High Productivity and Photosynthetic Flexibility in a CAM Plant

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Summary. In the annual succulent \textit{Mesembryanthemum crystallinum} growing \textit{in situ}, the balance between \textit{C}_{3} and CAM carbon fixation shifted rapidly in response to changes in water availability. When water was plentiful, \textit{M. crystallinum} fixed carbon dioxide by the \textit{C}_{3} pathway and grew at rates comparable to other \textit{C}_{3} species. Under drought conditions, \textit{M. crystallinum} fixed carbon by the CAM pathway at an average rate which exceeded 1 nanomole of carbon dioxide per square centimeter of leaf surface per second, a very high rate for a CAM plant.

Introduction

Crassulacean Acid Metabolism (CAM)—the process by which many succulent plants fix external carbon dioxide to form organic acids in the dark and refix internally generated carbon dioxide to carbohydrates in the light—is generally considered to be an adaptation to arid environments which achieves water conservation at the expense of slow growth. The transpiration ratio (g H\textsubscript{2}O transpired/g CO\textsubscript{2} assimilated) of plants using CAM ranges from 25 to 125 whereas that of \textit{C}_{3} and \textit{C}_{4} plants ranges from 450 to 600 and 250 to 350 respectively (Szarek and Ting, 1975). By this measure, CAM plants are at least two times more efficient in their water use than are \textit{C}_{3} or \textit{C}_{4} plants. The maximum carbon fixation rates of \textit{C}_{3} and \textit{C}_{4} plants, however, are typically several times faster than those of CAM plants: \textit{C}_{3} rates vary between 1 and 6 nMoles CO\textsubscript{2} cm\textsuperscript{-2}s\textsuperscript{-1}, \textit{C}_{4} between 2 and 5, and CAM between 0.1 and 0.8 (Black, 1973; Mooney et al., 1976).

\textit{Mesembryanthemum crystallinum} is an annual CAM plant which has spread rapidly along the coast of California (Moran, 1950; Philbrick, 1972). In the laboratory studies of Winter (Winter, 1974a, b) this species rapidly shifted the balance between \textit{C}_{3} and CAM carbon fixation as water stress varied: \textit{C}_{3}

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was the predominant method of carbon assimilation when water stress was low, but CAM assimilation increased as water stress increased. The maximum carbon fixation rates measured in these studies were 0.47 nMole CO$_2$ cm$^{-2}$ s$^{-1}$ for C$_3$ and 0.13 nMole CO$_2$ cm$^{-2}$ s$^{-1}$ for CAM (Winter, 1974b). Such low rates seem inconsistent with $M$. crystallinum's success in Mediterranean climates. The present study examined whether or not $M$. crystallinum growing under natural conditions exhibited rapid growth rates as well as a flexible carbon fixation response to water stress.

Materials and Methods

A small population of $M$. crystallinum grows along a raised path which borders the salt marsh formed by San Francisco Bay at Palo Alto, California. Atriplex semibaccata, Mesembryanthemum nodiflorum, and the Eurasian grasses, Hordeum vulgara, Lolium multiflorum, Bromus rigidus, and Bromus mollis, are the other major species at this site. The present study was conducted entirely on one patch of $M$. crystallinum 3 m $\times$ 1.5 m. Such a small sample site was chosen to reduce microclimate variation.

During the 1975 growing season (February through July), measurements were made on one age class of $M$. crystallinum which had germinated in mid-January (Age Class 1) and on another which had germinated in mid-February (Age Class 2). From February to May, both age classes grew as low-lying rosettes which had two major leaf pairs set perpendicularly. The plants assumed at the end of May a reproductive growth form with many branches bearing comparatively small leaves. Flowering occurred from the middle of June through July. By August, most of the plants had set seed and died.

On each sampling date, three soil cores from the soil surface to 7 cm deep were taken at random points in the plot and sealed in cans. Three plants from one age class and three from the other, all of which had been marked the previous sampling date, were photographed against graph paper to determine plant surface area. Six neighboring plants, similar in size and stage of development to the first six, were photographed for plant area and marked for the next sampling date. At dawn, the first six plants were sampled. Discs of known area were punched from a leaf of both major leaf pairs for the Age Class 1 plants and from a leaf of the older leaf pair for the Age Class 2 plants. These discs were either kept on dry ice or sealed in cans. Samples from the opposite leaves of the same plants were taken again at dusk and kept on dry ice.

The soil samples were weighed, dried for 72 h at 105°C, and reweighed to calculate soil moisture in percent dry weight. The leaf samples which were kept on dry ice were weighed, ground with a mortar and pestle, boiled in 15 ml of water for 3 minutes, and titrated to an end point of pH 6.4 with 0.01 normal sodium hydroxide to determine both fresh weight per unit area and titratable acidity per unit fresh weight. In $M$. crystallinum, the change in titratable acidity to a pH of 6.4 results from the accumulation of malate at night and the breakdown of malate during the day by the CAM process (Winter and Lüttge, 1976); therefore, the change in titratable acidity is an accurate measure of the amount of CO$_2$ fixed by CAM. The leaf samples which were sealed in cans at dawn were dried for 72 hours at 70°C and weighed to calculate plant dry weight per leaf area. The dry plant samples were then analyzed for carbon isotope ratio ($^{13}$C/$^{12}$C) with a mass spectrometer (Troughton et al., 1974).

The relative growth rates for plants with the rosette growth form were determined using the change in plant area from one sampling date to the next and the conversion factor between leaf area and dry weight. Precipitation was measured at the Palo Alto Weather Station located 3 km from the field site.

Plants for CO$_2$ and H$_2$O exchange analysis were excavated with the surrounding soil on March 29 and June 6. The plants were enclosed in a cuvette identical to that pictured in Bartholomew (1973) and were monitored with a CO$_2$ and H$_2$O exchange system similar to that described in Björkman et al. (1973). For the measurements of the dark carbon fixation rates, the temperature and humidity of the chamber were changed every hour to match the temperature and humidity.