Simulation of plant temperature and water loss by the desert succulent, *Agave deserti*

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Summary. A simulation model has been developed to describe the thermal relations of individuals of an important group of desert succulents, the agaves, similar to previous modeling efforts on cacti. The model utilizes an energy budget approach to evaluate the effect of various morphological and microclimatic parameters on plant temperature and water loss. For an *Agave deserti* 0.5 m tall with a basal rosette of 60 leaves, the predicted surface temperatures differed by an average of only about 1°C from those measured in the field in the western Sonoran Desert. Simulations indicated that leaf and stem temperatures as well as plant water loss were especially sensitive to changes in air temperature. Nocturnal stomatal opening reduced leaf surface temperatures by only 1.4°C. Increasing the shortwave absorptance from the measured value of 0.45 to 0.80 caused the maximum leaf surface temperature to increase 8°C. Stimulated increases in plant size markedly reduced the diurnal range of stem tissue temperatures, and simulated decreases in size reduced the diurnal range in leaf surface temperatures. The small stature of *A. utahensis* would result in higher minimum leaf temperature and may account for its survival at a cold site in Nevada. Water loss per plant varied approximately as the square of the linear dimensions, which may help explain the decreasing height of agave species with increasing aridity from central Mexico northward. Thermal buffering of the meristematic region in the stem apex by the surrounding massive leaves may also be quite important for the growth and distribution of agaves.

Introduction

Many aspects of the physiology and ecology of desert succulents depend on temperature, such as stomatal opening, nocturnal acidity increase, water-use efficiency, tissue survival, and ultimately plant distribution. Thus, prediction of surface and internal temperatures is an important objective for understanding the special morphology and adaptations of this group. In contrast to the relatively thin leaves of C₃ and C₄ plants, the massive photosynthetic organs of succulent CAM plants can store a considerable amount of heat. Consequently, special modifications of the conventional leaf energy budget analysis (Gates 1980) are necessary to predict temperatures for plants where heat storage and internal heat conduction must be considered.

Lewis and Nobel (1977) developed a computer simulation model involving the division of cactus stems into discrete subvolumes or “nodes” to examine thermal relations, an approach commonly adopted by heat transfer engineers for systems that are too complex to yield analytical solutions (Kreith 1973). In formulating the model the plant is visualized as a set of isothermal nodes, and an energy budget including terms for shortwave irradiation, infrared radiation, latent heat, convection, conduction, and heat storage is calculated for each node. Iterations are performed by computer until the energy into each node minus the energy out equals the energy stored, taking into consideration the interaction between nodes, such as by heat conduction. Such a nodal analysis has been applied to a variety of cactus species to investigate the effects of different morphological and environmental parameters on surface temperature and plant distribution (Nobel 1980a, b). Although the Cactaceae may be the most conspicuous group of succulents in the North American deserts, the Agavaceae and Crassulaceae are also important components of the desert flora whose thermal relations have received relatively little attention (Curtis 1936; Gates 1980). In this study, energy budget modeling using a nodal system has been extended to *Agave deserti*, a leaf succulent common in the Mojave and Sonoran Deserts.

The simulation model for *A. deserti*, which incorporates the radiation interception model developed for this species by Woodhouse et al. (1980), helped quantify the effect of various parameters on its surface and internal temperatures. *A. deserti* is characterized by a basal rosette of massive, opaque leaves that can have temperatures substantially different from air temperature, since a significant amount of mass is available for heat storage relative to the surface area for energy dissipation. The relatively complex geometry of the rosette form of *A. deserti* influences the interception of shortwave irradiation as well as infrared (longwave) and convective exchanges, which in turn affects interior temperatures. The apical meristem is embedded inside a central region of folded, developing leaves which together with the massive mature leaves can buffer the effects of changes in leaf surface temperature, delaying temperature extremes at the meristem and reducing their diurnal range.

After constructing the model, the simulation predictions were compared with field measurements for its verification. The effects of changes in environmental and morphological parameters such as plant size, shortwave absorptance, and stomatal conductance on the thermal relations of *A. deserti*...
were then analyzed quantitatively. Finally, the influences of temperature and water loss on distribution of agaves were considered.

Materials and methods

Plant material

_Agave deserti_ Engelm. (Agavaceae) was investigated at the University of California Philip L. Boyd Deep Canyon Research Center in the western Sonoran Desert (33°88′ N, 116°24′ W). A large natural population of _A. deserti_ occurs in this region at elevations between 250 and 1,600 m. The computer model was based on morphological measurements on a representative plant that was 0.50-m tall and had 60 unfolded leaves approximately 0.35 m long. This plant occurred at an elevation of 850 m and exhibited the radial symmetry typical of solitary agaves.

Plant properties

The conductance to water vapor loss (_g<sub>ww</sub>_ ) was determined in the field on 14–15 February 1981 with a Lambda Instruments LI-60 diffusion resistance porometer and an LI-20 sensor. Values were routinely obtained at midlength on leaves oriented approximately 45° to the horizontal; stomates were substantially open (_g<sub>ww</sub> > 1.5 mm s⁻¹) from 2200 to 0500 h. Surface temperatures were measured with 0.13-mm-diameter copper-constantan thermocouples or an infrared thermometer (Barnes Engineering PRT-10). Internal leaf temperatures were measured with thermocouples 0.51 mm in diameter.

Shortwave absorptance was determined with an integrating sphere radiometer using solar irradiation (Dunkle et al. 1960; Smith and Nobel 1977). Leaf absorptance, calculated by subtracting leaf reflectance from 1.00 (transmittance was zero), averaged 0.45 ± 0.04 (standard deviation for eight measurements). The thermal conductivity was determined from the heat flux measured with calibrated heat flux plates (Thermonetics HC21-18-10EC); the leaf tissue at 25° C had a thermal conductivity that was 73% of that for water. Additional data on morphology were obtained from Woodhouse et al. (1980).

An _A. deserti_ of similar dimensions to that above was used in the determination of the heat convection coefficients for the four cardinal directions and various nodes for wind speeds from 0.5 to 5.0 m s⁻¹. The nodal convective heat flux was calculated from measurements of the temperature gradient in attached leaves oriented at 0°, 45°, and 90° to the horizontal. Shortwave irradiation, net longwave irradiation, and latent heat were negligible during the measurement of the convection coefficient. All outputs from thermocouples and thermopiles were recorded with a Doric Digitrend 220 data logger. Compared to the previously determined heat convection coefficient for the barrel-shaped stem of _Ferocactus aeanthodes_ (Lewis and Nobel 1977), the heat convection coefficient was 4.5 times greater for the nodal region at the leaf tip (Fig. 1a), 0.7 at midleaf, and 0.4 times as large for the nodal region at the leaf base.

Microclimatic measurements

Microclimatic measurements were made in the field on partially cloudy winter days (14–15 February 1981). Relative humidity was recorded with a WeatherMeasure II311 hygrothermograph located 0.5 m above the ground. Shielded thermocouples were used to measure air temperature near the plant and at 2 m. The mean hourly water vapor concentration was 4.5 ± 1.7 g m⁻³. Effective environmental IR temperatures were determined with an infrared field thermometer directed to the sky or horizontally in the four cardinal directions. The mean hourly sky temperature was −8.6 ± 5.1° C. Total solar irradiation on a horizontal surface was measured hourly with a Kipp & Zonen CM5 Moll-Gorczyński pyranometer and amounted to 14.3 MJ m⁻² day⁻¹, of which about 32% was diffuse. Diffuse irradiation was determined by occluding direct solar irradiation from the pyranometer. Wind speeds at various heights were measured using Thornthwaite 106 cup anemometers, e.g., the mean hourly wind speed at 2 m was 1.38 ± 0.40 m s⁻¹. The wind speed in m s⁻¹ at a particular node (_v<sub>node</sub>_ ) was generated from a regression equation relating node height in m (_h_) and prevailing wind speed at 2 m above the ground in m s⁻¹ (_v<sub>2m</sub>_): _v<sub>node</sub> = (0.083 + 0.78 _h_ −0.16 _h_²) × _v<sub>2m</sub>_.

Computer simulation model

To describe the energy balance with heat storage and conduction, an _A. deserti_ 0.50-m tall (Woodhouse et al. 1980) was modeled as nearly 800 isothermal subvolumes or nodes (Kreith 1973; Lewis and Nobel 1977). The temperature of each node was affected by the temperature of all neighboring nodes, the initial temperature estimate being based on the temperature distribution of the previous hour. Subsequent iterations were used to correct the temperature of each node until the net flow of energy between nodes was zero.

Each leaf consisted of three interior nodes and nine massless exterior (surface) nodes (Fig. 1a) of which three were on the upper surface and on each of the two lower surfaces. The stem (Fig. 1c) had 8 pie-shaped interior nodes plus a central interior node in each of 6 levels on top of which were 8 unfolded leaves each consisting of a single interior and exterior node (Fig. 1b). Heat conduction occurred across the surface areas common to two adjacent nodes, the conduction path lengths being between nodal centers of mass (Kreith 1973). In the energy balance of an exterior node, radiation, convection, latent heat, and heat conduction were included, whereas an interior node

![Fig. 1a-c. Schematic illustration of nodal arrangements.](image_url)