

## Thermal ecology of an embedded dwarf succulent from southern Africa (*Lithops* spp: Mesembryanthemaceae)

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The 'stone plants' of southern Africa (*Lithops* spp.) live embedded in the hot surface layers of the soil: a 'window' for admitting light into the leaf is the only part of the plant exposed to the air. Many of the common mechanisms for keeping the leaves of desert plants cool are therefore ineffective for leaf temperature control in these plants. Model simulations and experimental measurements in the field indicate that leaf temperatures of *Lithops* are governed by three principles: (1) leaf and soil temperatures are strongly coupled; (2) variations of the surface energy budgets of the leaves alone have little effect on leaf temperature; (3) variation of window clarity causes significant variation of leaf temperature. Among the implications of these principles for the thermal ecology of *Lithops* and other embedded dwarf succulents are: (1) thermally coupling the plant and soil combines the plant's thermal capacity with the soil's and reduces daily variation of leaf temperature; (2) the steep vertical heterogeneity of temperature that is typical in soil keeps the deeper areas of the plant (containing the chlorenchyma) cool relative to the hotter surface regions of the plant during the hottest periods of the day; (3) variation of leaf color has little effect on leaf temperature, so that leaf color may be selected primarily for reasons other than for temperature adaptation; (4) variation of window clarity is probably the sole thermal adaptation to hot conditions that embedded dwarf succulents can employ.

### Introduction

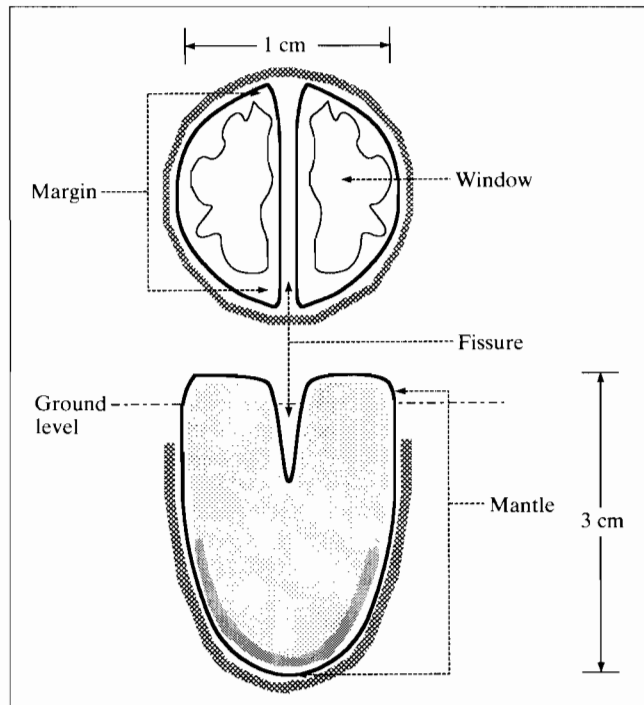
*Lithops* (Mesembryanthemaceae) is a genus of leaf succulents endemic to the arid zones of southern Africa (Cole, 1988). These plants are unusual in two respects. First, most of the body of the plant lies buried in the upper few centimeters of soil: little or none of the plant extends above the soil surface. The only portion of the plant exposed directly to air is a flat face that lies roughly flush with the ground surface (Fig. 1). *Lithops* share this habit with several other genera of Mesembryanthemaceae popularly known as the subterranean dwarf succulents, although embedded dwarf succulent is a more accurate description. Second, the face of the plant is often clear, forming a 'window' that admits light into the interior of the plant (Fig. 1).

Although *Lithops* show certain typical adaptations to desert life, like succulence and

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crassulacean acid metabolism (Cockburn, 1974), their unusual features appear to preclude many of the thermal adaptations presumed to be common among desert plants (Nobel, 1983; Gates, 1980; Hadley, 1972). *Lithops* leaves are completely embedded in soil: they therefore cannot orient away from direct sun or engage in self-shading. *Lithops* do not have an erect habit: they therefore can neither escape hot surface boundary layers nor cool their leaves convectively. The water reserves of *Lithops* are small and rainfall in their habitats is scarce and unpredictable: cooling of the leaves by evapotranspiration would presumably have to be infrequent. *Lithops*' small size makes their thermal capacity small: their ability to use thermal inertia to damp daily variations of leaf temperature will therefore be limited.

Because the soil surface is typically the hottest environment to be found in deserts (Cloudsley-Thompson, 1977; Graetz & Cowan, 1979), it is reasonable to suppose that plants like *Lithops* either must endure very high temperatures through the day, or have some unique adaptations to this harsh thermal environment. This paper deals with this supposition, approaching it in two ways. First, we use a numerical model of leaf temperature in an embedded dwarf succulent, and evaluate how effective certain possible



**Figure 1.** Schematic diagram of a *Lithops*. *Top panel:* View looking down on a plant. *Bottom panel:* Cross-sectional view of a plant (the ephemeral roots are not shown). The plant has the overall shape of a right circular cone with a blunted apex. In a plant *in situ*, the blunt apex of the cone is embedded pointing down into the soil, while the base of the cone, or face, is exposed at the soil surface. An individual plant normally has two leaves, which together form the head. The head in an adult plant is roughly 1 cm in radius at the face and roughly 3 cm long. Each leaf in a head is separated from the other by a fissure. Light is admitted to the interior of the leaf through a central window in the face that is bounded by a pigmented zone called the margin. The interior of the leaf is filled with transparent water-storage tissues, and the photosynthetic cells of the plant are located along the inner surface of the frustum of the cone, or mantle. The mantle is usually surrounded by a sheath consisting of the dried remnants of old leaves. ■, sheath; ▨, chlorenchyma; ▩, water storage tissue.

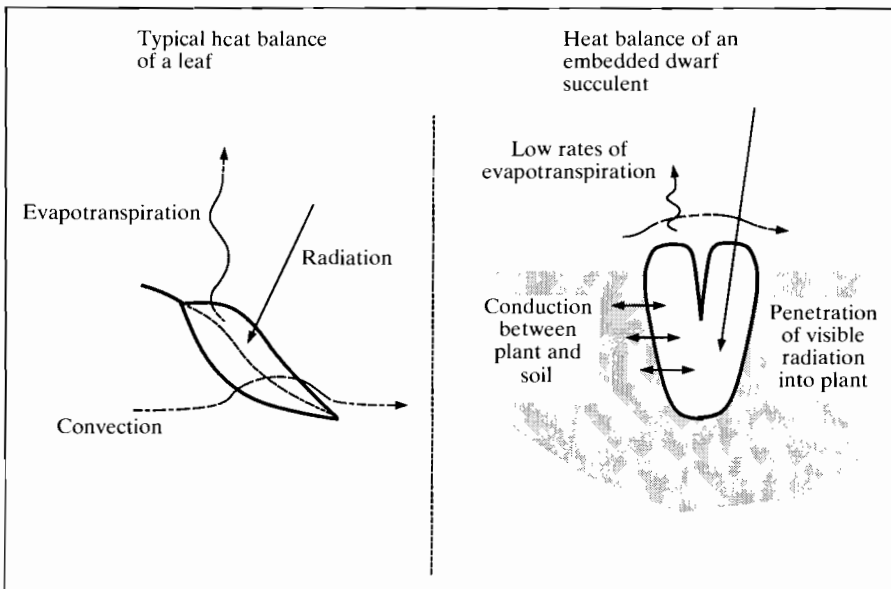
adaptations might be in altering *Lithops* leaf temperature. Second, we measure and experimentally manipulate the leaf temperatures of two species of *Lithops* under field conditions. The aim in these experiments is to evaluate what *Lithops* leaf temperatures actually are in nature, and whether there are any special adaptations for keeping the leaves cool.

### Simulations of *Lithops* temperatures

A 'typical' leaf surrounded on all sides by air exchanges heat with the surroundings by radiation, convection to the air, and evaporation (Fig. 2). The heat balance of a leaf of a subterranean dwarf succulent like *Lithops* may be atypical in several ways (Fig. 2). (1) Conduction to and from the surrounding soil may be a significant component of the leaf's energy budget. (2) Convection heat exchange with the air is probably very small, both because of the small leaf area exposed to the air and the low wind speeds expected to occur close to the surface of the ground. (3) Radiation should be absorbed not only at the leaf face, but also within the leaf, after its transmission into the plant through the window.

We use a numerical model to simulate the distribution of temperature in a cylindrical plug of soil containing a *Lithops* in the center. The model is a conventional steady-state finite difference model (Thomas, 1980) that accounts for the unique attributes of the heat balance of a subterranean dwarf succulent. The soil plug is divided into a series of 900 cylindrical and toroidal nodes. Temperatures of the nodes are estimated by solving the nodes' energy balance equations. Heat exchange between nodes is assumed to be by conduction only. Heat exchange between the surface and environment is modelled using standard models of radiative and convective heat exchanges at soil surfaces (Rosenberg, 1974; Campbell, 1977; Monteith, 1973). Details of the model and the PASCAL code for implementing it are available on request from the senior author.

We simulated the effect of three alterations in the thermal properties of the plant, and



**Figure 2.** The heat balance of a 'typical' leaf compared with that of an embedded dwarf succulent like *Lithops*.

**Table 1.** *Standard conditions for simulation of Lithops temperatures*

Property	Value	Units
Soil conductivity	0.30	$\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$
Soil absorptivity (short-wave)	0.50	
Soil emissivity (long-wave)	0.95	
<i>Lithops</i> internal conductivity	0.60	$\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$
<i>Lithops</i> facial absorptivity (short-wave)	0.50	
<i>Lithops</i> facial emissivity (long-wave)	0.95	
<i>Lithops</i> internal transmissivity	0.10	
Surface irradiance (direct)	800	$\text{W m}^{-2}$
Ratio of diffuse to direct irradiance	0.20	
Air temperature	25.00	$^\circ\text{C}$
Wind speed	2.00	$\text{m s}^{-1}$

two alterations in the properties of the soil. For the plant, we altered (a) the absorptivity of the face of the leaf to visible light (equivalent to changing the color of the face), (b) the long-wave emissivity at the leaf face, and (c) the transmission of visible light into the plant (equivalent to altering the clarity of the window). For the soil, we altered (a) the absorptivity of the soil surface to visible light, and (b) the thermal conductivity of the soil.

We assess the effects of variation in these plant and soil properties by comparing them against benchmark "Standard Conditions", chosen to represent a plant in dry sandy soil during typical sunny day conditions. These conditions are detailed in Table 1. The effect of departure from the standard conditions is depicted as a temperature change map, which shows how the distribution of temperature is changed by the alteration of the property.

## Simulation results

### *Alteration of leaf properties*

With one exception, altering the properties of the plant does little to alter leaf temperature (Fig. 3).

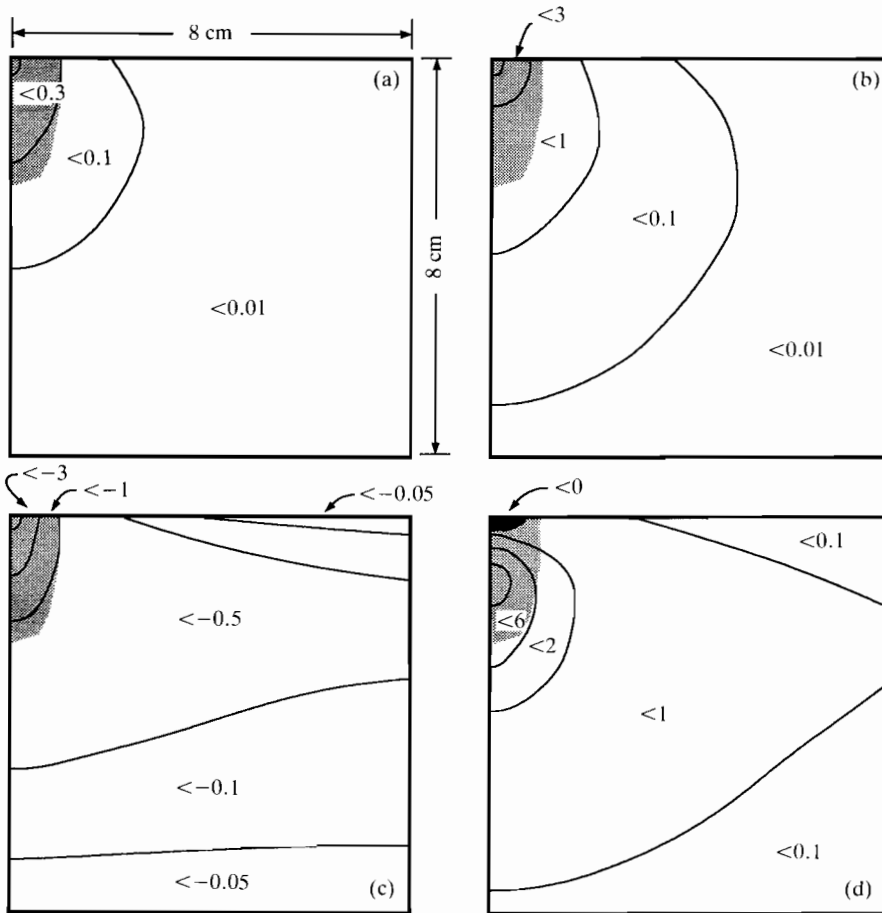
Reducing facial emissivity from 0.95 to 0.5 warms the surface of the plant by less than  $0.5^\circ\text{C}$  [Fig. 3(a)]. This is attributable to a lower re-radiation of energy from the surface of the plant. There is little change of temperature of the surrounding soil.

Increasing facial absorbance of visible light from 0.5 to 0.9 increases the surface temperature of the plant by  $1\text{--}3^\circ\text{C}$  (Fig. 3(b)). Reducing facial absorbance of visible light from 0.5 to 0.1 reduces surface temperatures by  $1\text{--}3^\circ\text{C}$  [Fig. 3(c)]. In both cases, the regions of the plant containing chlorenchyma – the outer margin of the leaf, the deeper regions of the leaf and the mantle – change in temperature by less than  $1^\circ\text{C}$  [Fig. 3(b, c)]. There is little change of temperature of the surrounding soil.

Clarity of the window has the most significant effect on leaf temperature [Fig. 3(d)]. When window clarity is increased by the amount indicated, surface temperature of the leaf is reduced slightly. This is attributable to the lower proportion of incident light dissipated as heat at the face. In the plant interior, however, leaf temperature is dramatically increased, by  $2\text{--}6^\circ\text{C}$  [Fig. 3(d)], with the increase being highest in the center of the plant.

### *Alteration of soil properties*

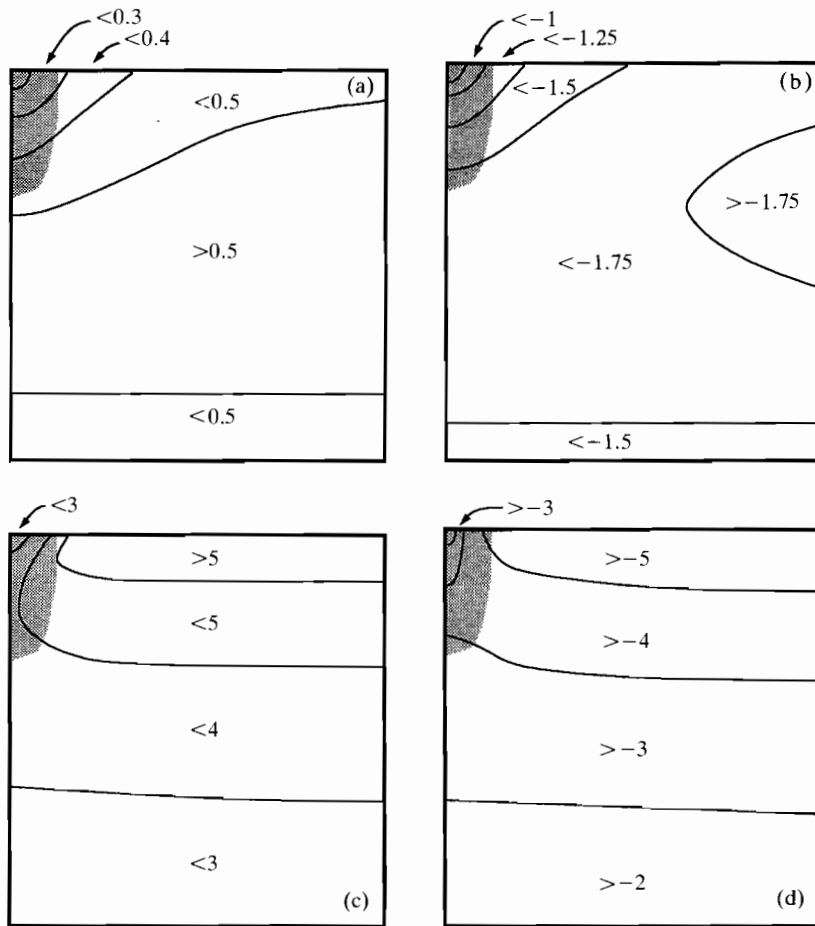
Changing conductivity of the soil significantly altered soil temperature, but had mixed



**Figure 3.** Maps of temperature change in plant and surrounding soil that result from the indicated changes in properties of plant. The stippled area indicates the location of the plant. The curved lines indicate isopleths for temperature difference from the Standard Conditions (Table 1). The numbers indicate the temperature deviation in  $^{\circ}\text{C}$  for the indicated region. For example, the region bounded by the isopleths for  $+0.3^{\circ}\text{C}$  and  $0.1^{\circ}\text{C}$  will change by  $<0.3^{\circ}\text{C}$ . *Panel (a)*: The effect of reducing emissivity from 0.95 to 0.5. *Panel (b)*: The effect of increasing absorptivity of the leaf face from 0.5 to 0.9. *Panel (c)*: the effect of lowering leaf face absorptivity from 0.5 to 0.1. *Panel (d)*: the effect of increasing transmittance from 0.1 to 0.5.

effects on leaf temperature. Reducing soil conductivity  $0.3$  to  $0.1 \text{ W m}^{-1}\text{ }^{\circ}\text{C}^{-1}$  increased leaf surface temperature by less than  $0.3^{\circ}\text{C}$ , and mantle temperature increased by no more than  $0.5^{\circ}\text{C}$  [Fig. 4(a)]. Increasing soil conductivity from  $0.3$  to  $0.9 \text{ W m}^{-1}\text{ }^{\circ}\text{C}^{-1}$  more substantially reduced soil temperature and reduced mantle temperature of the leaf by  $1.0$ – $1.5^{\circ}\text{C}$  [Fig. 4(b)].

Changing the soil's absorbance of radiation significantly altered leaf temperature, mostly because change of leaf temperature is being forced by changes of soil temperature [Fig. 4(c–d)]. When soil absorptivity is increased from  $0.5$  to  $0.9$ , mantle temperature of the leaf is increased by  $4$ – $5^{\circ}\text{C}$ , with leaf surface temperature increasing slightly less,  $3$ – $5^{\circ}\text{C}$  [Fig. 4(c)]. Reducing soil absorptivity from  $0.5$  to  $0.1$  brings about similar, though opposite, changes of temperature. Mantle and leaf interior temperatures are reduced by  $3$ – $5^{\circ}\text{C}$ , and leaf surface temperatures are lowered by  $2$ – $5^{\circ}\text{C}$  [Fig. 4(d)].



**Figure 4.** Temperature difference maps for the effect of varying certain properties of the soil. Conventions as in Fig. 3. *Panel (a)*: The effect of reducing soil conductivity from  $0.3$  to  $0.1 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1}$ . *Panel (b)*: The effect of increasing soil conductivity from  $0.3$  to  $0.9 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1}$ . *Panel (c)*: The effect of increasing absorptivity of the soil surface from  $0.5$  to  $0.9$ . *Panel (d)*: The effect of lowering soil surface absorptivity from  $0.5$  to  $0.1$ .

## Field observations of *Lithops* temperatures

### *Materials and methods*

*Species.* We carried out field measurements of leaf temperature on two species: *Lithops comptonii* in the Ceres Karoo of South Africa and *L. gracilidelineata* in the Hamiltonberg of Namibia. The two species of *Lithops* differ considerably in habitat, facial color and window clarity. *L. comptonii*'s face is dark green to purplish in color and has one of the clearest windows to be found in the genus (Cole, 1988). *L. gracilidelineata*'s face is very light in color and has one of the most opaque windows to be found in the genus (Cole, 1988).

*Habitats.* *L. comptonii* var *comptonii* is confined to a small area northeast of the town of Ceres, in the southwestern Cape Province of the Republic of South Africa. The area is known cartographically as the Ceres Karoo, but is ecologically more properly classified as part of the Succulent Karoo (Hoffman & Cowling, 1987). The Ceres Karoo is dominated

by the low scrubby vegetation known locally as the Karoo Shrubland. The study area is a mountain valley, with average elevation roughly 700 m.

The Ceres Karoo is located in South Africa's winter rainfall climate zone. The climate of this area is poorly characterized and is very unpredictable and heterogeneous (Venter *et al.*, 1986). The Ceres Karoo falls within the 400–500 mm isohyet for mean annual rainfall: roughly 20 per cent of this occurs in the summer. Mean annual temperature is 17.5–20°C, and the mean daily maximum temperature for January is 32°C. Roughly 90 days through the year experience air temperatures greater than 30°C, and between 10–30 days per year have air temperatures less than 0°C. The annual potential evapotranspiration is roughly 1700 mm. In December, potential evapotranspiration is roughly 230 mm, with a rainfall deficit of 210 mm. In June, the potential evapotranspiration is roughly 80 mm with a rainfall deficit of about 20 mm (Venter *et al.*, 1986).

The study area for *L. comptonii* was situated in a gravel flat adjacent to a gypsum quarry. The plants are found in loose, friable soils, comprising either gypsum clay or sand. Much of the site is covered by gravels of quartz, chert, ironstone and gypsum. The gravels are typically smaller than 10 mm diameter, and the color of individual pebbles ranges nearly from black to white. Areas that contained *L. comptonii* typically did not contain any shrubs or other erect vegetation, so there was little possibility of shading by other plants.

*L. gracilidelineata* are found in the Namib Desert, north of the Kuiseb River. All known sites of the species are found within 100 km of the Atlantic coast, as far north as the Brandberg (21°S, 14°30'E) and as far south as the Hamiltonberg (23°S, 14°50'E). The Kuiseb River divides the southern dune sea of the Namib Desert from the northern gravel plains. The Namib gravel plains are roughly 300–600 m elevation, with scattered rocky outcrops 500–1000 m elevation (one, the Brandberg, rises to 2700 m). *L. gracilidelineata* is found on some of these rocky outcrops. The population we studied is probably var *waldroniae* (*sensu* Cole, 1988), and is located in the Hamiltonberg, a chain of uplifted blocks of marble and ironstone. The highest point in the Hamiltonberg is 549 m: the outcrops at the study site rose less than 50 m from the gravel plain, for site elevations of 300–400 m. The site is within the boundaries of the Namib Naukluft National Park.

Individual *L. gracilidelineata* are located in jumbles of marble boulders near the tops of the outcrops, in small pockets of windblown sand that gather in hollows in the rocks and in spaces between boulders. The soil is stabilized by a very thin crust, and is very friable when this crust is broken.

The climate of the Namib also is poorly characterized (Schulze, 1965). It is very arid: the Hamiltonberg falls within the isohyet for < 100 mm mean annual rainfall, and rainfall is evenly distributed through the year. However, like other parts of the coastal Namib, significant amounts of water are imported by intrusion of coastal fogs: rocky outcrops, or Inselbergs, like the Hamiltonberg, are particular beneficiaries of this water. The area is very sunny: Walvis Bay, the nearest weather station, receives more than 80 per cent of the potential annual insolation: the figure for the inland areas is higher (Schulze, 1965).

#### *Instrumentation and field methods*

Temperatures of plants and soils were measured using 30 Ga Type K (chromel-alumel) thermocouples. Temperatures frequently measured were: temperature of the leaf face ( $T_{ls}$ ), temperature of the leaf interior, typically 1 cm into the plant from the face ( $T_{li}$ ), temperature of the soil surface 1 cm from the outer edge of the margin ( $T_{ss}$ ) and soil temperature 1 cm below the surface and 1 cm from the outer edge of the plant's margin ( $T_{sd}$ ). Thermocouples were implanted into the leaves by pushing the tip into the leaf at the desired place. Any resulting leaf wound was sealed with cyanoacrylate adhesive. Soil thermocouples were placed as desired and secured with small clips.

Temperatures of thermocouples were measured in one of two ways. For intermittent measurements, a hand-held digital thermocouple thermometer was used (Model 871,

Omega Engineering, Stamford, Connecticut). For measurements requiring continuous monitoring, a computer-driven data logging system was employed. The system included a battery powered microcomputer (TRS-80 Model 100, Tandy Corporation, Fort Worth, Texas), and a multiplexed 16 channel analog-digital converter (ADC-1, Remote Measurement Systems, Seattle, Washington). Data were recorded onto magnetic tape and later transferred to another computer for analysis. All thermocouples were calibrated against a mercury standard thermometer referable to the South Africa Bureau of Standards.

Meteorological measurements were made using a field-portable meteorological station (Model 101, MC Systems, Cape Town). Air temperatures were measured using shielded solid-state temperature sensors, which also were calibrated against a mercury standard thermometer. Wind speed was measured with a cup anemometer, mounted on a 2 m high mast (stall speed about  $0.2 \text{ m s}^{-1}$ ). Solar insolation was measured using a Monteith tube solarimeter (Delta-T Devices, Cambridge, England), mounted 5 cm from the surface of the ground. Occasional measurements of soil surface reflectivity also were made using the tube solarimeter. Incident radiation was measured with the sensor side up. Reflected radiation was measured by orienting the sensor side down. Surface reflectivity was taken to be the ratio of the two measurements.

#### *Plant facial reflectivity*

Plant facial reflectivity was altered by gluing small aluminum foil disks on the leaf surface. The disks were either left shiny, which gave very high surface reflectivity, or painted with matt black lacquer, which gave very high surface absorbance. Good thermal contact between the foil and leaf face was ensured by using sufficient adhesive to cover the leaf face, and by gently molding the foil cap to the leaf face. Measurements were done around the austral autumnal equinox of 1988, when ambient temperatures of both regions are at their maximum.

For *L. comptonii*, three plants, designated Plants 1, 2 and 3, were chosen for this experiment. The plants chosen were 'double-headed', comprising two pairs of leaves growing from a single rootstock. Each head was designated a (control) or b (experimental). In each plant, four thermocouples were implanted: one each for leaf surface temperature ( $T_{ls}$ ) and leaf interior temperature ( $T_{li}$ ) for both heads a and b. Additionally, a thermocouple to measure  $T_{sd}$  for each plant was positioned near the plant. The facial reflectivities of the plants were altered according to the protocol summarized in Table 2. Temperatures were monitored for a 24 h period commencing on 19 March 1988.

For *L. gracilidelineata*, fifteen plants around the study site were chosen and divided among three groups: Control, Absorptive and Reflective. The group Control left the plants untouched. In the group Absorptive, matt black aluminum caps were fitted to the plant faces. In the group Reflective, plants were fitted with shiny aluminum caps. On the days 29–30 March, the temperatures in and around the plants ( $T_{li}$ ,  $T_{ls}$ ,  $T_{sd}$ ,  $T_{ss}$ ) were measured

**Table 2.** *Experimental design for facial reflectivity experiments on L. comptonii*

Leaf	Plant		
	1	2	3
a	Control	Control	Control
b	Control	Reflective cap	Absorptive cap



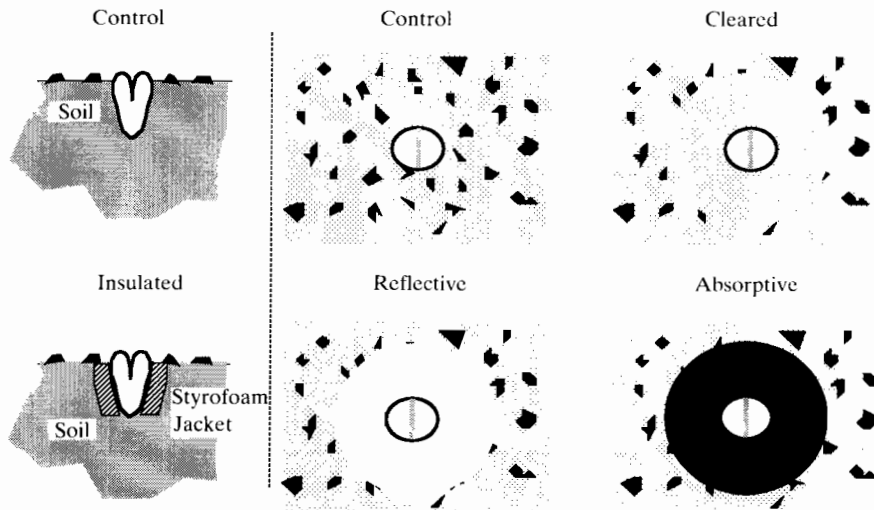
at noon (around 12h00), midafternoon (around 15h00) and evening (around 18h00). The results were analysed in a two-way analysis of variance, with surface reflectivity (Absorptive, Reflective or Control) and location of temperature ( $T_{sd}$ ,  $T_{ss}$ ,  $T_{li}$  and  $T_{ls}$ ) as the main effects. Separate analyses were done for noon, midafternoon and evening.

### Soil reflectivity and soil conductivity

These experiments were carried out on *L. comptonii* only: they were not possible for *L. gracilidelineata*.

On the evening of 19 March 1988, twenty-five plants were segregated into five groups. Within each group, the plants were in close proximity to one another. Each of the five plants in a group was subjected to a different treatment (Fig. 5). The Control treatment did not alter the substratum in any way. For three treatments, the reflectivity of the substratum for a 5 cm radius around the plant was altered. For the Cleared treatment (Fig. 5), the gravel overburden was cleared away, exposing the underlying soil. The Reflective treatment fitted the plant with a circular 'collar' of shiny aluminum foil. The Absorptive treatment cleared away the gravel overburden and painted the exposed soil with matt-black spray lacquer (the leaf surface was left unpainted). In the fifth treatment, Insulated, soil from around the plant was carefully dug away and replaced with a 'jacket' of polystyrene foam. The top layer of soil and gravel was then replaced.

At around 1330 h on the next day, 20 March, temperatures in and around each plant were measured once. Temperatures measured were  $T_{ls}$ ,  $T_{li}$ ,  $T_{ss}$ , and  $T_{sd}$ . Results were analysed in a two-way analysis of variance, with treatment (Control, Cleared, Reflective, Absorptive and Insulated), and location of temperature ( $T_{ls}$ ,  $T_{li}$ ,  $T_{ss}$ ,  $T_{sd}$ ) as the main effects.



**Figure 5.** Schematic diagram of experimental design for soil reflectivity and soil insulation experiment for *Lithops comptonii*. *Left panel:* Control and experimental conditions for the Insulated experimental group. *Right panel:* Control and experimental treatments for soil reflectivity experimental groups. Terms explained in text.

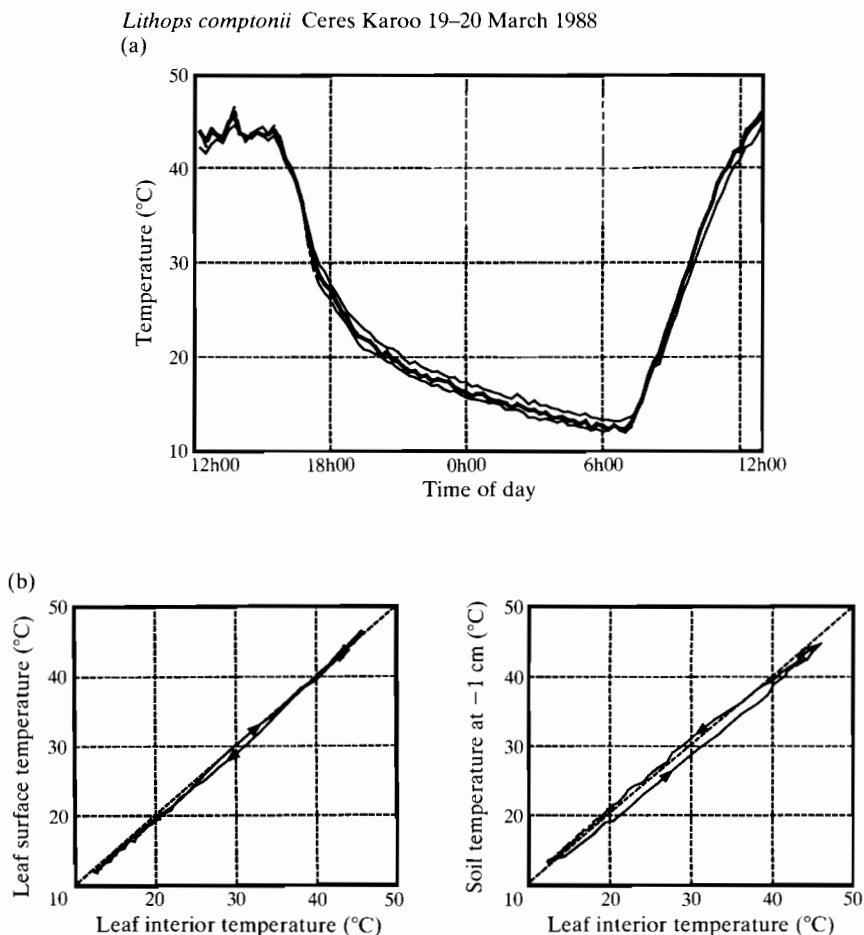
## Results

### *Observations on Lithops comptonii*

All observations and experiments were carried out on 19–20 March 1988. Both days were sunny and clear, with daytime air temperatures reaching a maximum of 27°C, wind speeds at 50 cm above ground averaging roughly 1.5 ms<sup>-1</sup> and maximum insulations of 850 W m<sup>-2</sup>.

*Daily course of temperature.* We monitored the daily course of leaf surface temperature ( $T_{ls}$ ) and leaf interior temperature ( $T_{li}$ ) for three plants. Soil temperature at -1 cm ( $T_{sd}$ ) also was measured. Records for all three plants were similar: a representative record for one is shown in Fig. 6.

The range of temperature experienced by the plant through the day was 12–46°C [Fig.



**Figure 6.** Temperatures in and around a *Lithops comptonii* in the Ceres Karoo on 19–20 March 1988. *Panel (a):* Daily course of temperature for the leaf interior (heavy solid line), leaf surface (dotted line), and the soil 1 cm from the plant and 1 cm deep (thin solid line). *Panel (b):* Phase diagrams for the covariation of leaf surface temperature and soil temperature at -1 cm, both with respect to leaf interior temperature. Arrow indicates direction of temperature change. Diagonal line is the line of equality for the two plotted temperatures.

6(a)]. Leaf surface temperature was virtually identical to leaf interior temperature through the day [Fig. 6(b)]. Soil temperature is slightly damped and lagged in phase with respect to leaf interior temperature [Fig 6(b)].

*Average midafternoon temperatures.* Temperatures of 62 separate plants were recorded from 13h00–15h15 on 20 March 1988. Four temperatures in and around each plant were recorded:  $T_{ls}$ ,  $T_{ss}$ ,  $T_{li}$  and  $T_{sd}$ .

Temperatures during this time averaged roughly 41–44°C (Table 3). There were significant differences between the four temperatures ( $F = 34.271$ ,  $P < 0.0001$ ). The hottest temperatures were found at the soil surface and in the leaf interior.

The leaf surface was significantly cooler than the leaf interior (Fig. 6(a);  $t = 6.22$ ,  $P < 0.0001$ ). The average and modal values for  $T_{ls} - T_{li}$  were about  $-1.1^\circ\text{C}$ , and 0 to  $-1^\circ\text{C}$ , respectively [Fig. 7(a)]. Leaf interior temperatures were on average  $2.1^\circ\text{C}$  warmer than soil temperatures at  $-1$  cm (Fig. 7(b);  $t = 11.17$ ,  $P < 0.0001$ ). The leaf surface was on average  $1.4^\circ\text{C}$  cooler than soil surface temperature (Fig. 7(c);  $t = 8.05$ ,  $P < 0.0001$ ).

*The effect of plant facial reflectivity.* The effect of capping the head is presented as the time course of the temperature difference between the experimental head (head b) and its companion uncapped, or control, head (head a).

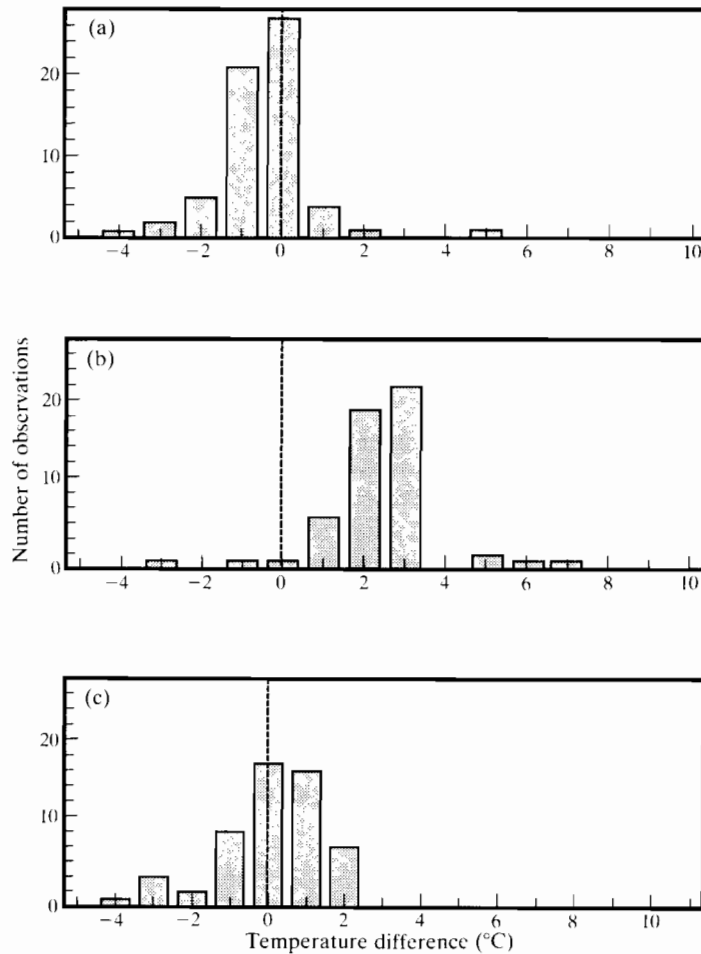
Altering facial reflectivity significantly altered the daily course of leaf facial temperature [Fig. 8(a–c)]. For the plant in which neither head was capped,  $T_{ls}$  of the two heads did not differ through the day [Fig. 8(a)]. The leaf fitted with the reflective cap has a cooler surface during the day and a warmer surface at night than does its uncapped companion [Fig. 8(b)]. Conversely, the leaf with the absorptive cap is warmer during the day than is its uncapped companion head b [Fig. 8(c)].

Altering facial reflectivity appears not to affect leaf interior temperature in any obvious way. There were clear differences between the interior temperatures of experimental and control leaves for each plant, including the uncapped head of plant 1. However, the time course of  $T_{li,a} - T_{li,b}$  is roughly the same both for plants with an absorptive cap [Fig. 8(f)] and plants with a reflective cap [Fig. 8(e)].

*The effect of soil reflectivity and soil conductivity.* Temperatures differed significantly between experimental groups ( $F = 107.729$ ,  $P < 0.0001$ ), and between locations in and around the leaf ( $F = 19.070$ ,  $P < 0.0001$ ). There was no significant treatment by location

**Table 3.** Midafternoon temperatures of *Lithops comptonii* in the Ceres Karoo on 20 March 1988. The HSD range shows the bounds of the range (mean  $\pm 0.5 \times \text{HSD}$ ) where HSD is the honestly significant difference calculated according to the method of Sokal and Rohlf (1969). The HSD is calculated at the 95% confidence level. [Min-Max] shows the bounds of the range of observed data

Location	Average	S.E.M. (°C)	HSD range [Min-Max]
Soil at $-1$ cm	41.5	0.18	41.2–41.8 [38.3–46.6]
Leaf interior	43.5	0.13	43.2–43.8 [41.3–46.2]
Soil surface	43.7	0.19	43.4–44.1 [40.5–47.4]
Leaf surface	42.5	0.19	42.2–42.9 [38.3–47.7]

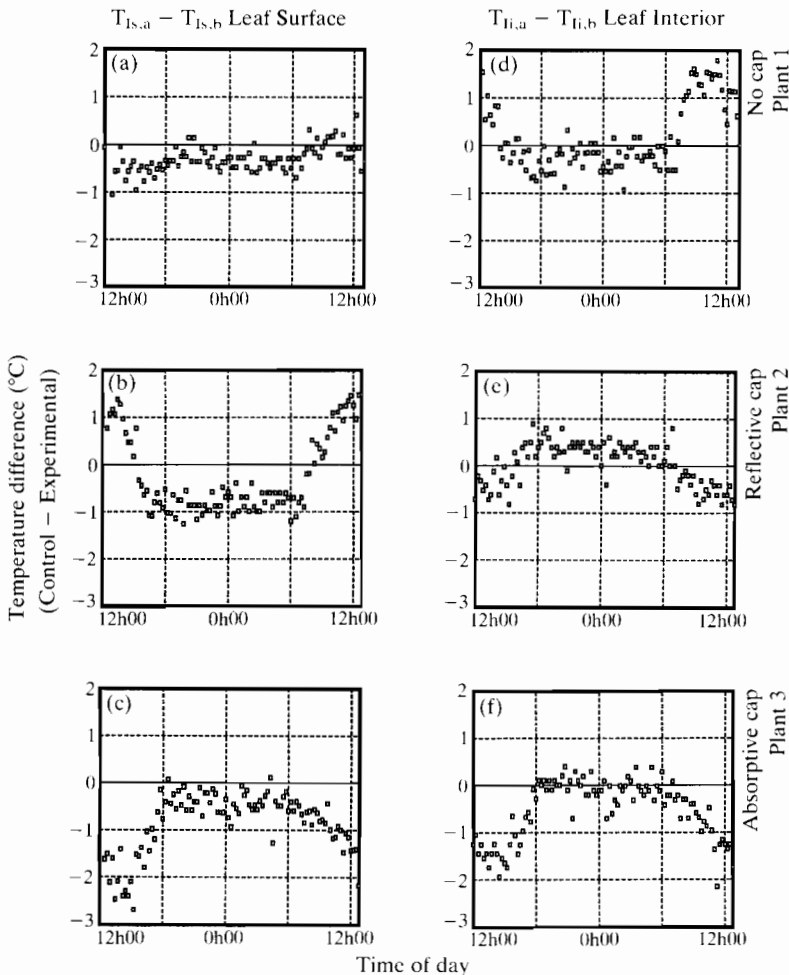
*Lithops comptonii* Ceres Karoo 20 March 1988

**Figure 7.** Temperature differences in and around *Lithops comptonii* in the Ceres Karoo at midafternoon on 20 March 1988. *Panel (a)*: Temperature difference between the leaf surface and leaf interior. *Panel (b)*: Temperature difference between the leaf interior and soil at -1 cm. *Panel (c)*: Temperature difference between the leaf surface and the soil surface 1 cm away. Numbers on the abscissa are the upper range of the interval indicated by the bar. Vertical dotted line indicates the bar for -1 to 0°C.

interaction ( $F = 1.158$ ,  $P = 0.3274$ ). Insulating the plant with polystyrene foam or blackening the soil around it both significantly increased main effects temperature to 49–50°C (Fig. 9). A reflective substratum significantly reduced main effects temperatures to roughly 36°C (Fig. 9). Removing the gravel overburden slightly cooled the plants, but not significantly so (Fig. 9).

*Distribution of plants and soil reflectivity.* We distinguished three types of substrata in the study area: clay with no gravel overburden, clay and sand with a gravel overburden, and loose sandy soil. On 19 March 1988, between 1050 h and 1315 h, we surveyed twenty-nine locations distributed among the three substratum types, and determined substratum reflectivity, the presence or absence of *L. comptonii* and, when plants were present, leaf interior temperature ( $T_{li}$ ).

*Lithops comptonii* Ceres Karoo 19–20 March 1988

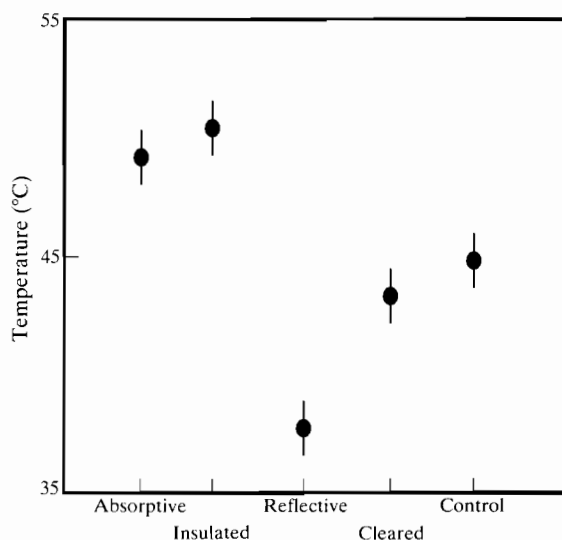


**Figure 8.** Results of plant surface reflectivity experiment for *L. comptonii*. Temperature differences between the uncapped head (head a) and the capped head (head b). Left vertical series of graphs (panels a, b, c) indicates the temperature differences between the surface of the uncapped (Control) head and the surface of the capped (Experimental) head. Right vertical series (panels d, e, f) of graphs indicates the temperature differences between the interior of the uncapped (Control) head and the interior of the capped (Experimental) head. Top horizontal series (panels a, d) indicates the temperatures for the plants with no caps on either head (plant 1). Middle horizontal series (panels b, e) indicates temperatures when head b is fitted with a reflective cap (plant 2). Bottom horizontal series (panels c, f) indicates temperatures when head b is fitted with an absorptive cap (plant 3).

*L. comptonii* were found in fifteen of the localities (Table 4). No plants were found in any of the localities with loose sandy soils. Half the sites with gravel overburden had plants growing in them. All the clay sites had plants (Table 4).

The reflectivities of the substrata ranged from 0.37 to 0.16. The darkest soils were found among the gravels and the lightest were found among the clays. Leaf interior temperatures during the measurements averaged  $38.7^{\circ}\text{C} \pm 3.5^{\circ}\text{C}$  (SD). There was no significant correlation between substratum reflectivity and leaf temperature ( $t = -1.493$ ,  $P = 0.080$ ,  $n = 15$ ).

*Lithops comptonii* Ceres Karoo 20 March 1988



**Figure 9.** Results of soil properties experiment for *L. comptonii*. Closed circles indicate main effect mean values and vertical bars indicate  $\pm$  one-half the Honestly Significant Difference (HSD), calculated at  $P = 0.05$ . Non-overlap of the bars indicates the means are significantly different.  $\phi$ , mean  $\pm$   $\frac{1}{2}$ HSD.

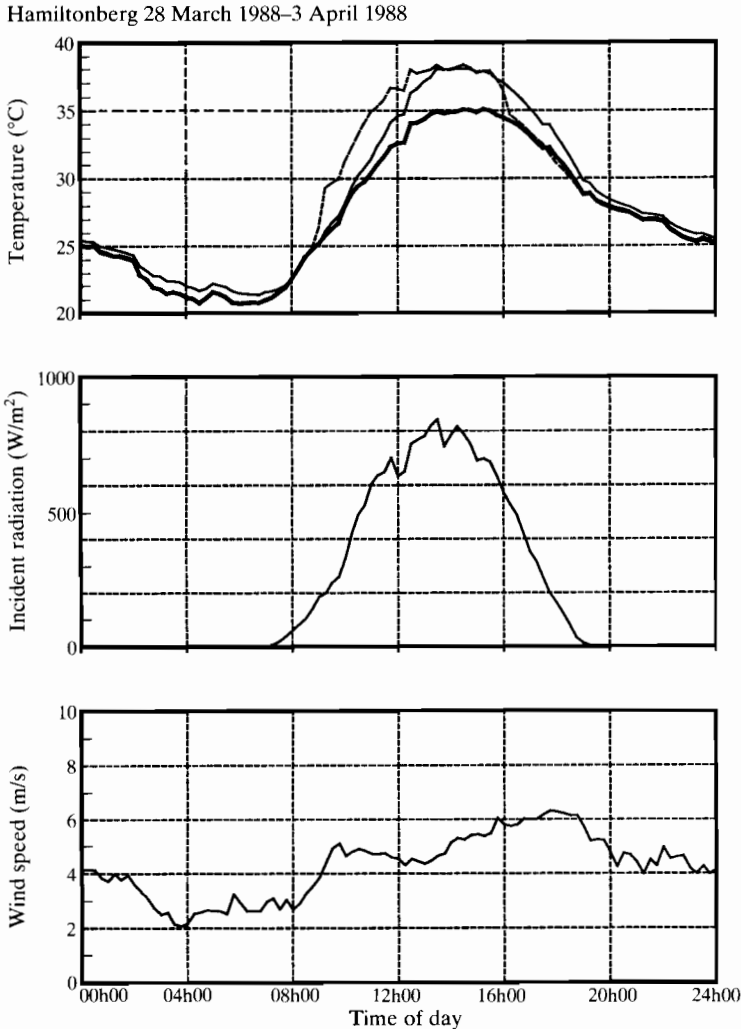
#### Observations on *Lithops gracilidelineata*

Observations on *Lithops gracilidelineata* were made during two periods: one from 17–20 January 1988, and one from 27 March–3 April 1988. The hottest months in this area of the Namib are March and April. In January, the site was surveyed for plants, individual plants were marked and preliminary observations of leaf temperature made. In March, a more detailed series of observations was carried out. Most of the results reported here are from the March observations.

*Meteorological conditions in March–April 1988.* In March, air temperatures at +1 m above the ground typically approached a maximum of 40°C during the day [Fig. 10(a)], although some days were considerably cooler. Minimum night time temperatures ranged from 28°C to as low as 12°C. Air temperatures at +10 cm above the ground could be as much as 7°C warmer than the air temperatures at +1 m, but only during a limited period during midday [Fig. 10(a)]. For most of the day, air temperatures at +1 m and +10 cm were indistinguishable [Fig. 10(a)].

**Table 4.** Presence of *Lithops comptonii* in and reflectivities of the various substrata at the Ceres Karoo study site. *N* indicates number of sites checked. Sites present indicates numbers of sites containing plants

Substrata	N	Reflectivities			Maximum	Minimum
		Sites present	Average	s.d.		
Sandy	9	0	0.320	0.021	0.349	0.291
Clay	10	10	0.342	0.022	0.373	0.298
Gravel	10	5	0.224	0.037	0.284	0.159



**Figure 10.** Meteorological data for the Hamiltonberg study site for the dates 27 March–3 April 1988. *Panel (a):* Air temperatures at ---, +1 cm; —, +10 cm; —, +1 m from the ground. *Panel (b):* Incident solar radiation. *Panel (c):* Wind speed recorded at +1 m.

Through the entire study period, daytime conditions were generally clear and sunny [Fig. 10(b)]. Peak solar radiation averaged  $850 \text{ W m}^{-2}$ . On 28–29 March, there were minor accumulations of cloud at midday. Coastal fog descended on the site on the nights of 1 April and 2 April.

Winds were typically high in the afternoon, but calm in the late night and early mornings [Fig. 10(c)].

*Lithops* leaf temperatures compared with those of other plants. At mid-afternoon on 20 January 1988, leaf temperatures of *L. gracilidelineata* were compared with other plants in the Hamiltonberg (Table 5). Of all the plants examined, which covered a diversity of plant types and habitats, *L. gracilidelineata* clearly experiences the highest midday temperatures (Table 5).

**Table 5.** *Temperatures of Lithops gracilidelineata in the Hamiltonberg, compared to other local plants. Comparisons made on 20 January 1988 for temperatures from 1500–1600 h*

Species	Comments on species	Mean temperature +/- SD N
<i>Aloe</i> sp.	Large bushy rosette of thick lanceolate leaves.	36.4
	Rosette is 1 m or more in diameter and individual leaves are 10–20 cm wide at the base and tapering to a sharp tip. Light purplish in color. Occurs at tops of ridges	0.9 10
<i>Euphorbia lignosa</i> Marloth	Leafless stem succulent, 1 m high. Photosynthetic stems roughly 0.5 cm in diameter. Bush emerges from rock clefts as a large dome shape up to 1 m in diameter. Occurs near top of ridges	34.0 1.7 10
	<i>Kleinia longiflora</i> DC.	Small bush, with no leaves and photosynthetic stems. Stems purplish and upright, about 1 cm in diameter. Bush cylindrical in shape, roughly 30–50 cm high and 20–30 cm in diameter. Occurs near tops of ridges
<i>Lithops gracilidelineata</i> Dinter	Described in text	41.1 2.6 10
	<i>Trichocaulon</i> sp.	Single photosynthetic stem, purplish in color, roughly 5 cm in diameter and 30–50 cm long. Surface highly sculptured. Emerges horizontally from deep clefts in rock. Occurs near tops of ridges
<i>Zygophyllum simplex</i> L.	Bushy plant, with sparse, tiny succulent leaves, roughly 1 mm in diameter and 3 mm long. Bush is roughly 30 cm in diameter and is recumbent, placing leaves with 1–2 mm of the ground. Occurs low on the ridge slopes	36.5 1.5 10
	<i>Zygophyllum stapfii</i> Schinz	Bushy plant, roughly 0.5–1 m high. Disk shaped fleshy leaves roughly 2 cm in diameter. Occurs near top of ridges

*Daily course of Lithops leaf temperature.* The daily course of temperature for leaves and surrounding soil was recorded continuously for the days 27–30 March 1988. Additionally, on the days 28–30 March, temperatures of eighteen plants and adjacent soil around the study site were measured intermittently at four times through the day: morning (about 0900 h), noon (about 1200 h), midafternoon (about 1500 h) and evening (about 1800 h). For both continuously and intermittently monitored plants, the measured temperatures were:  $T_{ls}$ ,  $T_{li}$ ,  $T_{ss}$  and  $T_{sd}$ .

Maximum daytime temperature was reached at about 1400 h (Fig. 11(a); Table 6). Maximum  $T_{ls}$  averaged roughly 46°C (Fig. 11(a); Table 6), but could reach as high as 47–50°C. During the daylight hours, temperature within the plant varied considerably [Fig. 11(b)], especially compared to the temperature variation seen in *L. comptonii* [Fig. 6(b)]. Leaf interior temperature was delayed in phase and damped with respect to leaf surface temperature [Fig. 11(b)]. The leaf surface was on average 1.5°C warmer than the leaf interior at noon (Fig. 12(a);  $t = 5.75$ ,  $P < 0.0001$ ) and 0.7°C warmer than the leaf interior at midafternoon (Fig. 12(d);  $t = 1.95$ ,  $P = 0.03$ ), but was 0.7°C cooler than the leaf interior at evening (Fig. 12(g);  $t = -5.47$ ,  $P < 0.0001$ ).

Soil temperature at -1 cm ( $T_{sd}$ ) was slightly damped and delayed in phase with respect to temperature of the leaf interior ( $T_{li}$ ). The leaf interior was 1.7°C warmer than the

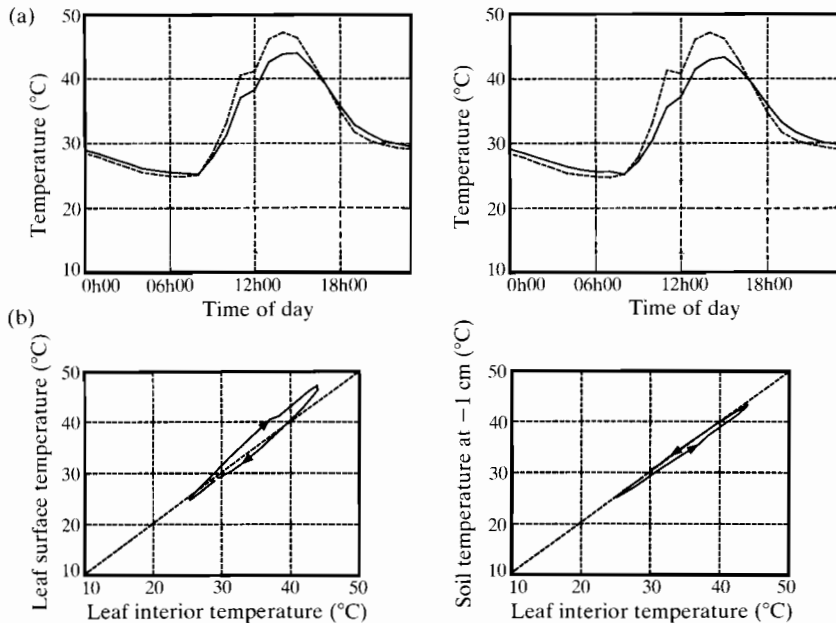


**Table 6.** Plant and adjacent soil temperatures ( $^{\circ}\text{C}$ ) for *Lithops gracilidelineata* 28–30 March 1988. Cells represent average temperatures. The HSD range is calculated at the 95% confidence limits

	Morning	Noon	Mid-afternoon	Evening
$T_{li}$	27.6	40.6	43.8	36.8
HSD range	(25.7–29.5)	(39.4–41.9)	(42.7–45.0)	(35.6–38.1)
[Min-Max]	[24.1–33.5]	[35.3–41.3]	[34.6–45.9]	[33.5–38.5]
$T_{ls}$	28.0	42.1	44.6	36.1
HSD range	(26.0–29.9)	(40.8–43.5)	(43.4–45.8)	(34.9–37.3)
[Min-Max]	[24.6–34.3]	[37.2–44.0]	[37.1–47.2]	[33.9–37.7]
$T_{ss}$	27.8	41.6	43.9	35.9
HSD range	(25.9–29.7)	(40.4–42.8)	(42.7–45.1)	(34.7–37.1)
[Min-Max]	[23.9–34.1]	[37.1–46.9]	[37.5–48.6]	[33.3–37.0]
$T_{sd}$	27.1	38.9	42.4	37.2
HSD range	(25.2–29.0)	(37.7–40.1)	(41.2–43.7)	(36.0–38.4)
[Min-Max]	[24.3–31.7]	[34.3–40.5]	[36.8–44.2]	[33.9–37.6]

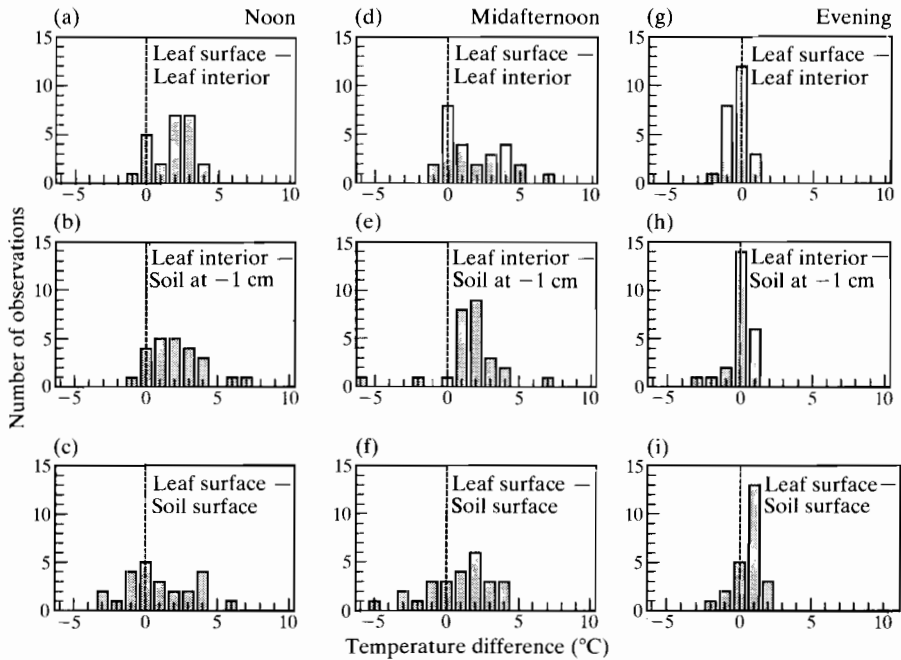
adjacent soil at noon (Fig. 12(b);  $t = 4.48$ ,  $P < 0.0001$ ) and  $1.2^{\circ}\text{C}$  warmer than the adjacent soil at midafternoon (Fig. 12(b);  $t = 2.79$ ,  $P = 0.005$ ), but was  $0.4^{\circ}\text{C}$  cooler than the adjacent soil at evening (Fig. 12(h);  $t = -2.08$ ,  $P = 0.02$ ).

The leaf surface was warmer than the adjacent soil surface by on average  $0.5^{\circ}\text{C}$  at noon

*Lithops gracilidelineata* Hamiltonberg 27–30 March 1988

**Figure 11.** Daily course of temperature of a *Lithops gracilidelineata* and the surrounding soil for the days 27–30 March 1988. *Panel (a)*: Average hourly temperatures for the leaf interior, — and leaf surface (left), --- and for the soil surface, - - -; and soil, — at  $-1\text{ cm}$  (right). *Panel (b)*: Phase diagrams for the covariation of leaf surface temperature and soil temperature at  $-1\text{ cm}$ , both with respect to leaf interior temperature. Conventions as in Fig. 6(b).

*Lithops gracilidelineata* Hamiltonberg 28–30 March 1988



**Figure 12.** Temperature differences in and around *Lithops gracilidelineata* in the Hamiltonberg on 28–30 March 1988. Each vertical series of graphs is similar in layout to Fig. 7. Each vertical series presents measurements done at Noon (panels a, b, c), Midafternoon (panels d, e, f) and Evening (panels g, h, i).

[Fig. 12(c)]; 0.4°C at midafternoon and 0.2°C at evening [Fig. 12(i)]. None of the temperatures differences between the leaf surface and soil surface are statistically significant.

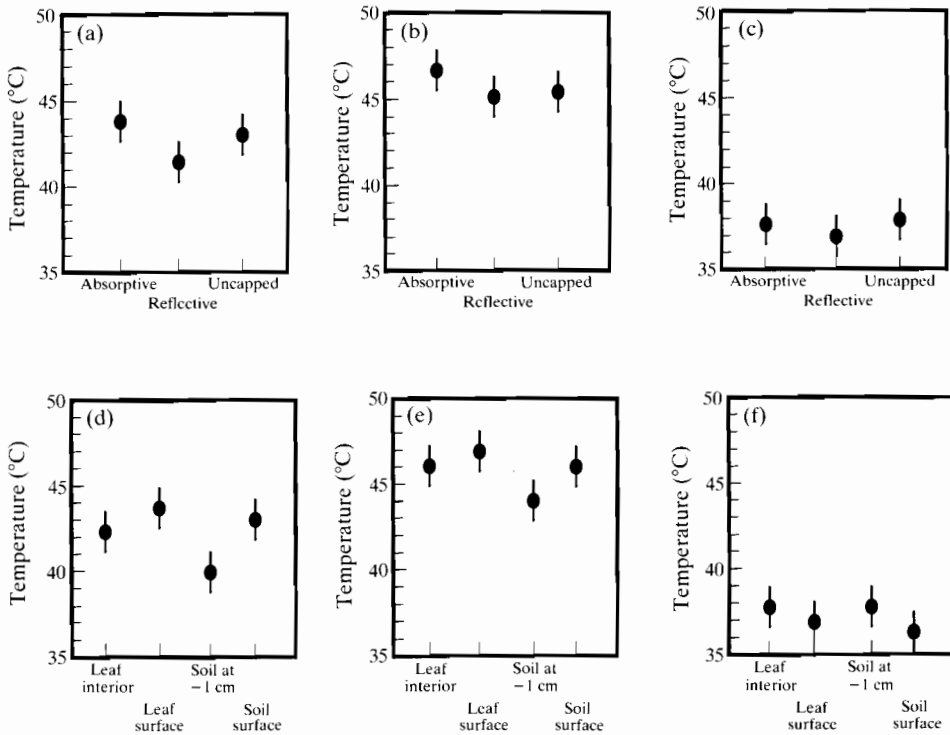
*The effect of plant facial reflectivity.* Plant facial reflectivity had a significant effect on leaf and surrounding temperatures at noon ( $F = 5.207$ ,  $P = 0.0065$ ) and midafternoon ( $F = 3.803$ ,  $P = 0.0243$ ), but not in the evening ( $F = 1.046$ ,  $P = 0.3539$ ). At the times when facial reflectivity had an effect, the temperatures in the Absorptive group were significantly higher – temperatures in the Uncapped and Reflective groups were never significantly different (Fig. 13). Nevertheless, difference between plants with absorptive caps and reflective caps was always small: roughly 1.6°C at noon [Fig. 13(a)] and roughly 1.4°C at midafternoon [Fig. 13(b)].

Significant variation between temperatures in and around the plant were evident at noon ( $F = 6.496$ ,  $P = 0.0004$ ), midafternoon ( $F = 4.394$ ,  $P = 0.0053$ ) and evening ( $F = 6.710$ ,  $P = 0.0003$ ). For the most part, the significant differences were between the soil surface and the soil at –1 cm, but at noon, leaf interior temperature was significantly warmer than soil at –1 cm [Fig. 13(d)]. Leaf surface, soil surface and leaf interior temperatures never were significantly different (Fig. 13).

At no time was there a significant surface reflectivity–location interaction (noon,  $F = 0.770$ ,  $P = 0.5944$ ; midafternoon,  $F = 0.432$ ,  $P = 0.8564$ ; evening,  $F = 0.317$ ,  $P = 0.9273$ ).

*Distribution of plants.* The dimensions of the soil pockets were measured for 20 individual

*Lithops gracilidelineata* Hamiltonberg 29–30 March 1988



**Figure 13.** Results of surface reflectivity experiment for *Lithops gracilidelineata*. Mean temperatures at three times of day (Noon, (a, d) Midafternoon (b, e) and Evening (c, f)). Closed circles indicate means  $\pm$  one-half the HSD at  $P = 0.05$ . Top series of panels (a, b, c): Temperatures at different reflectivities. Bottom series of panels (d, e, f): Temperatures in and around the plants. Left series of panels (a, d): Temperatures at Noon. Middle series of panels (b, e): Temperatures at Midafternoon. Right series of panels (c, f): Temperatures at Evening.

plants. On average, the depth of sandy soil in the pockets was about 18 mm (Table 7). Surface areas of the soil pockets could not easily be measured because of their highly irregular shapes, but their circumferences averaged 40 cm. Because of the small size and locale of the pockets, plants were usually in very close proximity to a large boulder, on average 25 mm, and never more than 12 cm (Table 7). The reflectivities of the various sites ranged from 0.19 to 0.40 (Table 7).

### Discussion

Most vascular plants can tolerate leaf temperatures as high as 55°C without ill effect (Nobel, 1983). Some low-lying cacti can briefly tolerate leaf temperatures of 60–70°C (Nobel *et al.*, 1986), and even some recumbent arctic and alpine plants can tolerate leaf temperatures as high as 45–47°C (Kappen, 1981). It is clear from our results, and from those of others (Eller & Grobbelaar, 1986) that leaf temperatures experienced by *Lithops* in nature are high – maximum daytime leaf temperatures of 40–50°C are apparently not uncommon (Tables 3, 6; Figs 6, 13), but these appear to be well within the thermal tolerances of most vascular plants. Nevertheless, it is equally clear that the embedded

**Table 7.** Characteristics of sites and plants for *Lithops gracilidelineata* in the Hamiltonberg

	<i>n</i>	Mean	s.d.	Minimum	Maximum
Depth of soil (mm)	20	17.7	7.0	29	8
Circumference of soil pocket (cm)	19	40.3	28.7	11	124
Distance to nearest boulder (mm)	33	25.4	32.2	5	121
Reflectivity	19	0.29	0.06	0.19	0.39

habit of *Lithops* poses some unique thermal challenges. The soil surface in a desert is an unusually hot microenvironment (Graetz & Cowan, 1979): in the Hamiltonberg, the embedded habit of *L. gracilidelineata* imposes on them the highest daytime temperatures experienced by any plant in the community (Table 5). Because the embedded habit of *Lithops* further appears to preclude most of the common thermal adaptations of desert plants, it is interesting to ask what thermal adaptations, if any, an embedded dwarf succulent might employ?

Both from theoretical and experimental results, leaf temperatures of an embedded dwarf succulent appears to be governed by three general principles. (1) Leaf temperature and soil temperature are strongly coupled. (2) Anything which alters the energy budget of the exposed surface of the plant *alone* will have little effect on temperature of the leaf interior. (3) Altering transmission of light into the plant is the only effective way leaf temperature of an embedded dwarf succulent can be altered significantly. Each principle carries with it implications for the thermal ecology of embedded dwarf succulents, which we shall consider in turn.

#### *Principle 1. Soil and leaf temperatures are strongly coupled*

It is clear from the data that temperatures of *Lithops* leaves and the surrounding soil are strongly coupled. Leaf temperature commonly differs from soil temperature by no more than a few degrees (Figs 6, 7(b, c), 11, 12; Tables 3, 6). Phase delays and damping between soil and leaf temperatures through the day are likewise small [Figs 6(b), 11(b)].

If soil and leaf are thermally coupled, it follows that a high soil temperature will inevitably lead to a high leaf temperature. This does not mean, however, that an embedded dwarf succulent must have extraordinary thermal tolerance. While surface temperatures in full sun in a desert can get very hot, the temperatures even a centimeter below the soil surface usually are more equable. At the hottest part of the day, there is a steep vertical gradient of temperature, and daily temperature fluctuations are considerably damped (Monteith, 1973; Campbell, 1977; Nobel, 1983). Thermally coupling a *Lithops* with the soil will impose similar temperature regimes on the plant (Eller & Nipkow, 1983, Eller & Grobbelaar, 1986). If the photosynthetic cells are located in the deeper parts of the leaf, their temperature will be governed by this more benign temperature regime. Only the surface (and principally structural) portions of the leaf will experience the extreme temperatures of the soil surface.

Thus, an embedded dwarf succulent need not develop extraordinary thermal tolerance (at least not in the chlorenchyma) to survive in the very hot microenvironment of the soil surface. It must, however, be the proper shape, one that exploits the vertical heterogeneity of soil temperature. This means having leaves with a relatively long vertical axis and narrow cross-sectional area, so that temperature-sensitive cells (like chlorenchyma) can be confined to the deeper regions of the leaf. Embedded succulents shaped like shallow disks or 'pancakes' should only be possible if the chlorenchyma develops extraordinary tolerance to high temperature (Nobel *et al.*, 1986).

Succulence is a widespread attribute of desert plants, and high thermal capacity of the leaves is thought to be an important consequence of this: a leaf with a high thermal capacity will be 'thermally damped' and so will experience smaller daily extremes of temperature than the air or a leaf with smaller thermal mass (Nobel, 1983). The larger the leaf, the more pronounced is this damping of temperature. The small size of embedded dwarf succulents would seem to indicate that daily course of leaf temperature might not be very effectively damped. However, thermal coupling between soil and leaf joins the plant's small thermal capacity to a heat sink with large thermal capacity, namely the soil. This means that a 5 g plant like *Lithops*, which in still air would have a time constant of less than 15 min., less in windy conditions (Turner, 1985), can have an apparent time constant on the order of hours when it is coupled to the soil's thermal capacity [Figs 6(a), 11(a)].

It has been suggested that the paper sheath surrounding *Lithops* (Fig. 1) insulates it from the hot soil and so keeps leaf temperature cool (Eller & Grobbelaar, 1986). It is not likely that thermally decoupling the plant and soil can work in this way, however. The plant's daily fluctuations of temperature can only be damped by the soil's thermal capacity if the leaf and soil can readily exchange heat. Insulating the plant from the soil will likely result in a leaf that heats faster and to higher temperatures than an uninsulated leaf. This is evident for *L. comptonii* insulated from the soil by jackets of polystyrene foam (Fig. 9).

Some species of *Lithops*, along with many other dwarf succulents, inhabit gravel plains covered with reflective quartz pebbles. It is popularly thought that this is a thermal adaptation for *Lithops*: the reflection of light from the quartz pebbles will result in lower soil temperatures and so afford protection against high leaf temperatures for the plants living there. This raises the interesting possibility that *Lithops* spp. might occur preferentially in soils with high reflectivities.

Such a thing is feasible. Simulating an increase of soil absorptivity from 0.1 to 0.9 brings about a 6–10°C increase of leaf temperature (Fig. 4). When absorptivity of the soil surface around *L. comptonii* is experimentally altered from 0.07 (Reflective) to about 1 (Absorptive), midday temperatures in and around the plant increase by 11.5°C (Fig. 9).

Natural variations of soil surface reflectivity are considerably less, however. For *L. comptonii*, the natural variation of surface reflectivity ranges only from 0.37 to 0.16 (Table 4), and appears to have no statistically discernible effect on leaf temperature. It is worth noting that similar natural variation of surface reflectivity is evident for the habitat of *L. gracilidelimitata* (Table 7). For *L. comptonii*, clearing away the dark gravel overburden to expose the lighter soil beneath had no significant effect on plant and soil temperatures (Fig. 9). In addition, *L. comptonii* in the Ceres Karoo is found only on the most reflective and the least reflective substrata, and not at all on substrate of intermediate reflectivity (Table 4). None of these observations is consistent with the idea that *Lithops* occur preferentially in soils of high reflectivity. Stability of soil, not soil reflectivity, is probably the most important factor determining where *Lithops* are found in a habitat (Cole, 1988).

*Principle 2: Altering the energy budget of the exposed face of the plant does not significantly alter leaf temperature*

It is clear, both from the simulation and experimental results, that an adaptation that alters the energy budget of the exposed plant face *alone* will have only a small effect on leaf temperature. Consider the simulated effect of altering plant surface absorptivity. Although substantial changes are seen in the surface temperature of the plant (Fig. 3), only small changes of temperature deeper in the plant are evident. The explanation for this is straightforward: the surrounding soil acts as a thermal 'shunt'. If an increased absorptivity warms the plant surface, it will lose heat both to the cooler interior of the leaf, to the above-ground surroundings and to the cooler surface soil. The simulations indicate that most heat moves between the leaf surface and soil surface and between the leaf surface and the

above-ground environment [Fig. 3(b)]. Conversely, little heat moves into the leaf interior (where the chlorenchyma are). A similar, though opposite, shunt of heat will defeat any attempt to cool the plant by increasing surface reflectance [Fig. 3(c)], or by evaporation from the exposed surface (Eller & Ruess, 1982, Eller & Grobelaar, 1986). These types of thermal shunts have been observed in laboratory measurements of leaf and soil temperatures of *Lithops* under simulated natural conditions (Eller & Nipkow, 1983).

This theoretical result is upheld by the temperatures of leaves capped with absorptive or reflective aluminum caps, which force surface absorptivities to vary from roughly 0.95 to 0.07. For *L. comptonii*, daytime surface temperature of leaves with reflective caps and absorptive caps differed by roughly 3°C (Fig. 8), in reasonable agreement with the theoretical calculations (Fig. 3). Yet no consistent effect on leaf interior temperature is evident (Fig. 8). Similar results obtain for *L. gracilidelineata*: on average, plants with reflective caps and absorptive caps differed in leaf interior temperature by only 1.5–2.5°C, significantly so only at 12h00 (Fig. 13).

These temperature differences are considerably less than the normal variation of leaf temperature within the habitat (Tables 3, 6), which has a range of nearly 10°C at certain times of the day. It is worth remembering that the natural variation of facial reflectivity is considerably smaller than that provided by the differently colored caps. It follows that considerable variation of leaf color can exist among a population of *Lithops* and little variation of leaf temperature will result. This may illumine a feature of *Lithops* that often invokes comment, namely its crypticity.

*Lithops*, as implied both by the generic name, and by some of their common names (e.g. 'stone plants', 'mimicry plants', etc.) are renowned for their cryptic appearance. Early reviews (Marloth, 1929; Schwantes, 1957) pointedly noted the accurate mimicry of shape, size, color and texture of stone-mimicking succulents to their surroundings. Southern Africa appears to have a large number of presumed plant mimics of stones (Wiens, 1982), the most dramatic example being *Lithops*. In these plants particularly, there usually is a very close match of leaf shape, size, color and texture with the surrounding gravel substrata: *Lithops* fanciers emphasize that the plants are very hard to locate (Cole, 1988).

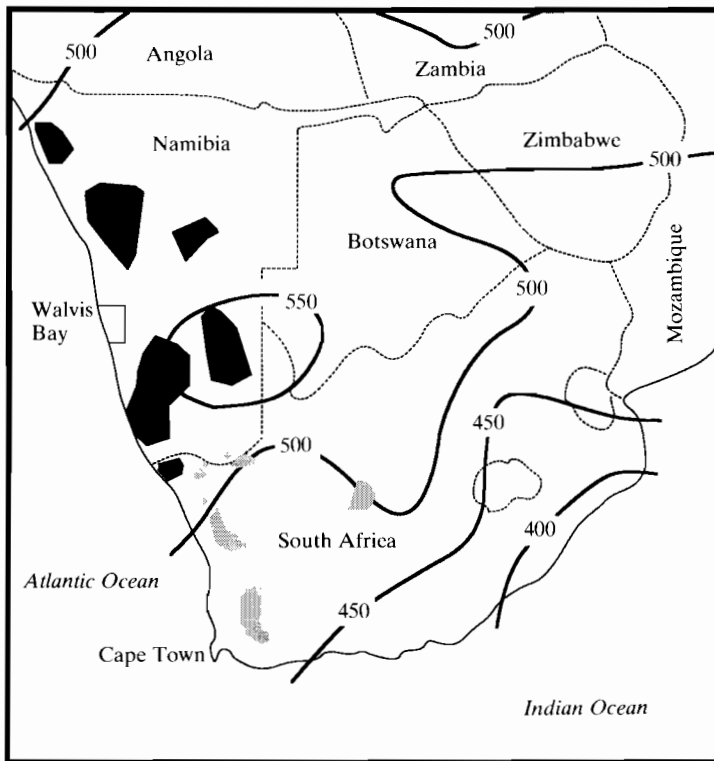
The fact that humans find it difficult to see *Lithops* in no way demonstrates that the plants actually are stone mimics, of course. Most evidence for the supposed mimicry of *Lithops* is circumstantial. For example, *Lithops* are rarely found with herbivore damage. Those animals that have been seen browsing on *Lithops* (ostrich, guinea fowl, various species of bustard and francolin, various mammals including porcupines, gerbils, hares, baboons, and small buck) are visually oriented herbivores (Cole, 1988). It is a logical, albeit risky, step to assume that *Lithops* are rarely eaten by herbivores because the herbivores cannot easily see them.

Crypticity is difficult to demonstrate conclusively (Barrett, 1987), and any claim that a plant is cryptic usually must first deal with two complicating factors: (1) the plants may be adequately defended against herbivores by other means, such as chemical or mechanical defense, or (2) the color of the plant may be determined by other factors, such as temperature control. With respect to other defenses, *Lithops* and other of the dwarf succulents appear to be palatable to a wide range of herbivores, provided the herbivores can find them (Herre, 1971; Cole, 1988). We believe our results weaken the hypothesis that color of *Lithops* can be explained as an adaptation for temperature control.

We have shown that color has a small effect on leaf temperature. It follows that large variation of facial color among *Lithops* should confer little thermal benefit, or impose little thermal cost, on the plant. This may in turn leave leaf color to be selected predominantly by other factors, including perhaps how well color serves to conceal the plant from visually oriented herbivores. It is worth repeating that this is so only because of the thermal 'shunt' to the soil that is peculiar to a subterranean dwarf succulent: color would not be so 'free' to vary without thermal cost if the plant were thermally isolated from the soil.

*Principle 3: Clarity of the leaf face substantially affects leaf temperature*

For light to reach the chlorenchyma of a *Lithops*, it must be transmitted through the window into the plant. The simulations show that leaf temperature of an embedded dwarf succulent can be altered significantly only by altering the transmission of light into the plant [Fig. 3(d)], consistent with experimental results obtained by others (Eller & Grobbelaar, 1986). A simulated increase of transmittance of light into the plant from 0.1 to 0.5 (equivalent to increasing the clarity of the window) causes the leaf interior to increase in temperature by 2–6°C and the plant surface to cool by about 0.5°C [Fig. 3(d)]. The cooler surface and warmer interior are readily explained by the fact that radiation dissipated as heat at the surface when transmittance is low is dissipated as heat deeper in the plant when transmittance is higher (Eller & Grobbelaar, 1986).



**Figure 14.** Map showing distribution of solar radiation (in  $\text{cal cm}^{-2} \text{day}^{-1}$ ) in southern Africa, and distributions of *Lithops* spp. identified by Cole (1988) as having well-developed clear windows (stippled fill) and *Lithops* spp. identified by Cole (1988) as having opaque or reduced windows (solid fill). Plants with well-developed clear windows included seven species and four varieties (*L. dinteri* Schwantes, two varieties; *L. divergens* L. Bolus; *L. olivacea* L. Bolus, two varieties; *L. otzeniana* Nel; *L. salicola* L. Bolus; *L. viridis* H. Lüsckh.; *L. comptonii* L. Bolus). Plants with opaque or reduced windows included nine species and 19 varieties (*L. francisci* (Dinter & Schwantes) N.E. Br.; *L. gracilidelineata* Dinter, three varieties; *L. hookeri* (Berg) Schwantes; *L. karasmontana* (Dinter & Schwantes) N.E. Br., four varieties; *L. meyeri* L. Bolus; *L. pseudotruncatella* (Berger) N.E. Br., seven varieties; *L. schwantesii* Dinter, five varieties; *L. vallis-mariae* (Dinter & Schwantes) N.E. Br.).

Two consequences follow from this. First, temperature distribution within an embedded dwarf succulent should vary with respect to clarity of the window. Second, window clarity may be an effective thermal adaptation for embedded dwarf succulents.

When the window is opaque or translucent (i.e. transmittance is small), one expects leaf surface temperatures to be warmer than leaf interior temperatures. When the window is open and transparent (i.e. transmittance is large), one expects the reverse: the leaf interior should be warmer than the leaf surface [Fig. 3(d)].

The temperature distributions measured in the clear-windowed *L. comptonii* and the more opaque-windowed *L. gracilidelineata* are as predicted by the model. In *L. comptonii*, the leaf interior is warmer at midday than the leaf surface [Fig. 7(a); Table 3], although the temperature difference is small and the most common values fall within 0–1°C [Fig. 7(a)]. The opposite is true for *L. gracilidelineata*: leaf interior temperatures through the day are on average 1–2°C cooler than leaf surface temperatures (Table 6; Figs 11, 12). Additionally, the leaf surface of *L. gracilidelineata* is slightly, but not significantly warmer than the soil surface [Figs 12(c), 14(f)]. In *L. comptonii*, however, the leaf surface is significantly cooler than the adjacent soil surface [Fig. 7(c)]. This is as predicted for a clear-windowed plant [Fig. 3(d)].

If *Lithops* window clarity does affect leaf temperature, might variation of window clarity serve as a thermal adaptation? For example, plants that live in relatively cool and less sunny environments might have clearer windows than plants living in hotter and sunnier environments. This does appear to be the case: if one examines the distributions of those species unambiguously identified by Cole (1988) as having either clear or opaque windows, it is apparent that the clear-windowed species are found in sunnier regions than are the relatively opaque windowed species (Fig. 14). Such a comparison is complicated by a number of factors, among them the high degree of variation in window clarity or window form even within a species (Cole, 1988), and the generally poor characterization of microclimate in the southern African region.

To summarize, *Lithops*, and presumably other embedded dwarf succulents, live in a thermally harsh environment, the hot surface soils of the desert. Owing to the strong coupling of soil and leaf temperature, the thermal adaptations common to other desert plants, such as altering surface reflectivity, self-shading, evapotranspiration, will not be much use to an embedded dwarf succulent like *Lithops*. One of the only effective thermal adaptations available to this plant happens also to be one of its unique attributes: a window in the leaf surface. Variations of window clarity can bring about substantial variation of leaf temperature and of temperature distribution in and around the plant. *Lithops* may use variation of window clarity as a compensatory device to keep leaf temperatures similar over a wide range of climates. Confining the photosynthetic cells deep in the plant (which goes hand-in-hand with the presence of the window) keeps these cells out of the harsh temperature regimes that exist at the surface. It appears that only the structural parts of the leaf will experience the most extreme temperatures.

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