The Microenvironment Associated with *Welwitschia mirabilis* in the Namib Desert

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Welwitschia mirabilis (Hooker fil.) creates an island of relatively moderate thermal and moisture regimes below its large leaves. In the environmentally stressful habitat in which the plant occurs, soil temperatures may be 40 °C lower below the plant than in nearby unshaded areas, and the plant thereby provides critical shelter to many desert organisms.

INTRODUCTION

Plants modify the environment in which they grow by creating shade and shelter and by accumulating wind-blown debris, silt and sand in addition to the litter they themselves produce. Although the shade and litter associated with desert plants is usually far less than that of plants in temperate and tropical forests and grasslands, even a little shade and organic matter, particularly if concentrated around shrubs, may be of significance locally in a hot desert environment (Noy-Meir, 1979/80).

Welwitschia mirabilis (Hooker fil.) is a long-lived gymnosperm which occurs in discrete localities (Kers, 1967; Rodin, 1953) in the Namib Desert. This plant has long straplike leaves (0,5 to 1,0 m broad and 1,0 to 2,0 m long) which create an effective umbrella of shade below the plant. *Welwitschia mirabilis* often occurs in environmentally stressful areas where other plant cover is sparse. Despite the possible importance of the climate-moderating effect of *W. mirabilis* to animals, this aspect has not received any direct attention. Schulze, Eller, Thomas, Willert and Brinckmann (1980) have examined the thermal relationships of *W. mirabilis* and state that these plants modify air and soil temperatures quite considerably. Their study, involving *W. mirabilis* in a grassland and a cool coastal region of the Namib, recorded that air and soil temperatures below the leaves were equal to, or slightly lower than, ambient air temperature despite high temperatures on the insolated soil surface. Unfortunately, they do not give quantitative data concerning the insolated soil surface temperatures. Furthermore, the leaves themselves were only 4–6 °C above air temperature. This was thought to be due to the high reflectivity of the leaf (Schulze *et al.,* 1980). The central layer of the cuticle contains crystals of calcium oxalate that may play an important role in reflecting radiant energy (Bornman, 1972) as may the fibre bundles that run parallel to the leaf axis (Eller, Willert, Brinckmann and Baasch, 1983).

The present study examines the extent to which *W. mirabilis* plants modify their local thermal and moisture environment in the central Namib Desert at a site about 70 km inland from the coast. At this site the insolated soil surface temperatures regularly exceed 70 °C and *W. mirabilis* represents the most abundant perennial vegetation. A moderate thermal climate below the plants could represent a critical refuge that enables animals to survive in this environment.

METHODS

Study site

All work was carried out at 'Welwitschia Wash' (15° 36′ E; 23° 37′ S), 20 km east of the Namib Research Institute. The wash is barren and *W. mirabilis* plants form the main constituent of the vegetation, the only other perennial vegetation of importance being *Adenolobus pechuelli, Orthanthera albida* and *Sutera maxii,* which provide little in the way of canopy cover. During the day, owing to direct radiation, re-radiation of heat from the steep rocky sides of the wash as well as lack of air movement in the wash, insolated soil surface temperatures may be extremely high, temperatures of 78 °C having been recorded during the study.

Soil Moisture

Samples for analysis of soil moisture were collected at 15h00 on three occasions (Table I). Soil samples were taken at a depth of 50 mm:

a) On the southern side but close to the stem of *W. mirabilis* plants.
b) In an exposed area, one to two metres south of the plant's leaf tips.

Soil moisture was determined gravimetrically by drying a pre-weighed soil sample in an oven at 70 °C for a minimum of four days.

Temperature measurements

Temperatures associated with *W. mirabilis* plants were measured using copper constantan thermocouples and a digital

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thermometer (Bailey Instruments, Model BAT-12). Thermocouples were 30 gauge and had tips embedded in epoxy. Readings were taken at approximately hourly intervals for 24 to 48 hours on three occasions in 1982. On each occasion, soil surface temperatures were also measured at an exposed site close to the *W. mirabilis* plants. Air temperature in the shade was measured at a height of 1 m with a mercury thermometer.

1) From 17h30 on 25 January 1982 to 17h30 on 26 January 1982 the following temperatures were measured: soil surface temperature below *W. mirabilis* leaves where the ground was covered with a 20–30 mm layer of litter; 40 mm below the soil surface in an exposed area; 40 mm below the soil surface under *W. mirabilis* leaves, where the soil was covered with a 20–30 mm layer of litter.
2) From 12h00 on 19 April 1982 to 14h00 on 20 April 1982 the following temperatures were measured: soil surface temperature below *W. mirabilis* leaves, ground not covered by litter; surface temperature below *W. mirabilis* leaves, ground covered by 20–30 mm layer of litter; under a 40–50 mm layer of litter in the stem depression.
3) From 19h00 on 21 February 1982 to 18h00 on 23 February 1982 the following temperatures were measured on the east and west sides of the plant: soil surface temperature below leaf tips of plant; soil surface temperature about 30 mm from the stem of the plant and under a 20–30 mm layer of litter.

RESULTS

Soil moisture

The percentage soil moisture at a depth of 50 mm (Table 1) was significantly higher below *W. mirabilis* plants than at nearby exposed areas ($P < 0{,}001$ for 10 February 1983 and 13 August 1983 and $P < 0{,}01$ for 7 April 1983, *t*-test for two means). The percentage soil moisture was not higher on days during which fog was experienced in the mornings (10 February and 7 April) than on a fogless day (13 August).

Table 1
Mean $(\bar{X})$ and standard deviation *(S.D).* of the percentage soil moisture in soil samples from below leaves of *W. mirabilis* and exposed sites nearby; *n* represents the number of samples taken.

Date	*n*	Percentage soil moisture below plant $\bar{X} \pm S.D.$	percentage soil moisture at exposed site $\bar{X} \pm S.D.$
10 February 1983	9	0,41 ± 0,08	0,17 ± 0,03
7 April 1983	10	0,37 ± 0,08	0,26 ± 0,06
13 August 1983	20	0,43 ± 0,12	0,25 ± 0,07

Temperature measurements

On 26 January 1982 surface temperatures at the exposed site reached 78 °C while surface temperatures below the plant's leaf reached a maximum of just over 40 °C (Fig. 1).

Temperatures at the exposed site were greater than 40 °C for approximately 10 of the 24 hours monitored (Fig. 2).

Temperatures at a depth of 40 mm below the soil surface at the exposed site reached a maximum of just over 60 °C while at 40 mm depth below the plant, temperatures peaked at 36,6 °C and the range in temperature over 24 hours was 6,5 °C compared with a range of 36 °C at a depth of 40 mm at the exposed site.

On 20 April 1982, surface temperatures reached a maximum of 54 °C at the exposed site and 31,4 °C under *W. mirabilis*

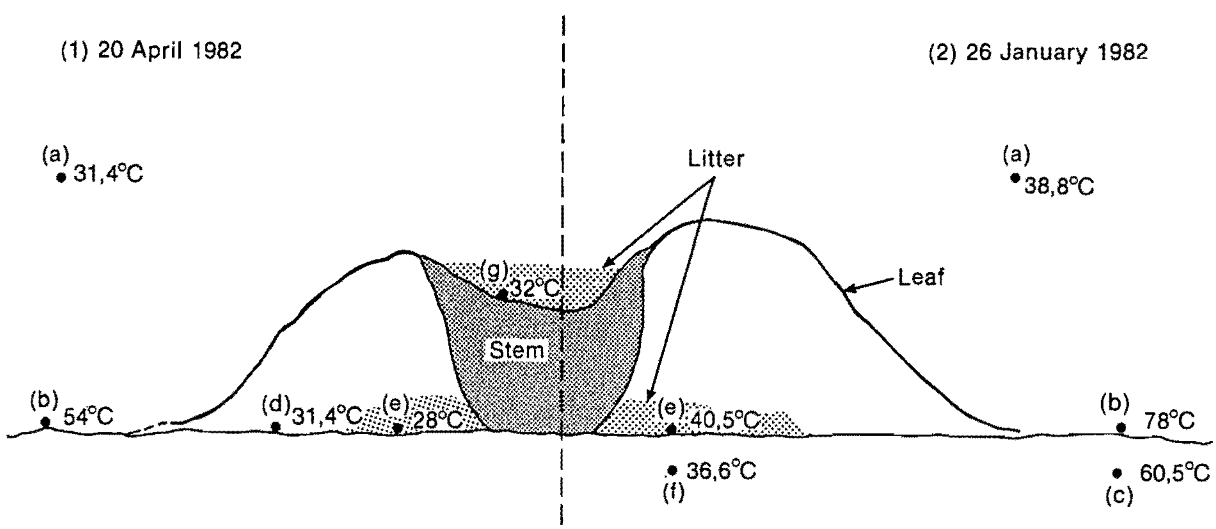

Fig. 1
Transverse section through *Welwitschia mirabilis,* showing maximum temperatures recorded on 1) 20 April 1982 and 2) 26 January 1982 in the following positions: **a**: 1 m above the soil; **b**: insolated soil surface; **c**: 40 mm below insolated soil surface; **d**: below leaves on shaded, litter-free soil; **e**: soil surface beneath a 20–30 mm deep layer of litter; **f**: 40 mm below soil surface that was covered with a 20–30 mm deep layer of litter; and **g**: in stem depression under a 40–50 mm deep layer of litter.

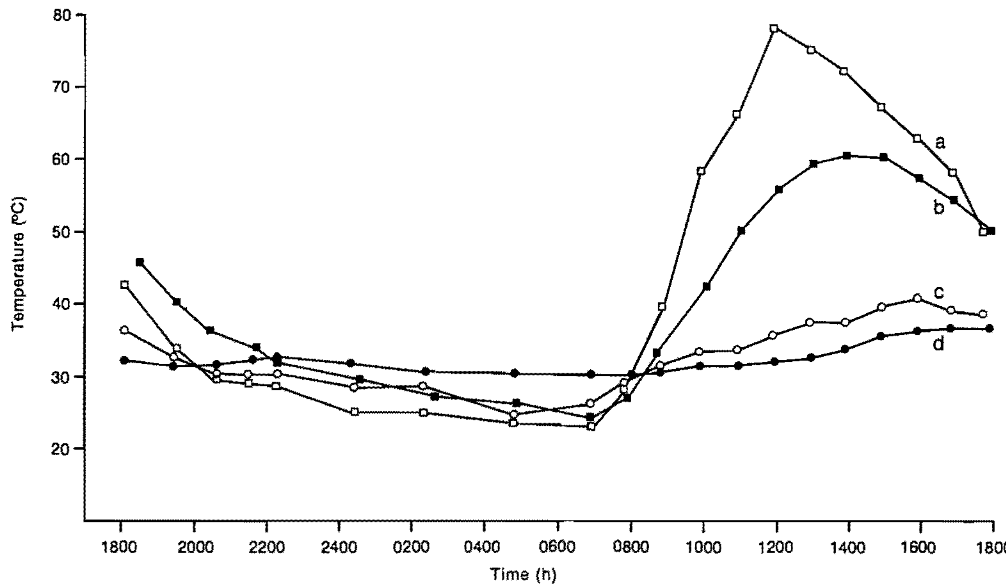

Fig. 2

Temperatures recorded during 25 and 26 January 1982: **a**: on exposed soil; **b**: at 40 mm depth below exposed soil; **c**: below *W. mirabilis* leaves – on the soil surface; and **d**: at 40 mm depth. Soil was covered by 20–30 mm litter for (c) and (d).

leaves (but not covered with litter), while temperatures under *W. mirabilis* leaves, where the ground was covered with litter, reached 28 °C. The maximum temperature under litter in the stem of the plant was 34 °C (Fig. 1). Whereas the range of temperatures was 18,5 °C for bare soil surfaces below the leaves and under the stem litter, the range was 10 °C below litter under the leaves (Fig. 3).

On 20 February 1982, exposed surface temperatures reached a maximum of 67 °C (Fig. 4). At any one time temperatures on the east and west side of the plant varied considerably, both at the leaf tips and close to the stem in constant shade.

Temperatures on the east side peaked earlier, the maxima were lower than those on the west side, and exhibited a smaller range. Even the frayed leaf tips moderated ground temperatures considerably. At 14h00 the difference in temperature between the soil surface below leaf tips and exposed soil surfaces was approximately 10 °C (both east and west sides); however, at 16h00 the temperature below leaf tips on the west side was virtually the same as the exposed soil surface, while the temperature on the east side below leaf tips was 15 °C lower.

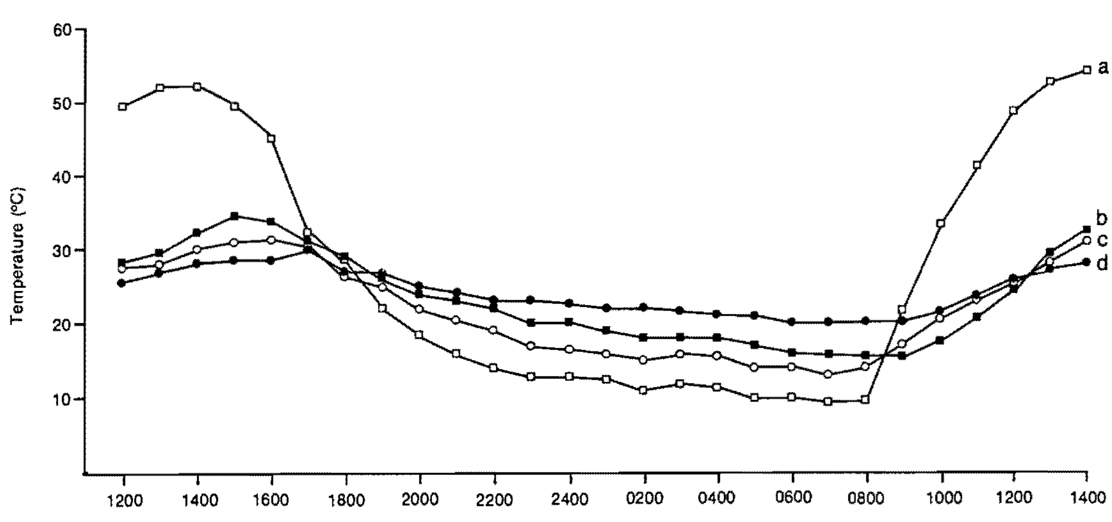

Fig. 3

Temperatures recorded during 19 and 20 April 1982: **a**: on exposed soil; **b**: under 40–50 mm litter in *W. mirabilis* stem depression; **c**: below *W. mirabilis* leaves – on bare ground; and **d**: soil surface under 20–30 mm litter.

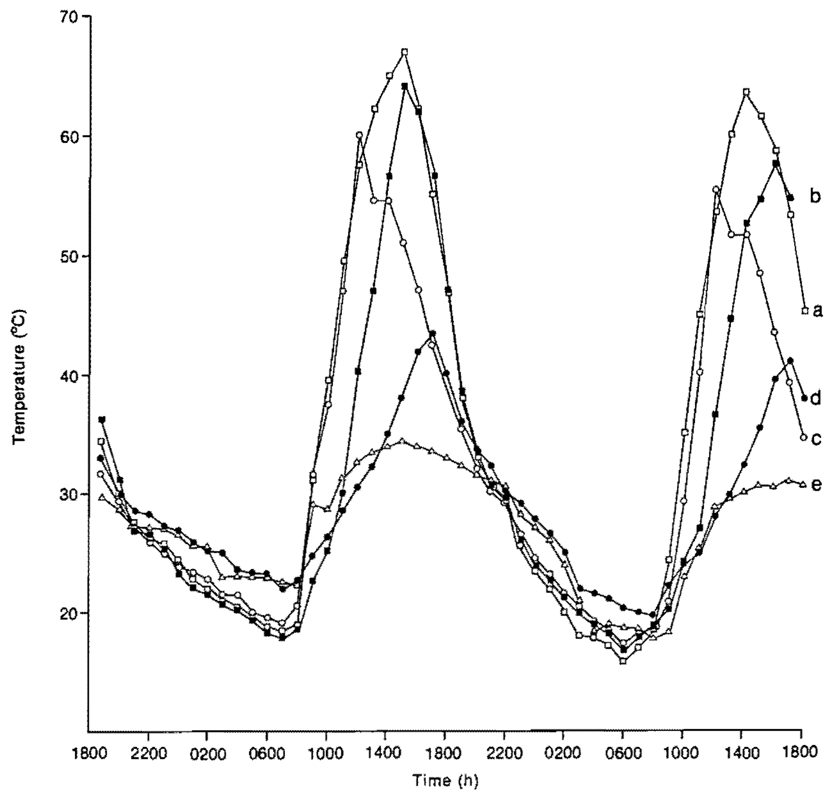

Fig. 4

Temperatures recorded during 21, 22 and 23 February 1982: **a**: on exposed soil; **b**: soil surface under western leaf tips; **c**: soil surface under eastern leaf tips; **d**: soil surface west of stem; and **e**: east of stem. (d) and (e) were under 20–30 mm litter.

DISCUSSION

Welwitschia mirabilis creates a microclimate below its leaves in which temperature and moisture regimes are considerably more moderate than those prevailing in the harsh environment in which it lives. Thus when the temperature of exposed soil was over 70 °C, soil temperatures below *W. mirabilis* plants barely reached 40 °C. Even soil temperatures below frayed leaf tips were substantially lower (up to 15 °C) than at exposed sites under certain conditions. Furthermore, temperatures varied considerably depending on the point of measurement relative to the plant. Since leaves tend to become frayed at the tips, temperatures were generally higher with increasing distance from the stem. Thermal regimes at easterly and westerly positions under the plant displayed considerable differences and the amount of litter collected within the stem depression and at the base of the stem moderated temperatures. There is therefore a mosaic of temperatures within the microhabitats associated with *W. mirabilis* at any one time.

Microhabitats associated with desert plants often provide favourable conditions for arthropod activity (Charley and West, 1977; Sartos, DePree and Whitford, 1978) and for refuge and feeding of other animals (Cloudsley-Thompson, 1962; Larmuth, 1979; Seely, De Vos and Louw, 1977). The microhabitats below *W. mirabilis* attract numerous animals, including birds, snakes, small mammals, lizards, chameleons, scorpions, spiders and a variety of insects (Bornman, 1971). Marsh (1987) has also established that a relatively rich micro-arthropod community flourishes in the soil mound below this species. Many of the large animals do not live permanently below *W. mirabilis* nor do they utilize the plant as a food resource. Their occasional presence below the plant is probably largely due to the thermal refuge that the plant provides. Furthermore, it is likely that the humidity beneath the plants is greater than elsewhere because of transpiratory water loss and this may also enhance the attractiveness of the microenvironment for animals. The presence of a permanent diverse micro-arthropod fauna below the plants and their scarcity elsewhere in this habitat (Marsh, 1987), is largely because of a relatively rich food resource base in the form of litter but their ability to persist there can also be attributed to the more favourable microclimate created by the plant.

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