Atmospheric Water Uptake by an Atacama Desert Shrub

Abstract. Nolana mollis, *a succulent-leaved shrub of the extreme coastal desert of Chile, has the capacity to condense water on its leaves out of unsaturated atmospheres. Metabolic energy would have to be expended to move this water either from the leaf surface directly to the mesophyll or, when dripped to the soil, from there into the roots. Because of the unusual aridity of its habitat and of the utilization of water-use-efficient metabolism by* Nolana, *at least during certain periods, such an energy expenditure could be effective.*

The sparse coastal vegetation of the Atacama Desert of northern Chile is composed primarily of succulents and succulent-leaved shrubs (*1*). In the region between 26°30′S and 25°15′S, where annual precipitation is less than 25 mm, one of the principal dominant shrubs is *Nolana mollis* (Phil) Johnston. Its succulent leaves are always wet to the touch and often covered with visible water droplets, while adjacent plants of other species are normally dry.

We investigated the source of this leaf moisture on shrubs growing at Pan de Azucar, a valley draining into the Pacific Ocean north of Chañaral at 26°15′S. *Nolana* is found abundantly in this valley from the immediate coast to some 20 km to the east, near the crest of the first coastal range. Beyond this boundary there is no plant life until the foothills of the Andes.

The climate of Pan de Azucar is controlled by the cold water offshore. High fog, which breaks in the afternoon, is a characteristic feature of the area. The weather observed during separate days, one clear day and one characterized by high fog, typifies the climatic features of the region (Fig. 1). Air temperatures are moderate and saturation deficits generally low. The dew point is fairly constant at about 10°C, since it is controlled primarily by the ocean temperature. Relative humidity seldom exceeds 80 percent, even at night, since the fog does not generally reach ground level. Nighttime dew formation on the soil surface occurs irregularly, and rainfall is a rare event. It is thus apparent that the normal source of leaf surface moisture on *Nolana* cannot be fog, dew, or precipitation.

The surfaces of the leaves of *Nolana* are covered with salt glands (Fig. 2). These salt glands occur in depressions on the leaf surface and are connected to each other by a series of troughs or canals. Salt glands have not previously been reported in this family (Nolanaceae) (*2*).

The gland-produced salts that cover the leaves of *Nolana* are effective in condensing moisture from unsaturated atmospheres. Blotter paper saturated with the liquid collected from the leaf surfaces was nearly as effective in accumulating moisture overnight as blotters soaked in saturated NaCl. Blotters soaked in the surface liquid from *Nolana* leaves and left suspended vertically in the air overnight accumulated 13 μl cm^{-2}. Blotters impregnated with saturated NaCl accumulated 14.5 μl cm^{-2}; blotters with 1*N* NaCl, 3 μl cm^{-2}; and untreated control blotters, 0 μl cm^{-2}. Water collected directly from leaves in the morning with a micropipette amounted to 9.5 μl per centimeter of surface after a night the highest humidity was 82 percent. Leaves that had been rinsed well with distilled water the previous afternoon, on the other hand, did not accumulate surface water.

Leaves of *Nolana* have high total concentrations of chloride (12 percent, dry mass) and sodium (6 percent) as well as calcium (3 percent) and magnesium (2 percent). More than half the electrolytic activity of the liquid covering the leaves of *Nolana* can be attributed to NaCl (*3*).

Simulations utilizing the energy budget equation (*4*) and the characteristics of the salts found on the surfaces of the leaves (20.45 μmole equivalents of NaCl per square centimeter) allowed calculation of the amount of water that would accumulate on leaves through dewfall or direct atmospheric transfer for a series of atmospheric relative humidities (Fig. 3). At humidities above 85 percent, substantial amounts of water can be accumulated on leaves within a single hour.

Table 1. Atmospheric leaf water accumulation at various relative humidities and energy requirements for water transport to mesophyll.

Relative humidity	Water accumulated* (μl cm^{-2} hour^{-1})	Energy	
		Required† (mJ μl^{-1} cm^{-2} hour^{-1})	Available from respiration‡ (mJ cm^{-2} hour^{-1})
0.99	20	1.5	35
0.95	13	2.7	35
0.90	6	7.0	35
0.85	3	14.1	35
0.80	2	20.2	35

*Based on computer simulations; see legend to Fig. 3. †Calculated from work/mole = *RT* ln (*e*, leaf surface)/(*e*, leaf interior). The leaf surface vapor pressure was calculated from a surface salt concentration of 20.45 μmole of NaCl per square centimeter and the water volumes were obtained from approximations of Raoult's law. The tissue water potential was set at −1.5 MPa or relative vapor pressure of 0.99. This is the leaf water potential measured at dawn with thermocouple psychrometers. ‡Calculated on the basis of a measured (as CO_2) respiration rate at 20°C of 0.149 μmole cm^{-2} hour^{-1}, and if 50 percent of the energy released is available for work. Respiration rates were measured on plants grown at a coastal habitat in northern California (Bodega Head) with a thermal regime similar to that at Pan de Azucar. Measurements were made with an infrared gas analysis system (*13*).

An important question is whether the water that is accumulated on the leaves of *Nolana* is available to the plant for metabolism. We consider two possible pathways for water movement, one from the leaf surface directly into the leaf mesophyll, and the other from the leaf surface to the soil surface and hence into the roots. Both of these pathways require an energy expenditure.

Since the leaves are covered with salt, the water on their surfaces is at a high osmotic concentration. The concentration decreases as water accumulates. With an accumulation on the leaf surface of 20 μl cm^{-2}, which would occur after 1 hour at a humidity of 99 percent, 1.5 mJ of metabolic energy would be required to move 1 μl cm^{-2} hour^{-1} (Table 1). This is only a fraction of the energy available from respiration. At lower humidities with lower water accumulations and higher osmotic concentrations, the energy expenditure for water uptake would become quite high. Since the major nonrestrictive pathway from the leaf surface to the mesophyll would be through the stomates, and since the stomates are positioned above the leaf surface, this pathway is unlikely.

Water accumulated on the leaves at night often drips off and wets the soil surface. This water contains dissolved salts, and hence the surface soil has a high osmotic concentration. The upper centimeter of soil had an osmotic concentration of −4.5 MPa at water saturation (*5*), and yet live roots were observed. At midday, plants of *Nolana* had a leaf water potential of −2.5 MPa. Under these conditions, at 20°C, 2.01 mJ of energy would be required in order to take up 1 μl hour^{-1} from a saturated soil. Thus, as much as 16.6 μl cm^{-2} hour^{-1} could be taken up if all the respiration energy were used. Under well-watered conditions, *Nolana* would lose on a sunny day about 13 μl cm^{-2} hour^{-1} through transpiration, and on a foggy day about 7 μl cm^{-2} hour^{-1} (*6*). Thus, all the water requirements of *Nolana* could be met through energy expenditure from respiration. However, obviously not all respiration energy can be allocated to water uptake. Water uptake by roots against energy gradients has been implied by the work of others (*7*).

The water loss rates of *Nolana* are probably considerably less than those indicated for the well-watered plants, since *Nolana* has a carbon isotope ratio of −20.1 parts per thousand (*8*), indicating that it may fix at least some of its carbon through crassulacean acid metabolism (CAM) (*9*) and thus has the potential of fixing light energy during the day with stomata closed. With the much greater water-use efficiency of CAM photosynthesis, *Nolana* could benefit from the relatively small amounts of water obtained by atmospheric condensation.

Certain plants can take up water from saturated atmospheres (*10*), but water uptake from unsaturated atmospheres has been documented primarily in insects and arachnids (*11*). In mites (*12*), as with *Nolana*, hygroscopic salts, produced in salt glands, are the means by which water is absorbed. Metabolic energy must be expended to move the water that is captured by the leaves of *Nolana* into the plant by any given pathway.

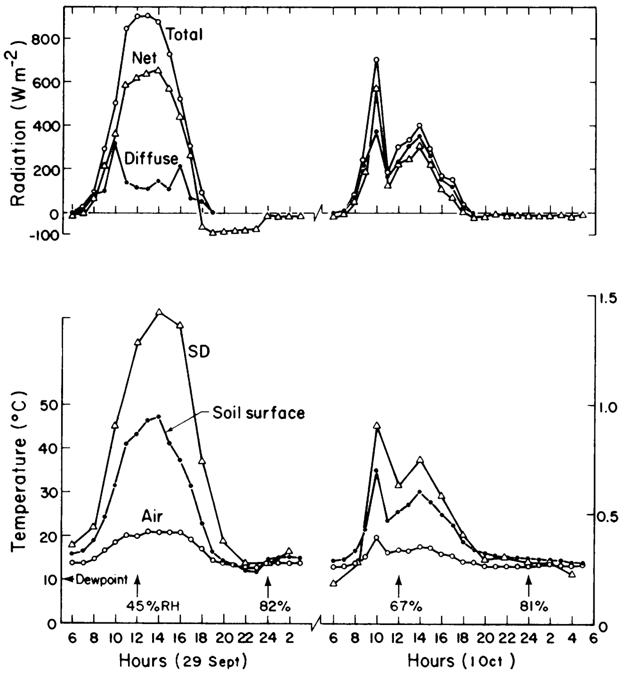

Fig. 1. Microclimatic characteristics of a clear day (29 September) and of a foggy day (1 October) at Pan de Azucar, Chile. Air temperature and humidity measurements were taken at a height of 0.5 m.

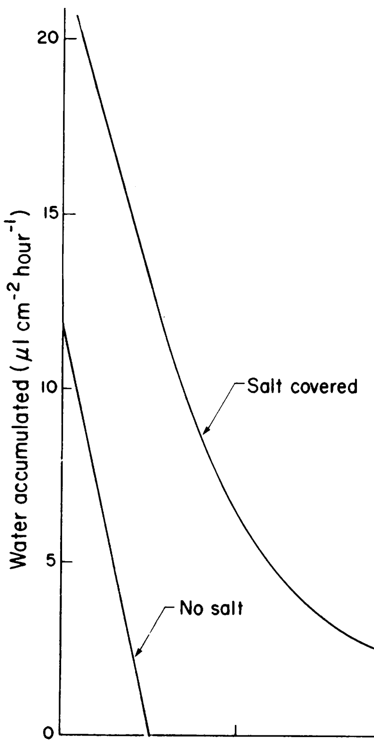

Fig. 2 (left). Scanning electron micrograph of leaf surface of *Nolana mollis*, showing salt gland in a depression. Fig. 3 (right). Simulations of hourly water uptake by leaves of *Nolana* at different relative humidities. The environmental conditions used for the energy budget simulations were typical of nighttime conditions. Leaf resistance, 99 sec cm^{-1}; wind speed, 50 cm sec^{-1}; downward infrared radiation, 279 W m^{-2}; and air and soil temperatures, 15°C. The water uptake under natural or "no salt" conditions is the result of dew formation. The salt concentration of the leaf was set as saturated sodium chloride (osmotic potential about −40 MPa). Simulations were done on a minute-by-minute basis and totalized for an hour.

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6. Transpiration rates were measured on plants growing at a coastal site at Bodega Bay, Calif., and on plants grown in a growth chamber (20° to 15°C) at Pan de Azucar on a clear day and on a foggy day.
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13. A Peltier-based cuvette was used for holding attached samples at a controlled temperature, CO_2 concentration, and humidity. Photosynthesis, respiration, and transpiration can be measured with this system (C. Field, unpublished).
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