Optical properties and succulence of plants in the arid Richtersveld (Cp., Rep. South Africa)

Botanica Helvetica *93:* 47-55 (1983)

Optical properties and succulence of plants in the arid Richtersveld (Cp., Rep. South Africa)

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Received January 19, 1983

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Abstract

Eller, B.M., E. Brinckmann, and D.J. von Willert. 1983. Optical properties and succulence of plants in the arid Richtersveld (Cp., Rep. South Africa). Botanica Helvetica *93:* 47-55. The leaf spectral properties of different plants growing in the southern Namib desert (Richtersveld area) were determined for the wave range from 400 to 1350 nm and weighted mean values calculated. The absorption values for the visible global radiation (400 to 750 nm wave length) do not differ from each other and those of mesophytic leaves. On the contrary, the absorption for the infrared part of global radiation (750 to 1350 nm wave length) increases with increasing succulence. Comparable leaf types show similar absorption for global radiation. Ecological aspects of leaf spectral properties are discussed.

Introduction

Perennial plants growing in arid environments are intriguing as they can survive over long periods of high radiation and temperatures without rainfall. The plants, especially the succulents growing in the Richtersveld are examples of this type of plants. The vegetation belongs to the Western Cape Domain of the Karoo-Namib region (Werger 1978). Even if one considers that the radiation regime under which the plants grow is very rigorous, one observes a variety of leaf shapes, surface structures, sizes and colouration, contrary to expectations that natural selection principles would lead to more uniformity. Energy balance considerations would predict that the leaves should be small and thin to increase their convective heat transfer and highly reflective or transmissive to reduce the amount of energy they absorb. However, though some of the leaves are small and others show higher degrees of reflection many have high mass to surface area ratios and show no marked increases in reflectivity. To get a clearer understanding why these differences in leaf morphology exist a study of the optical properties of some perennial plants growing at Numees in the Richtersveld (Cape Province, Rep. South Africa) was made.

Material and methods

Leaf samples were collected at the measuring site and sent by air courier to Zürich where the measurements on leaf optics were made. Plants of *Ozoroa dispar* (Presl.) R. & A. Fernandes were raised from seeds at the Technische Hochschule Darmstadt under climatic conditions similar to the natural habitat. A description of the topography, climate, and vegetation at Numees is given elsewhere (von Willert et al. 1980). The leaf types investigated were:

a) Succulent leaves. (1) Plants growing close to the ground: *Othonna opima* Merxm. has pointed cylindrical upright leaves, max. length approx. 10 cm, max. diameter approx. 1.5 cm. The leaves are light green in colour and highly succulent with water content of 93.5%. *Cotyledon orbiculata* L., pointed cylinders, max. height approx. 9 cm, max. diameter approx. 1.5 cm. *Prenia sladeniana* (L. Bol.) L. Bol., approx. circular, max. diameter 3.0 cm, max. thickness 0.5 cm. *Cheiridopsis sp.* having leaves of triangular cross-section, max. width approx. 1cm, height approx. 5 cm. *Delosperma pergamentaceum* L. Bol., leaves of more or less triangular cross-section, max. length 4 cm, width approx. 1 cm. The leaves are green-grey with a leathery epidermis. (2) Tree and shrub species: *Aloe ramosissima* Pill., with leaves of max. length 20 cm, max. width approx. 2 cm. *Tylecodon paniculatus* (L.f.) Toelken, oval shaped leaves, max. length 8.0 cm, max. width 3.0 cm, thickness about 0.3 cm.

b) Non-succulent leaves. *Ozoroa dispar* (Presl.) R.WA. Fernandes small tree growing out of deep rock crevices, with oval shaped flat leaves, max. length approx. 6 cm, max. width approx. 3 cm. The leaves are thin, brittle and xeromorphic. Dark green intervenal areas are traversed by transparent veins. The water content of the leaves is 55%.

c) Stem succulents. *Brownanthus schlichtianus* (Sonder) V. Bittrich & Ihlenfeldt, upright cylindric stems of approx. 20 cm height and 1.0 cm in diameter. During the investigation period *Brownanthus* carried no leaves.

Spectral properties were determined using an integrating sphere and a spectroradiometer ISCO SR as described by Eller (1972). Measurements were taken over the wave length range from 400 to 1350 nm for the reflectivity r (= reflected/inciding radiation) and the transmissivity t (= transmitted/inciding radiation). The absorptivity a was calculated by the expression

$$a = 1 - (r + t).$$

For the ultraviolet below 400 nm and the infrared in the wave band 1350 to 3000 nm approximations of the spectral properties were made by the methods of Eller (1979) taking the value at 400 nm for the ultraviolet region and a value of absorptivity of 0.96 and reflectivity of 0.04 for wave lengths above 2300 nm. Between the values at 1350 and 2300 nm a linear approximation of the trend in the spectral properties was chosen, giving an error considerably lower than if the global energy in this wave bands was neglected (Eller 1979). To get the true spectral coefficients for reflected, transmitted and absorbed global radiation energy weighted mean spectral properties (x*) for the different wave ranges were claculated using the spectral energy distribution of global radiation given by Gates (1966) with an irradiance of 892 Wm^{-2}. Calculations for a wave length range from λ_1 to λ_2 were made using the equation

$$x^* = \int_{\lambda_1}^{\lambda_2} x(\lambda)\ E(\lambda)\ d\lambda \Big/ \int_{\lambda_1}^{\lambda_2} E(\lambda)\ d\lambda$$

x (λ) = optical property (reflectivity, transmissivity or absorptivity at wave length λ

E (λ) = irradiance of global radiation at wave length λ

Also determined was the surface expansion (surface (cm^2)/fresh weight (g)) of the leaves.

Results

Fig. 1 compares the spectral properties of the succulent leaf of *Othonna opima* and the sclerophyllous leaf *Ozoroa dispar,* two extremely differing leaf types found in the Numees area. In the visible spectrum both leaf types show similar absorptivities which do not differ from that of typical mesomorphic leaves (Eller, 1971). In the near infrared region, however, the succulent *Othonna opima* has high absorptivities compared with the values of *Ozoroa dispar*.

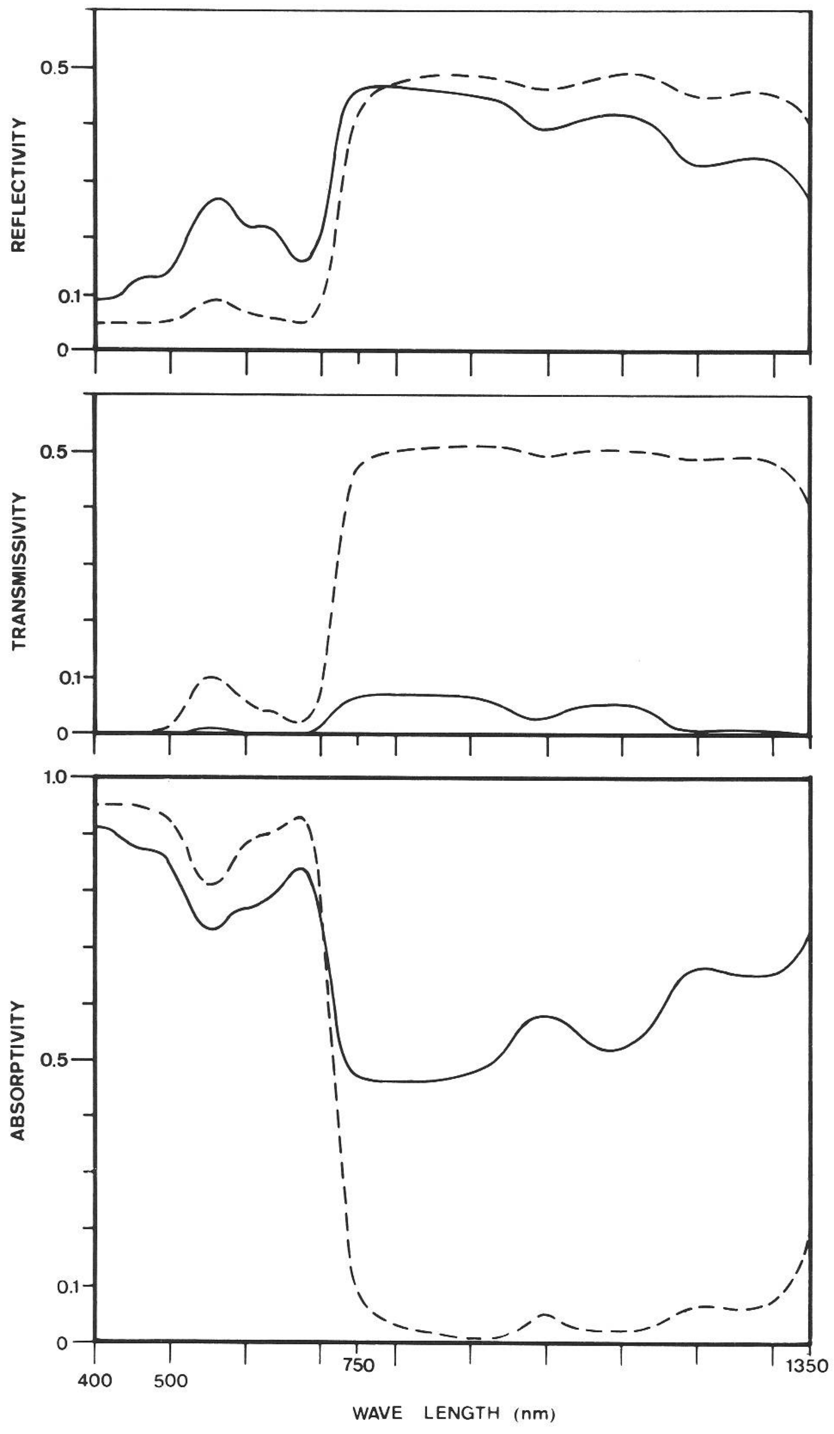

Fig. 1
Optical properties of *Othonna opima* (————) and *Ozoroa dispar* (– – – –) leaves.

Table 1

Spectral properties and surface expansion of different species growing at Numees (Richtersveld, Rep. South Africa).
Surface expansion S= surface in cm^2/fresh weight in g, weighted mean values of reflectivity (r), transmissivity (t) and absorptivity (a) for the wave ranges VIS (400...750 nm), IR1 (750...1350 nm) and G (300...3000 nm) calculated for a global radiation (G) of 892 W m^{-2} after Gates (1965).

	S (cm^2g^{-1})	r_{VIS} (%)	r_{IR1} (%)	r_G (%)	t_{VIS} (%)	t_{IR1} (%)	t_G (%)	a_{VIS} (%)	a_{IR1} (%)	a_G (%)
Cheiridopsis sp.	3.80	28.0	46.7	33.4	1.4	11.4	4.6	70.6	41.9	62.0
Othonna opima	3.91	20.1	42.1	26.9	0.7	4.7	2.0	79.2	53.2	71.1
Cotyledon orbiculata	4.15	32.9	53.7	38.8	0.2	1.8	0.7	66.9	44.5	60.5
Delosperma pergamentaceum	4.62	40.5	54.9	43.1	0.2	0.9	0.4	59.3	44.2	56.5
Brownanthus schlichtianus	5.21	19.9	45.5	27.7	0.1	1.7	0.6	80.0	52.8	71.7
Aloe ramosissima	5.55	28.9	55.2	36.7	1.0	7.7	3.1	70.1	37.1	60.2
Tylecodon paniculatus	8.55	16.2	43.4	24.9	3.8	32.0	13.3	80.0	24.6	61.8
Prenia sladeniana	8.55	23.0	38.6	27.4	9.0	36.1	17.5	68.0	25.3	55.1
Ozoroa dispar	41.67	8.7	47.1	22.8	7.0	49.5	22.3	84.3	3.4	54.9

Table 1 shows the weighted mean leaf spectral properties and the surface expansion of representative species growing in the Numees area. In the visible (VIS) wave band the difference in the absorptivity between the highest and the lowest is 25.0 % while the difference in the near infrared (IR 1) is 49.8 %. For the total range of global radiation it is 16.8 %.For reflectances in the VIS and IR 1 the range is 31.8 % and 16.6 % and for transmittances 8.9 % and 48.6 %, respectively. Hence the main differences in absorption of global radiation of the leaves lie in the near infrared band. These differences are due to lower transmittances associated with succulence and water content. For *P. sladeniana*,

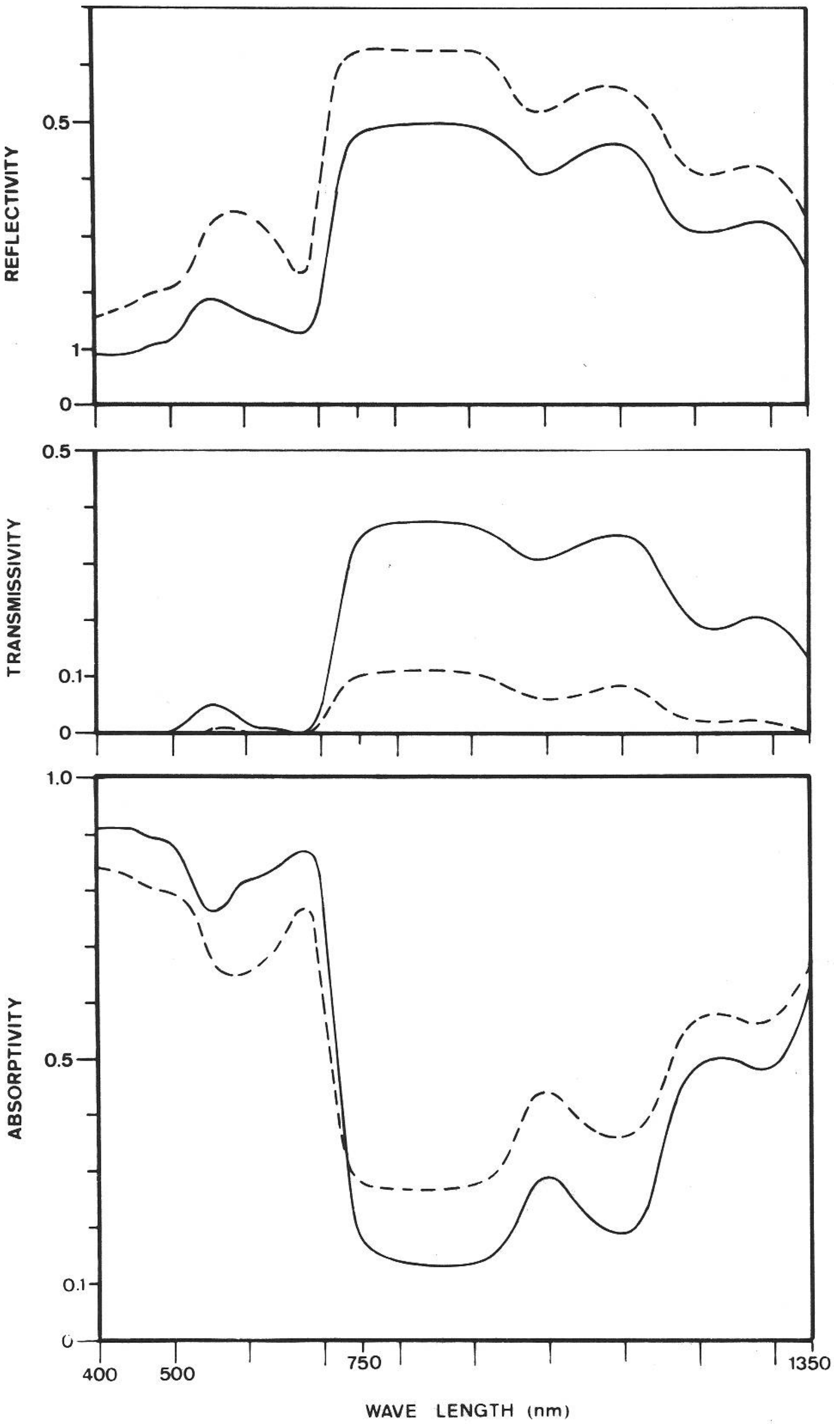

Fig. 2
Optical properties of *Tylecodon paniculatus* (———) and *Aloe ramosissima* (– – – –) leaves.

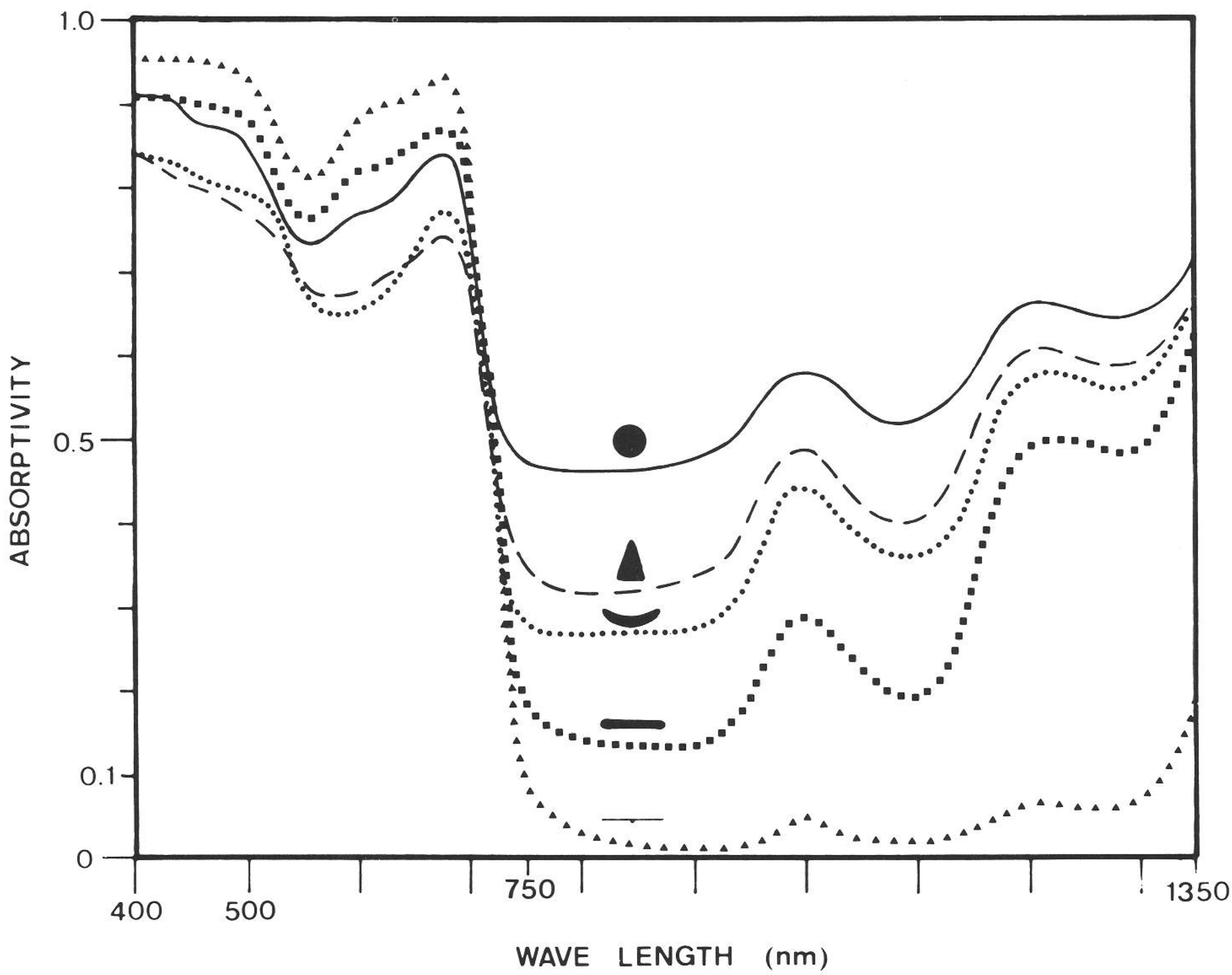

Fig. 3
Absorptivities of leaves with different leaf expansion coefficients S (surface in cm^2/fresh weight in g). Inserted into the fig. are scetches of leaf crossections. ——— *Othonna opima* (S = 3.91), – – – – *Cheiridopsis sp.* (S = 3.80), ˙˙˙˙˙˙ *Aloe ramosissima* (= 5.55), ■ ■ ■ ■ *Tylecodon paniculatus* (S = 8.55), ▲ ▲ ▲ ▲ *Ozoroa dispar* (S = 41.67).

T. paniculatus and *O. dispar* the spectral properties of both the upper and lower leaf surfaces were determined but the differences were only minor. Removal of the light waxy bloom on *P. sladeniana* leaves had little effect on the absorptivity as it decreased the reflectivity by 5% and increased the transmissivity by approx. equal amounts. This is unlike the effect of waxy blooms found in other species which decrease the absorption (Thomas and Barber, 1974; Eller and Willi, 1977). A comparison of the juvenile and old leaves of *Cheiridopsis sp.* showed no difference in transmission. However, the reflectivity of the juveniles is about 8% higher over the wave length range 400 to 1350 nm.

Fig. 2 compares the spectral properties of *A. ramosissima* and *T. paniculatus*. These are interesting as both types of leaves have similar leaf positions but *T. paniculatus* shows periodic leaf-fall in summer. The leaves are of comparable width and thickness. The weighed mean absorptivities for global radiation are almost the same (Table 1). The more leaves xeromorphic of *A. ramosissima* absorb more in the IR 1 while those of *T. paniculatus* do so in the VIS. Transmittances are higher in *T. paniculatus* while reflectances are higher in *A. ramosissima*. The similar global absorptivity (a* Table 1) is reached by different means in these two plants.

Fig. 3 shows the wide range of leaf absorptivities that exist in the Numees area. In the visible the lowest value lies only about 30 % below the highest value, while in the infrared the range is 95 %. The large variation in the absorptivities in the infrared can be correlated with leaf cross-section which are also given in Fig. 3.

Discussion

Contrary to what might be expected in an environment subject to high iraadiance the range of absorption coefficients for global radiaton, 0.717 to 0.549 is higher than that reported for mesophytic leaves, 0.6 to 0.5 (Gates et al. 1965). Most of the measured leaves have absorption coefficients greater than 0.6. Though reflectances can be higher e.g. *A. ramosissima, C. orbiculata, Cheirodopsis sp.* and *P. cf. subnudosum* than those of mesophytic species one cannot generalize that leaves in arid environments always have higher reflectivities. Sinclair and Thomas (1970) also found that the reflectivities of leaves in arid regions of South Australia were not consistently higher than those of mesic environments.

In succulent plants leaf transmittances are low because they cannot avoid the consequence of their functioning as water stores. This is seen by the low transmittivities and the consequently high absorptivities in the near infrared wave band, 750 to 1350 nm where the absorptance peaks for the leaves are the same as those for water. In the photosynthetically active spectral band (400 – 750 nm) the absorptances of *C. orbiculata, Cheiridopsis sp., A. ramosissima* and *P. sladeniana* tend to be lower than those of mesophytic leaves. This might be an adaption to reduce the radiation load of these plants as it seems that the irradiances would nearly always be high enough to saturate the photosynthetic mechanism of these plants growing in a desert environment.

There is a diversity in the shape of succulent leavens and their absorptivity for solar radiation does differ to a great extent. The difference in absorptivity between the highest *(P. cf. subnudosum)* and the lowest *(P. sladeniana)* is 16.6 %. From the energy balance viewpoint a high energy input resulting from a high absorptivity must disfavour plants in their struggle to survive if they get no compensation by other morphological or physiological adaptions. Certainly the position of the leaves either in respect to their insertion high above soil surface or their inclination plays a major role. Direct solar radiation (S) inciding with a zenith angle (z) of 37.8° would be absorbed by the upright growing round leaf of *O. opima* (^{a}O = 0.711) with a maximum value of 0.435 x S (S x a_o x sin z). The same value results for a horizontally exposed leaf area of *P. sladeniana* (S x a_p x cos z) withan absortivity (a_p) of 0.551. In fact all plants with absorptions greater than 0.60 have their leaves (or stems in the case of *Psilocaulon)* in an upright position. *T. paniculatus* and *A. ramosissima* with absorptivities of 0.618 and 0.602, respectively seem to be exceptions. Juvenile plants of these species, however, have their leavens in a more upright position than adults. Taller plants have more or less horizontally growing leaves, but they have an improved convective energy dispersal due to a better air circulation at greater distance from the soil surface. In the case of small growing plants with not upright leaves, e.g., *P. sladeniana* a lowered absorptivity compensates the unfavoruable position.

It would be premature to try to explain the diversity of growth forms of succulent leaves of plants growing in the same habitat in terms of energy balance, but it is apparent that a rigorous selection for uniformity in absorption or leaf size and shape is lacking. Growth forms, position and some physiological features such as transpiration cooling also play an important role in the energy budget which determines leaf temperature with its implications on leaf and eventually plant viability (Smith 1978). Further investigations in the field must lead to a better knowledge of the pathways by which evolution of the different life forms a succulent vegetation has occured.

The work was supported by the Swiss National Science Foundation grant no 3.438-0.78 and the Deutsche Forschungsgemeinschaft. We thank S. Treichel for providing plant material of *Ozoroa dispar* and D.A. Thomas for helpful discussion.

Zusammenfassung

Die spektralen optischen Eigenschaften der Blätter einer repräsentativen Auswahl von Pflanzen aus der südlichen Namib-Wüste (Richtersveld) wurden für den Wellenlängenbereich von 400 bis 1350 nm bestimmt und die Mittelwerte berechnet. Die Absorptionswerte im sichtbaren Wellenlängenbereich (400...750 nm) sind für die untersuchten Spezies etwa gleich groß und nicht wesentlich von denen mesomorpher Blätter verschieden. Im Gegensatz dazu nimmt die Absorption im infraroten Anteil der Globalstrahlung mit steigender Sukkulenz zu. Morphologisch ähnliche Blätter haben bezüglich der gesamten Globalstrahlung ähnlich Absorptionswerte. Sich aus den Unterschieden in den optischen Eigenschaften ergebende ökologische Aspekte werden diskutiert.

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