

Osmotic Relations of Some Plants of the Northern Marshall Islands¹

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ABSTRACT: Osmotic relations of several strand species were investigated by determining osmotic potentials (ψ_{π}) and sodium contents of leaf samples collected in the field, by measuring the electrical conductivity of groundwaters and soil solutions, and by growing seedlings in the greenhouse in culture solutions with varying levels of added salt. Mean ψ_{π} of the field-collected leaves ranged from -1.9 to -3.1 M Pascals, compared with that of seawater at -2.7 M Pa. Sodium contents of the leaves were high, commonly being 1 to 3% of the dry weight. Groundwaters mostly ranged in electrical conductivity from 16 to 50 mmhos/cm (equal to about 0.86 to 2.7 M Pa ψ_{π}). In culture solutions, seedlings of four shrubby species (*Cordia subcordata* Lam., *Guettarda speciosa* L., *Scaevola sericea* Vahl, and *Tournefortia argentea* L.f.) and a native variety of squash (*Cucurbita pepo* L.) all grew well at solution ψ_{π} of -0.28 M Pa, but were depressed to about 50% yield at -0.42 M Pa. The woody species declined to about 10–20% yield at -1.4 M Pa, and grew only a little at -2.8 M Pa (a solution equal in ψ_{π} to that of seawater).

THE VEGETATION OF THE ATOLL beaches and small islets in the northern Marshall Islands is dominated by a few species growing as shrubs or small trees (Fosberg 1953). Although usually healthy, they are often widely spaced and slower in growth than the same and other species growing in interior parts of the larger islands (for photographs see Gessel and Walker 1987). Such a pattern was attributed some time ago to effects of salinity (Fosberg 1949). However, Stone (1951) observed a similar pattern on Arno Atoll, which is farther south and with higher rainfall, and suggested that soil fertility might be a factor as well. On Kapingamarangi, in the Caroline Islands, Niering (1957) contended that salinity was the major cause of such a vegetational pattern and classified the more common species into several groups with respect to salt tolerance. As might be expected, *Guettarda speciosa* L., *Scaevola sericea* Vahl, and *Tournefortia argentea* L.f. were included in his most tolerant category, but *Cordia sub-*

cordata Lam. was considered somewhat less tolerant.

Salinity is most likely responsible for this pattern of vegetation, because plants growing on atolls are inevitably exposed to appreciable salinity. The main objectives of this study were to study osmotic relations and degree of salt tolerance of several atoll species. Osmotic potential (ψ_{π}) and mineral analyses of field-collected leaf tissue, electrical conductivity of groundwaters and soil samples collected in the field, and the growth of plants in the greenhouse in solution cultures containing varying levels of salt were used to ascertain the real or potential salt tolerance and water-absorbing ability of *G. speciosa*, *S. sericea*, *T. argentea*, *C. subcordata*, and an atoll variety of squash, *Cucurbita pepo* L.

MATERIALS AND METHODS

Osmotic Potentials of Leaves

Samples of fully expanded leaves, usually 10 to 20 g, were collected from healthy plants on Rongelap Atoll, packed tightly into heavy-

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weight plastic bags, kept cool, then frozen within 1 to 2 hr. They were transported in dry ice-cooled chests to the University of Washington laboratories in Seattle, where they were stored in a room at -15°C until used. Sap was expressed from the just-thawed samples using a small piston adapter in a Carver press. Promptly after expressing, the freezing point depression was determined by the method described by Loomis and Shull (1937). A number of possible errors may be involved in this method. The most likely to be serious are dilution of the sap by apoplastic or even cytoplasmic water, and adsorption of solutes by the residual pellet, both tending toward less negative values of ψ_{π} . Crafts et al. (1949) discussed limitations and sources of error of the method in detail. Despite the drawbacks of the technique, we believe that the data give a useful characterization of the leaves collected in the field.

Groundwaters and Soils

For groundwaters, well points on galvanized pipe (3 cm outside diameter) were driven into the soil and underlying coral sand to a depth that permitted removing water by inserting a plastic tube attached to a suction hand pump. Water was commonly reached at 1 to 2 m depth. Samples were collected at about 20 locations on Rongelap Atoll. Electrical conductivity was read within 2 days of collection.

About 15 soil pits were dug on or near the beaches, normally to a depth of 1 to 1.5 m. Roots were most numerous in the upper 20–30 cm, but living roots were almost always found down to the bottoms of the pits and sometimes extended vertically into the underlying strata. In several instances groundwater was reached, with roots seen to be in contact with it.

Samples of soil collected from the sides of the pits were returned to the laboratories in Seattle, where soil solutions were extracted from saturation pastes using a pressure plate apparatus at 1.5 M Pa pressure. Conductivities of the saturation extracts were corrected to four times the water content of the soil after extraction, because water content (percentage

dry weight) at field capacity is about four times the content at -1.5 M Pa tension.

Mineral Analyses of Leaves

Fully expanded leaves were collected on Rongelap Atoll in mesh bags, usually separating upper (younger) and lower (older) portions. These were air-dried in the field, transferred into plastic bags, transported to the University of Washington laboratories, ground to 20 mesh, dried to constant weight in an oven at 80°C , then analyzed by the following methods: Ca by oxalate precipitation and titration, Mg by MgNH_4PO_4 precipitation and colorimetric assay, and K and Na by flame photometry (Jackson 1958).

Plant Growth at Varying Salt Levels

Seeds of the various species were collected on Rongelap Atoll, and the seed germinated and plants were grown in the greenhouse at the University of Washington. The methods used were adapted from Hoagland and Arnon (1950). The plants were supported by corks or plaster covers in 1/2- or 1-gallon (1.9- and 3.8-liter) Mason jars, one seedling per jar, usually with quadruplicate jars, and Shive-type capillary glass aerators were used. The compositions of the solutions are given in Table 1. Some of the solutions were salinized with NaCl alone, but in others extra Ca was included as well, both because soil solutions and ground waters in the atoll environments contain appreciable Ca (often 4 to 8 mM) and because Ca is known to ameliorate the adverse influences of high Na (Greenway and Munns 1980, Kent and Läuchli 1985). Extra salts were added as chlorides because the dominant anion in the atoll environment is chloride.

RESULTS

Osmotic Potentials of Leaves

These are listed in Table 2. Only a few values are more negative than that of seawater (-2.7 M Pa), but all are negative enough to allow water absorption from most of the

TABLE 1
COMPOSITIONS OF THE CULTURE SOLUTIONS

SOLUTION	ψ_{π} (M Pa)	KH ₂ PO ₄	KNO ₃	Ca(NO ₃) ₂ (mM)	MgSO ₄	NaCl	CaCl ₂
A	-0.03	0.50	2.50	2.50	1.00	0.10	—
B	-0.28	0.50	2.50	2.50	1.00	40	2.50
C	-0.48	0.50	2.50	2.50	1.00	80	—
D	-0.62	0.50	2.50	2.50	1.00	110	5.50
E	-1.39	0.50	2.50	2.50	1.00	270	15.0
F	-1.43	0.50	2.50	2.50	1.00	300	—
G	-2.77	0.50	2.50	2.50	1.00	600	—

NOTE: All cultures received micronutrients as follows (μ M): B, 23; Cu, 0.16; Mn, 4.6; Mo, 0.26; Zn, 0.38. Fe was supplied in 0.5% FeSO₄ · 7 H₂O solution, 0.5 ml per liter added twice weekly. Solutions were changed twice monthly; solution volumes were made up every other day with distilled water.

TABLE 2
OSMOTIC POTENTIALS OF LEAF TISSUE* COLLECTED ON RONGELAP ATOLL IN SEPTEMBER

SPECIES	ISLAND	LOCATION	NO. OF SUBSAMPLES	MEAN ψ_{π} (M Pa)
<i>Scaevola sericea</i>	Rongelap	Rain gauge (near lagoon)	5	-1.99
	Rochi	Lagoon beach	2	-2.31
	Burok	Lagoon beach	2	-2.22
<i>Tournefortia argentea</i>	Rochi	Seaward beach	4	-2.43
		Lagoon beach	2	-1.97
	Burok	Lagoon beach	3	-2.08
		Seaward beach	2	-2.22
<i>Guettarda speciosa</i>	Burok	Lagoon beach	4	-2.23
		Seaward beach	3	-3.12
<i>Pisonia grandis</i> R. Br.	Burok	Seaward beach	2	-2.31
<i>Cordia subcordata</i>	Rochi	Lagoon beach	2	-3.09
<i>Pemphis acidula</i>	Island 13 (small islet)		2	-3.90

* Midribs were removed from the leaves at time of collection to minimize any dilution with apoplastic water when expressing sap.

groundwaters (see *Discussion*). The extreme ψ_{π} value of -3.9 M Pa was recorded for leaves of *Pemphis acidula* Forst. growing on a very small islet, which presumably had no freshwater lens. This species is commonly observed with the root systems under seawater at high tide (Fosberg 1953). Unfortunately, we could not germinate seeds of *P. acidula* for greenhouse study.

Rongelap island is a large island of over 500 ha, but the other islands listed are of moderate size (100–200 ha). There was a trend of more negative osmotic potentials in samples from the seaward beach than from the lagoon beach of Burok. This is consistent with

the greater water and salt stress on the seaward side of islands.

Electrical Conductivities of Groundwaters and Soil Solutions

The values for groundwaters from a large island (Rongelap), several moderate-sized islands of 100–200 ha area, and the very small Pokoreppu are given in Table 3. They can be converted to approximate equivalence in osmotic potential using the curve for NaCl, the dominant salt present, in the handbook from the U.S. Salinity Laboratory (1954). The samples vary from those with little salt up to

TABLE 3
ELECTRICAL CONDUCTIVITIES OF GROUNDWATERS COLLECTED ON RONGELAP ATOLL

ISLAND	MONTH COLLECTED	LOCATION	NUMBER OF SAMPLES	MEAN ELECTRICAL CONDUCTIVITY** (mMhos/cm) \pm SD
Rongelap	Sept.	Lagoon beach (north end)	7	27.7 \pm 2.3
	Mar.	Pit 22 (in coconut grove)	2	15.0
	Sept.	Pit 22 (in coconut grove)	2	13.4
	Mar.	Pit 23 (in coconut grove)	1	17.2
	Sept.	Pit 23 (in coconut grove)	11	16.6 \pm 0.8
	Sept.	Near village well	6	2.61 \pm 1.7
Kabelle	Sept.	Lagoon beach (35 m from shore)	8	27.3 \pm 4.3
	Sept.	Lagoon edge of coconut grove	8	18.6 \pm 0.1
	Mar.	Old <i>T. argentea</i> grove	1	31.1
	Sept.	Old <i>T. argentea</i> grove	5	26.4 \pm 5.7
	Sept.	North end in scrub	6	45.1 \pm 0.6
Mellu	Sept.	Near lagoon beach	2	42.1
Naen	Sept.	Naen-Kar well	3	7.41 \pm 0.1
	Sept.	Lagoon side back from beach	4	30.0 \pm 0.2
	Sept.	Center of island	4	17.8 \pm 0.1
Eniaetok	Sept.	Center (in coconut grove)	5	25.7 \pm 0.7
Pokoreppu	Sept.	Center (very small islet)	4	50.6 \pm 0.13

* Electrical conductivity (mMhos) \times 0.04 to 0.045 = approximate ψ_{π} (M Pa) (U.S. Salinity Laboratory 1954, p. 15).

** Rongelap seawater measured 50.0 mMhos/cm.

some nearing or equaling the salinity of seawater. A characteristic cation composition was (mEq per liter): Ca, 14; Mg, 45; K, 5; Na, 270.

The low values of 2 and 7 mMhos ($\psi_{\pi} \cong 0.1$ to 0.4 M Pa) are from waters used for drinking by the native people upon necessity. Groundwaters in the areas where the species used in this study commonly grow are mostly in the range of 15 to 30 mMhos, or about 30 to 60% of the strength of seawater. Most of the samples included in Table 3 were collected in September, which is the "wet" season of the year (Arnow 1954). Conductivities might be expected to be higher in the "dry" season (December to March), but the only three cases for which we have such a comparison show merely a small trend in that direction.

Saturation extracts of soils from Rongelap and Kabelle islands proved to be only moderately saline. Soils from 12 pits showed mean conductivities (mMhos) as follows: A horizons, 1.96 \pm 0.97; B horizons, 1.53 \pm 1.02. Again these convert to approximate ψ_{π} values of -0.05 to -0.07 M Pa (U.S. Salinity

Laboratory, p. 15). It is true that depletion of moisture may be rapid from these coarse, excessively drained soils. This could result in soil solution conductivities as much as four times the values measured in the saturation extracts, if the soil water potential dropped to -1.5 M Pa (about the "permanent wilting" range). Because all species tested in the greenhouse grew well in solutions of conductivity 7.5 mMhos (about -0.28 M Pa ψ_{π}), such soil solutions would not exert stress.

Mineral Analysis of Leaves

The composition of a representative group of foliar samples is given in Table 4. Na is high in most of the samples, showing that these species have the ability to absorb and translocate this ion, an indicator that they are halophytic (Greenway and Munns 1980). Also there is a tendency for Na to be higher in lower (older) foliage. In the greenhouse material, very high Na uptake depressed the levels of the other cations, reducing Mg to possibly limiting concentrations.

TABLE 4

CATION COMPOSITION OF LEAF TISSUE FROM GREENHOUSE EXPERIMENTS OR COLLECTED ON RONGELAP ATOLL

SPECIES	LOCATION WHERE SAMPLED		Ca	Mg	K	Na	
			(% OF DRY TISSUE)				
<i>Scaevola sericea</i>	Greenhouse: Solution A		2.35	0.35	5.47	0.079	
			1.28	0.17	3.16	4.74	
	Solution C		0.67	0.14	1.82	5.52	
	Solution F		1.78	0.42	2.97	0.95	
	Rongelap I. near center of island	UL*	2.79	0.60	0.89	1.73	
		LL*	1.41	0.64	1.33	1.35	
	Rongelap I. near seaward beach	UL	2.27	1.24	0.48	1.34	
		LL	2.05	0.49	1.96	1.68	
	Kabelle I. on lagoon beach	UL	3.25	0.89	0.33	1.99	
		LL	2.66	0.37	4.39	0.11	
<i>Tournefortia argentea</i>	Greenhouse: Solution A		4.27	0.21	2.94	2.29	
			2.35	0.082	1.72	7.04	
	Solution C		2.79	0.54	2.70	1.59	
	Solution F		3.49	0.64	2.04	2.16	
	Kabelle I. near center of island	UL	3.96	0.52	2.13	1.99	
		LL	6.78	0.64	0.60	3.45	
	Kabelle I. on lagoon beach	UL	0.92	0.41	0.92	0.92	
		LL	1.32	0.29	0.59	0.39	
	<i>Guettarda speciosa</i>	Anielap I. near lagoon beach	UL	1.59	0.52	1.70	0.73
			LL	2.05	0.57	1.05	0.60
Kabelle I. on lagoon beach		UL					
		LL					

* UL = upper leaves; LL = lower leaves.

Plant Growth at Varying Salt Levels

In an initial trial, *S. sericea* and *T. argentea* were grown in solutions without extra Ca, and including a solution as strong as -2.7 M Pa ψ_{π} . The seedlings were transferred from sand flats into the unsalinized control solution and held there for 2 weeks, then transferred to the salinized solutions and grown for 4 months. Upon transfer to the -2.7 M Pa solution, the seedlings initially wilted, but regained turgor overnight. The yields of the *S. sericea* in that trial are given in Table 5, and the plants are depicted in Figure 1A. Growth declined with increasing salinity, until at -2.7 M Pa it was less than 10% of the control. The results with *T. argentea* (not given here) were similar to those of *S. sericea*.

When calcium was enriched in the medium (Table 6), the woody species endured the osmotic stress of -1.4 M Pa, but were depressed very much in growth. Nonetheless, this ability to grow at a salt concentration over one-half that of seawater indicated strong salt tolerance. The squash was not as

TABLE 5

YIELDS OF *Scaevola sericea* GROWN ON SALINIZED SOLUTIONS WITHOUT EXTRA CALCIUM

SOLUTION	OSMOTIC POTENTIAL (M Pa)	MEAN DRY WEIGHT YIELDS (g) \pm SD		
		SHOOT	ROOT	TOTAL PLANT
A	-0.03	9.89	2.73	12.6 \pm 0.71
C	-0.48	9.71	2.38	12.1 \pm 2.78
F	-1.43	2.22	0.54	2.76 \pm 1.53
G	-2.77	0.98	0.22	1.20 \pm 0.52

tolerant as the woody species, but it was stimulated by moderate salinity (-0.28 M Pa) and showed over 50% yield at -0.62 M Pa, which is exceptionally good for an herbaceous plant. Among the woody species, *C. subcordata* grew poorest in the more saline solutions, in agreement with the assessment in the field by Niering (1957) that this species is less salt-tolerant than *S. sericea* and *T. argentea*. Within a species, the root : shoot ratio did not vary much with salinity treatment, but *T.*



FIGURE 1. *A*, *Scaevola sericea* plants after 4 months' growth in the greenhouse in solutions of (left to right) -0.03 , -0.48 , -1.43 , and -2.77 M Pa osmotic potential (scale is in decimeters). *B*, *Cordia subcordata* plants after 4 months' growth in the greenhouse in solutions of (left to right) -0.03 , -0.28 , -0.62 , and -1.39 M Pa osmotic potential (scale is in decimeters).

TABLE 6
YIELDS OF PLANTS GROWN IN SALINIZED SOLUTIONS WITH EXTRA CALCIUM

SPECIES	SOLUTION	OSMOTIC POTENTIAL (M Pa)	MEAN DRY WEIGHT YIELDS (g) ± SD			LEAF DRY MATTER (%)
			SHOOT	ROOT	TOTAL PLANT	
<i>Scaevola sericea</i>	A	-0.03	44.2	11.5	55.7 ± 8.1	17.2
	B	-0.28	41.4	12.3	53.7 ± 13.4	12.4
	D	-0.62	24.4	5.01	29.4 ± 4.1	11.6
	E	-1.39	4.31	1.34	5.65 ± 1.3	11.2
<i>Tournefortia argentea</i>	A	-0.03	30.1	16.9	47.0 ± 2.6	16.0
	B	-0.28	15.0	8.69	23.7 ± 6.5	12.0
	D	-0.62	13.1	5.85	18.9 ± 4.1	10.7
	E	-1.39	7.02	3.23	10.2 ± 1.4	10.1
<i>Cordia subcordata</i> *	A	-0.03	21.1	17.4	38.5	22.4
	B	-0.28	16.1	11.7	27.8	19.2
	D	-0.62	8.07	5.14	13.2	18.4
	E	-1.39	1.06	0.59	1.65	20.5
Squash (<i>Cucurbita pepo</i>)	A	-0.03	15.0	3.68	18.7 ± 1.2	15.9
	B	-0.28	17.8	5.00	22.8 ± 2.4	15.9
	D	-0.62	8.75	2.76	11.5 ± 3.5	20.1
	E	-1.39	(All plants died in this solution)			

* Limited number of seedlings allowed only duplicate plants of *C. subcordata*.

argentea and *C. subcordata* had higher root : shoot ratios throughout than *S. sericea* and squash.

Succulence is a response of many species to salinity (Flowers et al. 1977). The percentage dry matter in the leaves is included in Table 6 as an indicator of succulence. Both *S. sericea* and *T. argentea* showed lower dry matter contents (i.e., greater succulence) with increasing salinity as expected, although the squash did not. *Cordia subcordata* showed only a small increase in succulence in more saline treatments. These results are in agreement with our observations in the field, where *S. sericea* and *T. argentea* often showed visible succulence (thicker, fleshier leaves) in sites where they are more exposed to salinity, but *C. subcordata* did not.

DISCUSSION AND CONCLUSIONS

Although all field collections treated here were from Rongelap Atoll, we have similar data (not included) for plant tissue and groundwater samples from Bikini Atoll.

Flowers et al. (1977) suggested that halophytes may be distinguished from glycophytes

(nonsaline-adapted plants) by their ability to go through the life cycle in the presence of at least 300 mM salt. By this criterion, it is doubtful if any of the species we studied would qualify as halophytes, since they yielded 20% or less of control weights at 300 mM salt (about -1.4 M Pa ψ_p), although we could not hold the plants long enough in the greenhouse to test completion of the life cycle. With less strict criteria, Greenway and Munns (1980) divided halophytes into one group that is strongly stimulated in yield by 100–200 mM chloride in the external medium and produces about 50% yield at 500–600 mM chloride, and a second group that is not stimulated in growth by salt, but grows well at 200–300 mM chloride, although declining markedly in yield as external salt reaches 400–500 mM. The atoll species studied here seem to fit reasonably well into this second category. There was only a small indication of stimulation of growth by added salt, although such a tendency may have been reduced by the inclusion of 0.1 mM NaCl in the control solution. Certainly these species survived in 300 mM salt, although they did not grow well at levels that high.

The ability to generate osmotic potential

and thus maintain turgor by the accumulation of Na (and usually Cl) in their tissues is a well-known characteristic of halophytes, and one possessed by these atoll species (Tables 2 and 4). Their osmotic potentials are negative enough to support gradients for absorption of water from rather saline substrates, assuming turgor pressure in the leaves to be small. This is a reasonable assumption, because we frequently observed slight wilting in the afternoons in *S. sericea* and *G. speciosa*. For example, if leaf ψ_{π} were -2.0 M Pa and leaf turgor pressure had declined to 0.3 M Pa, a shrubby plant could absorb water from a solution of ψ_{π} about -1.6 M Pa, more saline than most of the groundwaters measured. The presence of living roots at 1- to 1.5-m depths in most of the soil pits, some actually in water, shows that the groundwaters are certainly an available source of moisture for the plants. Indeed, during the dry season, water in the upper soil layers was obviously low at many sites. The higher Na contents of the greenhouse-grown *S. sericea* and *T. argentea* leaves than in field-collected material (Table 4) may be a further indication that the plants in the field are tapping groundwaters less saline than the salinized culture solutions.

These experiments show that seedlings of several species that occur on or near atoll beaches can endure exposure of the roots to osmotic concentrations equivalent to that of seawater, but do not grow much at such high salinity. Nonetheless these species often grow well in nature close to both the lagoon and seaward shores. Groundwaters in such locations are usually considerably less saline than seawater (Table 3), and the plants have extensive root systems penetrating to appreciable depths. These beach species can tolerate the salinity of most of the groundwaters and probably absorb much water from them, especially during the dry season.

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