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Solar energy input to plant surfaces: II. Leaf dimorphism of *Aloe dichotoma* Masson and diurnal absorption of global radiation

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Abstract

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Seedlings and young plants of *Aloe dichotoma* have their leaves in an almost upright position, on the contrary older but still immature plants have their leaves in a nearly horizontal position. Field measurements in the natural habitat near Springbock (Cp., RSA) concerning global radiation and climatic data for a quantification of the energy input were extended by modeling of direct and diffuse spectral solar radiation with the computing program ECOSOL (Flach and Eller 1990). Diurnal courses of global radiation impinging on a young and an older leaf were modeled. The diurnal course of global radiation is much more balanced for the young leaf. Together with the measured spectral absorptivities of the leaves the absorbed energy for different wavelength ranges and the absorbed quantum fluxes of PAR during a day were calculated for both leaves. The results are discussed in context with the load of thermic energy and its significance for both types of leaves.

Key words: Aloe, leaf dimorphism, optical properties, solar radiation.

Introduction

Succulent plants have usually thick and opaque photosynthetic organs which are generally not flat. Between the species of the about forty plant families which include plants that are succulent, a great variety of shapes of their organs occurs. The interception of solar radiation e.g. by the stems of columnar cacti or the leaf rosettes of *Aloes* is very complex. This is not only due to the different expositions of the parts of the plant performing photosynthesis and their mutual shading, they are also subject to changing irradiance caused by the variable position of the sun during its daily course.

Simulation of direct and diffuse radiation for any orientation of surface makes it feasible to analyse in detail the intercepted and absorbed irradiation. As it was shown in Flach and Eller (1990) the computing program ECOSOL is bestly suited for the simulation of clear sky global irradiation and its spectral power distribution for any orientation of the receiving surface. The first aim of this paper is to show how ECOSOL can be applied in connection with actual field radiation data and optical properties of plant surfaces to calculate diurnal courses of inciding and absorbed global radiation.

Recent investigations have focused on the interception of photosynthetic active radiation (PAR) and its relations to the CO_2-uptake of succulents and their productivity (for a review see Nobel 1988). However PAR interception is only one aspect concerning energy input to plants by the sun. The other aspect is the heat energy input by solar radiation in its entirety including infrared solar radiation converted into heat. A high heat energy input to an organ of a plant e.g. a leaf can cause an increase of its temperature to a letal level. Energy dissipation e.g. by convection is one feature to reduce head load to a plant, the other one is to reduce the input of solar energy (Gates 1980). The latter can be done in two ways: firstly by an increase of the angle of incidence of radiation and secondly by reducing the absorptivity of the receiving surface. An upright position of a leaf reduces absorption of solar energy for the timespan when the sun's zenith angle is low and the irradiance on a horizontal surface is maximal.

Reduction of total absorbed solar energy reduces also intercepted PAR. One might argue that optimizing PAR interception is always dominating for a plant but objections must be made if plants change their morphology significantly during their life cycle e.g. large *Aloes* like *A. dichotoma* Masson or *A. marlothii* Berger. Seedlings and young plants of *A. dichotoma* have their leaves in an almost upright position (Fig. 1 a). Older but still immature plants change to a habit as shown in Fig. 1 b with leaf size, exposition and colour which differ markedly from those of the small plants. This change occurs at a height of a about 0.5 m. Adults plants of *A. dichotoma* branches but the terminal leaf rosettes of the branches are very similar to that of older, immature plants as shown in Fig. 1 b. Small plants growing in the open are subject to the boundary layer of hot air adjacent to the soil surface. The leaves of the older individuals which are at greater distances from the soil omit this hot boundary layer.

The second aim of this paper is to gain information, how and to what amount the changing position of a young upright leaf to an older horizontal leaf can influence the diurnal course of PAR absorption, heat load and their daily ratios. One might argue, that it is trivial that a horizontal surface receives more solar radiation than an upright one, but this is definitely not even true for direct solar radiation at low elevation angles of the sun. Moreover this argument is completely incorrect for diffuse reflected solar radiation irrespective whether the reflection occurs at the environment or structures of the plant itself.

An attempt was made in 1979 to quantify by measurement the energy input from direct and diffuse solar radiation and also from radiation reflected by the environment in a habitat of *A. dichotoma*. Unfortunately changing weather conditions and the time schedule for other field work prevented the collection of data for the whole day. The modeling with ECOSOL (Flach and Eller 1990) however made it feasible to complete this data for a first investigation on the differences of energy input from global radiation to *A. dichotoma* plants of different age and morphology.

Material and methods

The plants under investigation were a young and an older but still immature individual of *Aloe dichotoma* with a height of 0.32 m and 1.9 m respectively. They were growing near Springbock (Cp., Rep. South Africa, 17°58′ east longitude, 29°41′ south latitude, 920 m altitude). The two individuals

Fig. 1. Young (a) and older (b) but immature plant of *Aloe dichotoma* in their natural habitat near Springbock (Cp., Rep. South Africa) showing their leaf dimorphism.

showed the typical vertical and horizontal exposition of their leaves corresponding to their state of development. The leaf dimorphism of the two plants used for the measurements is shown in Fig. 1.

On December 21 horizontal pyranometer (Kipp and Zonen, Delft, NL) and quantum sensor (LICOR inc., Lincoln, Nebraska, USA) data were collected together with air temperature and humidity measurements with an aspirated psychrometer (Haenni, Jegenstorf, CH). True leaf surface temperatures were determined at noon by an infrared radiation thermometer KT 16 (Heimann, Wiesbaden, FRG). Because of changing weather conditions the measurements were omitted in the afternoon and evening. At midday near the time of culmination spectral irradiation impinging on the upper and lower leaf side of one of the topmost leaves of the older plant and on the adaxial side of a leaf of the young plant were measured by a spectroradiometer ISCO (Lincoln, Nebraska, USA) at 12h47, 13h02 and 13h30 local standard time. The remote head of the spectroradiometer was exposed straight above and below (i.e. facing down) the leaf for the adult plant and for the young plant between two leaves facing the bud of the rosette. For December 21 the sun reaches at culmination its shortest zenith distance of the year.

For the modeling of the radiation data with the computing program ECOSOL the atmosphere model MODMISU (Flach and Eller 1990) for dry and hot conditions and the aerosol model RURAL (Selby et al. 1976) were chosen. The choose of the atmosphere model was done under consideration of the measured climatic data. For the characterization of the actual turbidity conditions one has to choose for the calculation procedure an aerosol model and an appropriate sea-level meteorological range as explained in Flach and Eller (1990). For the estimation of the sea-level meteorological range the modeling of the global spectrum at 12h47 on the horizontal upper leaf surface and of the daily course of horizontal global radiation were performed with several values for this parameter. With a value of 15 km for the sea-level meteorological range the modeling fitted best the measured global spectrum at 12h47 and the pyranometer data in the morning hours. For these measurements the weather conditions were nearly clear. All modeled radiation data were performed with the mentioned value of 15 km.

The spectral distribution of solar radiation impinging on the abaxial leaf surface of the older plant has mainly its origin in diffuse global radiation with a considerable part of radiation reflected

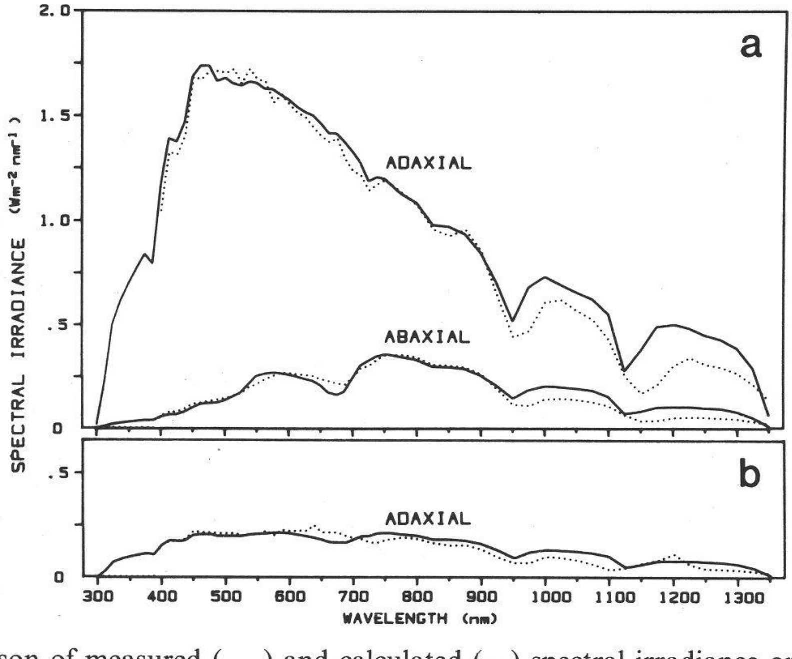

Fig. 2. Comparison of measured (....) and calculated (—) spectral irradiance on the adaxial and abaxial leaf surface of the older (a) *Aloe dichotoma* and on the adaxial side of a leaf of the young plant (b) on December 21 at 12h47, 13h02 and 13h30 local standard time respectively near Springbock (Cp., Rep. South Africa).

by the environment. The increase at 700 nm (Fig. 2a) is due to the reflection properties of the underlying leaves. To model this spectrum the reflection properties of the adult leaves of *A. dichotoma* were used. The spectral optical properties were measured between 400 and 1500 nm by means of the spectroradiometer ISCO with an integrating sphere as described by Eller (1972). The extension below 400 nm to 300 nm and above 1500 nm up to 3000 nm was made according to Eller (1979). For the radiation impinging on the the adaxial leaf surface of the young plant a likewise considerable part is due to reflected radiation at the inner parts of the rosette i.e. leaves, bud and stem and the surrounding environment. Thus the reflection properties of the abaxial surface of the young leaves (Fig. 4c) together with those ones of general soils (ALLSOIL, Flach and Eller 1990) served as input data set for the modeling.

The instantaneous amount of global radiation, which is absorbed by a plane surface element of a leaf, is calculated after:

(1) $$G_{a,i} \int_{300\,nm}^{3000\,nm} G_i(\lambda) \cdot a(\lambda)\, d\lambda$$

with $G_i(\lambda)$ = spectral global radiation inciding on the leaf element i, and $a(\lambda)$ = spectral absorptivity of the leaf surface.

The shape of the succulent leaves was modeled in a first approximation by an elongated pyramid with a cross section of an isoscale triangle. The basis of the triangle corresponds to the upper leaf surface and the two legs to the lower. The angle between a leg and the basis was determined from the measured thickness and the width of the leaf. The spatial orientation of the three sides of the pyramid was then determined considering that the young and the older leaf were attached to the stem in the northeasterly direction (azimuth angle = 210°, south = 0°).

The instantaneous energy input, i.e. the absorbed global radiation per unit area for the whole leaf is calculated by the weighted mean:

(2) $$\bar{G}_a = \frac{\sum_{i=1}^{n} G_{a,i} \cdot A_i}{\sum_{i=1}^{n} A_i}$$

with A_i = area of the i-th leaf element and $\sum_{i=1}^{n} A_i$ = total leaf area.

Results and discussion

The diurnal courses of the irradiation on the three surfaces of both pyramids were modeled with the parameters and data described in the preceding section. The measured and modeled spectral distributions of global radiation and the horizontal daily courses are given in Figs. 2 and 3 respectively. Fig. 4a and b show the measured spectral absorptivities of the adaxial and abaxial leaf side of the older and the young plant together with the spectral reflection properties of the adaxial and abaxial leaf side of the older and young plant respectively. In Fig. 5 the absorbed spectral distributions, i.e. the products $G_i(\lambda) \cdot a(\lambda)$ after (1), calculated for the radiation data and the spectral absorptivity from Figs. 2a and 4a respectively are given. Fig. 6a and b show the results of the calculations for each side of both pyramids separately and in Fig. 6c the diurnal courses of the weighted mean according equation 2. The diurnal courses of the absorbed radiation for each surface of both pyramids are essentially of the same shape, as the spectral composition of global radiation does not change significantly for zenith distances smaller than 75° (Szeicz 1975), i.e. between 7h03 and 18h28.

The young leaf in the vertical position receives a daily course of irradiation which is much more balanced. The maximal value is about half the maximum for the horizontal exposition and the irradiation is even more reduced at midday when the horizontal leaf

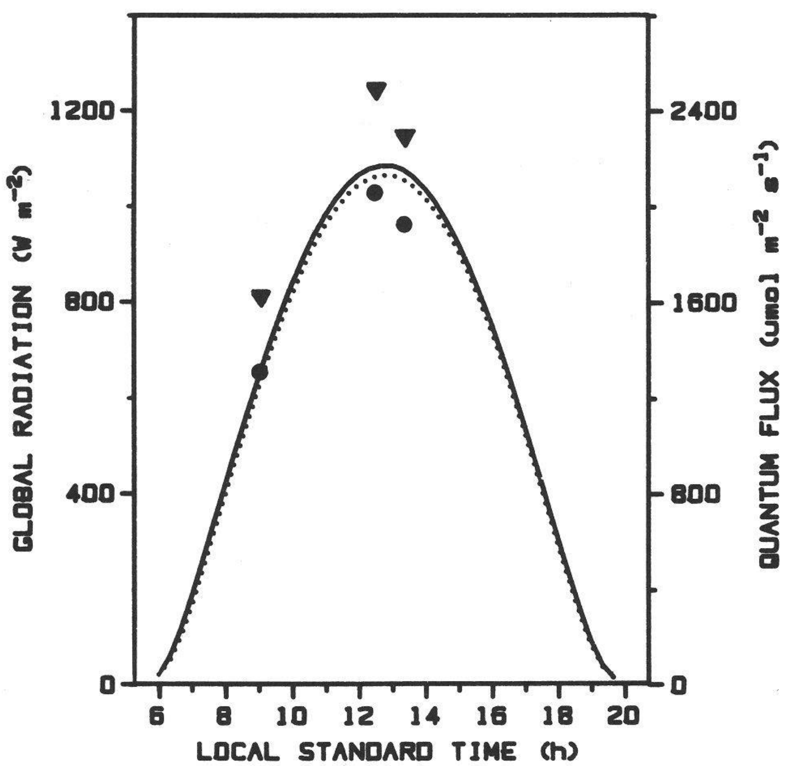

Fig. 3. Modeled daily course of horizontal global radiation (—) and quantum flux (....) for a sea-level meteorological range of 15 km and measured horizontal global radiation (●) and quantum fluxes (▾) on December 21 at Springbock (Cp., Rep. South Africa).

receives its maximal radiation input. In the late afternoon and early evening hours (17 h–19 h) the radiation input for the vertical leaf remains on a relatively high level between 200 and 300 W/m^2, whereas the values for the horizontal leaf drop continuously to zero.

This radiation input in the early evening hours probably enhances the CO_2-uptake of the young leaf for the given azimuthal position, as this timespan corresponds to phase 4 of the diurnal cycle of CO_2-uptake of a CAM plant like *Aloe* (Osmond 1978). If the plant's water status allows open stomata then CO_2-uptake is possible during this timespan. This statement of a prolonged evening is only valid for this orientation of both leaves in the north-easterly direction (southern hemisphere). A north-westerly orientation would rather result in favouring the morning hours and with this phase 2 of the diurnal course of CO_2-uptake of CAM plants (Osmond 1978).

In Table 1 the absorbed quantum (PAR) and energy fluxes of different wavelength ranges integrated over the whole day (December 21), the adaxial and abaxial leaf temperatures and the air temperatures at leaf height (all temperatures measured at noon) are compared for the young and the older leaf. The young leaf absorbs per unit area 67% of the photosynthetic quantum flux absorbed by the older leaf. However comparing the absorbed energy in the infrared region the young plant amounts only to 58% of the older. This is mainly due to the different absorption properties from young and adult leaves. This means, when comparing equal amounts of absorbed photosynthetic active radiation the young leaf is less loaded by thermic radiation. The energy input from total global radiation reaches two maxima, one in the morning (10 h–11 h) and one in the afternoon (17 h–18 h), and shows a minimum near midday when air and leaf temperatures are high

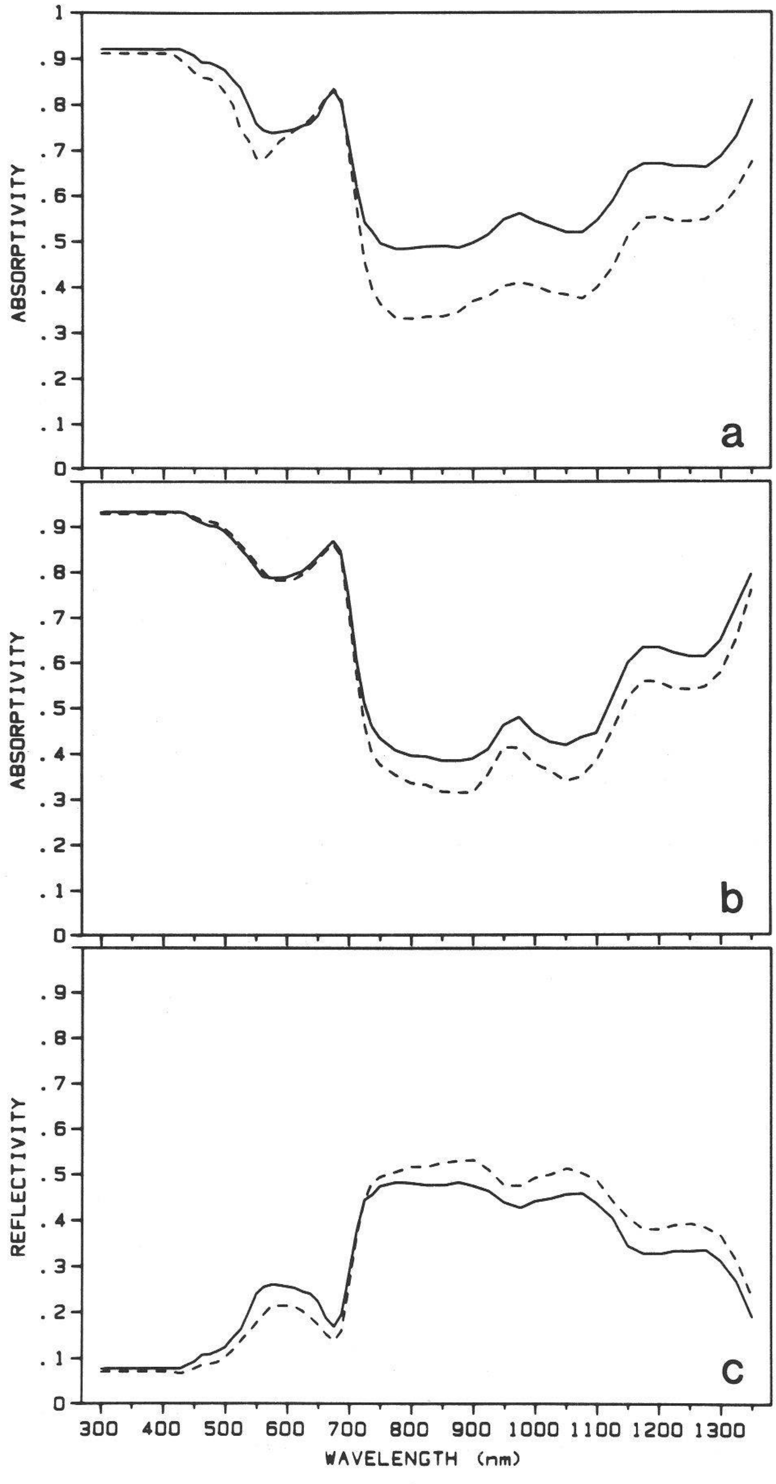

Fig. 4. Measured spectral absorptivity for an adaxial (—) and an abaxial (---) leaf surface of the older (a) and the young (b) *Aloe dichotoma* and measured spectral reflectivity (c) of the adaxial (—) and abaxial (---) leaf surface of the older and the young plant respectively.

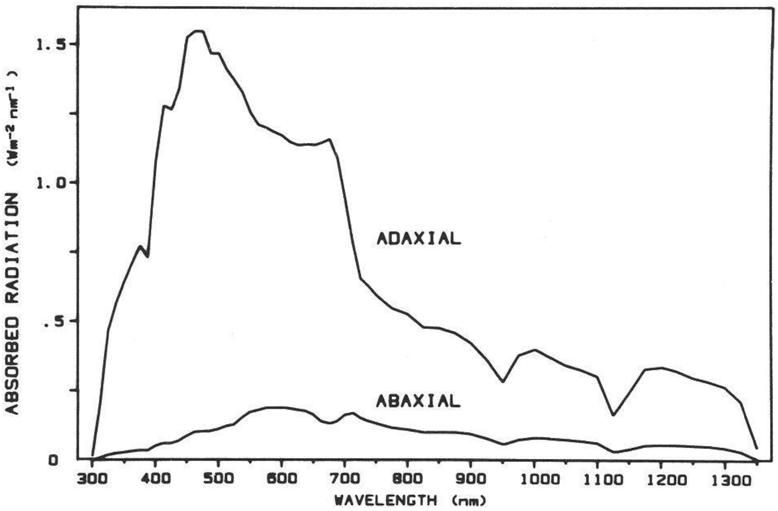

Fig. 5. Calculated absorbed radiation of an older *Aloe dichotoma* leaf for the radiation data and spectral properties given in Fig. 2a and 4a respectively.

Table 1. Comparison of the absorbed global radiation per unit leaf area for different wavelength ranges and the absorbed quantum flux for the diurnal courses of irradiation according to Fig. 6 integrated for December 21 for the young and the older *Aloe dichotoma*, together with measured leaf and air temperatures at noon.

	Young plant (y)	Older plant (o)	(y/o) (%)
Wavelength range: UV and VIS (MJ m^{-2})	4.82	7.33	66
IR (MJ m^{-2})	3.04	5.26	58
Total global radiation (MJ m^{-2})	7.86	12.59	62
PAR (mol m^{-2})	17.9	26.9	67
Range of leaf temperature at noon (°C):			
adaxial	43–45	47–49	
abaxial	44–46	46–48	
Air temperature at noon at plant height (°C):	39.8	39.0	

and the influence of the boundary layer of hot air adjacent to the soil surface is strong for the young leaves. It can therefore be concluded that the heat load is significantly reduced for the upright leaf position of the young *Aloes*. The reduction of the infrared part of global radiation input is even enhanced for the young leaves compared to the input of PAR. This could favour establishment of young plants at their natural habitat, where a high solar radiation input persists throughout the year.

The greater heat load by the boundary layer of hot air adjacent to the soil surface may be balanced to some degree by a more effective heat dissipation of the young leaves. Vogel (1970) observed maximal heat dissipation from leaves when they are oriented obliquely to a free or forced airstream.

The presented results are first investigations concerning the ecophysiological significance of the observed leaf dimorphism of giant *Aloes* like *A. dichotoma*, *A. marlothii* and

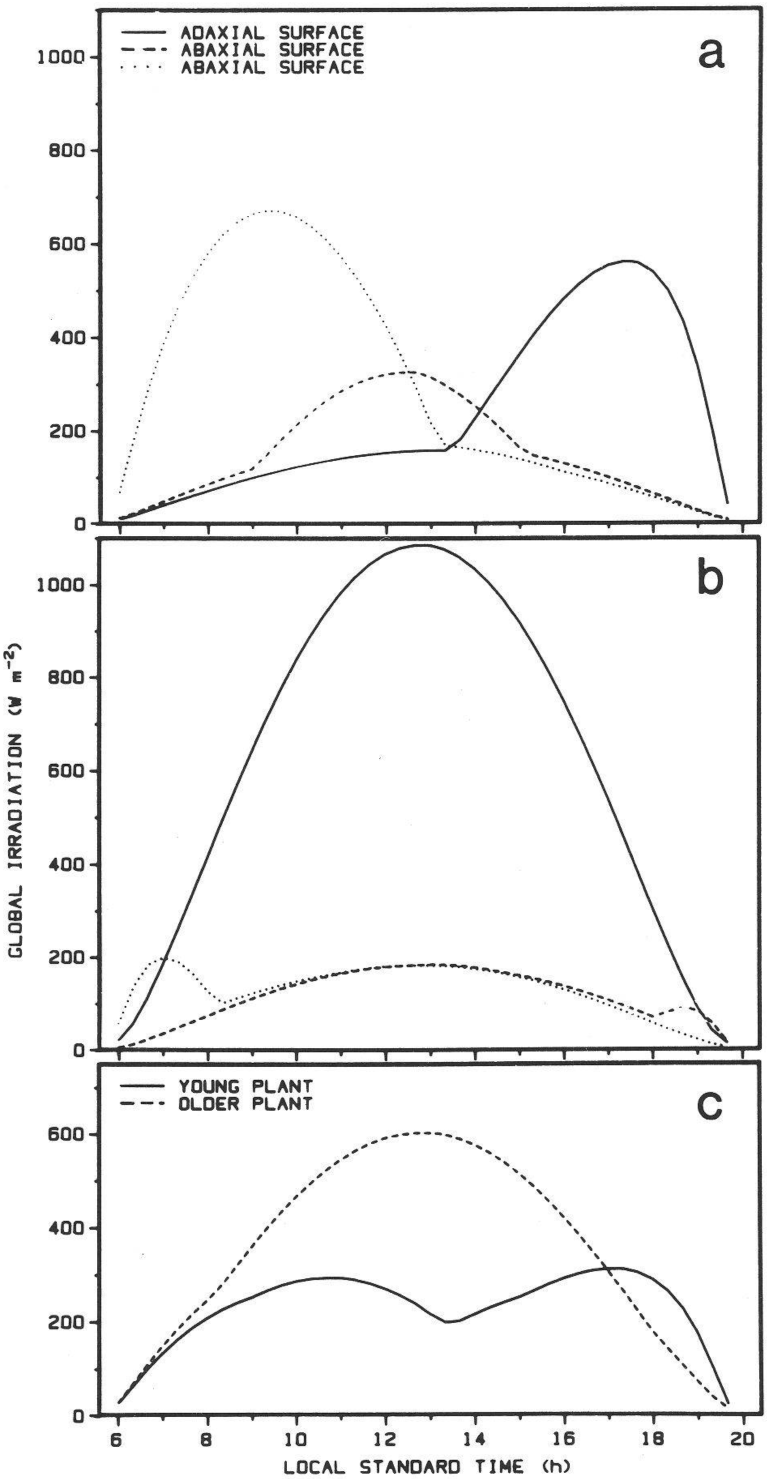

Fig. 6. Calculated diurnal courses of global irradiation on the three sides of the pyramids, which model the young (a) and the older (b) leaf of *Aloe dichotoma,* for December 21 at Springbock, and the weighted mean (c) for the three sides.

A. ferox Mill., but there is also a general tendency for an upright leaf orientation of small aloes, which have their leaves straight above the ground and which are growing in habitats of high irradiation. This can be observed for example for *A. claviflora* Burchell. and *A. hereroensis* Engler, which are growing in open spots and gravely planes. Further field investigations are needed to elucidate the significance of leaf exposition with respect to heat energy input to the leaves of that growth form of *Aloe*.

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