flare brightness—perhaps the most important single parameter. Plans are being made for photometric standardization of the films and for measurement with a contour densitometer similar to that described by Babcock (*3*). A "breadboard" of the densitometer is approaching the try-out stage, but the work goes slowly because of the pressure of other commitments. We do not expect to have any real brightness measurements, therefore, for some months.

The 504 flares observed so far already constitute a small but homogeneous statistical sample, and several interesting discoveries have emerged from preliminary studies. Space is lacking to discuss them here, but they do justify our efforts in building the flare recorder, and our hope that we may see eventually a whole chain of these instruments stretched around the world to keep a record of all the flares on the visible hemisphere of the sun.

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Technical Papers

Salt Hypertrophy in Succulent Dune Plants

Steve G. Boyce

Division of Biological Sciences, North Carolina State College of Agriculture and Engineering, Raleigh

Early German investigators (*1*) were the first to recognize that "many plants produce on the shore more succulent leaves than they do when grown inland, while the leaves of *Salsola Kali, Halogeton sativus,* and others, are thinner when the plants are grown upon a soil without salt, than is usual on plants growing on saline ground." Succulence of plants growing on saline soils has been attributed to the absorption of salts by the roots and their subsequent concentration in the mesophyll tissue, resulting in salt-induced hypertrophy (*2–4*). However, no previous investigation has satisfactorily explained the type of succulence found in dune plants near the strand.

Iva imbricata Walt. exhibits the typical succulent nature of plants found on coastal dunes. The leaves on the windward side of the plants toward the ocean are thick and succulent, whereas those on the leeward side of the same plant are thin, less succulent, and frequently coriaceous. The margins of leaves turned toward the ocean are thicker and more succulent than the leeward margin of the same leaves, and the tips of the leaves are more fleshy than the bases.

Succulence in dune plants has been considered to be a consequence of the more xeric habitat (*5*), of excessive transpiration (*6*), and of the salinity of the substratum (*7, 8*). Salinity of the substratum can be disregarded, since it has been shown that dune sands contain very little soluble salts (*9*). However, none of these proposals explains why leaves of an individual plant exhibit different degrees of succulence.

Previous studies on the coast have shown that droplets of sea water are ejected into the air by the bursting bubbles of the ocean; that these particles, concentrated by evaporation, are transported inland by winds and deposited on the coastal vegetation; and that the resultant killing of leaves and twigs by this concentration of salt is responsible for the zonation and spray form of the plants (*10–13*).

During a study of the coastal vegetation of Brunswick County, N. C., the author investigated the relation of salt spray to succulence. Succulent and nonsucculent leaves on the same plant of *Iva* were collected, the surface washed in distilled water, and 5 disks of equal area were punched from each leaf with a small rubber stopper punch. Each group of 5 disks was then macerated and titrated with $AgNO_3$ for halides. The 5 disks of the succulent leaves contained an average of 16.8 mg of Cl compared with an average of 4.5 mg of Cl in the disks of the nonsucculent leaves. (The titration data are expressed in terms of mg of Cl since the other halides make up such a small part of the salts of the ocean.)

The quantity of salt deposited on the different leaves was estimated with the use of oiled glass slides (*14*). Slides were exposed for 30 sec at different positions in an *Iva* shrub located on the top of the foredunes. The number and diameter of the deposited droplets were immediately determined with a microscope, which was protected from spray by a plastic cover. The average wind velocity from the ocean was 31 km/hr. The slides exposed on the windward side of the shrub caught an average of 1,900 droplets/cm²/min, which averaged 51 μ in diameter. Slides exposed on the leeward side caught an average of 490 droplets/cm²/min, which averaged 22 μ in diameter. Slides exposed at different positions in the shrub caught an intermediate concentration of droplets, both in number and in diameter. Obviously, the leaves on the windward side of the plant are receiving a much higher concentration of salt than the leaves on the leeward side.

Anatomical studies of the succulent and nonsucculent leaves showed a striking difference in the size of the cells. Table 1 shows this difference in *Iva*. The nonchlorenchymous parenchyma showed the greatest swelling, and the chlorenchyma and epidermal cells showed an intermediate swelling. The stomata showed no swelling at all, and about 60% of them were crushed shut by the swollen epidermal cells. There was no evidence of an increase in the number of cells. The swelling was due entirely to the enlargement of already existing cells.

TABLE 1

COMPARISON OF THE SIZE OF CELLS IN SUCCULENT AND NONSUCCULENT LEAVES OF *Iva*

Tissue	Succulent leaves (μ)	Nonsucculent leaves (μ)
Nonchlorenchymous parenchyma	102 × 262	68 × 82
Chlorenchyma	20 × 150	17 × 65
Epidermis	27 × 65	23 × 34
Stomata	24 × 40	27 × 34

Salt hypertrophy of *Iva* has been reproduced in the laboratory by placing strips of nonsucculent leaves in increasing concentrations of sea water. The concentration of the solution was increased until the cells showed incipient plasmolysis. As the cells regained turgidity, the concentration of the salt solution was increased. After repeating this procedure several times the cells had about doubled in size at the end of 72 hr. It was found that the cells swell more quickly when the sea-water solution is alternated with tap water. At present, no method has been found to induce the cells to return to normal size, though they can be plasmolyzed in saturated salt solutions.

Further investigation has shown that practically all dune species exposed to high concentrations of salt exhibit salt hypertrophy. The change in thickness of the leaves and the relative concentration of salts expressed in mg of Cl of a few representative species is given in Table 2. The succulent and nonsucculent leaves were removed from the same plant at positions of equal light intensity. All the species show the same type of swelling as *Iva*, the nonchlorenchymous parenchyma showing the greatest enlargement, with the chlorenchyma and epidermis showing slight enlargement, and the stomata exhibiting no enlargement. Salt hypertrophy has not been found in the grass species represented by *Uniola, Chloris, Spartina, Triplasis,* and *Andropogon*. However, titration of the leaves of these species showed they contained relatively low concentrations of salt.

Succulence in dune plants, then, is apparently due to the deposition of salt spray on the leaves and branches, resulting in salt-induced hypertrophy of local tissues. Hypertrophy seems to occur only on the leaves and branches on which the salt is deposited. Titrations indicate that after entrance the salts are translocated first to the tips of the leaves, inducing hypertrophy first in the tips, then along the margins, and eventually the entire leaf. There is no indication of the salts being translocated throughout the plant in sufficient concentrations to induce hypertrophy in protected leaves.

Salt hypertrophy is not confined to meristematic tissues but also occurs in leaves that become exposed to salt spray after maturity. Consequently, succulence does not seem to be associated with an influence of salts on the meristematic activities of cells but seems to be the result of salt accumulation in the vacuoles causing an increase in turgor pressure and resulting in the expansion of the cell walls. The primitive nonchlorenchymous parenchyma swell more than the more specialized chlorenchyma and stomatal cells.

TABLE 2

AVERAGE THICKNESS AND RELATIVE CONCENTRATION OF SALT OF A FEW DUNE SPECIES EXHIBITING SALT HYPERTROPHY. SUCCULENT AND NONSUCCULENT LEAVES WERE REMOVED FROM THE SAME PLANT

Species	Succulent leaves		Nonsucculent leaves	
	Thickness (μ)	mg Cl	Thickness (μ)	mg Cl
Iva imbricata Walt.	3,000	16.80	600	4.50
Atriplex arenaria Nutt.	656	5.40	335	1.05
Lippia nodiflora (L) Michx.	1,900	4.50	656	0.65
Physalis maritima M. A. Curtis	1,200	3.80	248	0.70
Chenopodium Berlandieri Moq.	1,230	3.80	349	0.65
Croton punctatus Jacq.	729	2.60	349	0.80
Ilex vomitoria Ait.	539	1.80	262	0.50
Baccharis halimifolia L.	656	1.60	286	0.45
Quercus virginiana Mill.	102	0.95	68	0.15

Salt hypertrophy is also correlated with the tolerance of species to high salt deposition. The species most tolerant to high salt concentrations have the greatest mass of nonchlorenchymous parenchyma and swell the most when subjected to high concentrations of salt, whereas the less tolerant species have little nonchlorenchymous parenchyma and swell the least. A more complete report of hypertrophy and injury of dune plants induced by high concentrations of salt will be published later.

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