

The Energy Balance of Leaves of the Evergreen Desert Shrub *Atriplex hymenelytra*

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Summary. *Atriplex hymenelytra* is an evergreen shrub distributed in the hot deserts of parts of Mexico and the southwestern United States. The leaves of the species have a number of characteristics that are adaptive in a hot, dry environment, some of which change seasonally. Steeply angled leaves reduce midday solar interception, yet result in relatively high interception when solar angles are low and vapor pressure deficits are at a minimum. The leaves substantially reduce their absorptance of incident radiation during the hot periods of the year by changing their moisture and hence dissolved salt contents. At these times the light intensity required for saturation of photosynthesis is low and a reduction in the radiation absorbed by the leaves therefore results in a greater water-use efficiency.

Introduction

Desert environments are characterized by high incoming solar radiation and limited moisture. Since the transfer of energy from a leaf through transpiration (latent heat) may often be greatly reduced during drought periods, it can be presumed that the energy transfer characteristics of the leaves of evergreen desert plants differ substantially from leaves of more mesophytic plants. There are indeed indications that the leaves of desert plants absorb relatively less radiation than plants in moister habitats (Billings and Morris, 1951), and that they have high coefficients of convection due to their generally small size (Gates et al., 1968).

Even the most severe desert habitat has at least some periods when moisture is relatively abundant. During these periods plants having relatively large leaves that absorb the incident radiation with high efficiency would be most adaptive. Leaf factors that maximize the absorption of radiant energy, such as horizontal orientation and low reflectance, characterize many drought-evading annuals and certain drought deciduous perennials.

What we ask is whether evergreen perennials, which maintain their leaves during drought as well as during moist periods, morphologically or physiologically adjust to these changing conditions, or whether they have evolved features that are an adaptive compromise between these environmental extremes. In this study we focus on the evergreen perennial shrub, *Atriplex hymenelytra*.

Materials and Methods

Atriplex hymenelytra is a long-lived desert shrub (Gulmon and Mooney, 1977) that is distributed in the hottest deserts of the United States and Mexico (Shreve and Wiggins, 1964). It is found on soils of moderate salinity (Hunt, 1966). These plants generally flower in the winter. Following anthesis a new crop of leaves is produced, at which time the previous year's leaves abscise. For a brief period both old and new leaves may be present.

Field studies were carried out on this species under both natural and irrigated conditions in its native habitat on the floor of Death Valley, California. Here mean annual rainfall is only 45 mm, and the mean daily maximum temperature varies from 18°C in the winter to a high of over 46°C in the summer. Some measurements were also made on transplanted plants grown at a cool coastal site at Bodega Head, California (Mooney et al., 1974).

Leaf absorptance, reflectance, and transmittance were measured on leaves using an Ulbricht integrating sphere (Rabideau et al., 1946) in monochromatic light as well as in broadband radiation (400–2000 nm). Seasonal changes in reflectance, presented here, were determined at 550 nm only. Measurements were made either at the field site or on fully expanded leaves that were collected at dawn and transported to the laboratory in moisture-proof containers on ice. Samples collected at dawn were also used for determinations of leaf moisture content, leaf size, and leaf specific weight. In most cases the values given represent means of five determinations.

Leaf anatomical features were determined on field material fixed in formol-alcohol and subsequently embedded and sectioned in paraffin.

Leaf chloride content was measured on extracts of ground dried leaf material in 0.1 N HNO₃ that were titrated with silver nitrate, using an Orion chloride specific-ion electrode (La Croix et al., 1970). Plant water xylem potential was determined on twigs at dawn with a pressure bomb (Scholander et al., 1965).

The photosynthetic light response of intact leaves and their conductance to water vapor loss were measured at various seasons on in situ plants, utilizing a gas system and a mobile laboratory previously described (Björkman et al., 1973).

For certain measurements plants were grown from seed in phytocells at Stanford, California under natural sunlight with close control of temperature and humidity (Björkman et al., 1973). These plants were grown in perlite with numerous automatic daily irrigations with nutrient solution.

Results

Leaf Structure

The newly expanded winter leaves of *Atriplex* had a specific weight (dry wt/leaf area) of less than 8 mg cm⁻². The specific weight gradually increased to a high of 22 mg cm⁻² by autumn. There were no apparent changes in leaf structure during this transition (Fig. 1) other than a substantial increase in the size of all cells.

As is characteristic of C₄ plants, *Atriplex hymenelytra* has Kranz anatomy. Stomata occur on both sides of the leaf. Measurement of the angle and direction of 50 leaves on field plants gave a mean angle of 70° from the horizontal with random orientation in relation to azimuth.

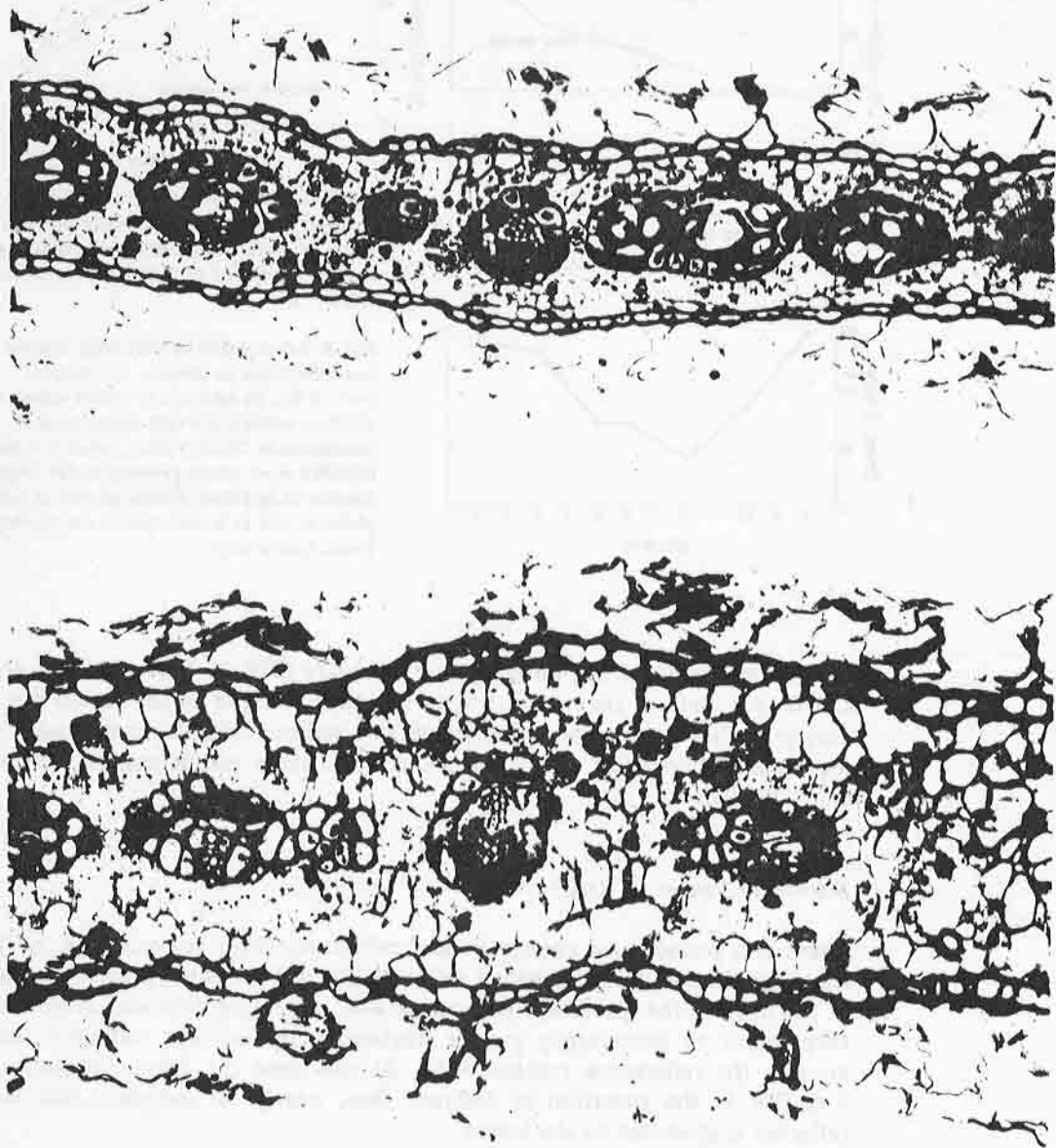


Fig. 1. Equal magnification cross sections of a newly expanded (*top*) and 1-year-old leaf (*bottom*) of *Atriplex hymenelytra*

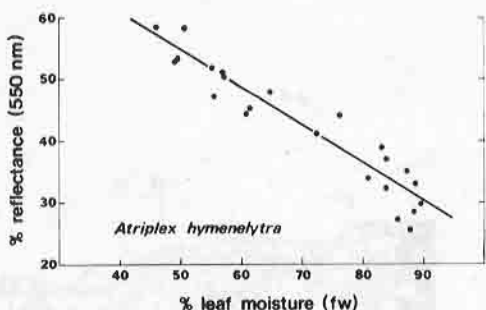
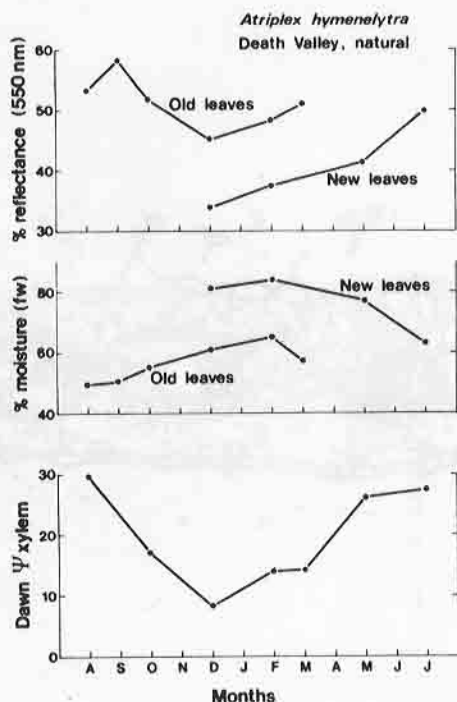


Fig. 2. Seasonal course of leaf reflectance, leaf moisture, and dawn xylem water potential of plants of *Atriplex hymenelytra* growing under natural conditions in Death Valley, California, during 1973–74

Fig. 3. Relationship of leaf water content and leaf reflectance in *Atriplex hymenelytra* ($r = -0.95$). In addition to plants sampled at different seasons growing under natural conditions in Death Valley, values are also included from plants growing under irrigated conditions in Death Valley, as well as from plants grown at a cool coastal site (Bodega Head, California)

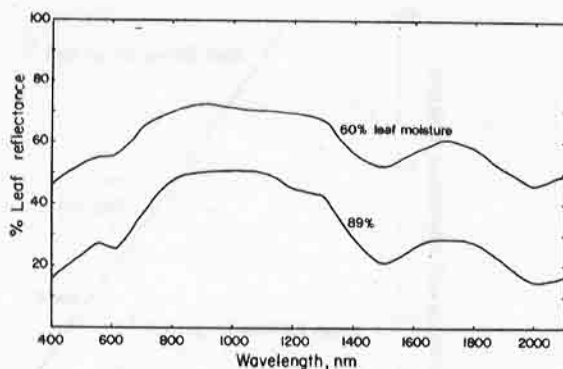
The leaf surfaces are covered with bladders (Fig. 1). The bladders are in a hydrated state in the young leaves, but they collapse as the leaves dry out during the hot summer period. Salts, mostly sodium chloride, contained within the bladders crystallize on the leaf's surface as these glands collapse (Mooney et al., 1974).

Seasonal Changes in Reflectance

There is a pronounced change in leaf reflectance with seasons (Fig. 2). New leaves produced during the winter reflect less than 35% of the incident radiation at 550 nm. As the leaves age coincident with increasing ambient temperatures, they reflect an increasingly greater fraction of the incident radiation. In the autumn the reflectance reaches 60%. At this time the leaves transmit only 1 to 2% of the radiation at 550 nm; thus, nearly all radiation that is not reflected is absorbed by the leaves.

During the winter, water stress is at a minimum (Fig. 2), and the leaves are fully hydrated. The new leaves that develop during this time have a higher water content than the previous year's leaves that still remain on the plant. Both new and old leaves show decreases in water content as the warm temperatures of summer appear.

Fig. 4. Reflectance of leaves of *Atriplex hymenelytra* with high and low water content (% fresh weight)



Leaf reflectance at 550 nm shows a strong inverse correlation with leaf water content (Fig. 3). The reflectance spectra of leaves of two different moisture contents (Fig. 4) indicates that the reflectance at 550 nm serves as a valid relative measure of the reflectance at all wavelengths in this 400 to 2000 nm range.

Leaf Rehydration

During the fall in Death Valley, leaves have a low water content and high reflectance, even when irrigated. At this time vapor pressure deficits are still high, and even irrigated plants do not fully rehydrate over the night, as indicated by dawn water potentials lower than -12 bar.

In a more direct experimental approach to determine the relation between leaf water content and reflectance, plants were covered with reflective plastic bags, and the changes in leaf water content and leaf reflectance were monitored. As shown in Figure 5, the reflectance of the leaves indeed decreased as the leaves gradually rehydrated. At the same time, the salt contained within the rehydrated leaves became diluted. Leaves at the beginning of the rehydration experiment contained $27 \text{ mg Cl}^- \text{ g H}_2\text{O}^{-1}$, and at the end only $16 \text{ mg Cl}^- \text{ g H}_2\text{O}^{-1}$. There was no change in the amount of chloride per dry weight of leaf (3.6%).

Co-Variance of Reflectance, Leaf Moisture, and Leaf-Salt Content

In the field, as the water content of the leaves decreases, the salt concentration increases. Thus, a high content of precipitated salts in the leaves, which is a likely source of a high reflectance, co-occurs with a low water content, which may also be expected to result in an increased reflectance. This makes it difficult to assess the effect of salt alone on leaf reflectance in field-grown material. In an attempt to separate the effect of salt and that of water content on leaf reflectance, plants were grown in phytocells under natural sunlight at 35°C day temperature and 23°C night temperature. One set of plants was irrigated

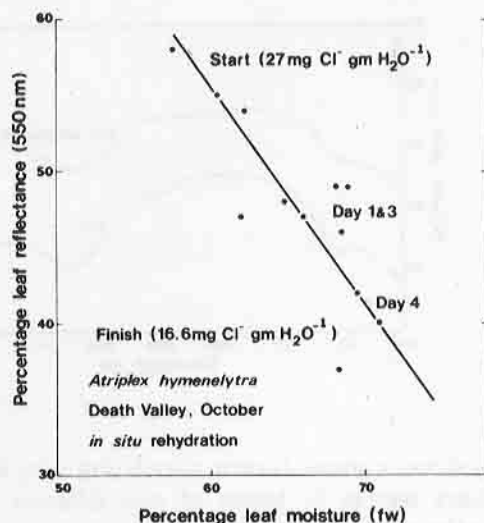


Fig. 5. Change in leaf reflectance and moisture content of an irrigated plant in Death Valley in which moisture loss was restricted by covering with plastic bags. Initially the leaves had 27 mg Cl/g H₂O. Due to dilution the salt content was reduced to 16.6 mg Cl/g H₂O by the fourth day of rehydration.

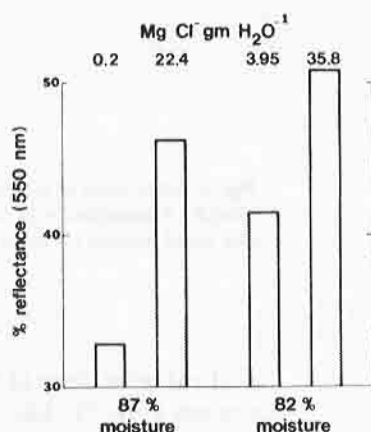


Fig. 6. Leaf reflectance vs. leaf moisture and leaf salt content. Plants were grown in controlled environments

with nutrient solution containing 1% NaCl, whereas another set received nutrient solution only. After one month under these conditions the leaf reflectance was measured. Irrigation was then stopped, and leaf reflectance was followed as the leaf water content of the leaves decreased.

At any given water content, plants with a higher salt content had a higher reflectance (Fig. 6). Conversely, among leaves having low salt content, those with a lower moisture content had a higher reflectivity. These measurements would indicate that changes in both salt content and water content are responsible for the changes in reflectivity.

Photosynthetic Light Saturation

In the native Death Valley habitat, maximum photosynthetic rates of *Atriplex hymenelytra* leaves are observed during early spring (Fig. 7). Light-saturated photosynthesis at this time exceeds 2 nmol cm⁻² s⁻¹. Stomatal conductance to water vapor transfer is high, about 0.9 cm s⁻¹. The light intensity required for saturation is 100 to 130 n einstein cm⁻² s⁻¹ (midday summer sunlight incident on a horizontal plane is about 200 n einstein cm⁻² s⁻¹). In late spring the photosynthetic rate declines, and during most of the year light saturation occurs at less than 75 n einstein cm⁻² s⁻¹. Therefore, at these times of the year reflectance will have little effect on photosynthesis at high light intensities. During the period of greatest drought stress (October) the photosynthetic rate

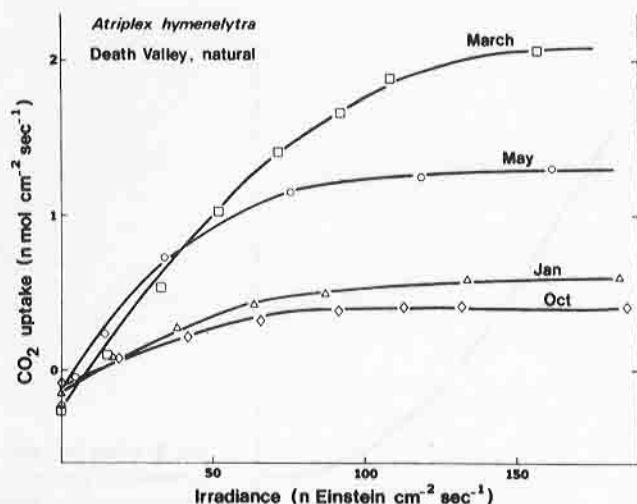


Fig. 7. Photosynthetic light response of intact leaves of *Atriplex hymenelytra* growing under natural Death Valley conditions during 1975-76. New leaves, normally produced in early winter, did not appear until late spring because of drought. The leaf conductances to water vapor during May, October, January, and March were, respectively, 0.1, 0.05, 0.3, 0.9 $\text{cm}^{-2} \text{s}^{-1}$

drops to a minimum value of 0.4 $\text{nmol cm}^{-2} \text{s}^{-1}$, and stomatal conductance to only 0.05 $\text{cm}^{-2} \text{s}^{-1}$. There is little difference in the temperature dependence of photosynthesis for *A. hymenelytra* during the different seasons (Mooney et al., 1976).

Leaf Size

The leaves collected in the field for reflectance and chemical analyses vary in size during the different seasons. The criterion for collection was that they be fully expanded sun leaves. The area of leaves collected from natural Death Valley habitat plants during the cool season averaged over 5 cm^2 , and those during the hot season, 2 to 3 cm^2 per leaf. As air temperatures during the late spring growing season increased, the newly produced leaves became smaller. It appears that at least some of the larger leaves abscised during the hot season, but this preliminary observation requires confirmation. Leaves from plants grown in a transplant garden in a cool coastal climate at Bodega Head, California, averaged 11 cm^2 per leaf.

To determine if leaf size was responding directly to temperature, plants were grown in the phytocells at a series of day/night temperatures: 42/35, 35/25, 25/20, and 16/10° C. Vapor pressure deficit was kept low in all treatments, and the plants were supplied with ample nutrients and water.

In these experiments the size of fully expanded leaves varied from an average of slightly less than 2 cm^2 at the hottest treatment (42° C) to over 16 cm^2 in the coldest (16° C) (Fig. 8).

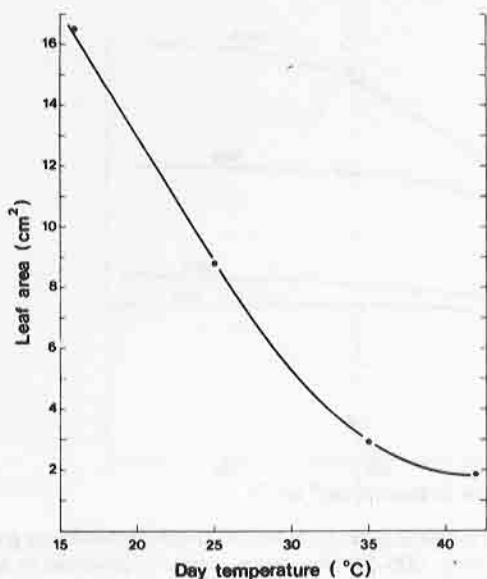


Fig. 8. Mean leaf size of plants of *Atriplex hymenelytra* grown at different day temperatures but similar vapor pressure deficits

Discussion

The leaves of *Atriplex hymenelytra* change their characteristics during the year in an apparently adaptive manner. During the cool season, when they are most photosynthetically active, they have a relatively high absorptance. During the hot, dry seasons, when photosynthetic rate and stomatal conductance are low, the leaves are highly reflective. In addition to the changes in the surface characteristics of the leaves during the season, there are changes in the sizes of newly produced leaves. The leaves produced during the coolest part of the growing season have nearly twice the area of those produced at the end of the growing season when it is hotter. The leaves of *A. hymenelytra* are relatively large in contrast to many desert evergreen shrubs. They are, however, held on the branches at a relatively steep angle, which minimizes their interception of midday sunlight. This leaf angle characteristic does not change seasonally.

To evaluate the possible adaptiveness of the above features, it is of course necessary to consider the potential gains as well as the losses that they confer on the plant. Although steep leaf angle reduces potential midday intercepted radiation, it results in potentially greater amounts of radiation being received during morning and afternoon periods when atmospheric vapor pressure deficits are lowest (Fig. 9). Considering interception by leaves held at 70° facing all directions, as occurs on *A. hymenelytra*, the average radiation interception is fairly constant during the day, about $100 \text{ n einstein cm}^{-2} \text{ s}^{-1}$ of photosynthetically usable radiation. Photosynthetic light saturation occurs at a relatively low radiation level in *A. hymenelytra*, which is in contrast to many other desert plants. Thus, even during the active spring period when light requirement for photosynthesis is at a maximum, the steeply angled leaves are near light saturation during most of the day. Thus, steep leaf angle results in very little loss,

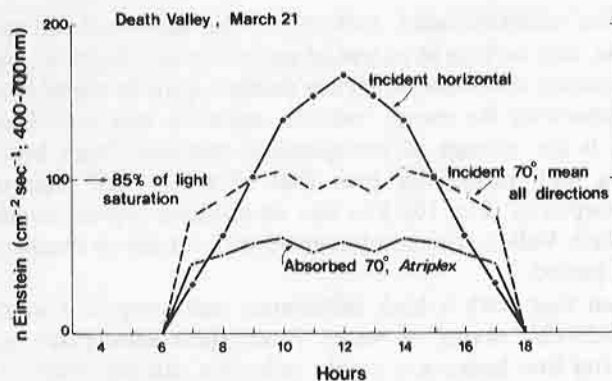


Fig. 9. Photosynthetically active radiation incident on a horizontal surface in Death Valley, California, on March 21, 1976; incident on a 70° angle surface facing all directions; and absorbed by *A. hymenelytra* leaves with the same angle features

Air temperature, 45°C
 Radiation, $1.5 \text{ cal cm}^{-2} \text{ sec}^{-1}$
 Conductance, 0.05 cm sec^{-1}
 Dew point, 10°C

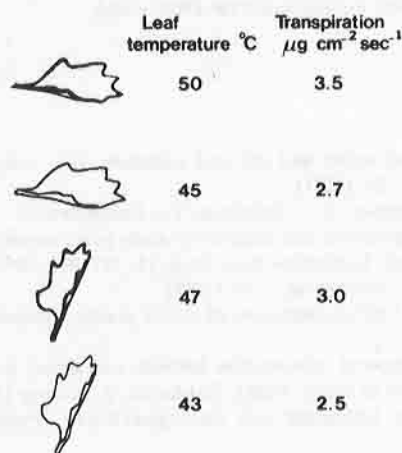


Fig. 10. Leaf temperature and transpiration of leaves of differing absorptances and angles as determined by the energy balance equation. All wavelength absorptances are as for a typical leaf (0.5) and for a summer *A. hymenelytra* leaf (0.25). Leaf conductance to water vapor transfer was measured on summer leaves. Environmental conditions are those characteristic of Death Valley at midday during the summer. Leaf orientation taken as horizontal or at 70° as indicated. Leaf size was 3.9 cm^{-2}

if any, of potential carbon gain in the plant but results in a reduced heat load and thus an improved water-use efficiency. During the summer drought period photosynthesis remains light-saturated for most of the day despite the very high reflectance of the leaves. This is apparently so because their photosynthetic capacity is much reduced during the drought period, and therefore the absorbed light required for saturation of photosynthesis is lower.

Since these leaf characteristics, minimizing the heat load, do not result in the loss of carbon, any savings in potential water loss can therefore be translated directly into increased water-use efficiency (carbon gain to water loss). To analyze these characteristics the energy balance equation was used (Gates, 1965). What we assess is the savings in transpiration resulting from having a steep leaf angle and a high reflectivity over that of a leaf held horizontally and with normal absorptivity (Fig. 10). For this we consider typical midday summer conditions in Death Valley. The conductances utilized are as measured on *Atriplex* during this period.

It can be seen that both a high reflectance and steep leaf angle (Fig. 10) result in a considerable saving of water. Since these effects are additive, the differences in water loss between a highly reflective, steeply oriented leaf (25% absorptance, 70° angle) and a normally reflective, horizontally oriented (50% absorptance, 0° angle) is as high as 30%.

Thus it would appear that the features described for *Atriplex* are indeed adaptive and that they represent one way in which plants can remain evergreen in an unusually hot and arid habitat.

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