Leaf Temperatures of Desert Plants

Abstract. Temperatures of small leaves of many desert plants are within $3^{\circ}C$ of air temperature in contrast to the temperature of Opuntia in the same locale; this plant has a temperature 10° to $16^{\circ}C$ above air temperature. Theoretical justification for the observation is given based on an energy budget analysis.

Solar radiation on plants growing in hot environments may cause their death if the plant temperature rises above a critical level. Several physiological processes-photosynthesis, respiration, enzyme activity, and protoplasmic streaming-begin to break down in most plants when the plant temperature exceeds 42° to 45° C (1). Temperatures as warm as 50°C have been measured in sunlit leaves of broad-leaved plants when the air temperature was $30^{\circ}C(2)$. Leaf temperatures exceeding the air temperature by 10°C are common. Transpirational cooling reduces leaf temperature (3) and may keep the sunlit leaves within a few degrees of air temperature.

Table 1. In full sun the leaf temperature of most desert plants is near the air temperature although the soil (often just a centimeter or two away) is very much above air temperature. The *Opuntia* is an exception. It can endure very high plant temperatures but suffers very little heat damage. These observations were made at Arches National Monument, Capitol Reef National Monument, and White Canyon, Utah, in August 1967.

Time	Temperat	Temperature (°C)	
x mite	Air	Leaf	
Artemesia tridentata			
0830	24	24	
1000	30	32	
1500	35	37	
Ephedra sp.			
0830	24	25	
1000	30	31	
Pinus edulis			
0830	24	23	
1100	30	33	
1300	32	34	
Juniperus sp.			
0830	24	23	
1000	30	30	
1400	32	33	
Graminaae*			
0830	24	23	
1000	30	30	
1200	32	35	
Onuntia sp			
0830	24 optimina sp.	34	
1000	30	45	
1030	30	46	
Gutierrezia sarothrae			
1000	26	27	
1400	33	31	
1630	31	30	
1050	Soil surface	50	
0830	24 Sou Surface	36	
1000	30	48	
1030	30	40	
1100	30	50	
1200	30	55	
1400	32	55	
1400	32	00	

* Not identified.

Desert plants often have little available water for extended periods. They must use other means to prevent sunlit leaves from becoming too warm when the air temperature rises to 50°C or more. The leaf temperatures of many plants of semiarid regions are very near air temperature. There are good physical reasons why the temperature of small leaves stays close to air temperature. Table 1 shows the leaf temperatures for fully sunlit leaves. Significantly, the leaf temperatures of all plants except Opuntia were within 2° or 3°C of air temperature. The blade temperatures of Opuntia were 10° to 16°C above air temperature. The temperatures of the sunlit soil surfaces were from 12° to 28°C above air temperature.

The temperature of a leaf in any environment depends upon the flow of energy between the leaf and the environment. The energy budget for a plant leaf is written as follows:

$$Q_{\rm abs} = \epsilon \sigma T_{l}^{4} \pm k_1 \left(V/D \right)^{\frac{1}{2}} \left(T_l - T_{\rm a} \right) +$$

 $L\frac{{}^{ids}(T_{i}) - r.h. {}_{s}\rho_{a}(T_{a})}{r_{i} + k_{2} \frac{W^{0.20}D^{0.35}}{V^{0.55}}}$ (1)

where $Q_{\rm abs}$ is the radiation (sunlight and thermal) absorbed (cal cm⁻² min⁻¹), ϵ is the emissivity of leaf surface, σ is the Stefan-Boltzmann constant (cal cm^{-2} $\min^{-1} {}^{\circ}K^{-4}$, T_i is the leaf temperature in degrees Kelvin in the radiation term and in degrees Celsius in other terms, k_1 is the convection coefficient, V is the wind speed (cm sec⁻¹), D is the leaf dimension in the direction of the wind (cm), W is the leaf width (cm), T_a is the air temperature (°C), L is the latent heat of evaporation of water (cal g^{-1}), $s\rho_l$ (T_l) is the density of water vapor at saturation within the leaf mesophyll at the leaf temperature (g cm⁻³), $_{s\rho_{a}}$ (T_a) is the density of water vapor at saturation of the air at the air temperature (g cm⁻³), r.h. is the relative humidity, r_i is the internal diffusion resistance to water vapor of the leaf (sec cm^{-1}), and k_2 is a coefficient for the external boundary-layer resistance. The total absorbed radiation is dissipated by reradiation, convection, and transpiration; only minute quantities are dissipated through respiratory action. The leaf temperature adjusts until the energy budget for the leaf balances.

The coefficients in Eq. 1 were confirmed in the laboratory. The transfer of heat and moisture from leaves and simulated leaves of blotter paper, mounted in a wind tunnel, was determined experimentally. The determination of these coefficients is very difficult, particularly for small leaves. The coefficients are:

If $W \gg D$, $k_1 = 10^{-3}$ If $W \ll D$, $k_1 = 16.2 \times 10^{-3}$ If W = D > 5 cm, $k_2 = 35 \times 10^{-3}$ If $W = D \le 5$ cm, $k_2 = 26 \times 10^{-3}$

Equation 1 was programmed for computer analysis for any given value of radiation absorbed, air temperature, wind speed, relative humidity, leaf size, and diffusion resistance. The computer solved the energy budget equation for leaf temperature and transpiration rate. Equation 1 is plotted to show transpiration rate as a function of leaf temperatures for leaves of different sizes and for different water vapor (diffusion) resistances (Fig. 1) (the constant environmental conditions are 1.2 cal cm^{-2} min⁻¹ radiation absorbed, an air temperature of 30°C, a relative humidity of 20 percent, and a wind speed of 100 cm sec $^{-1}$). These conditions were reasonably close to the conditions existing when some of the field observations were made. Clearly the temperature of a leaf measuring 1 by 1 cm or less will remain close to air temperature.



Fig. 1. Transpiration rate versus leaf temperature as a function of leaf size and internal diffusion resistance at 1.2 cal cm⁻² min⁻¹ of absorbed radiation, for an air temperature of 30°C, a relative humidity of 20 percent, and a wind speed of 100 cm sec⁻¹.

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This is the result of the convection term dominating the energy budget for small leaf sizes. Leaves larger than 1 by 1 cm may have temperatures very much above air temperature, particularly if the leaf's internal resistance to moisture is large. It would seem that there may be a physiological advantage for plants in arid or semiarid regions to have small leaves. Apparently, Opuntia, having large blades and using little water. has evolved a protein structure which is stable at high temperatures.

Measurements of surface temperature were made with a new pistol-grip infrared radiometer designed by the staff of Barnes Engineering Corporation. The radiometer weighs 1.1 kg, has a field of view of 20°, a time constant of 2 seconds, and an aperture of 1.2 cm. A germanium filter cuts out reflected sunlight, but the radiometer should not be used at the angle of specular reflection to the sun. Surface temperatures from -10° to 60°C were measured and were accurate within \pm .25°C. Surface temperatures of animals, plants, soil, and rocks, and sky and cloud temperatures were measured with the new radiometer.

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References and Notes

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Adoptive Autoimmune Encephalomyelitis in Inbred Guinea Pigs: Immunological and Histological Aspects

Abstract. Major variables which determine the induction and severity of adoptive autoimmune encephalomyelitis are the age and strain of the animal, and the amount of killed mycobacteria in the adjuvant. Control of these factors results in consistent production of this disease in high incidence and in severe form. The pathologic changes in the central nervous system can be correlated with the clinical disease. Maturity of the target tissues in the central nervous system of the newborn appears to be an important factor which distinguishes the response of the guinea pig from that of other species.

Adoptive transfer (1) of autoimmune encephalomyelitis (AE) between histocompatible guinea pigs (strain 13) has been regularly used recently to elucidate the mechanisms of autoimmune diseases (2). Nevertheless, the ease of reproducibility and the high incidence and severity of the passive AE has not been duplicated with other autoimmune systems (3), even when the same strain of guinea pig was used. This discrepancy has given rise to questions about the nature of the AE produced by adoptive transfer of lymph node cells in inbred guinea pigs. Difficulties encountered by others in inducing passive AE have warranted a delineation of the experimental variables which determine the outcome of appropriate transfers of adoptive autoimmune disease.

Strains 2/N and 13/N guinea pigs were used; adults were used as donors of lymph node cells (4) and animals of various ages were used as recipients. Donors were immunized with either guinea pig or rabbit spinal cord in complete Freund's adjuvant. Each

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animal received 0.5 ml of a water-inoil emulsion, incorporating 0.25 ml of 50 percent suspension of spinal cord in phenol water, 2.5 mg of killed Mycobacterium tuberculosis, and 0.25 ml of the oil phase (Arlacel A-Bayol 55) unless otherwise noted. A single immunizing dose was given intradermally into several sites in the nuchal region and the footpads. Most transfers

Table 1. Effect of strain and age of guinea pigs on incidence of adoptive AE. Donors and recipients were of the same strain. The results are expressed as the number of afflicted out of the total number tested. All donors were adults or old adults.

Recipient	Incidence of AE	
	Clinical	Death
	Strain 13	
Newborn	9/9	6/9
Young	23/27	16/27
Adult	14/14	13/14
Old adult	7/16	4/16
	Strain 2	
Young	0/9	0/9
Adult	0/3	0/3
Old adult	0/8	0/8

were carried out 5 days after sensitization of donors. The procedure of lymph node transfer was essentially the same as previously reported, except that, instead of stainless steel mesh, squares of nylon stocking were used to obtain uniform single-cell suspensions, and that, instead of Hanks's balanced salt solution, Eagle's Spinner medium containing glutamine was used (4). Recipient animals were weighed daily and observed for signs of clinical disease. Brain, spinal cord, and other tissues were taken for histologic examination at the time of death or of killing when moribund. Death from adoptive AE occurred usually from 8 days to 2 weeks after transfer.

Guinea pig spinal cord has been shown to be a more potent antigen than rabbit spinal cord in producing disease by active immunization (5); however, no difference attributable to these antigens was noted in the recipient animals under the conditions of these adoptive transfer experiments. This may be due to the fact that the donor animals had attained a size in which maximum sensitization occurred when either antigen was used. Consequently, for each age and strain group, the findings based on guinea pig and rabbit spinal cord antigens were pooled.

Successful transfers are more difficult with older recipients (Table 1). This is consistent with Celada's report of a barrier to syngeneic transfer of immune cells which increased markedly with age (6). However, in the guinea pig this might result from a dilution factor associated with a greater net increment of tissue of the central nervous system (CNS) or the reticuloendothelial system in the larger recipients. The resistance of strain 2/N animals to active AE is marked (7) but not absolute; full-grown female strain 2/N animals immunized with homologous antigen regularly develop florid, acute AE (5). However, even under optimum conditions for age and antigen (as with fullgrown adult donors to young recipients), transfers between strain 2/N guinea pigs resulted neither in overt clinical disease nor in histologic changes in the CNS without clinical disease (8).

As noted, 2.5 mg of mycobacteria per guinea pig were used routinely in the adjuvant for sensitization. Decreases below 1.0 mg caused a striking reduction in incidence of adoptive AE in recipients (8 of 9 had lethal AE at 1.0 mg; 0 of 9 had no signs of disease