

# CO<sub>2</sub> Exchange Pattern Under Natural Conditions of *Caralluma negevensis*, a CAM Plant of the Negev Desert\*

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## Abstract

*Caralluma negevensis* (Asclepiadaceae) is one of the few stem succulent plants of the Negev Desert. Its CO<sub>2</sub> exchange was investigated in the field under full sun radiation by using temperature and humidity controlled plant chambers. In April and May, the plant exhibited high rates of temperature dependent dark fixation of CO<sub>2</sub>, hence proving to be a CAM plant. During most of the light period it released large amounts of CO<sub>2</sub>. This loss was increased by temperature. In April (last period of the rainy season) the daily CO<sub>2</sub> balance of *C. negevensis* was positive. Already in May (beginning of the dry period) the carbon balance became negative, because high night temperatures inhibited CO<sub>2</sub> fixation, and high temperatures during the daily light period increased CO<sub>2</sub> loss. During the middle of the dry period (August), water stress prevented any net dark uptake of CO<sub>2</sub> at night. Regarding the photosynthetic productivity, *C. negevensis* is less adapted to the climatic conditions of the true, hot and dry desert than the arido-active desert shrubs without CAM. The high temperature level and the long lasting dry season apparently are the limiting factors for the succulent. This seems to be the reason, why *C. negevensis* prefers only shady habitats between rocks, avoiding full sun radiation. In these "ecological niches" conditions allow its existence in spite of the restrictions, which are evidently brought about by the Crassulacean Acid Metabolism.

Much laboratory work has been devoted, in recent times, to the biochemical and the physiological features of Crassulacean Acid Metabolism (CAM) in plants. Compared with this, our knowledge about the ecological significance of CAM, *i. e.* the behaviour of CAM plants under natural conditions, is still incomplete. Only little information is available in the literature on their photosynthetic productivity in the field, showing what special responses are brought about by the acid metabolism under different climatic conditions. AUBERT (1971), for instance, investigated the synthesis of organic acids and the stomatal regulations in cultivated *Ananas comosa* plants; BARTHOLOMEW (1973) studied the gas exchange of *Dudleya farinosa* in coastal California; SZAREK *et al.* (1973) and SZAREK and TING (1974) measured CO<sub>2</sub> uptake, acid metabolism, and diffusion resistance of *Opuntia basilaris* in the Colorado Desert in California. These investigations were carried out in regions where CAM plants are abundant within the vegetation and where climatic

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conditions seem to be favourable for them. However, there are other arid regions, where CAM plants are much less frequent. One example is the Central Negev Desert, where stem succulents of the *Cactus* type are represented only by a few *Caralluma* species, especially by *Caralluma negevensis* (as described by ZOHARY 1962). In the desert habitat these plants are not at all common, and the vegetation is dominated by arido-active dwarf shrubs. Perhaps the limits for successful growth of succulents with CAM are reached in such a type of desert as the Negev Desert. The question therefore arises as to the factors that determine their existence. In order to investigate this problem, CO<sub>2</sub> exchange measurements were carried out in the field with *Caralluma negevensis* as a representative of CAM plants.

## MATERIAL AND METHODS

The investigations were carried out near Avdat in the Central Negev Highlands of Israel. The mean annual precipitation in this area amounts to about 80 mm. The dry, rainless summer season lasts 6–8 months, and only during 4–6 months of the winter can rain be expected. The natural vegetation is characterized by a thin cover of dwarf-shrub formations (ZOHARY 1962; EVENARI *et al.* 1971). *Caralluma negevensis* (see ZOHARY 1962), belonging to the family of the *Asclepiadaceae*, is mainly growing within the region of the *Zygophylletum dumosi*, an association dominating on the slopes and on stone fields of the plateaus. Scattered in gaps and crevices between calcareous rocks, the succulent stems of *C. negevensis* are forming cushion-like 10 to 15 cm tall stands. The plant is only found in habitats where runoff water accumulates, therefore, it is living under a relatively good water regime. Within the shadow of rocks *C. negevensis* is at least partly protected against direct insolation.

A mobile laboratory, equipped with temperature and humidity controlled plant chambers, was used for measuring the gas exchange of the plants in the field. Details of the method of measurements and possible experimental errors have been described elsewhere (LANGE *et al.* 1969; KOCH *et al.* 1971; SCHULZE *et al.* 1972). The experiments with *C. negevensis* were performed three times in 1971: April 1–14 during the last period of the rainy season; May 3–10 at the beginning of the dry season; and August 2–9 in the middle of the dry season. The succulent plant stems, 5 to 12 cm long, were collected from their natural habitat about 2 km north of Avdat. The small roots were severed, and the whole shoots were placed into the gas exchange chamber. Occasionally it was necessary to remove the lower part of a shoot which was dry or etiolated; in this case the surface of the cut was sealed by vaseline. Within the gas exchange chambers the air temperature and the air humidity was controlled according to the ambient conditions occurring at a nearby stone pile which simulated the natural habitat of the plants, however, without any protection against direct sun radiation. Thus, the measurements were taken under temperature conditions which could be regarded to be the most extreme ones to which the plant is subjected in the desert. During the gas exchange measurements the temperatures of the enclosed plants were recorded by thermocouples which had been inserted into the tissue of sun exposed parts of the shoots. In addition to gas exchange studies under simulated natural conditions, experiments were carried out, in which the air temperature of the chambers was controlled at a constant level. — In intervals of several days the plant material was removed and replaced by newly collected shoots. The gas exchange data of the plants were related to dry weight, chlorophyll content, and surface area of the enclosed stems.

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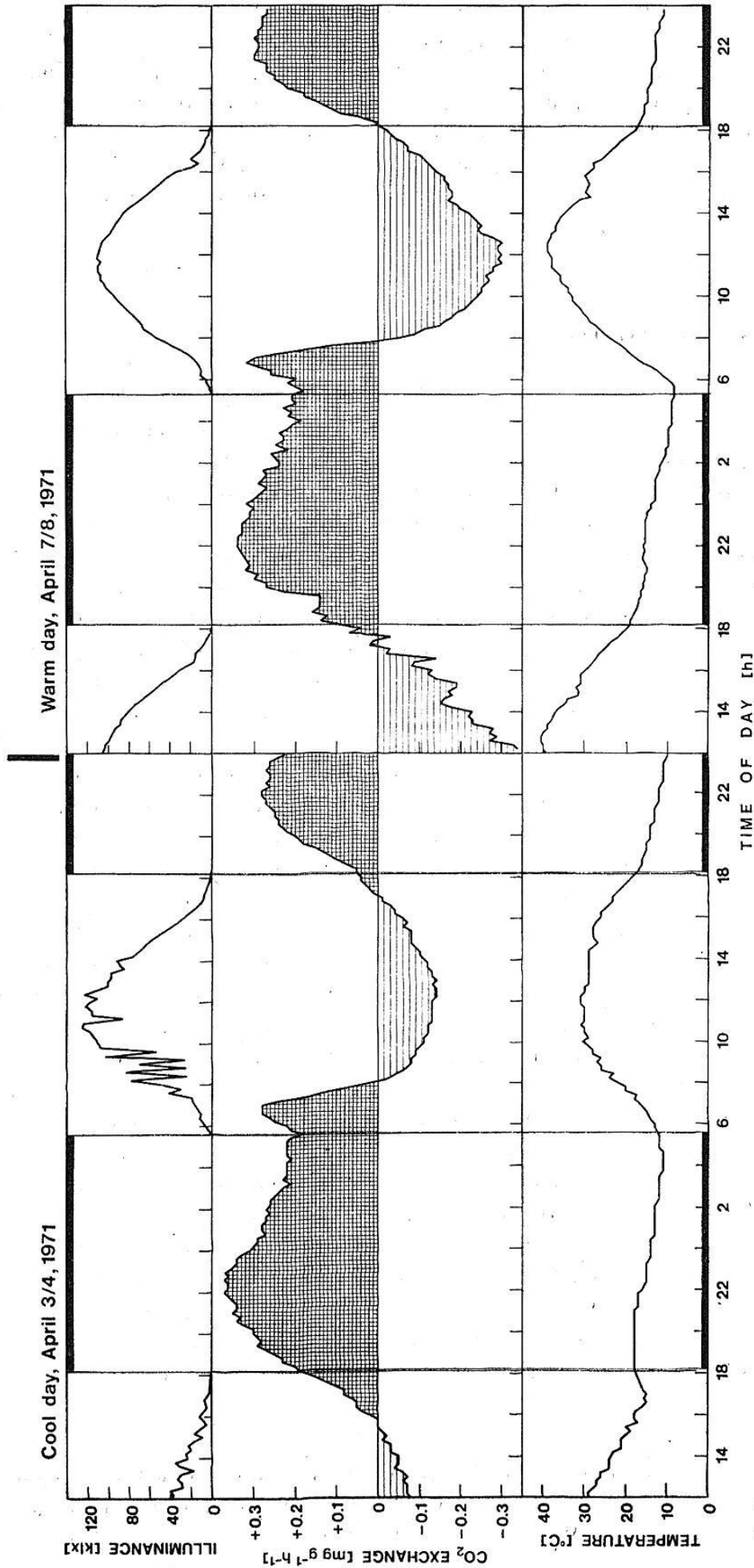


Fig. 1. CO<sub>2</sub> exchange of *Caralluma negevensis* in Negev Desert, Avdat, during the last period of the rainy season under cool (left) and warm (right) day time conditions. Diurnal course of CO<sub>2</sub> uptake (positive) and release (negative) in relation to dry weight; illuminance, and tissue temperature. The dark period is indicated by dark columns.

## RESULTS

In spring the *C. negevensis* plants in their habitat were fully turgid. Their appearance was fresh green, and they were actively growing. During the night the plants showed a high CO<sub>2</sub> uptake (see Fig. 1). This dark fixation started around sunset and rose to a maximum rate which was reached several hours after the beginning of the dark period. As is typical with most of the CAM plants and apparently depending on the charging of the malate pool, the CO<sub>2</sub> fixation rate decreased with progressing night time. However, it was still considerable at sunrise. Shortly after the beginning of the light period, the plants showed the well known burst of CO<sub>2</sub> uptake, followed by a sharp decrease. The CO<sub>2</sub> exchange passed the compensation point early in the morning. Thereafter, the plants were releasing CO<sub>2</sub> during the entire daylight period until dark fixation started again shortly after sunset.

The rate of CO<sub>2</sub> release during the light period appears to be highly temperature dependent. On the one hand this may be concluded from the shape of the CO<sub>2</sub> exchange curves (Fig. 1) which is evidently correlated to the temperature curves of the enclosed plants: the highest rates of CO<sub>2</sub> release took place during the midday period of highest temperatures. On the other hand, the temperature dependence of the CO<sub>2</sub> output is evident from a comparison of a cooler day with a warmer one (Fig. 1): on April 4 the maximum temperature of the plant tissue temperature of the insolated plant was 31 °C only, on April 7 and 8 the temperature of the plant reached 40 °C. This resulted in a much higher CO<sub>2</sub> output rate on the warmer days at noon. This temperature effect is obvious also from Fig. 2: on April 10 between 11.00 h and 13.00 h the temperature of the plant decreased, following a drop in solar radiation, caused by clouds. This temperature depression was clearly correlated with a depression in the CO<sub>2</sub> loss of the plant.

In a similar way also the dark fixation of CO<sub>2</sub> of the plants during the night depends on temperature. The natural night plant temperatures during the spring period of the year lay between about 9 °C and 19 °C. This seems to be optimal for the process of CO<sub>2</sub> fixation because an

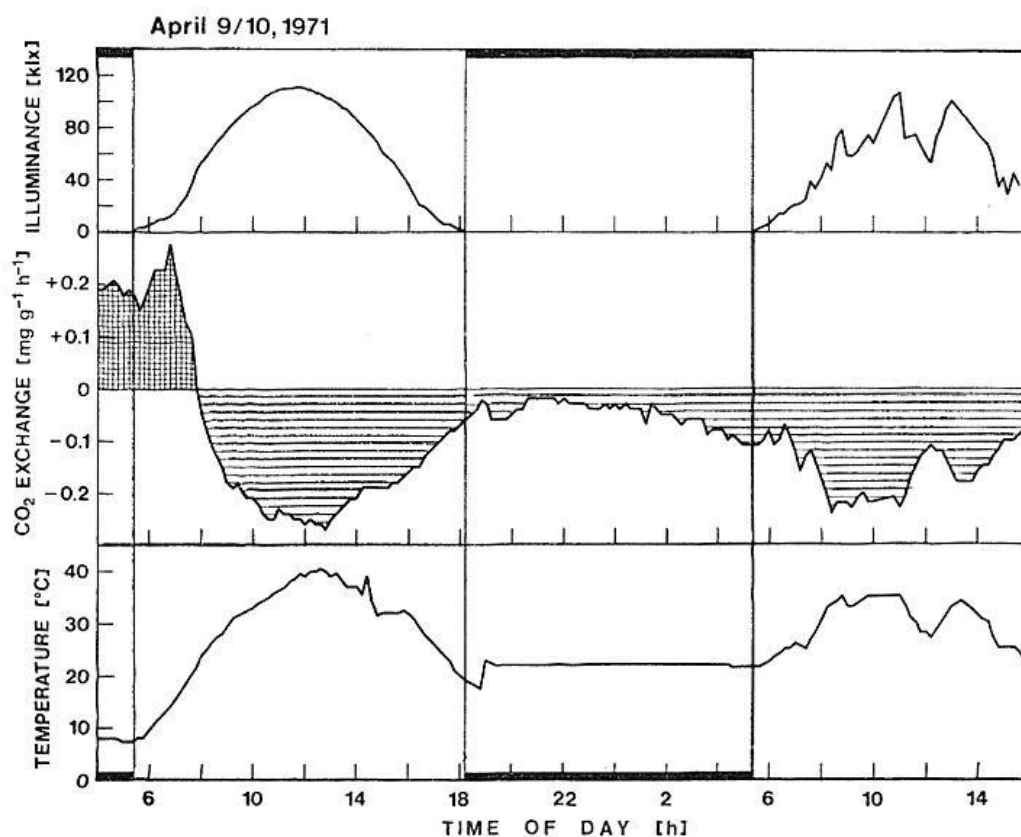


Fig. 2. CO<sub>2</sub> exchange of *Caralluma negevensis* during the last period of the rainy season under experimentally increased night temperatures (tissue temperature kept constant between 19.00 h and 15.30 h, April 10): April 9/10, 1971. For explanation see Fig. 1.



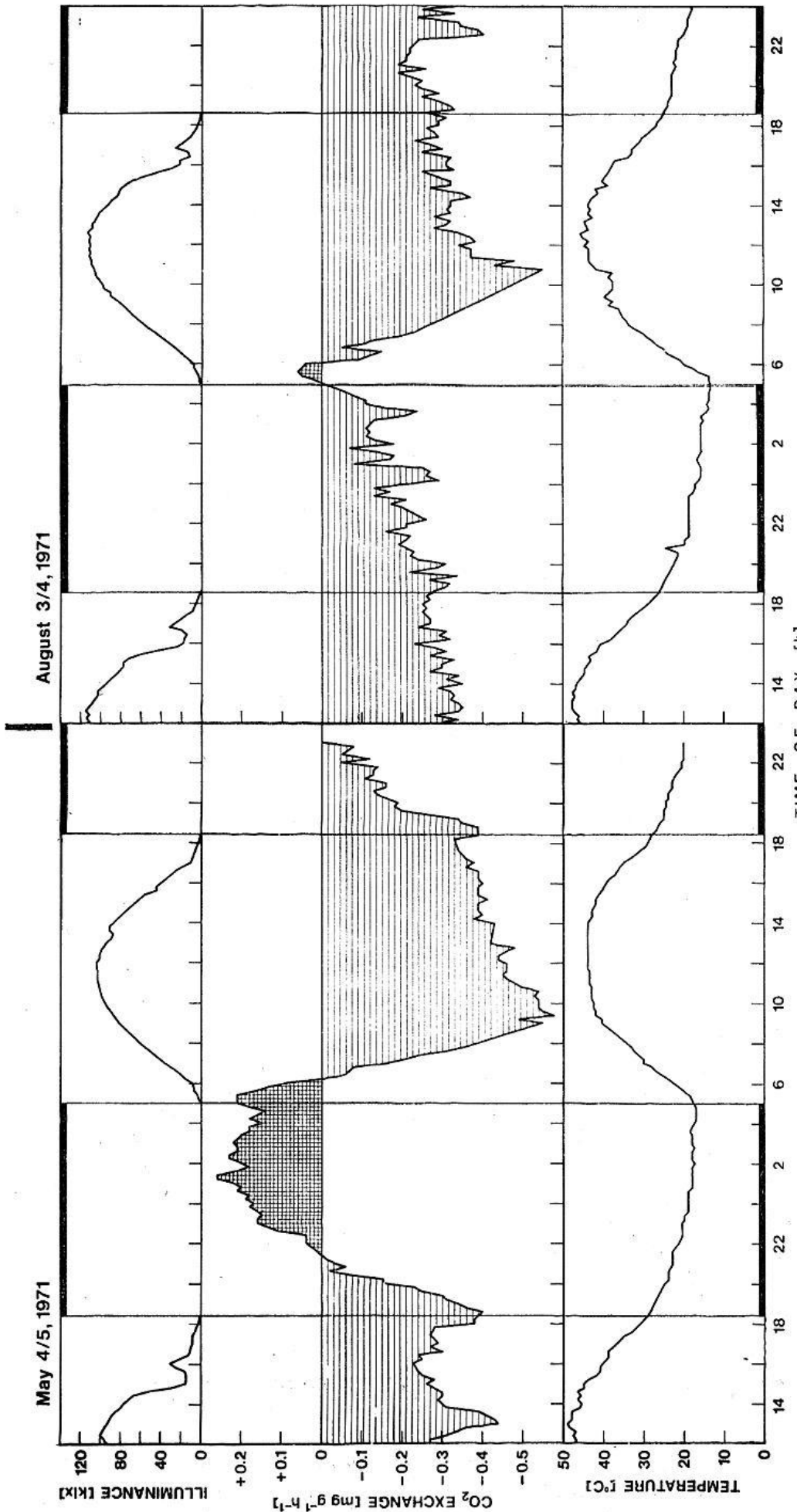


Fig. 3. CO<sub>2</sub> exchange of *Caralluma negevensis* at the beginning (May 4/5, 1971, left) and the middle (August 3/4, 1971, right) of the dry season. For explanation see Fig. 1.

artificial increase of temperatures resulted in a decreased rate of CO<sub>2</sub> uptake. High temperatures can fully inhibit the nightly net uptake of CO<sub>2</sub> (see Fig. 2). During the night of April 9/10 the temperature was experimentally held at 22 °C from 19.30 h to 5.30 h. In contrast to the preceding night under natural conditions, this temperature increase prevented any net CO<sub>2</sub> fixation. When compared with natural conditions, dark fixation of CO<sub>2</sub> was also decreased by lower night temperatures. At temperatures below 4 °C apparent CO<sub>2</sub> uptake ceased completely.

In spite of the CO<sub>2</sub> loss of the plants during the light period, a considerable positive CO<sub>2</sub>-balance resulted for *C. negevensis* under natural conditions in April. For April 4, the CO<sub>2</sub> loss amounted to 38 % of the CO<sub>2</sub> fixation within a 24 h period. This allowed for a dry weight related daily net gain of *C. negevensis* of 2.32 mg CO<sub>2</sub> g<sup>-1</sup>. The average daily net gain for five days during this period of the season amounted to 1.80 mg CO<sub>2</sub> per g dry weight, corresponding to 3.71 mg CO<sub>2</sub> per dm<sup>2</sup> surface area, or 1.63 mg CO<sub>2</sub> per mg chlorophyll content.

As the season progressed, the photosynthetic balance of *C. negevensis* decreased more and more, apparently because of increasing habitat temperatures. At the beginning of May, about two weeks after the last rain, the water relations of the plants were still favourable. At this time the shoots began flowering. As shown for a typical day of that period (May 4/5, Fig. 3), the CO<sub>2</sub> dark fixation was still high at night, and the CO<sub>2</sub> gain reached half of that in April. During the light period there was again a release of CO<sub>2</sub>. Due to higher temperatures at this period of the season, however, the CO<sub>2</sub> loss was much greater than in April. The plant lost so much CO<sub>2</sub>, that this could not be compensated by dark fixation, and hence the daily balance was no longer positive. On May 4, for instance, the CO<sub>2</sub> uptake was 1.64 mg CO<sub>2</sub> g<sup>-1</sup>. The CO<sub>2</sub> output during the light period amounts to 217 % of that. From this it follows that the plant lost 1.92 mg CO<sub>2</sub> g<sup>-1</sup> within 24 h.

Conditions during the middle of the dry period were even worse. In August the plants in their natural habitat were shrunk and had lost much of their turgidity. The shoots were flabby and greyish in colour. Under these conditions even their ability of nightly dark fixation ceased they were respiring all night (August 3/4, Fig. 3). Only a very short period remained with a weak apparent CO<sub>2</sub> uptake just after sunrise, corresponding to the burst of CO<sub>2</sub> uptake at this time of day earlier in the season. The CO<sub>2</sub> balance of *C. negevensis* resulted in being highly negative during this period. August 3, for instance, the plant lost 6.12 mg CO<sub>2</sub> g<sup>-1</sup> during 24 h under the extreme temperature conditions of the measurements.

## DISCUSSION

*Caralluma negevensis*, at least in spring and early summer, exhibits a high rate of dark fixation of CO<sub>2</sub>. Although no determinations of acid accumulation within tissues of the plants have been carried out, it may be concluded, that the CO<sub>2</sub> exchange pattern is caused by Crassulacean Acid Metabolism. The same characteristics are also reported from members of other genera within the *Asclepiadaceae* family, such as *Hoya carnosa* and *Stapelia variegata* (NUERNBERGK 1961).

It is well known that metabolic responses of CAM plants are to a large degree determined by temperature. At low temperatures the activity of the carboxylating enzymes dominates, at higher temperatures the decarboxylating processes are more active (see BRANDON 1967; KLUGE *et al.* 1973). In early spring the climatic conditions in the Negev Desert are characterized by relatively low night and moderate day temperatures. This seems to be optimal for malate synthesis at night; therefore, the net fixation of CO<sub>2</sub> is high. An experimental increase in temperature to 22 °C fully inhibits the net fixation of CO<sub>2</sub>, which agrees with the results of BRANDON (1967) on the temperature relations of the acidifying and deacidifying reactions in mitochondria of *Bryophyllum tubiflorum*.

The behaviour of *C. negevensis* during the light period is unexpected. The burst of CO<sub>2</sub>

324 uptake shortly after sunrise may be interpreted according to KLUGE (1968b) as photosynthetic assimilation of external CO<sub>2</sub> which continues until the malic acid is transported out of the vacuole and internal CO<sub>2</sub> becomes available (see BARTHOLOMEW 1973). At this time the plant begins to use predominantly its internal CO<sub>2</sub>. But, apparently more CO<sub>2</sub> is produced than can be fixed by photosynthesis. The result is a high, permanent CO<sub>2</sub> loss. Net release of CO<sub>2</sub> during the light period is often reported as a possible behaviour of CAM plants (see NUERNBERGK 1961; KLUGE 1968a). Most of the released CO<sub>2</sub> originates from decarboxylation of malate within the plant tissues. Another source is mitochondrial respiration. Both processes are highly accelerated by temperature. However, contrary to the behaviour of *C. negevensis*, the CO<sub>2</sub> loss of intact photosynthesizing organs of other CAM plants in laboratory experiments is usually restricted to the first phase of the light period, immediately after the burst of assimilation of external carbon dioxide. Moreover, at high illuminances the CO<sub>2</sub> output is usually small compared with the dark fixation rate.

Net loss of CO<sub>2</sub> by CAM plants in light is increased under all those conditions which diminish their photosynthetic efficiency. This is obvious, for instance, with *Tillandsia usneoides*, which exhibited CO<sub>2</sub> loss almost during the entire light period in experiments with low illuminances of 10 klx or with temperatures higher than 30 °C (KLUGE *et al.* 1973). The measurements on *C. negevensis* however, were carried out under the bright illuminance of the desert habitat, where light certainly does not limit photosynthesis. During noon time the shoots of *C. negevensis* reach high temperatures, which are typical for succulent organs at high radiation (HUBER 1935; GIBBS and PATTEN 1970). Such temperatures reaching 40 °C in April might surpass the optimum range for photosynthesis, increasing at the same time the malate decarboxylation rates as well as the mitochondrial respiration. From this, the temperature dependent high CO<sub>2</sub> release during the daylight period might be explained. However, since the compensation point already is surpassed early in the morning between 7.00 h and 8.00 h, at a tissue temperature of only about 22 °C and at illuminances between 40 and 50 klx it is improbable that the photosynthesis is already much inhibited at this time. Also the mitochondrial respiration will hardly be excessive at these temperatures. The only explanation is therefore the overflowing internal CO<sub>2</sub> production, generated from the previously synthesized organic acids. It seems as if no efficient diffusion barrier restricts the efflux of CO<sub>2</sub> out of the plant. Possibly, in contrast to the typical response of other CAM plants (see SZAREK *et al.* 1973), the stomata of *C. negevensis* do not fully close during the decarboxylating phase during the light period. More experimental evidence is necessary to answer this question.

At the beginning of the dry period in May, night as well as daytime temperatures were considerably higher than during the measuring time in April. Although during the night the tissue temperature of *C. negevensis* ranged between 17 °C and 29 °C (*e. g.* May 4/5), there was still a high dark fixation rate of CO<sub>2</sub>. The compensation point of night CO<sub>2</sub> exchange was reached at 23 °C. Since such temperatures during the experiments in April inhibited the CO<sub>2</sub> net uptake, a kind of temperature adaptation might have taken place. Similar acclimations have been reported from different *Opuntia* species in Arizona by NISBET and PATTEN (1974). However, as a result of high CO<sub>2</sub> losses during the hot light period, the CO<sub>2</sub> balance of *C. negevensis* became negative already at this time of the year. This was the case in spite of good water relations of the plants shortly after the last rain.

During the summer the *C. negevensis* plants were losing more and more of their water content. This drought effect resulted in an almost total absence of apparent dark CO<sub>2</sub> fixation. Although the temperatures, ranging between 14 °C and 26 °C at night (August 3/4), should have been favourable for acidification, no net CO<sub>2</sub> uptake existed. However, the persistent shoots were still alive, as shown by their high respiration rate.

In comparison with the dominating plants of the Negev vegetation, the photosynthetic productivity of *C. negevensis* under the extreme temperature conditions of a fully insolated habitat appears to be very ineffective (Table 1). Even during the first two weeks of April the daily photo-

Table 1

Daily net yield (+) or loss (–) of CO<sub>2</sub> of stems of *Caralluma negevensis* in comparison with twigs of arido-active desert shrubs during three different periods of the season (Avdat/Negev Desert, 1971). Figures in parentheses indicate the number of days which are taken for average.

	CO <sub>2</sub> yield or loss [mg g <sup>-1</sup> (dry wt.) d <sup>-1</sup> ]		
	April 1–14	May 1–14	August 1–14
<i>Caralluma negevensis</i>	+ 1.80 (5)	– 1.92 (1)	– 7.51 (5)
<i>Artemisia herba-alba*</i>	+ 9.78 (3)	+ 57.61 (3)	– 10.42 (4)
<i>Zygophyllum dumosum</i>	+ 23.38 (8)	+ 27.17 (8)	– 13.87 (5)
<i>Reaumuria negevensis</i>	+ 38.74 (8)	+ 21.17 (1)	– 3.40 (2)
<i>Hammada scoparia</i>	+ 37.23 (8)	+ 65.28 (8)	+ 27.93 (5)

\* Since no other data are available, values are indicated for March 24–30 instead of April 1–14.

synthetic net gain of twigs of the dwarf shrubs *Artemisia herba-alba*, *Hammada scoparia*, *Reaumuria negevensis*, and *Zygophyllum dumosum* was much higher than that of *C. negevensis*. This is true for the CO<sub>2</sub> gain in relation to dry weight, surface area, or chlorophyll content of the photosynthesizing organs. In May, when the CO<sub>2</sub> balance of the CAM plant *C. negevensis* already was negative, the productivity for the arido-active desert shrubs was optimal. In August, the daily CO<sub>2</sub> balance of *H. scoparia* was still positive. All the other investigated dwarf shrubs now exhibited a negative balance, but they had positive net photosynthesis at least at certain parts of the day. The balance of *C. negevensis* on the other hand was highly negative. Consequently, this plant spends a long time of the year in a condition of negative carbon balance, at least under the conditions of high insolation at which its CO<sub>2</sub> exchange was measured. Probably, in a more shady environment the organ temperatures of the plant would be lower and thus would improve its carbon balance. This fact apparently explains, why the plant evidently prefers shady habitats and is limited in its distribution within the Negev Desert to gaps and crevices between rocks. At such habitats *C. negevensis* obviously occupies its "ecological niche".

Regarding the photosynthetic productivity, the CAM plant *C. negevensis* seems to be much less successfully adapted to the climatic conditions of the Negev Desert than the arido-active dwarf shrubs without CAM. This may be the reason for the low competition strength of this succulent within the vegetation of a true desert. The high temperature level especially during the light period and the long lasting dry season apparently are the decisive factors which limit its productivity. Under these conditions the Crassulacean Acid Metabolism proves to be of no advantage to *C. negevensis*.



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