Ecophysiological studies on *Welwitschia mirabilis* in the Namib desert

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To determine which CO₂ fixation pathway is used by the gymnosperm *Welwitschia mirabilis* Hook. f. an extensive field study on diurnal CO₂ gas exchange, ¹⁴CO₂ incorporation, chemical composition, distribution pattern and variation of organic acids, and transpiration was made in the *Welwitschia* Flats of the central Namib desert.

The CO₂ gas exchange of *W. mirabilis* is that of a C₃ plant under air and conditions. No CO₂ uptake during the night was detected and the organic acids showed no day-night fluctuations that significantly exceeded the differences observed between the values obtained in a grid sampling over a whole leaf.

The daily water loss of *W. mirabilis* by transpiration is considerable, reaching a peak value of 1.9 mmol m⁻² s⁻¹ around noon. Problems with respect to water supply to maintain such transpiration rates are discussed. In spite of the evidence for a C₃-pathway the δ¹³C values are in the range of CAM plants. Reasons for such values in *W. mirabilis* are discussed.

Om vas te stel watte CO₂-assimileroorgroete deur die gynnosperm *Welwitschia mirabilis* Hook. f. benut word, is 'n uitgebreide veldstudie in die *Welwitschia* Vlakte van die sentrale Namibwoestyn uitgevoer waartydens ondersoek ingestel is na die etmaallike CO₂-gaswisseling, ¹⁴CO₂-assimilering, chemiese samenstelling, verspreidingspatroon en konsentrasieveranderingers van die organiese sure en die transpirasietempo van die plante.

Daar is bevind dat die CO₂-gaswisseling van *W. mirabilis* onder droë toestande ooreenstem met dié van 'n C₃-plant. Geen CO₂-opname kon snags waargeneem word nie en die ver­skil wat tussen die dag-en nagkonsentrasie van die organiese sure verky is, het nie noemenswaardig van die variasie verskil wat gekyktyd tussen verskillende punte op 'n blaar verky is nie.

*W. mirabilis* plante verloor daagliks, as gevolg van transpirasie, aansienlike hoeveelhede water. 'n Piekwaarde van 1.9 mmol m⁻² s⁻¹ word teen ongeveer 12hoo bereik. Probleme wat verband hou met watervoorsiening vir so 'n hoë transpirasietempo word bespreek.

Nietenaastande die getuenis dat *W. mirabilis* 'n C₃-roete benut, stem die plant se δ¹³C-waardes met dié van 'n C₃M-plant ooreen. Moontlike redes hiervoor word bespreek.


**Keywords:** *Welwitschia mirabilis*, Namib desert, ecology, ecophysiology, CAM

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**Introduction**

Since the discovery of *Welwitschia mirabilis* Hook. f. in 1859, this unique gymnosperm has been the subject of numerous investigations, firstly, as regards morphology and embryology (see references cited in Bornman et al. 1972 and Anon October 1977) but only recently in an effort to study how this plant manages to survive in habitats hostile to most other plants (Giess 1969; Gaff 1972; Bornman et al. 1973; Dittrich & Huber 1974; Schulze et al. 1976, 1980). *W. mirabilis* is endemic to the Namib desert which is to some extent analogous to the Atacama-Peruvian and the Baja California deserts with its shores bathed by a cold ocean current. The Namib is often foggy on its coastal edge but has sparse and episodic rainfall.

*W. mirabilis* has only two perennial leaves which emerge from a groove around the top of the stem. The leaves grow continuously at their bases and die off at their tips. Even after long drought periods the *W. mirabilis* leaves consist of sections which represent different leaf ages, from zero to about four or more years, provided that damage has not been done by browsing game or sand storms. The continuous increase of leaf age from the base of the leaf towards its tip allows for measurements not feasible with other plants which reveal the contribution of every leaf section with respect to the carbon balance of the whole plant and the distribution of inorganic ions, organic acids and amino acids, to leaf age.

Generally desert plants have small leaves. This fact is recognized as an important adaption for efficient convective energy transfer at high energy input to the leaf from absorbed solar radiation. A good convective cooling keeps leaf temperatures in a viable range (Gates & Papian 1971; Eller 1971). *W. mirabilis* with its large leaves is an exception to this generalization and therefore very high leaf temperatures at a high solar radiation input could be expected. Schulze et al. (1980), however, showed that the energy fluxes from reflection of the solar radiation at the upper leaf surface and a net thermal radiation loss from the lower leaf surface to the shaded soil below contribute substantially to balance energy fluxes at leaf temperatures only 4–6°C above the ambient air temperature.

Available data on water relations of *W. mirabilis* favour a direct water uptake of dew by the leaf via the stomata (Bornman et al. 1973). Spot measurements of stomatal resistance indicate that the stomata open more widely during the day than at night (Gaff 1972) and that the water loss at noon might be considerable (Walter 1936).
Investigations on the CO₂ fixation pathway in *W. mirabilis* give evidence of either C₃-photosynthetic CO₂ uptake (Gaff 1972) or Crassulacean acid metabolism (CAM) according to results from measurements of ¹⁴CΟ₂ uptake and δ¹³C values (Dittrich & Huber 1974; Schulze et al. 1976). Whatley (1975) found in chloroplasts of incomplete bundle sheaths of *W. mirabilis* a peripheral reticulum which in some respects resembled those of C₄-plants. Most of the investigations concerning CO₂ fixation have been done with plants or seedlings grown in greenhouses and in some cases the position of the measurements along the leaf axis is unclear. Although CAM has been proposed, only total acidity was measured without identifying the acids being involved in the proposed dark fixation of CO₂.

The information on the ecophysiology of *W. mirabilis* is patchy. Continuously recorded daily courses of transpiration with simultaneous measurements of ¹⁴CΟ₂ incorporation, and also the contents of inorganic ions and organic acids, are lacking. To obtain reliable information to clarify whether *W. mirabilis* carries out the C₃ type of CO₂-fixation or CAM, we decided to investigate *W. mirabilis* plants in their natural habitat in the central Namib desert.

**Material and Methods**

All measurements were made with naturally growing plants of the central Namib desert in the Wedwitscha Flats, about 45 km east of Swakopmund during April 1980 and August/September 1981. Some *W. mirabilis* plants were irrigated on August 24 and 28 and September 1, 1981 with a water supply equivalent to about 20 mm precipitation at each time. Determinations on these plants were made one week later.

Climatic conditions were recorded day and night. Air temperature and relative air humidity were measured by a shaded thermohygrograph (Lambrecht, Göttingen) at soil surface level. Leaf temperatures and the air temperature at 1.8 m above soil surface and near the *W. mirabilis* leaves were measured with copper-constantan thermocouples (wire diameter, 0.05 mm) connected to a reference temperature (TTYNG-EX, Hartmann & Braun, Frankfurt). Temperature measurements for energy balance calculations were made with an infra-red radiation thermometer (KT 16L, Heimann, Wiesbaden). An HR 33-T dew point microvoltmeter (Wescor, Logan) was used to determine the soil temperatures and the soil water potential at different depths as described earlier (von Willert et al. 1979). Leaf water potential was measured with Wescor L-51 leaf psychrometers attached to the lower epidermis. Dew was measured by dew fall discs. Calculations of dew point temperature and water vapour partial pressure deficit (VPD) were made from the recordings of the thermohygrograph. Evaporation was measured with a Piche evaporimeter (green filter paper no. 2653b, Schleicher & Schüll, Einbeck).

The global radiation fluxes were determined with a solarimeter (CM 5, Kipp & Zonen, Delft) and the total radiation (solar and thermal radiation) with a pyradiatormeter (PDI-QK, Observatorium, Davos). Most of the data were recorded on a 12-channel point recorder (Transcomp 250, Philips, Kassel). The electric power supply for the equipment was either 12 V DC from 90 Ah car batteries (gas analyser, pumps, recorder) or from a generator (balance).

Transpiration was estimated by the loss of mass method. For this purpose short leaves were torn longitudinally into strips which remained attached to the plant. Such a splitting often occurs naturally, either spontaneously or by distortion of the leaves during storms. The margins heal and prevent further damage of the formed leaf strips. After two weeks the artificially produced leaf strips were used for measurements. At that time microscopic examination of the margins revealed no difference compared with those resulting from naturally occurring splitting. For actual transpiration measurements the 10–15 cm long and about 2 cm broad leaf strips were cut close to the stem; the fresh cut was thoroughly sealed with vaseline. The mass of the strips was immediately determined by means of an AK 160 Mettler balance with and accuracy of 10⁻³ g. The leaf strips were exposed to the microclimatic conditions of the plant and the loss of mass was determined every 2 min for the next 10 min. Two samples of each leaf were used for one measurement. The loss of mass was linear over a period much longer than 10 min, and thus the requirement for reliable data was fulfilled (Slavik 1974). The projected leaf area was determined with a leaf area meter (LI 3100, Licor, Logan) at Bayreuth. Leaf conductance was calculated from the transpiration rate and the water vapour partial pressure difference between leaf and ambient air. Leaf and stem samples for the determination of stomatal frequency and epidermal structures were collected in FAA. For investigations with the scanning electron microscope at Zürich and Bayreuth the final preparation of the samples was made by critical point drying. CO₂ gas exchange was measured on intact growing leaves with an infra-red gas analyser (Binos 1, Leybold-Heraeus, Hanau). Rectangular plexiglass cuvettes (inside dimensions 30 × 80 mm, height 25 mm) were attached to the upper or lower surface with the longer side of the cuvettes parallel to the leaf veins. The cuvettes were carefully sealed (Terostat IX, Teroson, Weinheim) and the flow rate of the air passing through the cuvette was adjusted to 30 dm³ h⁻¹ for the untreated and 40 dm³ h⁻¹ for the irrigated plants. The air entered and left the cuvette via a tube nipple with an orifice of 5 mm in diameter. At an air flow of 30 dm³ h⁻¹ an air injection speed of 4.2 m s⁻¹ resulted, causing high turbulence in the assimilation chamber. Measurements of the air and leaf temperatures inside and outside the chamber revealed that the leaf-air temperature difference was of the same order of magnitude, 2°C–5.5°C around noon. Temperatures inside the cuvette never exceeded 42.5°C.

The ¹⁴CO₂ fixation experiments were carried out during the night and in the early morning. Small plexiglass cuvettes with a diameter of 20 mm (height 10 mm) were fixed on the leaf surface at different distances from the leaf base and on the green parts of the stem surface. The cuvettes were thoroughly sealed and connected in series with a sulphuric acid-containing bottle and an air pump in a closed air system. One cm⁻³ radioactive bicarbonate solution (1.85 × 10⁶ Bq cm⁻³, spec. activity 3.7 × 10⁶ Bq mmol⁻¹) was injected into the bottle and ¹⁴CO₂ was liberated by the acid. The concentration of total CO₂ did not exceed 1% (v/v). At the end of the fixation period leaf discs were cut from the fixation spots and immediately transferred to sample tubes containing I-propanol at 95°C. After heating to dryness the sample tubes were sealed. Radioactivity was analysed at Bayreuth. The discs were extracted with boiling water, and the radioactivity of aliquots of the extracts was determined by liquid scintillation counting.

For the determination of possible diurnal changes of organic acids and inorganic ions, samples were taken along and across the leaf blade at distances 50 mm apart, including
the youngest part of the leaf still hidden in the groove of the stem and also the dead end of the leaf at its tip. Samples were taken at the beginning and the end of the night. The fresh weight was determined, the samples were heated to 90°C for 15 min and dried for further processing at Bayreuth. Malate and citrate were determined enzymatically (Bergmeyer 1970). Proline was estimated by a colorimetric method according to Troll & Lindsley (1955). Sodium, potassium and calcium were determined by flame-photometry (Eppendorf, Hamburg) and chloride was determined by an electrotitric method (Chloride titrator, American Instrument Co., Silver Springs).

Results and Discussion

W. mirabilis and its habitat

The plan for extensive field investigations on W. mirabilis presupposed that, for simultaneous measurements and sampling, a large number of specimens of about the same size, age and physiological status were available. Therefore, it was decided to experiment on the large W. mirabilis population of the Welwitschia Flats in the central Namib desert. A segment of the population situated in the dry water-course parallel to the road to the famous 'Giant Welwitschia' was determined as the research site. All plants were recorded (position, size, sex) and a set of 22 plants, 12 male and 10 female, was selected for measurements. The experimental site (Figure 1) houses 215 plants, most of them about the same size and age.

In 1981, especially, the vegetation suffered severe damage from a long drought. The game (mainly zebras and antelopes) was deprived of its usual forage plants and was forced to feed on W. mirabilis. Many W. mirabilis leaves were detached from the stems but since the meristematic region of the leaf base, nesting in the groove at the margin of the stem, was not damaged, the detached leaf blades gradually became replaced by new ones. One could find plants with very short leaves (10 – 15 cm). Our observations imply that this leaf length is equivalent to the growth of an undamaged leaf during one year under dry climatic conditions. We measured growth rates (increase in leaf length) of 0,25 to 0,8 mm d⁻¹. Growth rates of the same magnitude were found by Moise, Swakopmund (personal communication by H. Walter, Stuttgart), while in another habitat (Brandberg area) the growth rate from March 1977 until September 1982 was 0,2 – 0,25 mm d⁻¹.

Within our measuring period in August/September 1981 all weather conditions typical for the dry period in the central Namib desert occurred — clear hot days with cool nights, foggy days and the ‘föhn’ wind condition. Dew fall and fog were not as frequent as might be extrapolated from the total number of fog days at the coast (Walter 1936). Only two days with fog, one with soil wetting driving fog and three nights with dew fall were observed during our investigations. The highest value for dew fall was 0,2 mm per night (23/24 August). In Figure 2 the data for temperature and relative air humidity from August 31 until September 30 are shown.

Figure 1 Distribution pattern of the 215 Welwitschia mirabilis plants found in the experimental area in the Welwitschia Flats. ● male plants (113), + female plants (102). In the middle of the figure the position of a steel barrel is given as a landmark. The total settling area of W. mirabilis in this water run-off is 40 205 m². The mean area for one plant is 187 m².

Figure 2 Air temperature and relative air humidity at the experimental site in the Welwitschia Flats from August 31 until September 9, 1981. The arrow indicates the beginning of the ‘föhn’ condition. Noon of each day is marked by the date.
are presented. During the night of August 31 to September 1 a NE ‘föhn’ wind arose which can be observed rather often during the cool season in this area. Owing to this weather change, the night temperatures did not fall below 17°C (compared with 3°C – 8°C one week earlier) and the relative humidity of the air did not exceed 40% (compared with 80% – 100% one week earlier). On the afternoon of September 4 the wind direction changed to SW and the typical diurnal course of temperature and humidity was restored in the following days. On September 7 and 8 the Welwitschia Flats were covered by fog in the morning until about 10h00. An extraordinarily strong sand storm from September 1 to September 3, with high wind speed, caused damage to the plants. This storm brought heavy mechanical stress to the leaves by bending and twisting them and numerous leaves were split into strips. The leaf and the stem surfaces on the windward side were abraded by the sand laden wind. Figure 3 gives an impression of the visually observable damage to the leaves. The green leaf surface first turned yellowish, then a light brown and after some days the leaves with the most damage showed a slightly brick-red colouring. Samples from intact and damaged leaf surfaces were collected in FAA for further investigation with the scanning electron microscope (SEM). Most astonishing was the absence of any detectable difference between the epidermal and cuticular structure of the damaged and undamaged leaf samples examined with the SEM. Sections of an injured leaf examined with the light microscope revealed that not the epidermis itself but the subepidermal cell layer was deformed. The observed changes in colouring may result from changes of the reflection power of the cells adjacent to the epidermis, but an esterification of xanthophylls, which can occur if cells are injured, and the xanthophylls being released into the cytoplasm might be responsible for the formation of the brick-red colouring (Goodwin 1976; Simpson et al. 1976). The Meteosat image of the large scale weather conditions in the southern part of Africa (Figure 4) on the second day of the sand storm (September 2, 1981) not only reveals how far the sand plume is driven into the ocean but also illustrates the various weather conditions that can occur in the different W. mirabilis habitats on the same day — hot weather and a sand storm in the central Namib and overcast or even foggy conditions in the Skeleton Coast region to the north. Satellite images could be used for long term studies of the variation of climatic conditions at the different W. mirabilis habitats (Brinkmann et al. 1979).

Transpiration

Plants growing in dry habitats very often have amphistomatic leaves (Parkhurst 1978) and there is a tendency for thick leaves to have stomata on both surfaces (Mott et al. 1982). W. mirabilis with its amphistomatic leaves fits well into this category. Bornman et al. (1972) reported equal stomatal frequencies (250 mm⁻¹) for both surfaces. To ascertain whether the stomatal frequency depends on the season or the year the different leaf zones have grown, a total of 306 countings on leaves of four plants (2 male, 2 female) with leaf lengths of 68 – 190 cm were performed. Countings were made every 3 cm along the leaf axis and also at several distances from the leaf base across the blade. It was not possible to recognize variations that were attributable either to the sex of a plant or to the seasonal growth periods or growth in a particular year. The mean values are, for the upper epidermis 86,8 ± 10,7 stomata mm⁻¹ (highest value 117, lowest value 66) and for the lower epidermis 61,4 ± 9,8 stomata mm⁻¹ (highest value 88, lowest value 46). Thus our countings do not support the high value given by Bornman et al. (1972).

The gymnosperm type stomata are arranged in rows (Figure 5a) and are deeply sunken into the epidermis. The cross-section (Figure 5b) illustrates how a pair of subsidiary cells reduces the stomatal groove at the bottom to a narrow furrow. This pair of subsidiary cells probably reduces the stomatal conductance significantly. The subepidermal tissue between the rows of stomata consists of fibre bundles. They run parallel to the leaf axis and ensure that under mechanical stress the leaf will rather split lengthwise than

![Figure 3 Welwitschia mirabilis leaves after the heavy sand storm (September 2, 1981). The arrows point to transition zones from injured parts of the leaf to zones that were partly protected by other leaf sections (right side) or a flower stalk (left side).](image-url)
crosswise. The fibre bundles may also act as micro-windows (Schanderl 1935) or as a diffuse reflecting apparatus for solar radiation. In fact, W. mirabilis leaves have a high reflectivity for infra-red solar radiation (Schulze et al. 1980). The stem is also green at its margin around the groove from which the leaves emerge and carries about 25 stomata mm⁻² (Figure 5c). The cross-section of such a stoma (Figure 5d) shows that it is completely blocked by wax. The ¹⁴C₀₂ incorporation experiments (see section on C₀₂ gas exchange) gave no evidence that such stomata are functional.

Figure 6 shows the transpiration of W. mirabilis after a long drought period. The water loss by transpiration is that of a plant with more or less open stomata. The leaf conductance is high in the early morning. It is attenuated with increasing evaporative demand showing a midday depression but increased again in the afternoon with decreasing water vapour partial pressure deficit.

The mean daily water loss of the four investigated plants was 0.96 dm³ m⁻² total leaf surface area. Considering that the average projected leaf area of the 215 plants in our measuring site was 0.5 m² this value implies an average water loss per plant of one dm³ day⁻¹. This water cannot be replaced by dew fall because it never exceeded 0.2 mm or 0.2 dm³ m⁻² per night (Walter 1936, and our own measurements). In the subsection of the Welwitschia Flats used for our investigation, each plant could have the use of 187 m² (mean value) settling area for water harvesting. Taking this area into account a precipitation of only 2 dm³ m⁻² (2 mm rainfall), if wholly available to the root system, would be sufficient to cover the plants annual transpirational water loss. But nobody can assume that every drop of such a rainfall could be harvested by the rooting system.

The capability of the leaves or the stem to store water could help to maintain a high transpiration rate. Gaff (1972) argued that the storage capacity of the leaves would be insufficient to supply water for transpiration during a long drought. The leaf water content as a percentage of the dry matter, measured in 1980 and 1981 (without detectable precipitation between the two measurements), is presented in Figure 7. Evidently no significant decrease of the leaf water content occurred between 1980 and 1981. Walter (1936) measured, around noon, a water loss of about 16% of the fresh mass per hour and from our transpiration measurements we get the same value or 25%–32% of the leaf water content. A leaf with 0.5 m² projected area has a fresh mass of 760 g; contains 420 g water and transpires 1000 g water a day. Hence, the leaf water content is only 42% of the daily water loss by transpiration and cannot contribute substantially to it. Waring & Running (1978) showed that an old stand of Douglas fir can store a considerable amount of water in sapwood (270 m³ ha⁻¹, equal to 27 mm precipitation) of which 75% is stored in the stem. Although W. mirabilis can store water in the sponge-like...
stem and root tissue, their volume cannot be compared with the stems of large trees. We must assume that the water holding capacity of the stem and the roots can at best merely buffer water loss and gain over short periods.

The leaf water potential of plants without a significant water storage capacity is forced to follow the daily water loss by transpiration. Measurements of leaf water potential (Figure 8) made at Torrabay in 1977 correspond in their daily course with the measured course of their transpiration rate (Figure 6). After the transpiration is attenuated in the afternoon, a recovery of the leaf water potential to less negative values is attained within a short time. During the night a further water supply eventually leads to the same values as those of the preceding morning. Such a coincidence of the transpiration and the leaf water potential pattern allows only one interpretation: the plant can replace its water loss owing to transpiration at a high VPD by a surplus in uptake at times with a low VPD and during the night when the stomata are closed. With decreasing water reserves in the rooting area a plant has to increase its suction force by decreasing its osmotic potential and/or its turgor. One can hardly say that *W. mirabilis* leaves tend to wilt during the drought periods to a detectable degree. After the extraordinary rain in 1935 Walter (1936) measured osmotic potential values in *W. mirabilis* leaves of $-3.2$ to $-3.4$ MPa whereas we obtained values of $-5.5$ to $-8.0$ MPa after the long drought.

The results presented and the fact that *W. mirabilis* preferably grows in dry water run-offs (Kers 1967) which get additional water from surface run-off from surrounding

Figure 5 Stomata of *Welwitschia mirabilis*. (a) Upper leaf surface, (b) Cross-section of leaf stomata, (c) Stem surface and (d) Cross-section of stem stomata. (Preparation and photographs a, b: U. Jauch; c,d: M.Kaib).
Transpiration, leaf conductance and microclimatic parameters of *Welwitschia mirabilis* in the Welwitschia Flats on September 10, 1981.

Figure 6

areas after rainfall, must lead to the hypothesis that *W. mirabilis* can only grow in places which provide water from well supplied underground structures. The soil of our study site in the Welwitschia Flats showed a well developed calcic horizon starting at a depth of about 30 cm. Assuming that between this horizon and the bedrock further soil horizons are capable of retaining water, then such a water resource could be the key to explain how *W. mirabilis* plants can replace their water loss by transpiration. Whether *W. mirabilis* roots can penetrate a calcic horizon or not is controversial (Giess 1969) but we must suggest that *W. mirabilis* can tap water reservoirs below this horizon which cannot be used by other plants. New plants could establish themselves if they reach this water resource after germination and before the water content of the upper soil layers is exhausted. The fact that *W. mirabilis* seedlings have a fast growing tap root (35 cm after 10 weeks in greenhouse culture) and that seedlings only establish episodically after very abundant rainfall periods support this suggestion.

Energy Balance

The energy balance consideration of Schulze *et al.* (1980) assumed the lack of a significant energy dissipation by transpiration, and the long wave radiation from the sky was based on calculations according to Swinbank’s formula. To complete the information, additional determinations of the energy balance of a horizontally growing *W. mirabilis* leaf were made.

Global radiation (G) and total radiation (Solar and thermal radiation, $R_{\text{tot}}$) were measured and the atmospheric reradiation ($R_{\text{atm}}$) was calculated according to the formula

$$R_{\text{atm}} = R_{\text{tot}} - G$$  \hspace{1cm} (1)

True surface temperatures were measured with an infra-red radiation thermometer, and a mean wind velocity was determined by a hot-wire anemometer. The optical properties of *W. mirabilis* were taken to be those given by Schulze *et al.* (1980). For the long wave emissivity ($\varepsilon$) of the soil and the leaf, a value of 0.96 was used (Wong & Blevin 1967; van Wijk & Scholte Ubing 1966). The transpiration was assumed...
to be of the same magnitude as was found for other *W. mirabilis* individuals during the measuring period.

If $R$ is the radiation budget, $B$ the energy dissipation by transpiration, $C$ the convective cooling, $S$ the stored heat and $M$ the energy exchange by metabolism, then the energy balance of a leaf is

$$R - B - C - S - M = 0 \text{ (2)}$$

With the weighted mean absorption $a^*$ (56.6%) for the *W. mirabilis* leaf the absorbed energy from global radiation was calculated by

$$G_a = a^* \cdot G \text{ (3)}$$

The thermal radiation fluxes from the soil ($R_s$) and the upper ($R_{LU}$) and the lower ($R_{LL}$) leaf surfaces were calculated according to the Stefan-Boltzmann law and the thermal long wave radiation budget with the formula

$$R_{th} = \varepsilon \cdot (R_{atm} + R_0) - R_{LU} - R_{LL} \text{ (4)}$$

The overall radiation budget is then

$$R = G_a + R_{th} \text{ (5)}$$

The transpirational energy loss ($B$) was calculated from the transpiration rate $B'$ and the heat of evaporation $c_v$

$$B = c_v \cdot B' \text{ (6)}$$

Inserting (5) and (6) into (2) and assuming the metabolic energy exchange and the value of the stored heat are negligible we get

$$C' = R - B \text{ (7)}$$

where $C'$ is the convective energy exchange from both leaf surfaces. Taking $C'$ as the energy balance residue, the convection coefficient $h_c'$ for a known leaf ($T_L$) and ambient air temperature ($T_A$) can be calculated from the formula

$$h_c' = C'/(T_L - T_A) = 2 \cdot h_c \text{ (8)}$$

For $T_L$ a mean value of the upper and the lower leaf surface temperature was taken. The value $h_c'$ divided by two gives the convection coefficient for one leaf surface.

On the other hand, the convection coefficient ($h_c$) and the convection ($C$) of a flat leaf can be calculated by the equations

$$h_c = k \cdot (v/D)^{1/2} \text{ (9)}$$

where $v$ is the wind speed, $D$ the leaf dimension and $k$ a constant and consequently

$$C = h_c \cdot ((T_{LU} - T_A) + (T_{LU} - T_A)) \text{ (10)}$$

The quotient

$$q = C/C' \text{ (11)}$$

allows comparisons of the convection calculated as the residue of the measured energy balance with the convection calculated according to equations (9) and (10) which are empirical formulae derived from measurements made with non-biological sheets.

To minimize errors arising from larger changes of the environmental conditions, mainly the radiation fluxes, the energy balance parameters were measured around noon on a clear day. The results are summarized in Table 1. Calculations were made for a horizontally exposed leaf section, 6 cm from the leaf margin. The wind speed was variable resulting in a mean velocity of 1.5 m s$^{-1}$.

The basic features of the energy input onto a plant leaf is the radiation budget $R$. Around noon about 400 W m$^{-2}$ enter the leaf system from absorbed short and long wave radiation ($T_1$, R). As already shown by Schulze *et al.* (1980) the soil surface shaded by a horizontally exposed leaf is cooler than the lower leaf surface. Thus, a net long wave radiation loss of 34 to 56 W m$^{-2}$ could be measured. These values are of the same magnitude as those calculated by Schulze *et al.* (1980). Together with the long wave radiation loss by the upper leaf surface the thermal net radiation has values between $-72$ and $-135$ W m$^{-2}$ (Table 1, $R_{th}$).

Our results from transpiration measurements require that one takes into account the energy loss by transpiration (mean value 58 W m$^{-2}$, Table 1) which balances about 14% of the mean total energy input ($R$) by radiation. This contribution of the transpiration to the energy dissipation must be considered as important for the *W. mirabilis* leaves to keep leaf temperatures during hot days at sublethal levels, as has been shown by Smith (1978) for other desert plants with large leaves.

Most astonishing is the absence of a significant temperature difference between the upper and the lower leaf surfaces (Table 1) and in cases of a difference the upper surface tends to be slightly cooler than the lower surface. Schulze *et al.* (1980) measured larger temperature differences between the upper and the lower leaf surfaces. We measured both surface temperatures with the same infra-red radiation thermometer which samples true surface temperatures and avoided errors that could arise from transmitted or reflected infra-red radiation. We must assume that the transpiration of the upper surface prevails which ensures a better cooling of the upper surface compared with the lower and so compensates for the higher energy input from solar radiation to the upper surface. Our estimates of the stomatal frequencies gave higher values for the upper surface, and for *Ledebouria ovatifolia* (Bak.) Jess., which also has more stomata on the adaxial leaf surface than on the abaxial, it is known that the energy loss by transpiration lowers leaf temperatures by 4 K – 6 K (Eller & Grobbelaar 1982).

The convection $C'$ (Table 1) as the residue of the energy balance calculations is higher than the convective loss calculated with equations (9) and (10). The quotient $q$, however, has values that match results from other investigators (Raschke 1956; Parlangue *et al.* 1971; Pearman *et al.* 1972). These authors consider a value of $h_c$ that is two to three times higher than $h_c'$ closer to reality for the energy transfer from leaves. Our measurements support this opinion.

Figure 9 summarizes the energy balance considerations giving a clearer picture of the energy fluxes, mainly the magnitude of the long wave radiation fluxes, than tabulated values. It also shows to what extent the high reflectivity of the *W. mirabilis* leaf protects it from overheating.
Table 1 Energy balance of a horizontally exposed leaf section of \textit{Welwitschia mirabilis} Hook. f. around noon. Welwitschia Flats, September 8, 1981. Leaf 18 cm above soil surface, leaf section 15 cm from leaf base and 6 cm from leaf margin, mean wind velocity 1.5 m s\(^{-1}\)

<table>
<thead>
<tr>
<th>Energy Balance</th>
<th>Symbol</th>
<th>Equation ((^{\text{b}})measured)</th>
<th>11h30</th>
<th>12h00</th>
<th>12h30</th>
<th>13h00</th>
<th>13h30</th>
<th>14h00</th>
<th>Mean value</th>
</tr>
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<tbody>
<tr>
<td>Radiation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Global radiation</td>
<td>(G)</td>
<td>((W \text{ m}^{-2}))</td>
<td>814</td>
<td>867</td>
<td>920</td>
<td>920</td>
<td>903</td>
<td>850</td>
<td>879 ± 43</td>
</tr>
<tr>
<td>Atmospheric reradiation</td>
<td>(R_{\text{atm}})</td>
<td>((W \text{ m}^{-2}))</td>
<td>420</td>
<td>405</td>
<td>391</td>
<td>413</td>
<td>433</td>
<td>453</td>
<td>418 ± 22</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambient air</td>
<td>(T_{A})</td>
<td>(^\circ\text{C})</td>
<td>20,5</td>
<td>22,5</td>
<td>23,5</td>
<td>24,0</td>
<td>24,5</td>
<td>25,0</td>
<td>23,3 ± 1,6</td>
</tr>
<tr>
<td>Leaf: upper surface</td>
<td>(T_{LU})</td>
<td>(^\circ\text{C})</td>
<td>27,5</td>
<td>25,0</td>
<td>29,0</td>
<td>27,0</td>
<td>29,0</td>
<td>29,0</td>
<td>27,8 ± 1,6</td>
</tr>
<tr>
<td>lower surface</td>
<td>(T_{LL})</td>
<td>(^\circ\text{C})</td>
<td>28,0</td>
<td>25,0</td>
<td>30,0</td>
<td>28,0</td>
<td>31,0</td>
<td>31,0</td>
<td>28,8 ± 2,3</td>
</tr>
<tr>
<td>Soil surface (shaded)</td>
<td>(T_{S})</td>
<td>(^\circ\text{C})</td>
<td>22,0</td>
<td>22,0</td>
<td>23,5</td>
<td>24,5</td>
<td>26,5</td>
<td>25,0</td>
<td>23,9 ± 1,8</td>
</tr>
<tr>
<td>Radiation budget</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Absorbed global radiation</td>
<td>(G_{a})</td>
<td>((W \text{ m}^{-2}))</td>
<td>461</td>
<td>491</td>
<td>521</td>
<td>521</td>
<td>511</td>
<td>481</td>
<td>498 ± 24</td>
</tr>
<tr>
<td>Thermal radiation budget</td>
<td>(R_{\text{in}})</td>
<td>((W \text{ m}^{-2}))</td>
<td>-104</td>
<td>-76</td>
<td>-135</td>
<td>-85</td>
<td>-83</td>
<td>-72</td>
<td>-92.5 ± 23.5</td>
</tr>
<tr>
<td>Total radiation budget</td>
<td>(R)</td>
<td>((W \text{ m}^{-2}))</td>
<td>357</td>
<td>415</td>
<td>386</td>
<td>436</td>
<td>428</td>
<td>409</td>
<td>405 ± 29</td>
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<tr>
<td>Energy balance</td>
<td>Transpiration</td>
<td>((\text{mg m}^{-2} \text{s}^{-1}))</td>
<td>23,9</td>
<td>23,1</td>
<td>21,7</td>
<td>21,7</td>
<td>24,2</td>
<td>27,8</td>
<td>23,7 ± 2,25</td>
</tr>
<tr>
<td>Energy dissipation</td>
<td>by transpiration</td>
<td>((W \text{ m}^{-2}))</td>
<td>58</td>
<td>56</td>
<td>53</td>
<td>53</td>
<td>59</td>
<td>68</td>
<td>58 ± 5,6</td>
</tr>
<tr>
<td>Energy balance residual</td>
<td>(B)</td>
<td>((W \text{ m}^{-2}))</td>
<td>229</td>
<td>359</td>
<td>333</td>
<td>383</td>
<td>369</td>
<td>341</td>
<td>347 ± 30</td>
</tr>
<tr>
<td>Convection coefficient</td>
<td>(h_{c})</td>
<td>((W \text{ m}^{-2} \text{K}^{-1}))</td>
<td>8</td>
<td>21</td>
<td>72</td>
<td>55</td>
<td>55</td>
<td>34</td>
<td>41 ± 19</td>
</tr>
<tr>
<td>Convection</td>
<td>(C)</td>
<td>((W \text{ m}^{-2}))</td>
<td>280</td>
<td>97</td>
<td>232</td>
<td>135</td>
<td>213</td>
<td>193</td>
<td>192 ± 66</td>
</tr>
<tr>
<td>Quotient of convection</td>
<td>(q)</td>
<td>((\text{measured}))</td>
<td>1,1</td>
<td>3,7</td>
<td>1,4</td>
<td>2,8</td>
<td>1,7</td>
<td>1,8</td>
<td>2,1 ± 1,0</td>
</tr>
</tbody>
</table>

Figure 9 Energy balance and global radiation energy fluxes of a horizontally exposed leaf section (6 cm from the leaf margin) of \textit{Welwitschia mirabilis} around noon on September 8, 1981 in the Welwitschia Flats (Figure based on the mean values of Table 1).

Transpirational cooling and net thermal radiation loss are important factors in the energy balance, but around noon with the energy input by solar radiation at its peak, convection is an attribute which significantly enhances the energy dispersion from the leaf.

The energy balance was only measured round about noon to elucidate how \textit{W. mirabilis} can keep its leaf temperature in a viable range during the time of the highest radiation input. At other times of the day the importance and magnitude of the different energy balance terms vary according to the reigning radiation regime. Figure 10 gives an example of the daily course of the three important radiation fluxes: global radiation, atmospheric reradiation and net radiation (short and long wave) in the Welwitschia Flats on a clear day in August/September.

\textbf{CO}_2 gas exchange

To decide whether a plant species fixes CO\textsubscript{2} only during the day via Rubisco (C\textsubscript{3}-pathway) or to some extent also during the night via PEPC (C\textsubscript{4}-pathway), one has to apply at least three criteria: firstly, is there a net CO\textsubscript{2} uptake during the night or at least a refixation of respiratory CO\textsubscript{2}; secondly, are there diurnal fluctuations in malate, citrate and other acids with an increasing content during the night; and lastly, are the \delta^{13}\text{C} values intermediate between those of C\textsubscript{3} and C\textsubscript{4} plants. In addition, CAM plants tend to have low daytime transpiration rates owing to stomatal closure under conditions of water stress.

Several investigators have reported seasonal changes in the ability to fix CO\textsubscript{2} during the night (see Kluge & Ting 1978 and references cited therein). Yet no reports exist of a CAM plant under severe water stress which exhibits a net CO\textsubscript{2} uptake during the night; and lastly, are the \delta^{13}\text{C} values intermediate between those of C\textsubscript{3} and C\textsubscript{4} plants. In addition, CAM plants tend to have low daytime transpiration rates owing to stomatal closure under conditions of water stress.

Diurnal recordings of the CO\textsubscript{2} gas exchange of different \textit{W. mirabilis} individuals clearly demonstrated that they do not have CO\textsubscript{2} uptake during the night (Figure 11a). Following night respiration, CO\textsubscript{2} uptake reaches a maximum in the early morning and decreases with increasing air

\textbf{Table 1 Energy balance of a horizontally exposed leaf section of \textit{Welwitschia mirabilis} Hook. f. around noon. Welwitschia Flats, September 8, 1981. Leaf 18 cm above soil surface, leaf section 15 cm from leaf base and 6 cm from leaf margin, mean wind velocity 1.5 m s\(^{-1}\)}}
temperature showing sometimes a second photosynthesis peak in the late afternoon. A set of plants were irrigated. This treatment, however, did not induce a nocturnal CO₂ uptake but increased CO₂ uptake during the day (Figure 11b). This reaction is typical of a C₃-type plant growing under arid conditions (Schulze & Hall 1982). Within our three week measuring period in 1981, with weather conditions that favour CAM, our measurements on several plants never gave evidence of a CO₂ uptake during the night (von Willert et al. 1983).

Measurements on leaf zones of different ages confirmed the absence of a net CO₂ uptake during the night (von Willert et al. 1983). As shown in Figure 12 the photosynthetic potential of leaf parts decreases with increasing leaf age. Calculations of the diurnal CO₂ balance showed clearly that the older parts of the leaf blade had a net carbon loss (Figure 11c) and therefore remained alive at the expense of the younger parts. To confirm the gas exchange measurements a series of ¹⁴CO₂ fixation experiments were conducted. Neither that plants with their natural water status nor the irrigated plants showed a significant CO₂ uptake during the night (von Willert et al. 1982), whereas considerable activity could be demonstrated during the day.

*W. mirabilis* is amphistomatic and measurements with cuvettes positioned opposite each other on the upper and lower leaf surface were made to ascertain whether both leaf surfaces show the same CO₂ gas exchange pattern. Figure 13 confirms that both surfaces have about the same rate of respiratory CO₂ release during the night but the rate of CO₂ uptake through the upper surface is higher than through the lower leaf surface. This is to be expected from the higher energy input from direct solar radiation through the upper than through the lower leaf surface, which only gets radiation transmitted through the leaf tissue adjacent to the upper surface or radiation reflected from the environment.

**Chemical composition**

The criteria mentioned for CAM involves the fixation of CO₂ into organic acids and this cannot necessarily be ascertained unequivocally by merely measuring the net CO₂ exchange of the leaves (Szarek & Ting 1974). Samples for the determination of organic acids were taken, in rows at 5 cm intervals, from the leaf base to the tip. One set of samples was harvested in the evening and another in the morning at a distance of 10 cm from the first set. A typical result is shown in Figure 14. Maximum differences in the malate content between a pair of samples from the same leaf zone (distance from leaf base) are ± 26 μmol/g dry matter. If we compare the average malate content of a larger number of leaves in the morning and evening, then in about 50% of the leaves malate increases whereas in the other a decrease is observed. The difference never exceeded 30 μmol/g dry matter.

A grid pattern (5 cm × 5 cm) sampling over the whole leaf blade showed for each leaf age a randomly distributed malate and citrate content (Figures 15 & 16). Dittrich & Huber (1974) reported an increase in titratable acid from 48–60 μeq/g fresh mass which is equivalent to 12 μmol malate/g dry matter. This was taken as further evidence for CAM in *W. mirabilis*. Our results (Figures 14, 15, 16) do not support this conclusion. Certainly a high content in organic acids alone is no proof for CAM. An interpretation of the unexpected high malate and citrate content in *W. mirabilis* leaves is not yet possible.

Measured δ¹³C values of *W. mirabilis* from different natural habitats have been interpreted in favour of the occurrence of CAM (Schulze et al. 1976). Our values, determined on three plants from our measuring site, vary from −17.77 to −19.64. If all our results from the CO₂ gas exchange measurements and the determination of the organic acid contents are taken into account, these δ¹³C values cannot be taken as evidence for CAM. They could be interpreted as the result of the microclimatic conditions of the desert habitat, the high organic acid content of *W. mirabilis* leaves and the amino acids which are known to have higher δ¹³C values (Ziegler 1979; Schmidt & Winkler 1979; Farquhar et al. 1982). On the other hand Whatley (1975) observed anatomical structures which were at least to some extent similar to those of C₄-plants. Thus the photosynthesis of *W. mirabilis* could be intermediate between the C₃ and C₄ types as has been observed for other plants from dry habitats (Kennedy & Laetsch 1974; Sayre & Kennedy 1977; Apel et al. 1978). If we assume *W. mirabilis* to be
Welwitschia mirabilis

Fig. 11 (a) CO₂ gas exchange of *Welwitschia mirabilis* after a long drought period and (b) after irrigation; (c) Sketch of a *Welwitschia mirabilis* plant used for the investigations showing the age and the net CO₂ gas exchange during a 24-h period for the different leaf zones.

A C₃/C₄ intermediate then ecotypic differences could lead to a variation in the C₃/C₄ levels as has been observed for ecotypes of *Mollugo verticillata* L. by Sayre & Kennedy (1977). Such variations must lead to differing δ¹³C values for different habitats. Schulze *et al.* (1976) reported δ¹³C values ranging from −23.31 to −17.39 (variation 5.92) for different habitats whereas our determinations from the Welwitschia Flats vary only by 1.87. Further investigations are needed to localize the source of the unusual δ¹³C values of *W. mirabilis*. 
The distribution pattern of malate and citrate (Figures 15 & 16) reveals a dependence on leaf age (distance from leaf base). The same is valid to a much greater extent for Na, K, Ca and Cl ions (Figure 17). Most remarkable, however, is the amount of these inorganic ions and the steep gradients of Cl⁻ and K⁺. As far as it is known from determinations in other plants K⁺ and Cl⁻ have their highest concentration in young leaves and Na⁺ and Ca²⁺ are enriched with increasing leaf age. Na⁺ and Ca²⁺ ions are carried in the transpiration stream and the ions are deposited in the transpiring leaves (see reference citations in Kinzel 1982). The results of *W. mirabilis* agree very well with this ion distribution pattern. The balance of negative and positive charges owing to inorganic ions reveals a surplus of cations which, however, can be balanced by organic acids.

Proline is present in *W. mirabilis* leaves in very high concentrations. As far as is known *W. mirabilis* has the highest...
60% of its actual leaf water content per hour. For the halophytic *Zygophyllum stapfii* Schinz. growing in the same habitat, this value was only 0.7%. Although the problem of how the water that is lost by transpiration is being replaced remains to be settled, sufficient evidence indicating that the soil must be the source of this water is available. Dew fall alone cannot replace the daily water loss. The feasibility of high transpiration rates during drought periods enables *W. mirabilis* not only to perform the C₃-pathway of photosynthesis with usually higher yields than CAM (Larcher 1976) but also leads to a fairly high energy output by transpiration. Our transpiration measurements with leaf strips must be considered as a first approach to improving the knowledge about the transpiration of *W. mirabilis* in its natural habitat, but further investigations connected with the determination of the water status of the soil must be performed.

*W. mirabilis* has only two persistent leaves and therefore cannot reduce the water loss by simply reducing the number of leaves as other desert plants do, especially succulent shrubs. The leaf tip dies off owing to extensive water loss and/or negative carbon balance (Figures 11 & 12). Growth at the base is continuous, even during extreme drought periods. *W. mirabilis* can only adjust its leaf by varying the growth rate, whereas the die-off at the tip is the result of climatic conditions and age. Other plants of the Namib desert produce new leaves seasonally (e.g. *Pachypodium namaquanum* (Wyley ex Harvey) Welw., *Tylecodon paniculatus* (L.f.) Toelken, *Ozoroa dispar* (Presl) R. & A. Fernandes) namely, at the end of the seasonal drought period, or else they keep a few leaves at the tips of their branches to have the photosynthetic organs ready if it should actually rain in the rainy season. Most desert plants can also exhibit a very rapid leaf and branch growth after a rain and can profit from a renewed water supply very quickly. *W. mirabilis* exhibits another strategy. It keeps a more or less large leaf area in an active state and in this way maintains a standby status for a quick reaction with an improved water supply, as can be seen from our irrigation experiments (Figure 11). Field investigations on a large group of different succulents growing in the southern Namib revealed that during a long drought the CAM-type of photosynthesis cannot avoid steady decline of the viability of the plants and a slow but unavoidable final death of almost the whole vegetation (von Wilpert *et al.* 1983). *W. mirabilis* grows only in areas with a sufficient water supply enabling it to survive long drought periods.

It seems contradictory that *W. mirabilis*, growing in a habitat with climatic conditions favouring CAM (low night temperatures, frequently occurring fog or dew), covers its CO₂ demand only by daytime fixation and consequently has to replace a considerable water loss through transpiration. However, *W. mirabilis* has leaves of a size not only unusual for a desert plant but also unfavourable from the energy balance viewpoint. We must assume that for *W. mirabilis* the evolution of the large leaves paralleled the evolution of adaptations that compensate for this unfavourable size, such as, a high reflectivity for infra-red solar radiation or the rising of the leaves above the soil surface to improve convective cooling and also to allow a net thermal radiation loss to the shaded soil below the leaf (Schulze *et al.* 1980). It seems that these adaptations are insufficient to keep leaf temperatures in a viable range. The need for an additional energy disposal method when a high solar radiation input occurs can only be met by transpirational cooling, which
has been shown to be important also for other plants growing under similar radiation energy regimes (Lange 1959, 1962; Eller & Grobbelaar 1982).

One could argue that \textit{W. mirabilis} tolerates a high transpiration rate only in favour of a low leaf temperature and that because the stomata are open for transpiration, CO$_2$ uptake can also take place and consequently the plant does not need to assimilate CO$_2$ during the night. Such an assumption would be an oversimplification. Firstly, the transpiration measurements reveal a marked stomatal closure (Figure 6, leaf conductance) during the day and secondly, the carbon gain by photosynthesis is poor, even for very young leaf sections (Figure 11). Only watered plants show a good two-peaked photosynthetic curve and the maxima are on the lower margin of observed values for gymnosperms or even CAM plants (Larcher 1976). So it would be better to accept that the high transpiration rate of \textit{W. mirabilis} even in drought periods is an unavoidable consequence of the fact that it can only perform the C$_3$-pathway.

Acknowledgements

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