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Leaf Temperatures and Energy Balance of *Welwitschia mirabilis* in Its Natural Habitat

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Summary. *Welwitschia mirabilis* is a perennial desert plant with extremely large leaves (0.5–1.0 m broad, 1–2 m long). Leaf temperatures were measured in the field and the energy budget was calculated. The portions of the leaf which were kept above the ground had leaf temperatures which were only 4–6° C above air temperature. In the leaf portions which were in contact with the ground leaf temperatures were 6–12° C above air temperature (absolute maximum 51° C). The important feature in the energy budget of *Welwitschia mirabilis* is its high reflectivity (38% of the global radiation). Only about 56% of the global radiation is absorbed by the thick leathery leaves. The energy loss due to convection is of the same order of magnitude as the reflection and it is about the same in the portions of leaf on and above the ground. The difference in leaf temperatures found in these portions is due to the loss of thermal radiation from the section of leaf above the ground to the cooler ground which is shaded by the leaf. The provision of a heat sink due to the large area of shade cast by these large leaves is of significance to the existence of *Welwitschia mirabilis* in its arid habitats.

Introduction

Deserts are generally occupied by plants which are characterized by small leaves. This fact has been recognized as an important adaptation for efficient convective energy transfer at high solar radiation in order to keep leaf temperatures in a viable range at low transpiration rates (Raschke 1956; Campbell 1977). Even the zonation of the earth's vegetation has been described by characteristic leaf dimensions (Grisebach 1884; Schmithüsen 1968), and small leaves were found to be typical especially in perennials for arid regions, whereas large leaves (megaphylls: Raunkiaer 1934) are restricted to tropical humid habitats. Calculations on optimal leaf forms (Taylor 1975) even require that large leaves, i.e. those of banana, split into small ribbons in order to increase their convective energy transfer so that leaf temperatures are kept in a viable range when exposed to high radiation.

There is an exception to these generalizations, *Welwitschia mirabilis* Hook. fil. This is a perennial plant growing in the North Namib and its distribution reaches from the coastal fog desert across the subtropical grasslands into the savannah regions (Gieß 1969; Schulze and Schulze 1976). This species is characterized by two perennial extremely large leaves (Bornmann et al. 1972) which can break up into smaller ribbons. Leaf surfaces with a length of 1–2 m and a width of 0.5 m can frequently be found.

Since it is unclear how *Welwitschia mirabilis* resolves its energy budget in an environment of high radiation and very low water supply the present study was undertaken to measure leaf temperatures and global radiation in the range of its natural distribution in the Namib desert.

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Material and Methods

Diurnal courses of leaf and soil temperatures were measured using 0.1 mm and 0.05 mm copper constantan thermocouples (Wescor Microvoltmeter HR-33T). Global radiation was measured with a Lambda radiometer and evaporation with Piche evaporimeters (30 mm green disc). The investigations were carried out in the North Namib during March 1977. Spectral properties, reflectivity, transmissivity, and absorptivity in the wave length range from 400 to 1,350 nm were determined on cut material in the laboratory with an ISCO SR spectroradiometer and an integrating sphere (Eller 1972).

The investigations were made on plants of *Welwitschia mirabilis* growing in the range of its natural distribution (Gieß 1969; Volk 1966): (1) in the coastal fog desert at Torrabai and at the intersection of the coastal road with the Brandberg west road about 15–30 km inland, (2) in the grassland region of the abandoned farm at Wereldsend and in the region south of the Brandberg about half way between Brandberg West and Uis 70–80 km from the coast, and (3) in the region of the Mopane savannah at Bloemhof farm close to "Versteinerte Wald" about 140 km inland. The sites were the same as those used by Schulze et al. (1976) for carbon isotope ratio determinations. At each location individuals of average size were chosen for the measurements (Table 1). Leaf and stem sizes were quite similar for the grassland and the desert habitat. The plant population in the savannah area is younger, therefore very large size individuals are absent.

The energy exchange of *Welwitschia mirabilis* leaves was calculated according to equation (1)

$$R_N = (1-\rho-\tau)S + (L_u - \sigma T_u^4) + \sigma(T_s^4 - T_l^4) + C \quad (1)$$

where R_N is the net radiation of the leaf, S is the global radiation, ρ and τ are the reflectivity and transmissivity of the leaf, L_u is the atmospheric thermal reradiation which is received at the upper leaf surface from the sky, σ is the Stephan Boltzmann constant (5.57×10^{-8} Wm^{-2} K^{-4}), T_u, T_l, and T_s are the temperatures

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Location	Distance from coast (km)	Vegetation aspect	*Welwitschia mirabilis*		
			Stem size (m)	Length of measured leaf (m)	Width of measured leaf (m)
Bloemhof	140	savannah	0.26 × 0.12	0.56	0.12
Brandberg Wereldsend	70–80	subtrop. grassland	0.90 × 0.70 0.65 × 0.30	0.92 1.22	0.63 0.75
Torrabai, Brandberg West road	15–30	succulent and lichen desert	1.40 × 0.50 1.20 × 1.20	1.25 0.76	1.00 0.80

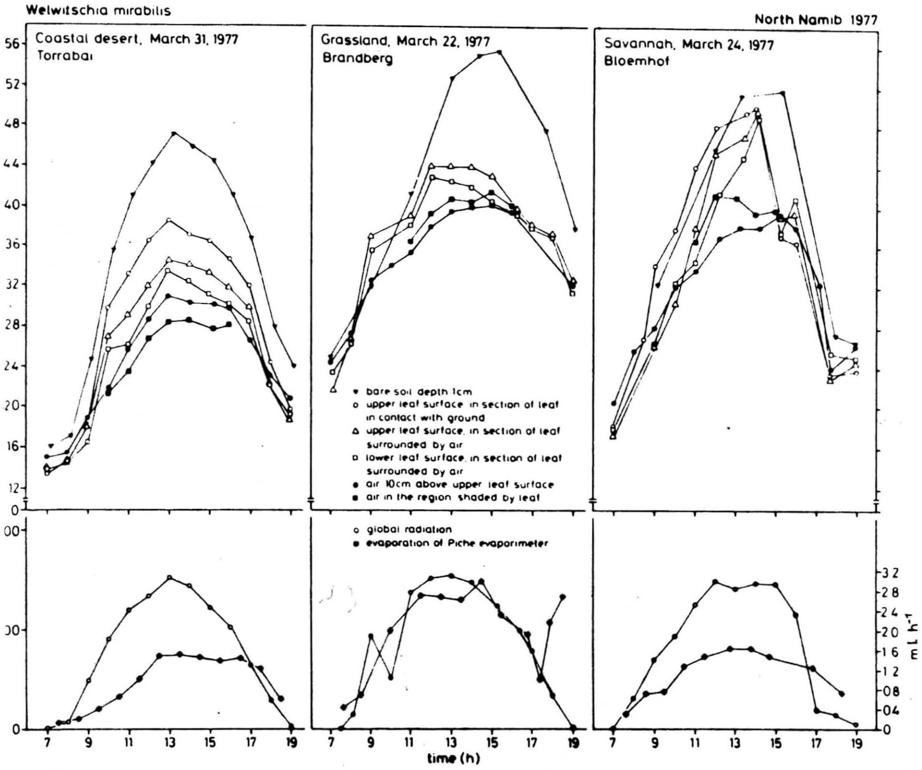


Fig. 1. Temperatures, global radiation, and potential evaporation in three contrasting habitats of *Welwitschia mirabilis*. In the coastal desert soil surface temperature in the shaded portion of the leaf is shown instead of air temperature

the upper and lower leaf surfaces and of the soil in the shade the leaf respectively, and C is the convection heat loss. R_N zero at thermal equilibrium. Measurements with a diffusion rometer (Körner and Cernusca 1976) showed no transpirational ter loss from the leaves during the day, therefore any evapo- ive energy loss is neglected. Also heat conduction to and from soil has been neglected as it was estimated to be very low to the dry soil conditions. The long wave radiation of the to the upper leaf surface (L_u) was calculated following Swin- ik's formula (see Monteith 1973):

$$=1.2\sigma T_a^4-171 \quad (2)$$

ere T_a is the air temperature, which was measured in this case m above ground. C was estimated as the residual term in (1). This was checked by calculating the heat transfer coeffi- it from the Nusselt-Reynold relationship (Monteith 1973). In cases the emissivity of the leaf was taken to be 1.

For leaf temperature investigations, flat, horizontally exposed tions of rigid leaves about 3–5 mm thick were chosen. Measuring points were in the middle portion of the leaf about 30–50 cm above the ground and where the leaf tip made contact with the ground. Thermocouple wires were taped to the leaf surface in order to achieve good thermal contact and the thermal junction was carefully pressed onto the epidermis. In all three habitats global radiation reached 750 Wm^{-2} at noon. Based on measurements made in the same region and period, diurnal courses are presented which are representative for cloudless summer day conditions. The weather may be changed by advection of hot air in the coastal area (Willert et al. 1979) or by summer rains.

Results and Discussion

The environmental conditions were different for the three habitats (Fig. 1). In the coastal desert, air temperatures (10 cm above leaf) were 15° C in the early morning and reached 30–31° C at noon, falling to 19° C at sunset. But in the grassland, air temperatures were above 24° C in the early morning and reached 49° C at

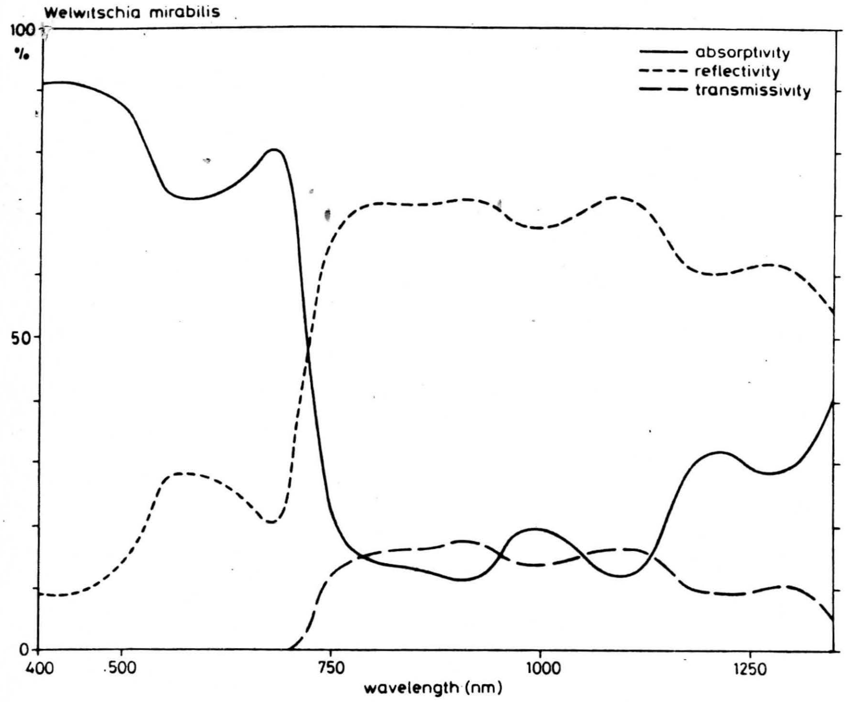


Fig. 2. Spectral properties of *Welwitschia mirabilis* leaves in the wavelength range of 400 to 1,350 nm

Table 2. Weighted mean spectral properties of *Welwitschia mirabilis* for different wave ranges at an incident radiation of 775 Wm^{-2}

Wave length (nm)	Reflectivity (%)	Transmissivity (%)	Absorptivity (%)
300– 400	9.3	0.002	90.7
400– 750	22.7	0.6	76.7
750–1,350	68.1	13.9	18.0
1,350–3,000	43.1	4.2	52.7
400–1,350	40.1	5.7	54.2
300–3,000	38.2	5.2	56.6

noon and were 32° C even after sunset. The air temperatures in the savannah were slightly lower, and similar differences existed in the temperatures of bare soil. At a soil depth of 1 cm, noon temperatures increased from the coast (47° C white sand) to the grassland (56° C red sand) and decreased again in the savannah (52° C white quartz gravel).

Temperatures of the upper leaf surface of *Welwitschia mirabilis* were highly dependent on whether or not the leaf was in contact with the ground. In its normal growth form the leaves emerge almost vertically from the stem (see Fig. 3). Then they curve around forming an arch with the highest point being near the middle of the leaf about 30–50 cm above the ground. Because of the width of the leaf (0.5 to 1.0 m) the soil under this leaf portion is shaded particularly at high solar elevation. The older portions of the leaf curl and touch the bare soil. For the portions of the leaf with both surfaces in contact with the air, the temperatures of the upper leaf surface were 4–6° C above air temperature at noon in the coastal desert and in the grassland region. But the small plants of the savannah region showed leaf temperatures of about 11° C above air temperature. The lower leaf surface of leaves from large plants at the coast and in the grassland was about 2° C cooler than the upper surface, however it was higher than the upper leaf surface temperature of small plants growing in the savannah.

For further analysis it is important to note that in spite of the extremely high temperatures of insolated bare soil, the soil and air temperature below the large leaves was about 2° C cooler than the air temperature in the coastal desert and it was about the same as the air temperature in the grassland.

Leaf temperatures increase as soon as the leaf is in contact with the ground. Upper leaf surface temperatures of 8–12° C above air temperature were observed. These temperatures come close to being lethal.

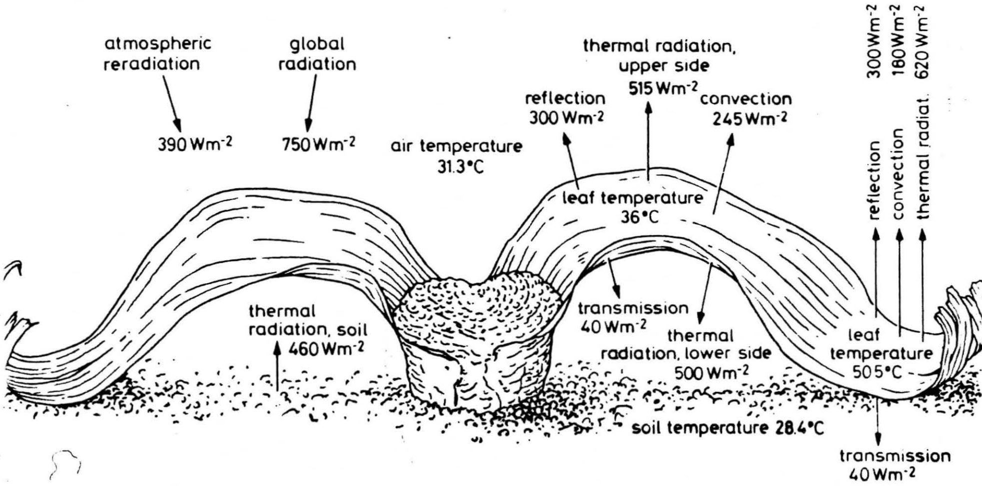
Figure 2 shows the spectral properties of *Welwitschia mirabilis* for the wave length range from 400 to 1,350 nm. Using the method of Eller (1979), weighted means of transmissivity, reflectivity and absorptivity in various wavebands are given in Table 2. For wave lengths below 400 and above 1,350 nm the weighted means were calculated on approximated spectral properties based on the measured values at 400 and 1,350 nm and an estimated absorptivity of 0.96 and a reflectivity of 0.04 for wave lengths greater than 2,500 nm (Eller 1979). Most important is the high reflectivity of the leaves in the near infrared. Additional measurements indicate that this spectral property is independent of the water content of *Welwitschia mirabilis* leaves. Thus the whole weighted mean absorptivity of the thick leathery leaf is only about 56% and comparable to thin mesophytic leaves in temperate zone species (Monteith 1973). Thick-leaved succulents of the Southern Namib have a considerably higher absorptivity (Eller et al., in preparation). Only for cacti has a similarly high reflectivity in the near infrared been reported by Gates (1965), but cacti can show temperatures ranging from 14 to 22° C above air temperature (Smith 1978) which is much higher than those found for *Welwitschia mirabilis*.

For conditions of high radiation, Table 3 shows the calculated energy budget of *Welwitschia mirabilis* in the different habitats. About 45% of the incoming global radiation is dissipated by reflection and transmission and, since transpirational water loss

· 3. The energy balance of *Welwitschia mirabilis* for the time of highest radiation in the various habitats

tion	Date/time	Loca-tion	T_u (°C)	T_a (°C)	ΔT_u (°C)	T_L (°C)	T_s (°C)	ΔT_l (°C)	S (Wm^{-2})	Reflect. (Wm^{-2})	Transm. (Wm^{-2})	$L_u - \sigma T_u^4$ (Wm^{-2})	$\sigma(T_l^4 - T_s^4)$ (Wm^{-2})	Con-vection (Wm^{-2})
.tal	31.3 10.00	mid	27.1	21.7	5.4	25.7	19.7	6.0	450	173	23	130	35	89
t	31.3 13.00	leaf	34.5	31.0	3.5	33.5	27.2	6.3	760	290	40	118	39	273
abai)	31.3 10.00	leaf	29.8	21.7	8.1	–	–	–	450	173	23	150	–	104
	31.3 13.00	tip	38.5	31.0	7.5	–	–	–	760	290	40	144	–	286
sland	22.3 11.00	mid	39.0	35.3	3.7	38.0	36.4	1.6	690	264	36	96	11	283
	12.00	leaf	44.0	38.0	6.0	43.0	39.2	3.8	758	290	39	114	27	288
ıdberg)	13.00		44.0	39.5	4.5	42.5	39.5	3.0	770	295	40	107	21	307
ane ınah	24.3 13.00	mid leaf	45.0	38.0	7.0	47	41.0	6.0	750	288	39	118	42	263
:mhof)	13.00	leaf	49.5	38.0	11.5	–	–	–	750	288	39	148	–	275
	14.00	tip	51.0	39.4	11.6	–	–	–	760	290	40	148	–	282

Upper side leaf temperature, T_a: Air temperature 10 cm above upper side, ΔT_u: Difference between T_u and T_a, T_l: Leaf ›erature on lower side, T_s: Soil temperature in the leaf shade, ΔT_l: Temperature difference between leaf and soil, S: Global ıtion, Reflect.: 300–3,000 nm reflection, Transm.: 300–3,000 nm transmission, $L_u - \sigma T_u^4$: Thermal net radiation upper side, $\sigma(T_l^4 - T_s^4)$: mal net radiation lower side



.. Energy budget of *Welwitschia mirabilis* on March 30, 1977 in the coastal desert area

ıeat conduction to the soil and heat storage are neglected, s assumed that the absorbed energy had to be released by ıal radiation and convective heat loss.

ıe main result is that *Welwitschia mirabilis* has a net loss ·rmal radiation from its lower leaf surface to the self-shaded herefore cooler soil. The proportion of energy loss by radia- from the lower surface is not large (about 5% of global ıion), but if the leaf is in contact with the ground this energy be dissipated by reradiation and convection from the upper ,urface only. For the given conditions of convective heat 'er this results in considerably higher leaf temperatures for leaf portions (Fig. 3). The temperature difference between ›oil and leaf tips of *Welwitschia mirabilis* might be explained e difference in reflectivity. At full sunlight the proportion ergy loss due to thermal long wave reradiation remains at : 20% of global radiation for leaf portions on and above ound. Under the considered conditions the convective energy loss is of the same order of magnitude as that of the reflection (average 34% of global radiation) and it is about the same for portions of the leaf above and in contact with the ground. The heat convection of 200 to 300 Wm^{-2} (Table 1) gives a heat transfer coefficient of 24 Wm^{-2}. From the Nusselt-Reynold relationship the calculated heat transfer coefficient for a wind velocity of 4 ms^{-1} and a characteristic leaf length of 0.5 m is 20 Wm^{-2}. It has been shown that under field conditions heat transfer coefficients can be higher than those calculated from the Nusselt-Reynold relationship (Pearman et al. 1972).

The highest recorded leaf temperature in portions above ground was 49° C but the highest leaf temperature at the leaf tip in contact with the ground was 51° C. This was observed in a small plant in the savannah which was not large enough to shade the ground sufficiently below the leaves and therefore was fully exposed to the high thermal reradiation of the bare soil or from quartz gravel. Young plants and leaf tips are most likely to suffer heat damage, and such damage was observed repeatedly.

Due to the combined effects of high near infrared reflectivity and the thermal reradiated loss to the self-shaded ground below the leaves at the given conditions of convective heat transfer, the absolute leaf to air temperature difference was surprisingly low even when compared to those of transpiring mesophytic leaves (Gates 1963) and those of small-leaved species of other arid regions (Lange 1959; Lange and Lange 1963). Large-leaved plants can achieve similar small temperature differences between leaf and air only by special adaptations such as leaf movement (Mooney et al. 1977) or by high transpiration rates (Smith 1978), but none of these plants has a leaf size of the order of square meters. The special growth form of *Welwitschia mirabilis* with large horizontally exposed leaves providing a large area of shade under the plant that can act as a heat sink in a desert environment seems to be an energy balance strategy unique to this plant species.

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