

- STOCKER, O. 1960. Physiological and morphological changes in plants due to water deficiency. Pp. 63-104 in *Arid zone research*. XV. Plant-water relationships in arid and semi-arid conditions. UNESCO, Paris.
- VOGEL, S. 1970. Convective cooling at low airspeeds and the shapes of broad leaves. *J. Expt. Bot.* 21:91-101.
- WEAVER, D. W. 1969. Geology of the Northern Channel Islands. Amer. Assoc. Petroleum Geologists Soc. Econ. Paleontologists and Mineralogists (Pacific Section).
- WERGER, M. J. A., and G. A. ELLENBROCK. 1978. Leaf size and leaf consistence of a riverine forest vegetation along a climatic gradient. *Oecologia* 34:297-308.

Zonation of Coastal Plant Species and their Correlation with Salt Levels in the Soil

Nancy J. Vivrette¹

Botany Department, University of California,
Berkeley, California 94720

INTRODUCTION

This study was an investigation of the processes leading to the establishment of a coastal vegetation pattern, and the factors which maintain or change a vegetation pattern over time. The simplest explanation for a zoned or banded distribution of species is the presence of an environmental gradient coupled with differential tolerance of the species to environmental factors in the gradient. An example is the banding of species at a right angle to onshore winds in exposed coastal regions. Onshore winds carry high levels of salt aerosol, and the strongest wind occurs closest to the ocean. This results in the deposition of high levels of salt aerosol and, consequently, leads to higher salt levels in the soil closest to the ocean. As the wind moves inland it carries less aerosol and the soil is less saline. Along this gradient the more salt-tolerant plant species would be expected in the regions close to the coast and less salt-tolerant forms would be expected in the interior soils.

Support for this hypothesis has been given in some preliminary work by Barbour *et al.* (1973), who found a strong association between species distributions and soil salinities. Lugo and Snedaker (1974) tested the hypothesis that soil salinities were responsible for zonation in mangrove regions and found that differential salt tolerance could not account for the zonation of species in mangroves. The present study was designed to test the hypothesis that differential salt tolerance can account for species distribution along a salt gradient on coastal headlands. To do this, I describe the zoned pattern along coastal headlands, examine the correlation of the distribution pattern with soil salinities, test salinity tolerances of the species involved in the pattern, and test these correlations with field manipulations.

DESCRIPTION OF THE STUDY SITE

The study was conducted on Fraser Point, the extreme western (and windward) end of Santa Cruz Island, 35 km off the coast of Santa Barbara, California. The study site was on the coastal headland 20 m above sea level, bounded on three sides by cliffs. The substrate is rocky with a shallow layer of soil varying in texture from clay to sand. Vegetation is a low-lying assemblage of annuals and perennials that appears to be sorted into bands paralleling the edge of the sea bluff.

The zonation of vegetation was quantified using two continuous line transects running from the seaward cliff (west) to the interior (east). Species were recorded at 10-cm intervals for 240 m (Fig. 1). A marked zonation is apparent for the three annual species. *Mesembryanthemum crystallinum* L. is found along the seaward edge of the headland, *Hordeum leporinum* Link. is found in the central portion of the headland, and *Lasthenia chrysostoma* (F. and M.) Greene is found in the most interior portion. The perennial species do not show as striking a zonation pattern. *Frankenia grandiflora* Cham. and Schlecht. is associated with the *Mesembryanthemum* and *Hordeum* zones. *Atriplex semibaccata* R. Br. is found in greatest abundance in the *Hordeum* zone. *Atriplex californica* Moq. in DC. and *Salicornia subterminalis* Parish. are

¹Present address: Ransom Seed Laboratory, 747 Knapp Dr., Santa Barbara, California 93108.

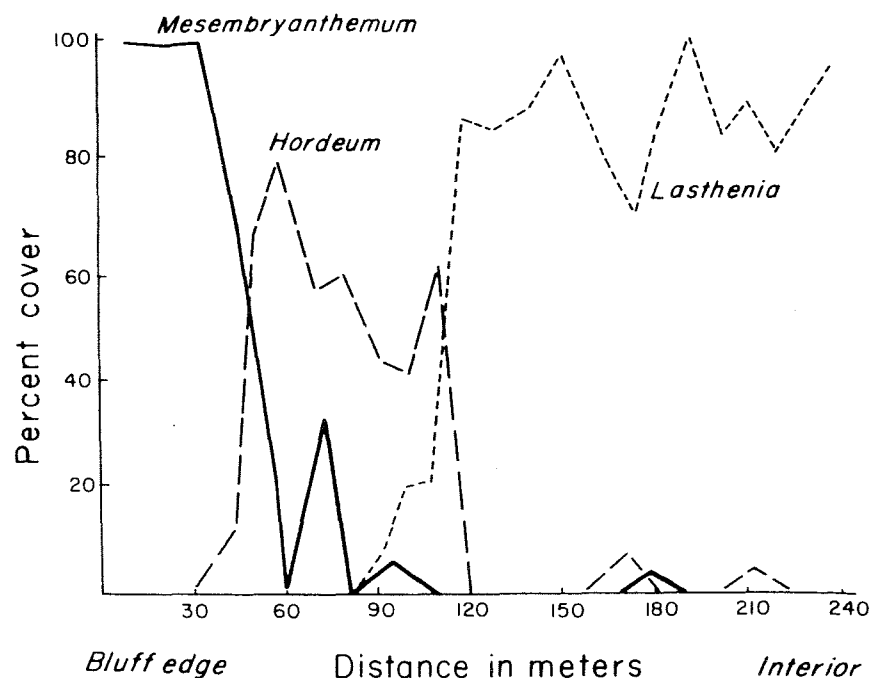


FIGURE 1. Distribution of annual species from the seaward edge of the bluff to the interior. Values are average per cent cover over 10-meter intervals.

associated with the *Lasthenia* zone. The annual species were chosen for further study since they must re-establish the banded pattern each season and are therefore suitable for experimental manipulation.

CORRELATION OF VEGETATION DISTRIBUTION WITH SOIL SALT LEVELS

If the zonation of the annual species is the result of differential salt deposition and accumulation from salt aerosol, there should be a correlation between the level of salt in the soil and the pattern of zonation. The expected salt levels would be high at the seaward edge and lower further inland. To measure salt levels in the soil, 100-g soil samples were taken to a depth of 2 cm at 10-m intervals from the seaward edge of the headland to the interior for 240 m. The soil was sifted to remove rocks, pulverized with a mortar and pestle, and then sifted again through a 0.01-mm pore soil screen. Two 20-g subsamples from each samples were shaken with 80 g of water for two hours. The extract was filtered through Whatman #1 filter paper and analyzed for total salts using freezing point depression with an Advanced Instruments Osmometer. Total salts are measured as milliosmols (mOsm) in the extract. Using this method, a one-molal solution of a nondissociating compound will have one osmol (Osm) activity or 1,000 milliosmols. Sea water is approximately 900 mOsm.

There is no correlation between soil salt levels and distance from the seaward edge of the bluff (Fig. 2). Up to a one hundredfold difference in soil salinity was exhibited at the same distance from the seaward edge of the transect.

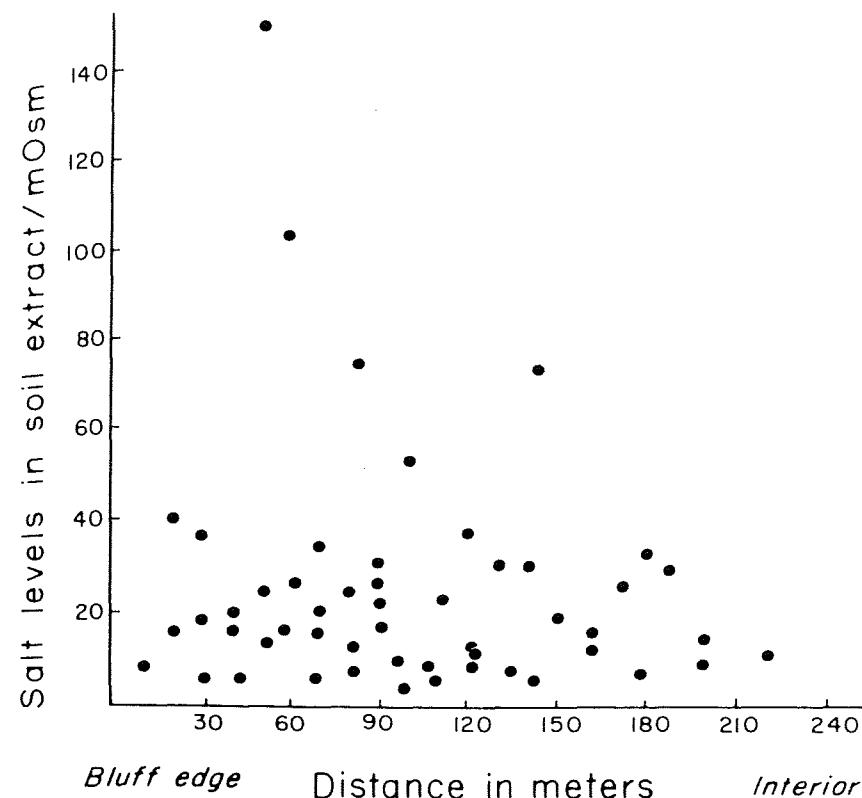


FIGURE 2. Soil salinity as a function of distance from the seaward edge of the bluff to the interior.

Mesembryanthemum crystallinum is known to greatly influence salinities in the surrounding soil (Vivrette and Muller 1977). To control for this influence, the soil samples were separated according to the species occupying them. The same gradient of high salinities on the seaward edge and lower salinities toward the interior would be expected for the soil beneath each species. Again, no decreasing gradient was observed (Fig. 3). On the other hand, there was a close association between the soil salinities and particular species. The variation in soil salinity found beneath the same species was much smaller than the variation in soil salinity between species. The large variation in soil salinity shown in Figure 3 can be explained in large part by the differential salinity associated with the various species.

I propose that the close association between soil salinity and the species occupying the soil is caused by species-specific mechanisms of salt uptake and release. Since the soil salinities are similar beneath a given species whether it is growing at the seaward edge or interior portion of the headland, differential salt recycling by the plants appears to have a greater influence on the soil salt levels than salt deposition from aerosol. If the soil salinities found beneath each species are used to plot their placement along a gradient of high to low salinities, the resultant species distribution appears as in Figure 4. However, this pattern does not match the actual distribution

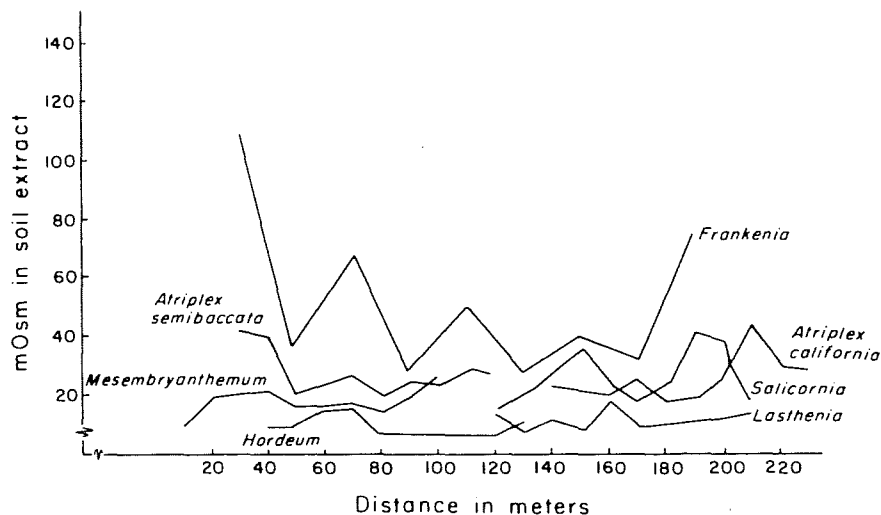


FIGURE 3. Soil salinity as a function of species from the seaward edge of the bluff to the interior.

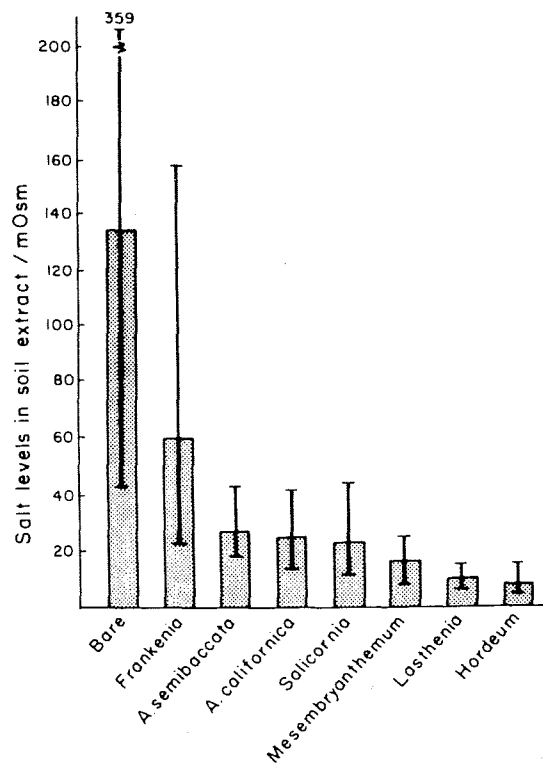


FIGURE 4. Salt levels in soils from bare ground and from beneath plant species ranked in order of average soil salinity (e.g., highest average salt concentrations were found in soil beneath *Frankenia*, lowest beneath *Hordeum*). The order of species is therefore the distribution of species expected on the basis of soil salinities alone.

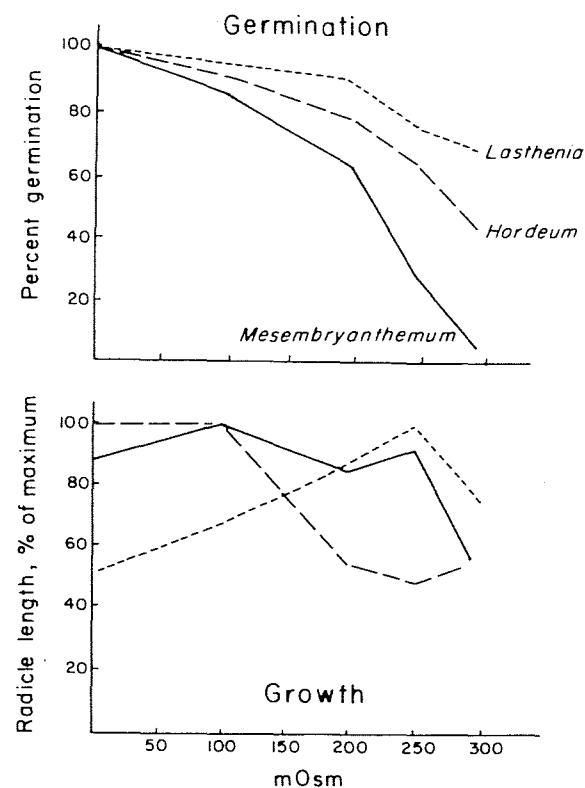


FIGURE 5. Germination and growth of the annual species under various levels of salinity. Each value is the average of 90 seeds.

of species observed on the headland. From this figure it is clear that the annual species have lower salinities than the perennials; the highest salinities are found beneath *Frankenia* and in bare soil.

SALT TOLERANCE OF THE ANNUAL SPECIES

It is possible that the differences in salinity associated with each species could be responsible for the distribution of the other species. Such a case has been described for *Mesembryanthemum crystallinum* (Vivrette and Muller 1977). Salt tolerances of the three annual species were tested using germinating seeds. Ten seeds were placed on a substrate of sand in each of a series of Petri dishes. The dishes were watered with either distilled water, 100-mOsm, 200-mOsm, 250-mOsm, or 300-mOsm NaCl solutions, representing the range of salinities observed in the soil extracts in the previous experiments. Each test consisted of three dishes, and the tests were repeated three times, for a total of 90 seeds per treatment.

Percent germination and radicle elongation were measured (Fig. 5). The salt tolerances of all three annual species are very broad. *Lasthenia* had the highest tolerance for salinity, although it is found on the interior portion of the headland. The distribution of species along the headland cannot be accounted for by differential salt tolerance. The close association between soil salinities and the species occupying the soil is more a function of the plants producing the salinity than the plants responding to a gradient of salinity.

TABLE 1. Seedling establishment in *Hordeum* and *Lasthenia* zones. Each value is the average of four subsamples.

	Average number of seedlings (range)		Seed added and clipped
	Control	Seed added	
<i>Hordeum</i> zone			
<i>Mesembryanthemum</i>	0	0.5 (0-2)	2 (0-3)
<i>Hordeum</i>	49 (40-62)	56 (33-80)	69 (52-94)
<i>Lasthenia</i>	0	8 (0-31)	47 (8-78)
Other	0	0	0
<i>Lasthenia</i> zone			
<i>Mesembryanthemum</i>	0	2 (0-12)	7 (0-19)
<i>Hordeum</i>	0	2 (0-5)	3 (0-10)
<i>Lasthenia</i>	145 (72-250)	159 (54-238)	207 (134-292)
Other	4 (0-10)	2 (0-5)	3 (0-10)

BIOTIC INTERACTIONS

The species distribution pattern seems to have no simple explanation. The sharp drop in occurrence of one annual species in the presence of another suggests that biotic interactions may play a role in zonation. If this hypothesis is correct, then each of the species should be able to grow in the other zones in the absence of the dominant species. To test this hypothesis, reciprocal transplants were performed. One control and two treatments were applied in the experiment, and each had two replicates. The control in each zone was an untreated 1-m² plot. The first treatment was a 1-m² plot with seed of the other zones added. The second treatment was a plot in which the dominant species was clipped to the ground, the clippings removed, and seeds of the other species added. A similar experiment had already been performed for the *Mesembryanthemum* zone (Vivrette and Muller 1977), so only the *Hordeum* and *Lasthenia* zones were included in the present experiment. The treatment was performed during the dry summer season when only the dead remains of plants were present. The results were recorded the following spring, after the winter rains had produced a new crop of plants. Seedling counts were taken in 10-cm diameter subsamples at the four cardinal compass points within the experimental plots.

The results of the transplant experiments are given in Table 1. When no manipulation is made, each zone is maintained by the dominant species. *Hordeum* grew in the zone it had occupied the year before; *Lasthenia* did the same within its zone. This persistent dominance was overcome slightly with the addition of seed from the other zones. Seed dispersal is apparently part of the explanation for the maintenance of the pattern over time. The clipped plots with seed added showed the strongest increase in seedling establishment of the other species. In the *Hordeum* clipped plot *Lasthenia* greatly increased in number. In the *Lasthenia* zone the increase in numbers of *Hordeum* and *Mesembryanthemum* seedlings was not as great, but the seedlings were large and occupied up to a quarter of the plot. This increase in the number and size of plants from the other zones following removal of the biomass of the dominant species suggests a strong biotic control of the pattern observed. These findings were reinforced during the drought year of 1976-1977. The *Lasthenia* zone was only sparsely occupied and the biomass was greatly reduced. Under these conditions, *Mesembryanthemum* invaded the *Lasthenia*

thenia zone and now shares dominance with the *Lasthenia*. Experiments are in progress to characterize the nature of this biotic interaction.

CONCLUSIONS

Differential salt tolerance of species along a salt gradient cannot account for the banded pattern observed for the annuals on Fraser Point, Santa Cruz Island. The soil salt levels remained in the range characteristic for each species regardless of the distance the species was found from the edge of the bluff. This close association between each species and the soil salt levels is due to characteristic mechanisms of salt recycling by the species growing in the soil, rather than to the species responding to a salt gradient.

ACKNOWLEDGMENTS

I wish to thank Mary Lu Arpaia, Linda Fox, J. Robert Haller, Deborah Mangis, and Robert Sheets for field and laboratory assistance. I also thank Dr. Carey Stanton and the Santa Cruz Island Co., and the staff of the University of California Santa Cruz Island Reserve. Illustrations are by Charlotte Mentges.

REFERENCES

- BARBOUR, M. G., R. B. CRAIG, F. R. DRYSDALE, and M. T. GHISELIN. 1973. Coastal ecology. Bodega Head. University of California Press, Berkeley, Calif.
- LUGO, A. E., and S. C. SNEDAKER. 1974. The ecology of mangroves. Pp. 39-64 in R. F. Johnston, ed., Annual review of ecology and systematics, v.5. Ann. Reviews, Inc., Palo Alto, Calif.
- VIVRETTE, N. J., and C. H. MULLER. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. Ecol. Monogr. 47:301-318.