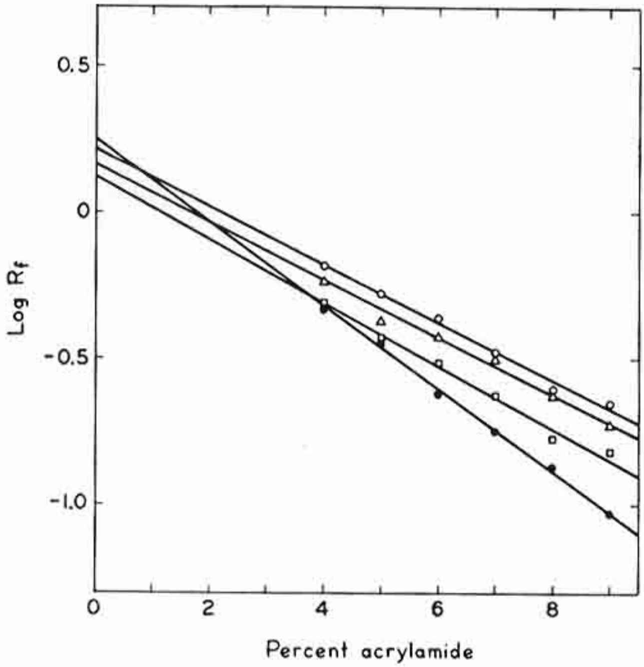

Fig. 21. Ferguson plots for phosphoenolpyruvate carboxylases from four C_4 species: open circles, *D. spicata;* open triangles, *A. sabulosa;* open squares, *A. hymenelytra;* filled circles, *T. oblongifolia.*

enzyme is about twice the molecular weight of the phosphoenolpyruvate carboxylases from the other three species. Whether or not the apparent size difference is an evolutionarily and structurally significant increase of the enzyme size is not yet known. The available information in the plant literature indicates a molecular weight of 350,000 for the phosphoenolpyruvate carboxylase from *Atriplex spongiosa* (Ting and Osmond, 1973).

Other C_4 plants, including *A. spongiosa* and plants in the Amaranthaceae related to *Tidestromia*, will be tested to see if *Tidestromia* has a unique phosphoenolpyruvate carboxylase or if there are apparently two size classes of phosphoenolpyruvate carboxylase among C_4 plants.

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PHOTOSYNTHETIC CAPACITY OF *in situ* DEATH VALLEY PLANTS

H. A. Mooney, O. Björkman, J. Ehleringer, and J. Berry

As part of our long-term studies on the physiological ecology of plants we have been concentrating our efforts on the characteristics of components of the native flora of Death Valley, California. While Death Valley is often identified as one of the hottest and driest environments on earth, these extremely high air temperatures (exceeding 50°C) occur only during the summer months (Fig. 22). In the winter months relatively cool temperatures (20°C) predominate, and in the spring and fall months air temperatures are

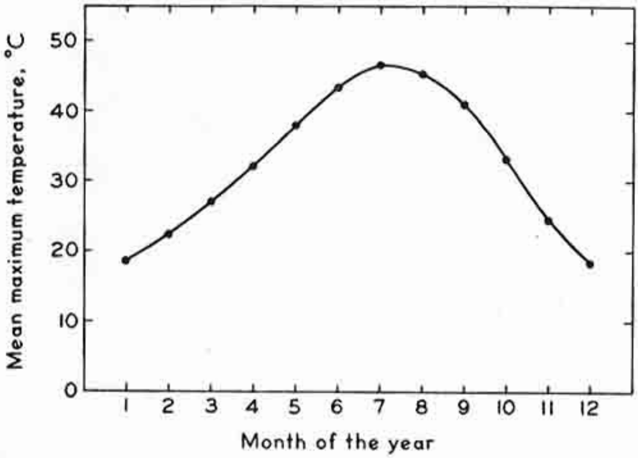

Fig. 22. The yearly course of mean maximum daily air temperatures on the floor of Death Valley, California.

often around 30°C. Consequently, Death Valley provides us with a broad variety of thermal environments and a unique opportunity to study the mechanisms plants possess to adapt to these seasonal thermal regimes.

We report here studies of the intrinsic photosynthetic capacities of several species in response to seasonal changes in thermal regimes of their natural habitat. The measurements were made on plants growing under natural conditions on the floor of Death Valley (*Year Book 73*, pp. 748–757).

Using the mobile laboratory, we measured the photosynthetic capacity of plants during the winter (January), spring (March), summer (late May), and fall (October) seasons. Plants studied included a winter annual (*Camissonia claviformis*), a summer-active herbaceous perennial (*Tidestromia oblongifolia*), and two evergreen shrubs (*Larrea divaricata* and *Atriplex hymenelytra*).

Under natural conditions the two evergreen shrub species were photosynthetically active throughout the year, although their maximum photosynthetic rates were considerably below those of the two that hold their leaves for a short period (Fig. 23). The two herbaceous species *Tidestromia* (C_4) and *Camissonia* (C_3) possess extremely high maximum photosynthetic rates

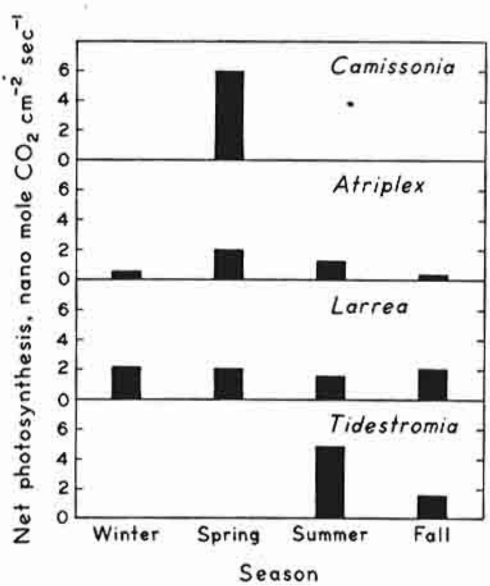

Fig. 23. Light-saturated rates of photosynthesis of four plant species native to the floor of Death Valley. Rates were measured on natural plants at leaf temperatures of 30°C, except *Tidestromia*, which was measured at 35°C. All measurements were made at 325 μbar CO_2, 21% O_2, and a water vapor pressure deficit of less than 15 mbar.

(exceeding 5 nmol CO_2 $cm^{-2}sec^{-1}$), yet their physiological activities are restricted for the most part to a single season during the year. There appears to be an inverse relationship between maximum photosynthetic rate and leaf longevity among the species in this study. Of the species with the highest rates observed, the winter-active annual *Camissonia* is a C_3 plant, whereas the summer-active herbaceous species *Tidestromia* is a C_4 plant.

At the 30°C measurement temperature, *Larrea,* the C_3 evergreen species, maintained a relatively constant photosynthetic capacity under natural conditions at all times of the year. This homeostasis persisted in spite of widely disparate midday seasonal air temperatures (20° to 45°C) and leaf water potentials (−25 to −50 bars). The unusual homeostatic adjustment comes about, in part, because of changes in the photosynthetic thermal optimum (Fig. 24). These data were obtained with plants receiving irrigation to eliminate the effect of water stress. Although the photosynthetic rate was relatively constant at the various seasonal temperature optima (2.4–2.7 nmol CO_2 $cm^{-2}sec^{-1}$), the temperature optimum shifted from 20°C during the cool season to over 30°C in the fall.

Atriplex, the C_4 evergreen species, exhibited its highest photosynthetic rate under natural conditions in the spring with newly produced leaves. The photosynthetic rates were reduced during the other season coincident with changes in leaf reflectivity (*Year Book 73*, pp. 846–852). Associated also with the lower photosynthetic rates were decreases in leaf water potential, leaf conductance, and leaf nitrogen. In contrast to *Larrea, Atriplex* showed little change in its temperature optimum for photosynthesis between seasons (data not shown). As shown in Fig. 25 the optimum temperature for photosynthesis was 30°C.

The summer-active C_4 plant *Tidestromia* is characterized by a very high photosynthetic rate during its principal growth period. In the summer months when *Tidestromia* is active, leaf temperatures may be in excess of 45°C. The optimum temperature for photosynthesis was similar (*Year Book 74*, pp. 743–751). Under spring and winter temperatures *Tidestromia* would have very low photosynthetic rates. The measured photosynthetic rates were lower in the fall, however, because of the onset of leaf senescence.

The C_3 winter-active annual *Camissonia* germinates following heavy winter rains and can, under certain conditions, complete its entire life cycle in six weeks. This short-lived species has a remarkable capacity to capture sunlight and fix carbon. *Camissonia* converted incident photosynthetically active radiation (400–700 nm) into

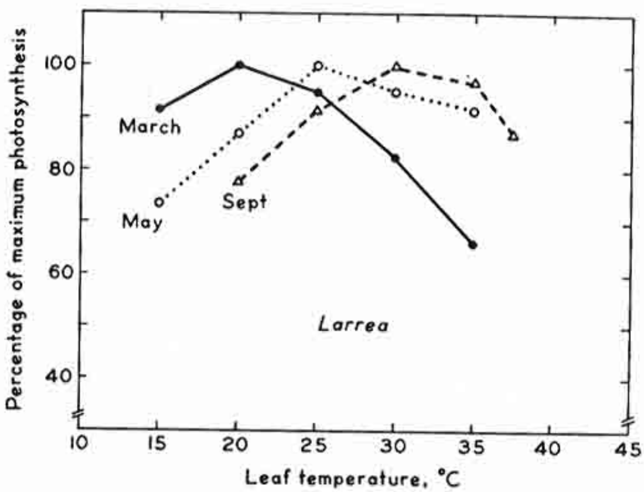

Fig. 24. Seasonal photosynthetic temperature responses of *Larrea* in Death Valley. These values were measured on irrigated plants under conditions of 170 nE cm^{-2} s^{-1}, an ambient CO_2 concentration of 325 μbar, and a water vapor pressure deficit of less than 15 mbar.

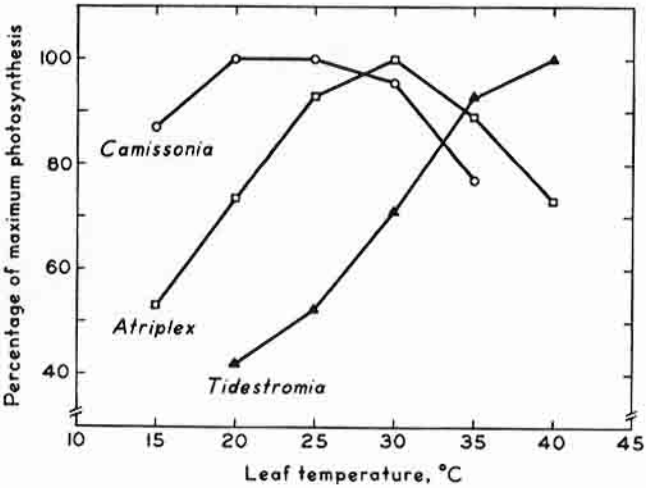

Fig. 25. Seasonal photosynthetic temperature responses of three plant species native to the floor of Death Valley. Measurement conditions as given in Fig. 24.

chemical energy with an efficiency of 8.5%. This is a consequence of the lack of light saturation at midday irradiances, a feature that is also characteristic of *Tidestromia* (*Year Book 70*, pp. 540–550). The *in situ* midday photosynthetic rate of *Camissonia* was nearly 6 nmol CO_2 $cm^{-2}sec^{-1}$, a rate that is higher than has been measured on such productive crop species as corn, sorghum, and sugar cane.

The thermal optimum of photosynthesis of the various species coincides with the prevailing temperatures during their principal growing period (Fig. 25). The winter-active C_3 *Camissonia* has a thermal optimum near 20°C and the summer-active C_4 *Tidestromia*, of over 45°C. The C_3 plant *Larrea* can potentially grow throughout the year, except during midsummer. This plant shifts its thermal optimum in concert with the prevailing air temperatures. The C_4 plant *Atriplex* grows only during the winter and spring months and maintains a thermal optimum at 30°C.

The major results from these studies will be published elsewhere in greater detail along with a full analysis of the physiological components responsible for the changing seasonal photosynthetic responses of the plants.

This work was supported in part by the National Science Foundation. We thank the U.S. Park Service in Death Valley for their considerate assistance.

LEAF ABSORPTANCE AND PHOTOSYNTHESIS AS AFFECTED BY PUBESCENCE IN THE GENUS *Encelia*

James Ehleringer

Among higher plants there is a trend toward increasing leaf pubesence (presence of leaf hairs) along environmental gradients of decreasing precipitation (Schimper, 1903; Warming, 1909; Clausen, Keck, and Hiesey, 1940). These hairs, covering the surface of the leaf, are generally considered to be an adaptive feature of plants occupying arid habitats. The reason is that pubescence can reduce the heat load of leaves by increasing the reflectance from the leaf surface, reducing the amount of radiation absorbed. The adaptive value