COMPARATIVE PHOTOSYNTHETIC CHARACTERISTICS OF COASTAL AND DESERT PLANTS OF CALIFORNIA

H. A. MOONEY[1], J. BERRY[2], O. BJÖRKMAN[2], AND J. EHLERINGER[3]

ABSTRACT

The photosynthetic characteristics of plants native to a Californian hot desert habitat, Death Valley, and a cool coastal locality, Bodega Head, were compared. The desert plants showed a variety of responses including species with C_3 and C_4 photosynthetic pathways, drought tolerance and intolerance, a wide range of thermal optima, and biochemical and morphological thermal acclimation. Most of the desert species have high photosynthetic light requirements for saturation and high photosynthetic capacities.

The coastal species in contrast had general uniformity in their photosynthetic responses, all having the C_3 photosynthetic pathway, similar photosynthetic thermal optima, comparatively low photosynthetic rates for a given growth form and low light requirements for photosynthetic saturation. They all show a strong stomatal response to changes in air humidity, a feature apparently lacking in at least some of the desert species.

The variability in responses of the desert species evidently relates to the large seasonal fluctuations in thermal regime and the low and seasonally unpredictable rainfall characteristic of Death Valley. The uniformity of the responses of the coastal plants relates in turn to the reduced thermal variation and more reliable precipitation of the coastal habitat.

RESUMEN

Se compararon las características fotosintéticas de plantas nativas tanto de un hábitat de desierto caliente (Valle de la Muerte) como de una localidad costera fresca (Bodega Head). Las plantas del desierto mostraron una gran variedad de tipos de

[1] Department of Biological Sciences, Stanford University, Stanford, CA 94305.

[2] Division of Plant Biology, Carnegie Institution of Washington, Stanford University, Stanford CA 94305.

[3] Department of Biology, University of Utah, Salt Lake City, UT 84112.

respuesta, incluyendo especies con vías fotosintéticas C_3 y C_4, tolerancia e intolerancia a la sequía, amplio rango de óptimos térmicos y bioquímicos además de aclimatación morfológica a la temperatura. La mayoría de las especies del desierto tienen requerimientos de luz altos para la fotosíntesis, así como alta capacidad fotosintética.

En contraste con lo anterior, las especies de la costa son uniformes en cuanto a su respuesta fotosintética, todas presentan fotosíntesis C_3, un óptimo térmico similar, tasas fotosintéticas comparativamente bajas para cada forma de crecimiento, así como bajos requerimientos de luz para saturación fotosintética. Todas muestran una fuerte respuesta estomática a los cambios de humedad atmosférica, siendo esta una característica que no se presenta en la mayoría de las plantas del desierto.

La variabilidad de respuestas de las especies del desierto está evidentemente relacionada con las amplias fluctuaciones estacionales en el régimen térmico y la baja e impredecible precipitación pluvial característica del Valle de la Muerte. A su vez, la uniformidad de respuestas de las plantas de la costa está relacionada con la reducida variabilidad térmica y la precipitación más predecible en el hábitat costero.

INTRODUCTION

California is a land of extremes. It contains one of the hottest deserts of the world, Death Valley, as well as habitats which are unusually moderate such as the immediate coastal regions of the northern part of the State, which have little difference in temperatures during or between days. These extreme habitats contain plants adapted to grow under these contrasting conditions. Here we compare the photosynthetic characteristics of a number of species which are native to Death Valley and to the coastal bluff habitats just north of San Francisco.

STUDY SITES AND METHODS

Death Valley receives on average less than 50 mm of rain during the course of the year (Fig. 1). This rain can come during any month. Temperatures are extreme with mean maximum temperatures exceeding 40°C for three summer months (Fig. 2). In the winter however, mean maximum daily temperatures can be less than 20°C. In contrast, at immediate coastal regions, as typified by Fort Ross, even in the warmest month mean daily temperatures are less than 20°C. Even though the coastal habitats are thermally moderate they are subject to the summer drought which characterizes most of mediterranean-climate California.

Thus, there is an extreme difference in temperatures between the coastal and desert sities. In addition, there is an equally great difference in the atmospheric aridity. In Death Valley, in the summer, atmospheric saturation deficits are often over 9 kPa, whereas at a typical coastal site, such as Pt. Reyes, saturation deficits are generally less than 1 kPa (Fig. 3).

Utilizing a mobile laboratory (Björkman, et al., 1973), or a portable controlled-environment cuvette (Field et al., 1982), gas-exchange characteristics were measured on intact leaves of plants growing in their native environment. Both of these systems permitted the control of temperature, humidity, light, and CO_2 concentrations within the cuvette.

Measurements were made principally at Furnace Creek, Death Valley under natural or irrigated conditions and at a coastal bluff site at the University of California's Bodega Marine Laboratory.

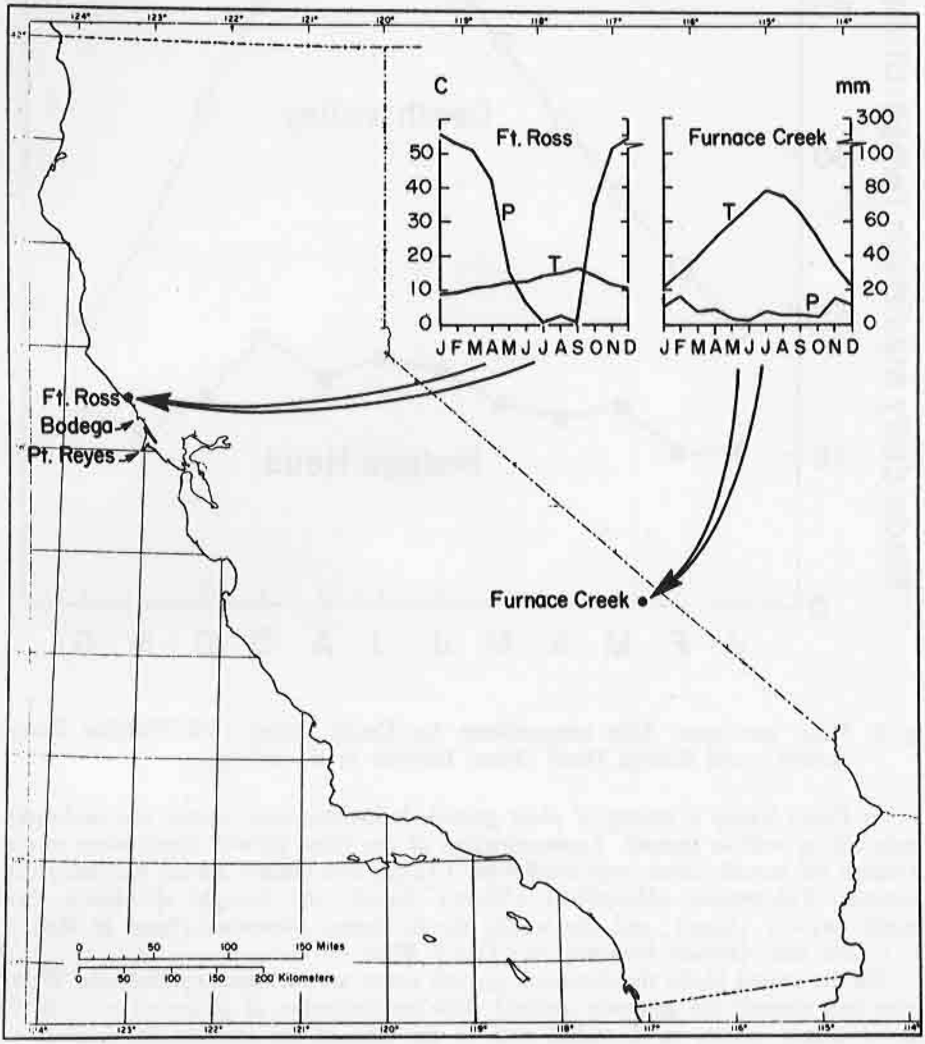

Fig. 1. Location and climatic characteristics of Californian coastal and desert study sites.

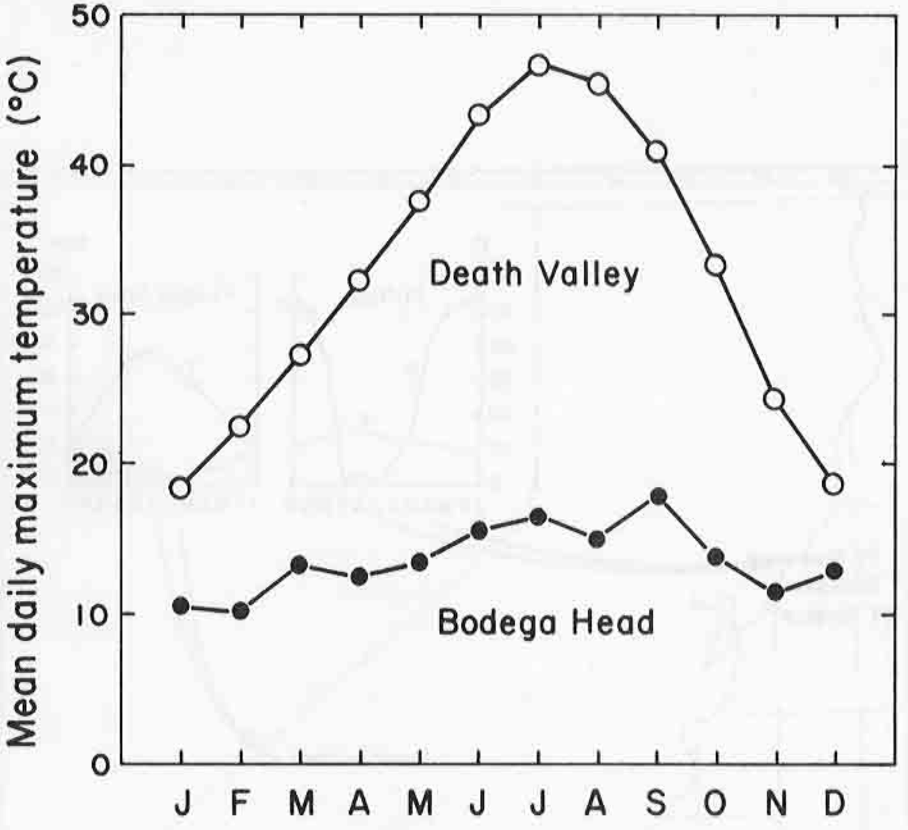

Fig. 2. Mean maximum daily temperatures for Death Valley (US Weather Bureau records), and Bodega Head (From Barbour et al., 1973).

In Death Valley a variety of plant growth forms co-occur: woody and herbaceous perennials as well as annuals. Representatives of the these growth forms were studied including the annual *Camissonia claviformis* (Torrey and Frem.) Raven, the herbaceous perennial, *Tidestromia oblongifolia* (Wats.) Standl., the drought deciduous shrub *Encelia farinosa* (Gray), and the woody shrubs *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. and *Atriplex hymenelytra* (Torr.) Wats.

On the coastal bluffs the dominant growth forms are herbaceous perennials. Woody plants and annuals are generally lacking with the exception of protected sites, in the case of woody plants, or disturbed sites in the case of the annuals. At Bodega the following herbaceous parennials were studied: *Ambrosia chamissonis* Less., *Eriogonum latifolium* Sm., *Ranunculus californicus* Benth., *Lupinus variicolor* Steud., *Fragaria chiloensis* (L.) Duchn. In addition some measurements were made on the naturalized annual, *Atriplex triangularis* Willd.

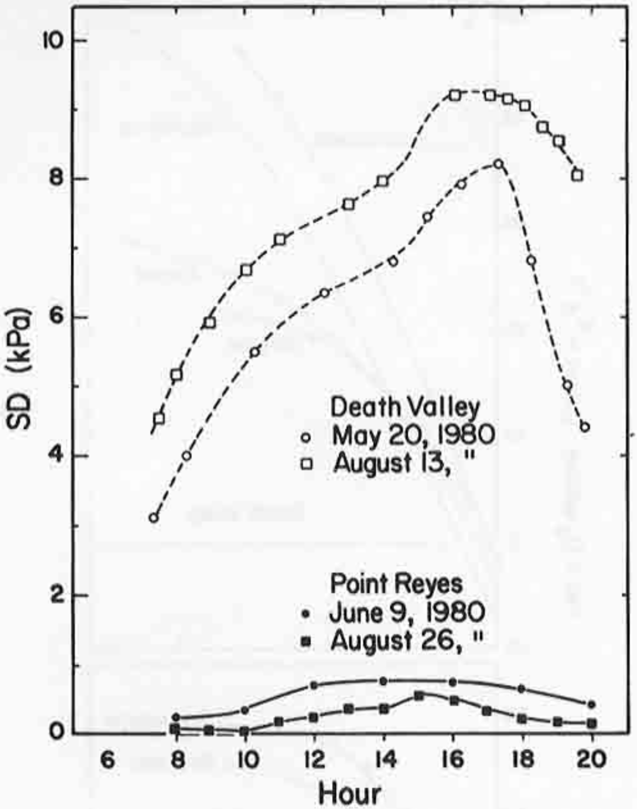

Fig. 3. Atmospheric saturation deficits at Death Valley and Point Reyes (From Roy and Mooney, unpublished).

RESULTS

Photosynthetic responses to Light

The plants studied at Death Valley generally have a high light requirement for photosynthesis (Fig. 4A). The annual, *Camissonia claviformis,* which was found to have one of the highest photosynthetic rates measured for plants (Mooney *et al.,* 1976a), does not deviate from the theoretical projection of the quantum yield until light levels nearly half of full sunlight. There are some exceptions to this general trend since at least one Death Valley species, the annual *Perityle emoryi* Torr. in Emory, has a relatively low light requirement (Armond and Mooney, 1978). In contrast to that found for desert plants, the leaves of all plants studied at Bodega had

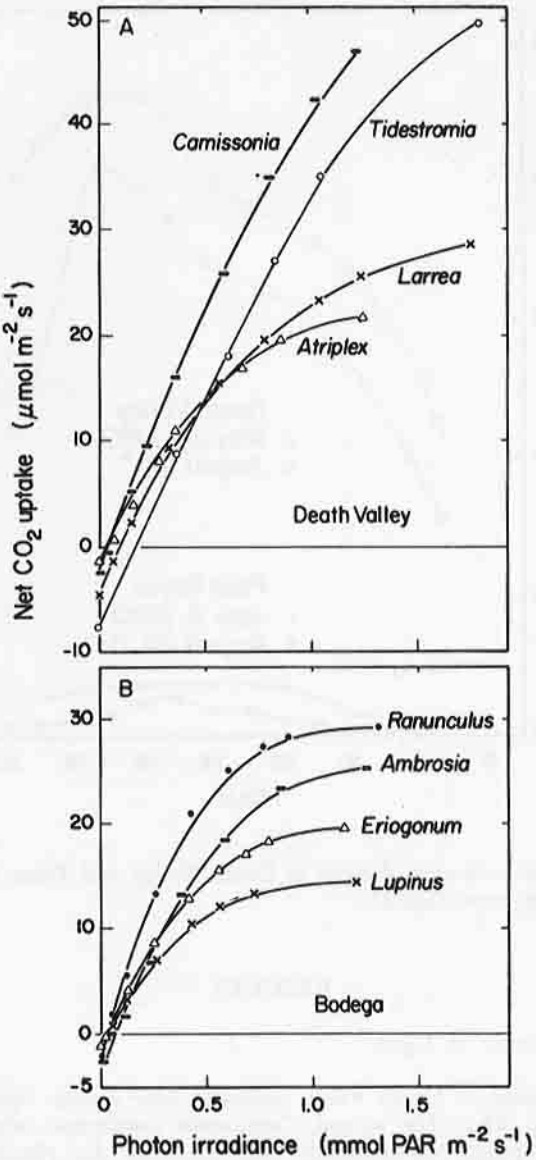

Fig. 4. Photosynthetic response to light of desert (A) and coastal species (B). The measurements for coastal species were all determined at 20°C. The desert species were determined at 30°C except for *Camissonia* which was measured at 20°C and *Tidestromia* at 35°C.

comparatively lower photosynthetic light requirements than those of desert plants (Fig. 4B).

Photosynthetic Responses to CO_2

The vegetation of Death Valley is dominated by plants which have both the C_3 and C_4 photosynthetic pathway. This is evident from their photosynthetic responses to CO_2 (Fig. 5A). *Atriplex* and *Tidestromia* are both C_4 species as is indicated by their zero CO_2 compensation points. *Camissonia, Encelia,* and *Larrea* on the other hand have CO_2 compensation points typical of C_3 species. The three Bodega species studied all show C_3-type CO_2 photosynthetic responses (Fig. 5B). C_4 plants do occur on the coast near Bodega but they are relatively rare.

Photosynthetic Responses to Temperature

The plants of Death Valley have diverse temperatures of optimum photosynthesis (Fig. 6B). *Tidestromia* has one of the highest photosynthetic temperature optima measured on land plants, 47°C (Björkman, et al., 1972). The winter-active annual Camissonia claviformis on the other hand has a photosynthetic temperature optimum near 20°C (Mooney *et al.,* 1976) which is about the same as that of *Larrea*, in the winter.

The evergreen shrubs of Death Valley which have leaves present during both the hot and cool seasons have dissimilar seasonal photosynthetic responses. One type is that typified by *Larrea* (Fig. 7) which has a strong capacity to acclimate biochemically to the changing seasonal temperature by a shift in the thermal photosynthetic optimum (Mooney *et al.,* 1976b, 1977a). This contrasts with behavior of leaves of *Atriplex hymenelytra* and *Encelia farinosa* (Fig. 8) which, although there are seasonal changes in rate capacity, the thermal optimum stays relatively constant. *Atriplex* and *Encelia* both adjust to the changing thermal environment principally by morphological rather than biochemical means (Mooney *et al.,* 1977b, Ehleringer and Mooney, 1978).

In contrast to the variety of thermal photosynthetic responses found in Death Valley plants those of Bodega are all relatively similar (Fig. 6B). Temperature optima are relatively low ($\simeq$25°C) and do not change markedly with season.

Photosynthetic Responses to Humidity

All of the plants which have been studied at Bodega have shown a strong stomatal response to humidity (Mooney et al., unpublished) as is typified by the response of *Fragaria* as shown in Fig. 9A. As vapor pressure deficit increases stomata close and transpiration either stays fairly constant or, in the example shown, actually decreases somewhat. Photosynthesis also declines but proportionately less than does transpiration. There have not been extensive studies of the humidity response of the Death Valley plants but it appears that for some species, at least, the stomata do not respond to changing humidity conditions at least under field conditions (Fig. 9B).

Photosynthetic Responses to Water Deficit

As with temperature, the plants of Death Valley show a variety of responses to drought stress. Some of the species have responses similar to mesophytes

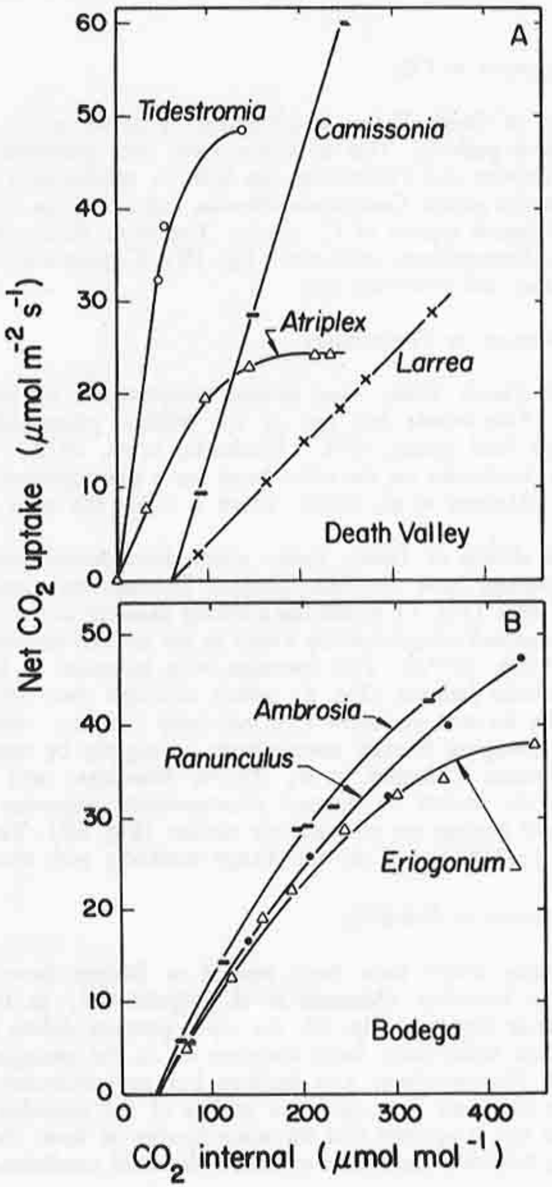

Fig. 5. Photosynthetic response to CO_2 of desert (A) and coastal species (5B). All determinations were made at light saturation and 20°C for coastal species and 30°C for desert species.

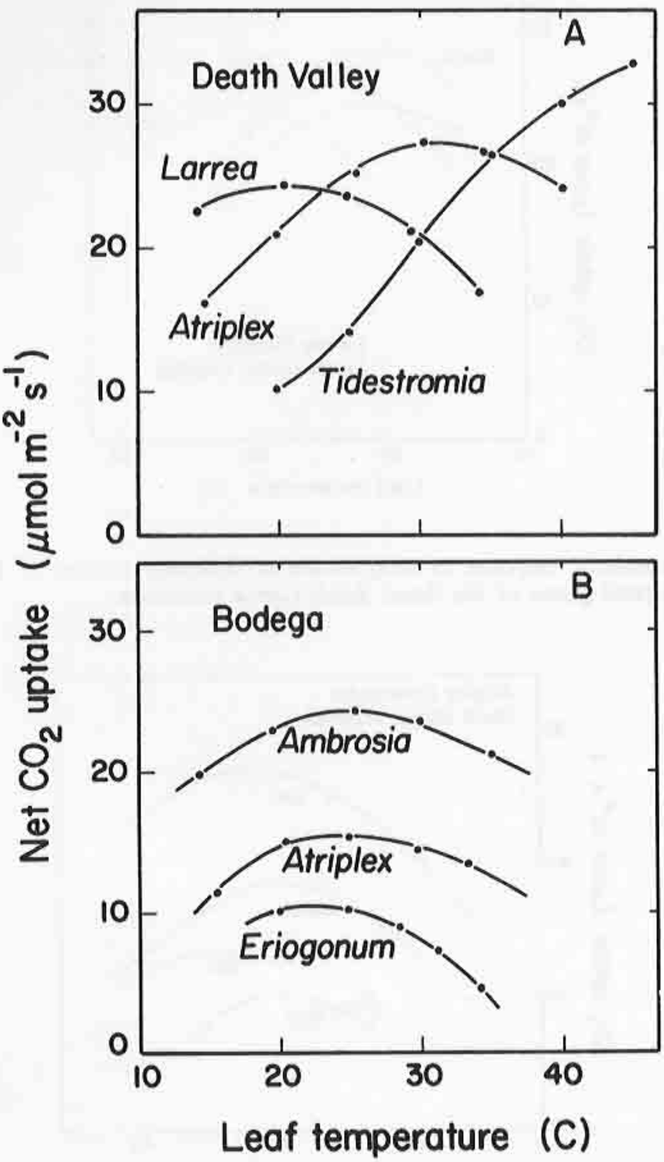

Fig. 6. Photosynthetic response to temperature of Death Valley (A) and coastal species (B). Determinations made under light saturation and normal air.

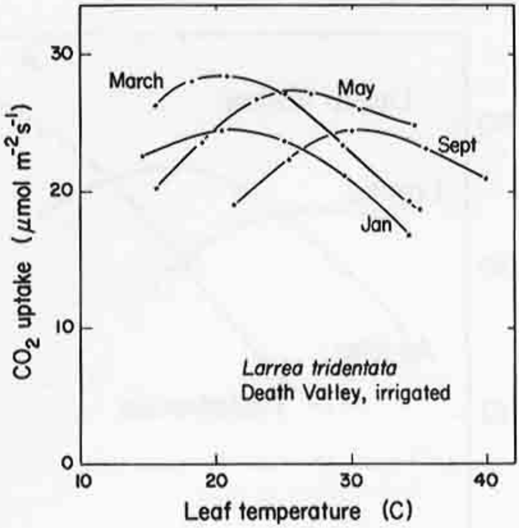

Fig. 7. Photosynthetic response to temperature at different seasons in Death Valley of irrigated plants of the desert shrub *Larrea tridentata*.

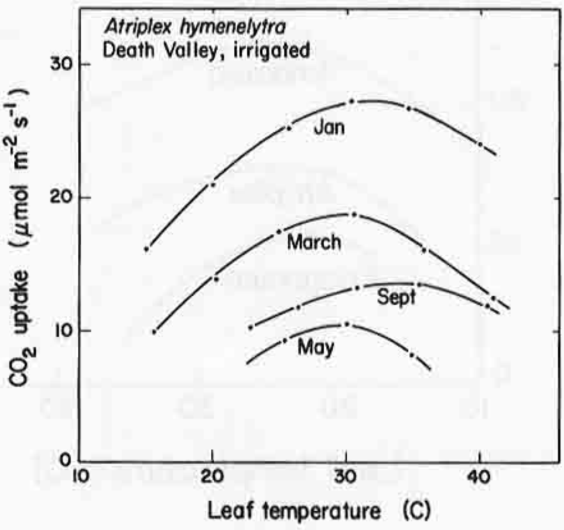

Fig. 8. Photosynthetic response to temperature at different seasons in Death Valley of irrigated plants of the desert shrub, *Atriplex hymenelytra*.

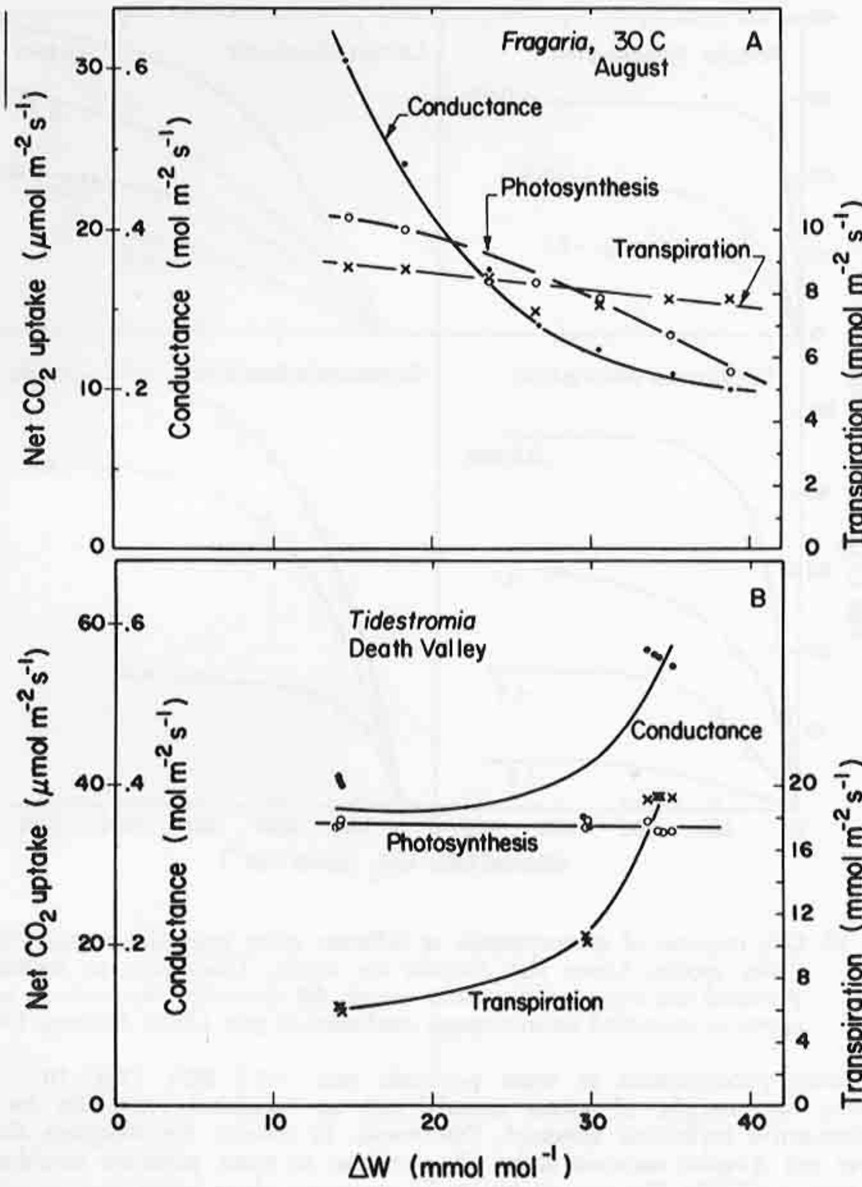

Fig. 9. Changes in conductance, photosynthesis, and transpiration to changing water vapor concentrations of a coastal species, *Fragaria* (A), and of a desert species, *Tidestromia* (B). *Tidestromia* determined at 35°C and *Fragaria* at 30°C.

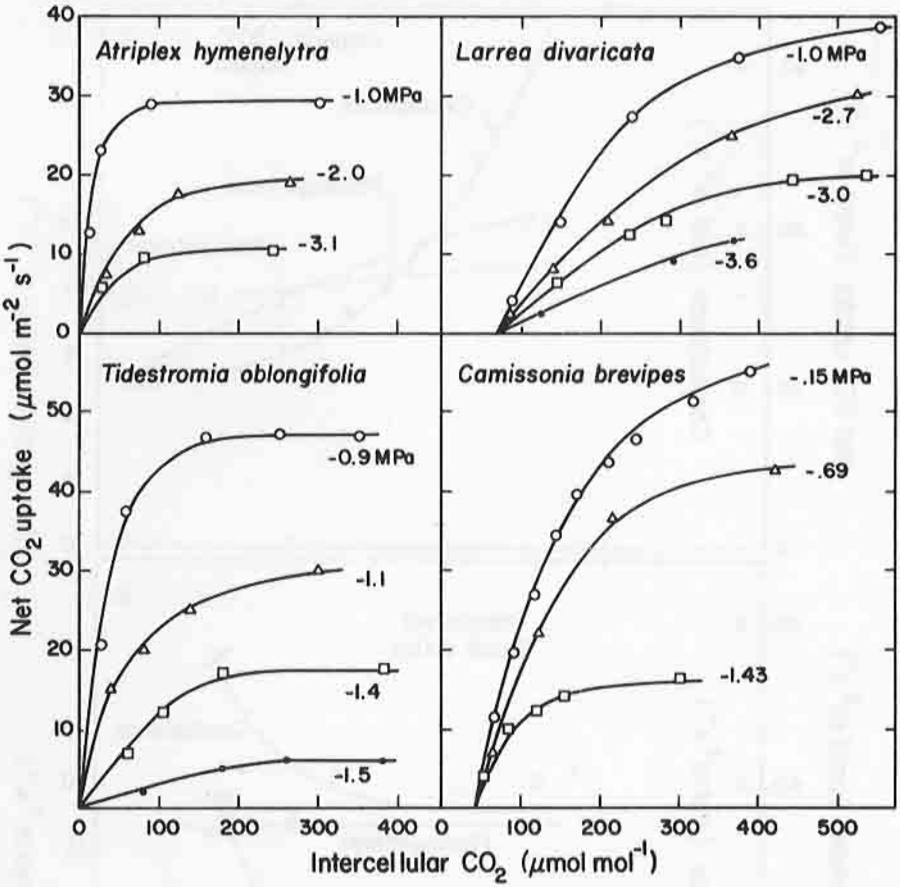

Fig. 10. CO_2 response of photosynthesis at different water potentials of four Death Valley species. *Larrea* and *Atriplex* are shrubs, *Tidestromia* an herbaceous perennial and *Camissonia* a winter annual. All determinations made on plants grown in controlled environmental conditions in pots (From Mooney, 1980).

and cease photosynthesis at water potentials near —1.5 MPa (Fig. 10). This is true, for example, of winter annuals, such as *Camissonia,* but also for the summer-active herbaceous perennial, *Tidestromia.* In contrast the evergreen shrubs, *Larrea* and *Atriplex* maintain active photosynthesis to water potentials considerably less than —3.0 MPa. The data shown are for pot-grown plants which were droughted. Under slower drought induction, as would occur in the field, the magnitudes of water potentials at a given photosynthetic capacity would probably differ from that shown. However the relative trend among species would be similar. There have not been detailed studies of the drought tolerance of the coastal plants but even during the summer drought measurements of midday water potentials are generally less than —2.0 MPa.

DISCUSSION

The extreme differences in habitat characteristics between coastal California and the extreme desert of Death Valley have selected plants with widely divergent physiological properties. Here wa have considered primarily the photosynthetic characteristics of these plants. In relation to the temperature response of this process it appears that there is little difference in the responses among coastal species at any given time or between seasons. This is to be expected since there is little change in habitat temperatures either diurnally or seasonally. This pattern contrasts sharply with that found in the desert. In the desert the habitat temperatures vary widely from winter to summer. Rainfall, although small in amount on average, can come during any season. Plants can most efficiently utilize this limiting resource if their photosynthetic machinery is adjusted to operate at the prevailing temperature when the moisture becomes available. Thus we see plants which are adapted to operate at low winter temperatures, such as *Camissonia* as well as extreme thermophiles such as *Tidestromia.* These plants are dormant when temperatures are not within their favorable ranges, although a certain amount of temperature acclimation is possible which prolongs their active period (Seemann *et al.,* 1979). In contrast, plants which are evergreen have adopted characteristics which permit them to be efficient at any temperature. *Larrea,* on the one hand, adjusts its temperature optimum biochemically whereas *Atriplex* does so by morphological means. Both types of behavior have been described for other desert evergreens (Pearcy, 1977; Ehleringer and Mooney, 1978). Those species which adjust to changing temperature do so in a variety of ways. In *Atriplex hymenelytra* leaves become more reflective in the summer as salts crystallize in their surface glands (Mooney et al., 1977b). In *Encelia farinosa* the same effect results from an increased surface hair density on leaves produced during the dry period (Ehleringer and Mooney, 1978). In both *Encelia* and *Atriplex* the leaves retained on the plants are smaller during the hot dry season than during the cool season resulting in more favorable convective characteristics.

Related to the differences in the seasonal thermal tolerance of the various desert species is their dissimilar responses to drought. As might be expected, the evergeen species exhibit a high degree of drought tolerance. For example, under field conditions *Larrea* showed no signs of drought effects on the quantum yield even at a water potential of —4.9 MPa (Mooney et al., 1977c). In contrast, those species wich are active principally during a single thermal period in the desert, either summer or winter, do not have the capacity to tolerate a high degree of drought. This is not surprising for the winter annuals, although they can acclimate somewhat to a reduced water availability as the summer drought period ensues (Seemann, *et al.,* unpublished). It is however somewhat unexpected that *Tidestromia,* which is only active during the summer drought period, is relatively drought intolerant. However, this species apparently only occupies microsites which have stored soil water (Gulmon and Mooney, 1977) and further it has very little internal resistance to the flow of water (Troughton *et al.,* 1974). Thus *Tidestromia* plants do not develop a water deficit even under very high evaporative demand.

Information is not available on the comparative drought tolerance of the coastal species which have been studied. However, it is unlikely that they have anything like the tolerance of the desert evergreens since they are not subjected to great water deficits. However the coastal habitat is water limited during the summer. It appears that one way in which the coastal plants cope with a limited water supply is by having an effective stomatal response to decreased humidity. At the coast humidity is generally high, however under certain conditions vapor pressure deficits can become high, particularly since the leaves of these plants are very close to the ground surface where leaf temperatures can be considerably greater than those reported in weather records. All of the coastal species studied (Mooney, *et al.*, unpublished) show very little change in transpiration with an increase in vapor pressure deficit at a constant temperature because of stomatal closure. Since photosynthesis is depressed proportionally less than transpiration with closing stomata this is a very effective response in terms of water-use efficiency or carbon gained per water lost.

One might anticipate a comparable water-saving behavior in the desert species but the limited work which has been done would indicate that this is not the case. It has been proposed (Mooney *et al.*, unpublished) that stomatal closure at low humidities would not be effective in Death Valley since humidities are generally always low and thus plants would have restricted photosynthesis with such a response. Further, transpiration, an important heat dissipating mechanism for leaves, would be blocked with stomatal closure. This could be potentially lethal under some Death Valley conditions.

The leaves of the desert species of a given growth form have higher photosynthetic capacities than the coastal species. This is the result of hte high conductances which characterize the desert species as well as the high concentrations of carboxylating enzymes which they have. Such concentrations are only possible with high leaf nitrogen contents. The coastal plants, perhaps because they co-occur in rather dense stands of vegetation, appear to be more nitrogen limited. A result of these differences is that the desert species can utilize higher light levels than can the coastal species. What is not clear is whether the differential light climates of these disparate habitats alone have selected for differences in the light responses of the native species or whether these different light responses are a necessary result of the different nitrogen economies of the leaves imposed by their respective habitats.

The diversity of physiological responses found in the plants of the desert, as contrasted with those found at the coast, is also seen in the variability in their photosynthetic pathways. In the desert there is a mixture of C_3 and C_4 species whereas at the coast all of the dominants are C_3. The greater potential water-use efficiency of C_4 species certainly suit them to the Death Valley conditions. However there is in addition to biochemical means, such as photosynthetic pathway, a variety of mechanisms which plants utilize to adapt to limited water regimes. Many of these mechanisms in various combinations are found in Death Valley C_3 and C_4 species. Further, tolerance to drought, which is not directly related to photosynthesis is under many conditions as important as the most efficient use of water in fixing carbon.

In summary, the desert represents a habitat offering many different climates throughout space and time. There are a wide range of adaptive modes found in the native plants which suit them for a given time period, or through either biochemical or morphological acclimation, for a series of different thermal regimes found through time. In contrast as the coast where the climate changes little through time the plants are all relatively similar in their photosynthetic characteristics which suit them to their relatively low temperature, low light environment.

ACKNOWLEDGEMENTS

We express appreciation to the National Science Foundation for supporting this work and to the personnel of the Bodega Marine Laboratory and the Death Valley National Monument for their considerable aid.

LITERATURE CITED

ARMOND, P.A., AND H.A. MOONEY. 1978. Correlation of photosynthetic unit size and density with photosynthetic capacity. **Carnegie Inst. Year Book 77:** 234-237.

BARBOUR, M.G., R.B. CRAIG, R.R. DRYSDALE, AND M.T. GHISELIN. 1973. **Bodega Head: Coastal Ecology.** Univ. Calif. Press, Berkeley. 338 p.

BJÖRKMAN, O., M. NOBS, J. BERRY, H. MOONEY, F. NICHOLSON, AND B. CATANZARO. 1973. Physiological adaptation to diverse environments; approachs and facilities to study plant response in contrasting thermal and water regimes. **Carnegie Institution Year Book 72:** 393-403.

EHLERINGER, J.R., AND H.A. MOONEY. 1978. Leaf hairs: effects on physiological activity and adaptative value to a desert shrub. **Oecologia 37:** 183-200.

FIELD, C., J.A. BERRY, AND H.A. MOONEY. 1981. A portable system for measuring carbon dioxide and water vapor exchange of leaves. **Plant, Cell and Environment.** In press.

GULMON, S.L., AND H.A. MOONEY. 1977. Spatial and temporal relationships between two desert shrubs, *Atriplex hymenelytra* and *Tidestromia oblongifolia* in Death Valley, California. **Jour. Ecology 65:**831-838.

MOONEY, H.A., J. EHLERINGER, AND J.A. BERRY. 1976. High photosynthetic capacity of a winter annual in Death Valley. **Science 194:** 322-324.

MOONEY, H.A., O. BJÖRKMAN, J. EHLERINGER, AND J. BERRY. 1976. Photosynthetic capacity of **in situ** Death Valley plants **Carnegie Inst. Year Book 75:** 410-413.

MOONEY, H.A., O. BJÖRKMAN, AND J. COLLATZ. 1977. Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. CO_2 exchange characteristics of intact leaves. **Plant Physiology 61:** 406-410.

MOONEY, H.A., J. EHLERINGER, AND O. BJÖRKMAN. 1977. The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra.* **Oecologia 29:** 301-310.

MOONEY, H.A., O. BJÖRKMAN, AND J. COLLATZ. 1977. Photosynthetic acclimation to temperature and water stress in the desert shrub, *Larrea divaricata.* **Carnegie Inst. Year Book 76:** 328-335.

MOONEY, H.A. 1980. Seasonality and gradients in the study of stress adaptation. pp. 279-294 in **Stress Physiology of Plants.** (Neil Turner and Paul Kramer, eds.). J. Wiley. N.Y.

PEARCY, R.S. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. **Plant Physiol. 59:** 795-799.

SEEMANN, J.R., W.J.S. DOWNTON, AND J.A. BERRY. 1979. Field studies of acclimation to high temperature; winter ephemerals in Death Valley. **Carnegie Inst. Yearbook 78:** 157-162.