Seasonal Shift from $C_3$ Photosynthesis to Crassulacean Acid Metabolism in *Mesembryanthemum crystallinum* Growing in Its Natural Environment*

Klaus Winter**, Ulrich Lütting, and Erika Winter
Institut für Botanik der Technischen Hochschule, Schnittspahnstr. 3–5, D-6100 Darmstadt, Federal Republic of Germany

John H. Troughton
Physics and Engineering Laboratory, Department of Scientific and Industrial Research, Lower Hutt, New Zealand

**Summary.** Changes in $\delta^{13}C$ value, diurnal malate content, water content and Na+, K+ and Cl− content of the annual *Mesembryanthemum crystallinum* (Aizoaceae) were followed in a natural population on a coastal cliff at the Mediterranean Sea shore close to Caesarea (Israel). Plants germinated in the middle of the rainy season in December 1976/January 1977. Diurnal malate fluctuations in the leaves were not detected until the end of March. Later on, at the start of the dry season, pronounced diurnal changes in malate developed. This was correlated with a progressive change in $\delta^{13}C$ value from about $-26^{0}/_{00}$ to about $-16^{0}/_{00}$ which is consistent with a change from normal $C_3$ photosynthetic $CO_2$ fixation to a predominantly nocturnal $CO_2$ assimilation pattern involving Crassulacean Acid Metabolism.

*Introduction*

The halophytic, annual *Mesembryanthemum crystallinum* (Aizoaceae) is capable of changing its mode of carbon assimilation from $C_3$ photosynthesis to CAM. This change has been observed when laboratory grown plants were exposed to root media of high salinity (Winter and von Willert, 1972; Winter, 1975), or low temperature, or oxygen deficiency (Winter, 1974a, b; Winter and Lüttinge, 1976). Each of these factors probably reduces the water availability in *M. crystallinum*. It has been suggested that a shift from $C_3$ to CAM could also occur during the

*The investigations were carried out during a stay of K.W. and E.W. at the Avdat Experimental Station, Negev, Israel, with the generous cooperation of Prof. Dr. Dr. h.c. M. Evenari*

**Present address and address for offprint requests:** Department of Environmental Biology, Research School of Biological Sciences, The Australian National University, P.O. Box 475, Canberra City, A.C.T. 2601, Australia

*Abbreviations.* CAM = Crassulacean Acid Metabolism; FW = fresh weight; DW = dry weight
life cycle of this species in its natural environment (Winter and Lüttge, 1976; Winter et al., 1976a; Winter and Troughton, 1978). In order to test this possibility we studied characteristics of carbon assimilation of a natural population growing in a coastal habitat of Israel.

Materials and Methods

The Study Site and the Plant Material

*M. crystallinum* is a winter annual which germinates during the wet winter and dies during the dry summer after having produced seeds. The *M. crystallinum* population studied occupied the upper part of a west facing coastal cliff on the Mediterranean Sea shore close to the ancient town of Caesarea (Israel) (Fig. 1). The study site is characterized by a mediterranean climate with wet winters and hot, dry summers; climatic features during the study period are shown in Figure 2. Average annual rainfall is about 500–800 mm. During winter and summer, maximum and minimum temperatures vary between 20 and 10°C and between 30 and 20°C respectively.

Sampling and Analysis

Soil and plant samples were taken at 6 to 10 day intervals. Leaf samples were collected at dawn and dusk. Once or twice every month more intensive sampling was done at 1½ to 3 h intervals throughout a day to follow water content and malate content of the leaves. Leaves were washed with distilled water and immediately frozen at −20°C in a propane-gas-refrigerator. After returning from the field leaf samples were freeze dried.

The freeze dried leaf samples were extracted with distilled water for 1 h at 80°C for Na⁺, K⁺, Cl⁻ and malate determinations. Na⁺ and K⁺ were determined using a flame photometer, Cl⁻ using a chloride-titrator, and l(-)-malate was determined enzymatically after Hohorst (1970).

Oven dried (80°C) leaf material was used for determination of carbon isotope composition (for details see: Winter et al., 1976b), which is expressed as δ¹³C in ‰ with respect to Pee Dee belemnite limestone (PDB) where

\[ δ^{13}C (‰) = \left( \frac{^{13}C/^{12}C_{\text{sample}}}{^{13}C/^{12}C_{\text{standard}}} - 1 \right) \times 1000. \]

Shoots (total above-ground phytomass of individual plants) were collected at dawn for fresh weight and dry weight measurement. They were separated into leaves and stems, weighed, and dried for 48 h at 80°C.

Relative growth rates (g g⁻¹ day⁻¹) were calculated using the following equation (Evans, 1972):

\[ \ln \text{DW}_2 - \ln \text{DW}_1 \]

\[ t_2 - t_1 \]

where DW₁ is the shoot dry weight (g) at day t₁, DW₂ is the shoot dry weight (g) at day t₂ and t₂ − t₁ refers to the period in days between t₂ and t₁.

Soil samples from 10 and 20 cm depth were sieved through a nylon net (1 mm mesh width) and soil water content was determined after samples had been dried for 48 h in an oven. Soil salinity was estimated by shaking 5 g of oven dried soil for 1 h with 125 ml water at room temperature. After leaving overnight, the supernatant was used for analysis of Na⁺, K⁺ and Cl⁻.

Air temperature and relative air humidity were determined with an aspiration-psychrometer or a thermohygrograph and light intensity was measured with a luxmeter.