes with these seeds were initially incubated as described above for 3 weeks and then transferred to a cold room (2°C) and treated with solutions cooled to the same temperature. After 10 days (*S. marina* and *E. parryoides*) or 20 days (*R. stenophyllus*), the dishes were removed from the cold room and incubated as described above. The incubation period ended when new sprouts ceased to appear. The seeds that failed to germinate in 50 or 100% sea water were then transferred to new dishes and germinated in distilled water. Germinated seeds were counted every day, calculating their proportion (%) of the total seed number in a given experimental variant.

RESULTS AND DISCUSSION

A high diversity of ecological conditions and, in particular, the dynamism and intensity of salinization on sea coasts imply interspecific differences in the degree of plant adaptation to this factor, which are expected to manifest themselves already at early stages of development, namely, during seed germination. Indeed, the analysis of data on seed germination in sea water of different concentrations (figure) revealed differences in seed tolerance to salinity between the species. Seed germination rate in distilled water proved to be high (over 50%) in all species except *Spergularia marina*; in 25% sea water, the germination rate remained at the control level in four out of the six coastal species but decreased in *S. europaea* and *R. stenophyllus*. Seed germination in the species not occurring in the coastal zone was suppressed almost completely. When 50% sea water was used, the seeds of *R. stenophyllus* failed to germinate, while the responses of other coastal species remained the same as in the previous variant. Seed germination in 100% sea water was observed only in true halophytes of the family Chenopodiaceae, but this process was markedly inhibited. The impairment of germination parameters at increased salinity was also observed in other halophyte species of this family, such as *Salsola iberica* (Khan et al., 2002) and *Kalidiopsis wagenitzii* (Sekmen et al., 2004).

The species specificity of adaptation to seed germination at increased salinity manifested itself most clearly when we analyzed the ratios of germination rates in sea water of different concentrations to those in the control (Table 2). The species were ranked in order of decreasing salinity tolerance of seeds, and representatives of the family Chenopodiaceae proved to be the best adapted species. Among them, *S. europaea* showed the highest salinity tolerance: its seeds germinated better in 100% sea water, whereas the highest germination rates in *S. komarovii* and *S. heteroptera* were recorded in variants with diluted sea



Germination rates of seeds treated with different concentrations of sea water.

water. These adaptive features may be accounted for by differences in the distribution (ranges) of these species. *Salicornia europaea* is a broad-range euhalophyte that grows both on sea coasts and in arid regions and, therefore, is naturally exposed to a wider variety of high salinities, whereas *S. komarovii* and *S. heteroptera* are coastal species confined to humid areas. Then follows the group of species whose seeds failed to germinate in 100% sea water but showed a fairly high germination rate when it was diluted. The seeds of species unadapted to high environmental salinity practically failed to germinate in sea water even when it was diluted fourfold.

Although halophytes of the family Chenopodiaceae grow in sea coast areas with different soil conditions (Shlyakhov and Kostenkov, 2000), all their habitats are characterized by strong salinization (Table 1). Thus, *S. komarovii* has established itself in the narrow, fragmentary band of marshes located in close proximity to the shoreline, where plants are affected not only by substrate salinity but also by salt water impulverization during storms. *Salicornia europaea* and *S. heteroptera* grow farther from the shoreline, in swamped depressions, where substrate salinity is also high. Other coastal species grow still farther from the shoreline. A comparative analysis of salinization along the Japanese coasts revealed the highest soil salinities in marshes, cliffs, and fore (unstable) dunes exposed to typhoons and storms (150–300 mmol/l NaCl or even higher), whereas those in hind (stable) dunes did not exceed 50 mmol/l NaCl, with rare exceptions (Mariko et al., 1992).

The relationship between habitat conditions and species specificity of seed germination at different salinities has been noted by a number of authors (Woodell, 1985; Ishikawa and Kachi, 2000; Espinar et al., 2005; Wetson et al., 2008). Analysis of our own and published data allows the conclusion that the observed rates of seed germination in different dilutions of sea water are consistent with ecological conditions in the habitats of maternal plants (see Table 1), which are characterized by different levels of soil salin-

Table 2. Ratios of seed germination rates upon treatment with different concentrations of sea water (SW) to those in the control with distilled water (DW)

Species	100% SW/DW	50% SW/DW	25% SW/DW
Salicornia europaea	0.61	0.37	0.39
Salsola komarovii	0.40	0.94	0.97
Suaeda heteroptera	0.28	0.97	1.00
Artemisia stelleriana	0	0.93	1.03
Spergularia marina	0	0.33	1.00
Rumex stenophyllus	0	0	0.73
Ermania parryoides	0	0	0.03
Polemonium boreale	0	0	0.01

Table 3. Germination recovery upon seed transfer to distilled water (DW) after incubation in 100% or 50% sea water (SW; above and below the line, respectively)

Species	Germination rate in SW, %	Germination rate after transfer to DW, %	Germination rate at the end of experiment, %	Germination rate in DW (control), %	Experiment/control ratio
Salicornia europaea	31 ± 2 / 19 ± 7	22 ± 7 / 22 ± 1	53 / 41	51 ± 2	1.04 / 0.80
Salsola komarovii	35 ± 4 / 83 ± 2	62 ± 7 / –	97 / –	88 ± 1	1.10 / –
Suaeda heteroptera	16 ± 6 / 56 ± 4	16 ± 1 / 3 ± 1	32 / 59	58 ± 4	0.55 / 1.02
Artemisia stelleriana	0 / 87 ± 3	92 ± 4 / –	92 / –	94 ± 2	0.98 / –
Spergularia marina	0 / 7 ± 2	10 ± 2 / 27 ± 1	10 / 34	21 ± 2	0.48 / 1.62
Rumex stenophyllus	0 / 0	96 ± 7 / 92 ± 4	96 / 92	98 ± 7	0.98 / 0.94
Ermania parryoides	0 / 0	5 ± 1 / 15 ± 5	5 / 15	62 ± 2	0.08 / 0.24
Polemonium boreale	0 / 0	5 ± 1 / 7 ± 2	5 / 7	71 ± 2	0.07 / 0.10

Note: (–) experiment in a given variant was not performed.

ity. Therefore, in the course of natural selection, sea coast species have developed various adaptive mechanisms allowing them not only to survive but even to produce viable seeds under stressful growing conditions.

The level of environmental salinity in coastal areas fluctuates significantly under the influence of many factors, including periodic inundation or impulverization with sea water (especially at the surf line), pouring rains, changes in temperature and wind direction, and partial desalinization by river waters in deltas and estuaries. Taking this into account, we performed a model experiment on seed germination under desalinization conditions, where the seeds that failed to germinate in 100 or 50% sea water were transferred to distilled water (Table 3). Comparing the results with the control (germination in distilled water alone), we found that the seeds of all coastal plants remained viable and resumed germination after being placed in distilled water. This recovery was species-specific, with germination rate in the majority of sea coast species rapidly reaching the control level and even exceeding it. Such salt stimulation was also observed in coastal plant species from other regions (Woodell, 1985; Weber and D'Antonio, 1999; Redondo-Gomez et al., 2008). Apparently, high environmental salinity is not necessary for seed germination in such species but can stimulate this process when the seeds are exposed to it. The seeds of plants unadapted to sea coast conditions showed practically no germination recovery, except for some *E. parryoides* seeds initially germinated in 50% sea water.

Therefore, only those species can survive on sea coasts in which stress caused by the action of sea water can be fully counterbalanced by adaptive mechanisms. The ability of seeds to retain viability in sea water and rapidly germinate upon transfer to fresh water provides for successful establishment of such plants in coastal areas. Situations combining the effects of exposure to sea water and subsequent abundant, often long rains are typical for the monsoon climate of the Russian Far East. Adaptation to such conditions is especially important for the species whose seeds fail to germinate at high salinity.

Thus, the result of this study indicate that the optimal salinity ranges providing for the most successful implementation of germination programs vary depending on plant species. The ability of coastal plants to produce high-quality seeds germinating at high salinities can be classified as a major adaptation to growing in such habitats. The results of simulation experiments on seed germination in a gradient of sea water salinity provide evidence for the adaptive potential of corresponding species in nature. With respect to salinity tolerance, the species included in the study can be arranged in the following descending series: *Salicornia europaea* > *Salsola komarovii* > *Suaeda heteroptera* > *Artemisia stelleriana* > *Spergularia marina* > *Rumex stenophyllus*. When the seeds that failed to germinate in sea water were transferred to fresh (distilled) water, the inhibitory effect of salinity was almost completely abolished in all coastal species, whereas the seeds of plants not adapted to sea coast conditions showed practically no germination recovery. The ability to timely implement the germination program in the period when salinity decreases (in the Russian Far East, during monsoon rains) is also a manifestation of the adaptive mechanism providing for the sustainable growth of these species in coastal plant communities.

Therefore, the species specificity of seed germination strategy in sea coast plants is a result of evolutionary adaptation to stressful growing conditions in their habitats.

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