



The Boyce Thompson Southwestern Arboretum near Superior, Arizona displays a wealth of cacti in greenhouses and on the grounds. The various forms, shapes, sizes and colors represent various adaptations of one basic life form successful in the desert because of crassulacean acid metabolism.

Crassulacean Acid Metabolism. The various types of cacti all have one overwhelmingly important adaptation which enables them to succeed under harsh desert conditions. This adaptation manifests itself both anatomically and physiologically. Anatomically the sign of the syndrome is the succulent condition; physiologically the indication is "crassulacean acid metabolism." When plant scientists finally became aware of the chemistry and functioning of succulent plants they began to relate physiology to internal anatomy and external morphology. Soon it became apparent that the succulent life form was exploiting diurnal changes in temperature and osmotic pressure to forge a new way of living.

There were several clues and questions which eventually led to an understanding of "succulentism" as a life form: 1) Although the photosynthesis of plants is based on the coming together of CO_2 and H_2O in the presence of chlorophyll in sunlight, the stomata of cacti and other succulents open only at night so that CO_2 enters the leaf in darkness! How could photosynthesis occur? 2) The plants are rooted in a shallow soil layer on the surface of the desert. This inhospitable layer would seem the least desirable for plant roots because it dries out so quickly and completely following precipitation. Why don't the roots extend deeper to moist soil? 3) Cacti and other succulents have a thick waxy epidermal covering and the stomata close in the daytime to very effectively isolate and insulate the internal tissues. How does transpiration occur? 4) The inner tissues are gel-like, containing large amounts of water and a veritable pool of organic acids [bitter when tasted]. Why is the gel so acid? 5) The life form is successful under a [subtropical] regime of hot days and cool nights with little or no winter freezing. Why is it relatively unsuccessful under fully tropical or temperate conditions?

The various answers and other bits of information proved to be pieces of a fantastic jig-saw puzzle which have now carefully been fitted together. The organic acids have proven to be in a temperature-dependent equilibrium with carbon dioxide, being upgraded by CO_2 when cool, but giving up CO_2 when warm. Thus, with stomata opening at night, carbon content of the succulent tissues increases in

proportion to the degree of coolness. During warm tropical nights relatively little CO_2 could be fixed to fuel metabolism. The shallow roots absorb water from even the lightest of rains, the water being quickly stored in the succulent gel with carbon-enriched acids. Such water-filled tissues are extremely susceptible to freeze damage and are at considerable disadvantage during temperate-zone winters. In the daytime the sun shines through the waxy epidermis, providing crucial warmth to split CO_2 chemically from the acids (and to vaporize H_2O), while providing light to photosynthetically combine captive CO_2 with captive H_2O to form sugar, the fuel which drives metabolism. Due to the thick waxy epidermis (and stomata closing through the daytime), the plant body literally acts as a "pressure cooker" to hasten the chemical reactions and to keep the captive CO_2 and water vapor from escaping! This manner of functioning is totally different from that of other plants. A broadleaf tree, for example, to bring water up from the depths of the ground, must transpire water vapor through the stomata to the atmosphere, creating an evaporative engine which pulls an unbroken chain of water molecules up through the vascular tissue from the roots eventually to the leaves to be used in photosynthesis. In such a "normal" plant the CO_2 constantly enters the leaves through the stomata throughout the day as some water vapor is transpired out to the surrounding air. But a cactus or other succulent would quickly lose its precious store of water if it transpired in this manner. Without significant transpiration (due to closing of stomata in daytime), cacti and succulents rely on osmotic pressure and capillarity to draw water up from the roots into the plant body, mechanisms incompatible with raising moisture from great depths of soil.

In the case of succulentism, the "goodness of fit" of the various pieces of the puzzle make a coherent whole which is so perfect as to suggest that other desert life forms must also have comparable secrets which we have not yet unlocked! The present issue of *Desert Plants* attempts to delve into the functioning of certain life forms of the Sonoran Desert. With regard to many of these we are as yet at a very imperfect state of knowledge. In several cases we have enough pieces to the jig-saw puzzle to see that a marvelous picture will someday emerge.