Distribution and control of photosynthetic pathways in plants growing in the Namib Desert, with special regard to *Welwitschia mirabilis* Hook. fil.

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CONTENTS

ABSTRACT

The present study investigates the physiological bases of species which compose the typical vegetation types of the Northern Namib: the savannas, the subtropical grasslands and the succulent deserts. The relative role in terms of vegetation cover and species diversity of the various pathways of photosynthetic production (Crassulacean acid metabolism, CAM type; C_4-dicarboxylic-acid metabolism, C_4 type; and Calvin type of CO_2-fixation, C_3 type) is determined and the environmental factors responsible for the distribution of the various metabolic types is discussed. In the savanna almost half of the total species and about two thirds of the vegetation cover belong to plants with the C_3 type of metabolism. C_4 plants dominate the zone of tropical grasslands, whereas CAM and the C_3 type of metabolism are most important in the coastal desert in terms of cover and species diversity. In the case of *Welwitschia mirabilis* representing the CAM type, water stress and saline conditions cannot explain the geographical variation of CAM. However, temperature seems to be a decisive factor. Night temperatures are probably too high for CAM in the grassland zone. In contrast to CAM is the C_4 metabolism: plants with this metabolism are specially adapted to the hot and dry climate of the inland region of the desert belt. It is probably too cold in the coastal area for the C_4 type of CO_2-fixation to be efficient enough competitively.

1 INTRODUCTION

During plant evolution various options of CO_2-fixation during photosynthetic production have evolved in plants, each adapted to special conditions of the natural environment (Evans, 1971; Marcelle, 1975). The normal type of CO_2-fixation operates via the Calvin cycle and to this group of so-called C_3 plants belongs the majority of higher plant species. They are most successful in moderate environments, but form an important part of the arid flora of the world as well. However, under extreme conditions of stress — especially those of water, high temperature and salinity — plants having other physiological pathways of CO_2-fixation seem to be better adapted (Hatch *et al.*, 1971). Grassulacean acid metabolism (CAM) is probably most commonly known (Kluge, 1972) and provides one way of increasing the efficiency of water use during photosynthetic production (Ting and Szarek, 1975). Under certain conditions of environmental stress, some species, mostly the succulents, close their stomata during the dry and hot part of the days and thus reduce water loss, whereas during the cool and more humid conditions prevailing at night they take up CO_2. It has been shown repeatedly that these species selectively opt between CAM and C_3 metabolism according to the environmental conditions prevailing (Osmond, 1973). But there is another specialized way of CO_2-fixation which is physiologically related to CAM. However, in contrast to CAM, where malate is formed and used in a night-day cycle, C_4-acids are respectively produced and metabolized in spatially separated mesophyll and bundle sheath cells. Also contrary to CAM plants, C_4 plants have been shown to be specially adapted to high temperatures and strong sunlight (Björkman, 1971). Due to an absence of photorespiration, they have a most efficient water use at a high absolute level of CO_2 uptake and waterloss with open stomata during the hot and dry time of the day (Pearcy *et al.*, 1974).

The ecological significance of various options of photosynthetic production in higher plants has often been stressed (Marcelle, 1975). However, little information is available on the geographical patterns, the relative role of such specially adapted plant species in the vegetation cover, and the environmental factors which are responsible for the distributional range (Moomey *et al.*, 1974; Osmond, 1975; Osmond *et al.*, 1975). This problem was investigated along a climatic gradient in an arid region of the Namib Desert, with its distinct distribution of savanna in the inland, grassland in the central region and succulent flora at the coast.

2 METHODS

The investigations were carried out in February 1975. Plant material (1—2 g fresh weight) of all species of representative sample plots, was collected on a transect from the inland to the coast in the northern (Khorixas-Torrabay) as well as in the middle (Uis-Brandberg West-Cape Cross) and in the southern (Gobabeb-Swakopmund) distributional areas of *Welwitschia mirabilis*. Since it was the general aim of this study to get to know more about the distribution of *Welwitschia* (see also Schulze *et al.*, 1976) the sample areas were selected according to the presence of this species. The vegetation cover was very dry during the time of investigation. Although an attempt was made to get as complete a species list as possible by collecting dead and remnant plant material from the various sites, it cannot be overlooked that in such an arid area species composition and cover might be completely different after a rain. The present study primarily includes, therefore, perennial phanerophytes, chamaephytes and hemicryptophytes, as well as annuals with woody stems.

Total plant cover and the cover of trees, shrubs, herbs, grasses and succulents were estimated. This proved to be difficult in some habitats because of the large scatter and patchy distribution of the vegetation. In the data following, average values were calculated on 2 to 3 independent estimates at each site.

The discrimination rate of heavier ^{13}C as compared with lighter ^{12}C during the process of CO_2-fixation was taken as an indication of the metabolic pathway exhibited by the various plant species (Smith and Brown, 1973). The discrimination rate was defined by the ^{13}C value:

$$\delta\,^{13}C = \frac{^{13}C/^{12}C\ \text{sample}}{^{13}C/^{12}C\ \text{standard}} - 1 \quad \times 1000 \quad ^0/_{00}$$

C_4 plants usually show a $\delta\,^{13}C$ value of about $-12\ ^0/_{00}$, and C_3 plants exhibit a $\delta\,^{13}C$ value of about $-27\ ^0/_{00}$. Succulent plants capable of CAM may vary within this range of discrimination rates because of their ability to change their metabolic pathway between light and dark fixation of CO_2 (Bender *et al.*, 1973). The determination of the ^{13}C and ^{12}C content was made with a mass spectrometer as described in detail by Osmond *et al.*, (1975). For *Welwitschia* the length of the green leaves and the stem diameter was determined. Total ash content was measured during the preparations for mass spectrometry. Chlorine (Cl^-) content was measured by titration.

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3 CLIMATIC CONDITIONS OF THE NORTHERN AND CENTRAL NAMIB

The Northern and Central Namib is a 50—150 km broad coastal zone ranging from the southern border of Angola to the Kuiseb river in South West Africa (Giess, 1970). It is characterized climatically by the cold Benguela current. There are few climatic data available for the Northern Namib. However, the principle change of climate from the coast to the inland becomes obvious from measurements made in the Central Namib by Besler (1972). Figure 1 shows only a few mm of rainfall at the coast. Rains are very rare; however, there are frequent heavy fogs and dewfalls. With increasing distance from the coast, precipitation by summer rains increases up to 100—150 mm at the inland border of the desert area (Walter, 1973). There is a cool, oceanic temperature climate at the coast with only 5° C temperature difference between the average minimum and maixmum day temperatures. With increasing distance from the coast, maximum temperatures increase rapidly. In Figure 1 the highest temperatures are reached about 60 km from the coast. But this station (Gobabeb) is still influenced by drifting coastal fogs, whereas the next station (Ganab) is already at the inland edge of the desert zone about 1 000 m above sea level. It is quite likely that higher average temperatures occur between these two stations. Night temperatures decrease in the vicinity of the coast because of increasing night radiation.

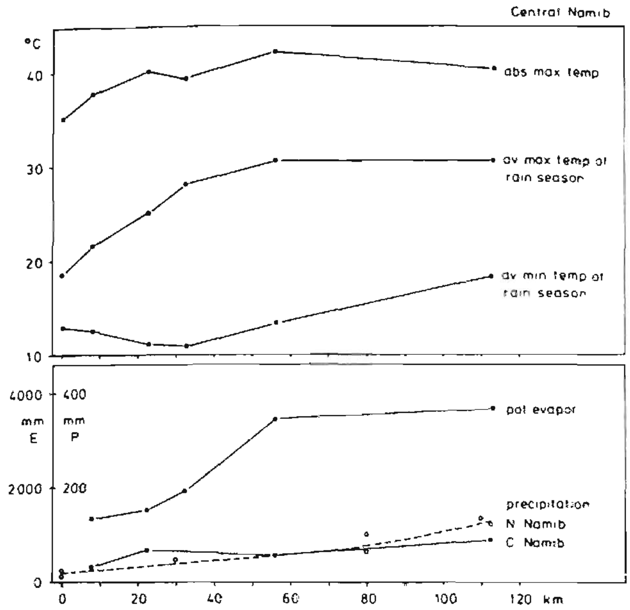

Figure 1. The change of absolute maximal temperature (abs. max. temp.), average maximal temperature of the rain season (av. max. temp. rain season), average minimal temperature of the rain season (av. min. temp. rain season), the potential evaporation (pot. evapor.) and precipitation in the Northern (N) and Central (C) Namib as related to the distance from the coast.

But further inland, night temperatures also increase considerably and, as was pointed out above, it is very likely that night temperatures are higher in the inland region of the desert area. Because of increasing temperatures, the aridity (expressed by the difference between potential evaporation and precipitation) increases two-fold in the inland area as compared to the coast.

4 RESULTS AND DISCUSSION

Figure 2 shows the change of relative cover of various morphogenotypes (trees and shrubs, grasses, succulents) in the vegetation along a transect from the inland to the coast in the Northern Namib. The data points indicate an average value of 2—3 independent estimates at similar sites because of the rapidly changing and patchy vegetation in an arid habitat. For detailed description of the vegetation see Walter (1973), Giess (1970) and Volk (1966). At about 140 km from the coast, the savanna, dominated by *Colophospermum mopane* (*Caesalpiniaceae*), has a total plant cover of about 15—25%, approximately two-thirds of which is trees, herbs and shrubs and one third is grasses. There is a very sparse cover of succulents. *Welwitschia* grows in some places (Plate 1, Farm Bloemhof) with numerous specimens of small stems (up to 28 cm stem diameter, 63 cm length of green leaf). Closer to the coast, there is an abrupt change in vegetation. The total plant cover decreases. Trees and shrubs can exist only on stony hill sites or as 'contracted' vegetation in the dry valleys. The vegetation is more and more dominated by grasses, which are eventually almost the only life form in this zone of subtropical grasslands. Plate 1 shows this region at 60 to 80 km from the coast. Also in this zone succulents have only a small cover. *Welwitschia* occurs with few but very large specimens (up to 78 cm stem diameter and 170 cm length of green leaves). With decreasing rainfall, not only does grass cover become sparse (Plate 2), but all other plants are rare. *Welwitschia* occurs as large plants which, however, often have very short leaves (up to 95 cm stem diameter, 35 cm length of leaves). There is another abrupt change in vegetation at the coastal zone. Following a 'full desert', where *Welwitschia* was found in some cases to be the only living plant species (Plate 3), there is the zone of heavy coastal fogs and dewfalls. It is dominated by succulent, evergreen dwarf shrubs and lichens (Plate 4). In this area large specimens of *Welwitschia* were found (up to 170 cm stem diameter, 135 cm length of leaves). Larger specimens of *Welwitschia* than those observed in this investigation were reported by Giess (1969) in a general survey of the distribution area and by Bornman *et al.*, (1972).

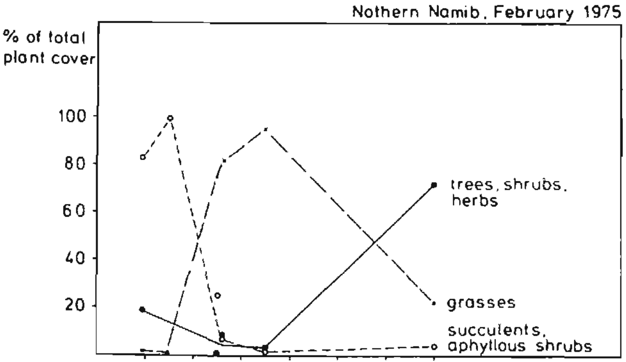

Figure 2. The change of total plant cover (%) of various morphogenotypes (trees-shrubs-herbs, grasses, succulents-aphyllous shrubs) as related to the distance from the coast.

The relative change in life forms and morphogenotypes on the transect from the inland to the coast — which also was found on an elevational gradient in Baja, California, and in Chile (Mooney *et al.*, 1974, a, Rundel and Mahu, 1976) — is accompanied by a corresponding change in the dominant option of photosynthetic pathways of the species present. Plate 5 shows the number of C_3, C_4 and CAM species in relative terms based on the total species number found in the different habitats. The relative proportion of C_4 species is small in the savanna. This vegetation type is dominated by C_3 species. There is also quite a variety of CAM plants. In the grassland area (70 km distance from the coast), there is a conspicuous increase in the relative number of C_4 species, whereas the relative number of C_3 and CAM species decreases. When considering only the perennial vegetation, the C_4 type would be almost the only morpho-genotype in this zone. Moving closer to the coast, the relative proportion of C_3 species increases slightly. More conspicuous is the large increase in relative number of CAM species and a strong decrease of the C_4 type. Table 1 shows the species being investigated so far. The C_4 species having a $\delta^{13}C$ value of —22 to

-25 ‰ belong to a great variety of families. This is different with the C4 species, which belong almost entirely to the *Gramineae*. The succulent species and the aphyllous shrubs, together with *Welwitschia*, are a very heterogenous group of plants. Some of the aphyllous succulent shrubs (e.g. *Arthraerua leubnitziae*) and some of the succulents (*Zygophyllum stapffii*) seem to belong to the C^3 type of metabolism. With some other species (*Hoodia currori, Sarcocaulon viminale*) it is not clear from the $\delta^{13}C$ ratio if they belong to the group of CAM or of C_4 plants. More work is necessary on this subject.

It is an important ecological question which environmental factors cause this typical zonation of vegetation in this area (see also Walter, 1936, 1959). For CAM plants this has been studied most extensively for *Welwitschia* (Schulze *et al.*, 1976). Figure 3 shows the $\delta^{13}C$ values of various C_3 and C_4 species and of *Welwitschia* as related to the geographic distance from the coast. It is obvious that *Welwitschia* does not have a constant $\delta^{13}C$ value as was found for C_4 plants ($-12{,}8$ ‰) or for C_3 species ($-23{,}6$ ‰). The differences between the $\delta^{13}C$ values of *Welwitschia* and the C_3 species is largest in the coastal zone but it is not statistically different from the C_3 species in the grassland area; however, it is again significantly different in the savanna. The data not only indicate that *Welwitschia* is capable of CAM, which has already been shown in the laboratory (Dittrich and Huber, 1975) and cytologically (Whatley, 1975), but that the proportion of CO_2 fixed via CAM is largest at the coast and smallest in the grassland region.

It has been observed that plants which are capable of performing CAM have the ability to change between CAM and C_3 metabolism and that various environmental factors may be responsible for such change (Neales, 1975; Osmond, 1975). Increasing salt stress was found repeatedly to induce CAM (Winter and von Willert, 1972). This factor does not seem to be responsible for the metabolic change in *Welwitschia*. Schulze *et al.* (1976) showed that the relative chloride content of leaf tissue increases from inland to the coast and shows no relation to the corresponding $\delta^{13}C$ value. Also, the ash content of the tissue, being a measure of the total anion and cation content, shows that the less negative $\delta^{13}C$ values are not obtained at high ash content, as would be expected if such a relationship existed. It was already shown by Walter (1936) that *Welwitschia* is not a typical halophyte.

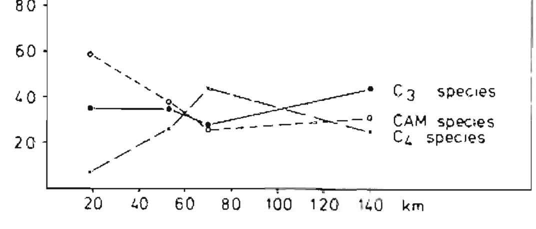

Figure 3. The change with distance from the coast of various types of CO_2 metabolism (C_3 species, CAM species. C_4 species) expressed in % of total species number in each vegetation zone.

Water stress was found to cause a change from the C_3 pathway to CAM (Kluge *et al.*, 1973). It cannot be ruled out that this factor causes a change in the metabolism of *Welwitschia*. In the savanna, for instance, sun-exposed plants showed less negative $\delta^{13}C$ values (i.e. more CO_2 fixed via CAM) than plants growing in the shadow of trees (Schulze *et al.*, 1976). However, it is not likely that water stress induces the change in metabolism on a broad geographical scale. The largest specimens, with fresh green leaves were found with CAM just in the coastal area, and not in the grassland zone where they did exhibit the C_3 metabolism which is usually found in non-stressed plants. In this region the total length of the yellow-green leaves was often reduced by dying of the leaf tips (Walter, 1973). There is no correlation between total leaf length and the $\delta^{13}C$ value. But this is not a final proof, since the $\delta^{13}C$ value represents the conditions during the period of active growth and it may be that water conditions during that time of year are better in the grassland zone than they are near the coast. Additional measurements are necessary to solve this problem.

Temperature was found to significantly influence CAM (Kluge *et al.*, 1973; Neales, 1973). Osmond *et al.* (1973) showed that for *Kalanchöe blossfeldiana* an increase of night temperature of only 3° C could determine whether or not CAM was possible. Figure 1 shows a very cool climate for the coast and an increase of night temperatures further inland. This increase would be in a range of temperatures that could cause a change from CAM to C_3 metabolism in other succulent species. The present data indicate that temperature regime and water stress as modifying factors determine the night fixation of CO_2 in *Welwitschia*. The high water use efficiency associated with CAM would allow a continuous growth at a low rate in the coastal climate. In the grassland zone the high night temperatures cause a change to C_3 metabolism, but since growth rates are larger with C_3 metabolism than with CAM (Osmond, 1975), this again may be advantageous for competition with other plants during the rainy season. The dying of leaf tips occurs then only in the dry season at a time when other perennial and annual species are dormant.

Contrary to the behaviour of CAM plants is the metabolism of that of the C_4 species. They were found to be specially adapted to hot conditions, with strongest production at a high light intensity (Björkmann, 1975). The distribution of C_4 plants, which in the study area are mainly represented by the grass type, strongly reflects this climate situation. The highest temperatures, which exist inland of the belt of coastal fogs, favours the existence of C_4 species. Besides a few annual herbs and some succulents, the vegetation is dominated by C_4 species. Only a relatively narrow range of conditions favours this metabolism. At the coast, as well as further inland,

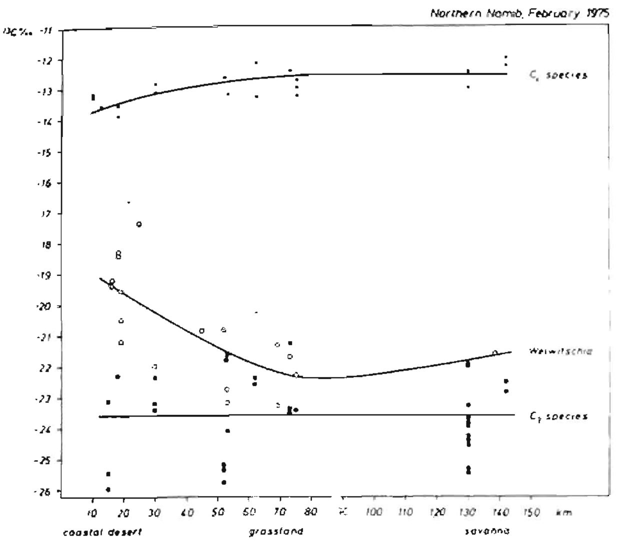

Figure 4. The $\delta^{13}C$ ‰ value of C_4 and C_3 species and of *Welwitschia mirabilis* as related to the distance from the coast and the according vegetation zones in the northern Namib.

the C_4 species are not as successful, which is obvious from the relative number of species as well as from the relative vegetation cover.

The C_3 species were found to be most important in the higher rainfall areas of the savanna. This metabolic type is almost absent among perennial plant species in the actual zone of the grassland, due primarily to drought and heat. It is surprising, however, that in the coastal area, which has been described as most extreme in terms of rainfall, the C_3 type of metabolism is quite successful again. In this range it is very often found even in aphyllous succulent dwarf shrubs. Although further experimental work is necessary, the present data indicate the influence of environmental conditions on the geograhpical distribution of various types of metabolic pathways which determine the specific vegetation cover.

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Table 1. List of investigated species. Average values of multiple determinations of the ^{13}C value are indicated by +.

	Family	Species	^{13}C ‰
1. C_3 plant species	Acanthaceae	*Monechma arenicola*	−22.85
		Monechma genistifolium	−22.60
		Monechma monechmoides	−21.50
		Petalidium engleranum	−24.31
	Amaranthaceae	*Celosia spathulifolia*	−22.33
	Asteraceae	*Dicoma tomentosa*	−23.49
		Geigeria alata	−23.48
	Burseraceae	*Commiphora angolensis*	−23.95
	Caesalpiniaseae	*Adenolobus pechuelii*	−25.39
		Colophospermum mopane	−22.54
	Capparaceae	*Cleome suffruticosa*	−25.22
		Maerua parviflora	−23.93
	Combretaceae	*Terminalia prunioides*	−22.02
	Convolvulaceae	*Merremia guerichii*	−25.46
	Euphorbiaceae	*Euphorbia glanduligera*	−23.50
		Euphorbia phylloclada	−22.12 +
	Fabaceae	*Indigofera auricoma*	−25.50
		Tephrosia dregeana	−23.23
	Heliotropiaceae	*Heliotropium oliveranum*	−24.14 +
	Loasaceae	*Kissenia capensis*	−21.28
	Mimosaceae	*Acacia robynsiana*	−25.82
		Acacia senegal	−24.42
	Pedaliaceae	*Sesamum schinzianum*	−25.36
	Periplocaceae	*Curroria decidua*	−23.30
	Polygalaceae	*Polygala guerichiana*	−23.73
	Rubiaceae	*Amphiasma merenskyanum*	−24.57
	Sterculiaceae	*Hermannia solaniflora*	−23.41
	Verbenaceae	*Chascanum garipense*	−23.14
2. C_4 plant species	Gramineae	*Enneapogon brachystachyus*	−13.26
		Eragrostis nindensis	−12.64 +
		Kaokochloa nigrirostis	−13.00
		Odyssea paucinervis	−13.24
		Rhynchelytrum villosum	−12.48
		Stipagrostis hirtigluma	−12.39 +
		Stipagrostis hochstetterana	−13.05 +
		Stipagrostis namibensis	−13.90
		Stipagrostis subacaulis	−13.31
		Stipagrostis uniplumis	−13.41 +
	Molluginaceae	*Mollugo cerviana*	−12.89
3. Succulents and aphyllous shrubs	Amaranthaceae	*Arthraerua leubnitziae*	−22.02 +
	Asclepiadaceae	*Hoodia currori*	−11.71
		Orthanthera albida	−20.12
		Sarcostemma viminale	−11.67
	Capparaceae	*Cadaba aphylla*	−16.93
	Euphorbiaceae	*Euphorbia transvaalensis*	−15.36
	Molluginaceae	*Gisekia africana*	−19.81
	Welwitschiaceae	*Welwitschia mirabilis*	−20.72 +
	Zygophyllaceae	*Zygophyllum simplex*	−14.03 +
		Zygophyllum stapffii	−23.25 +

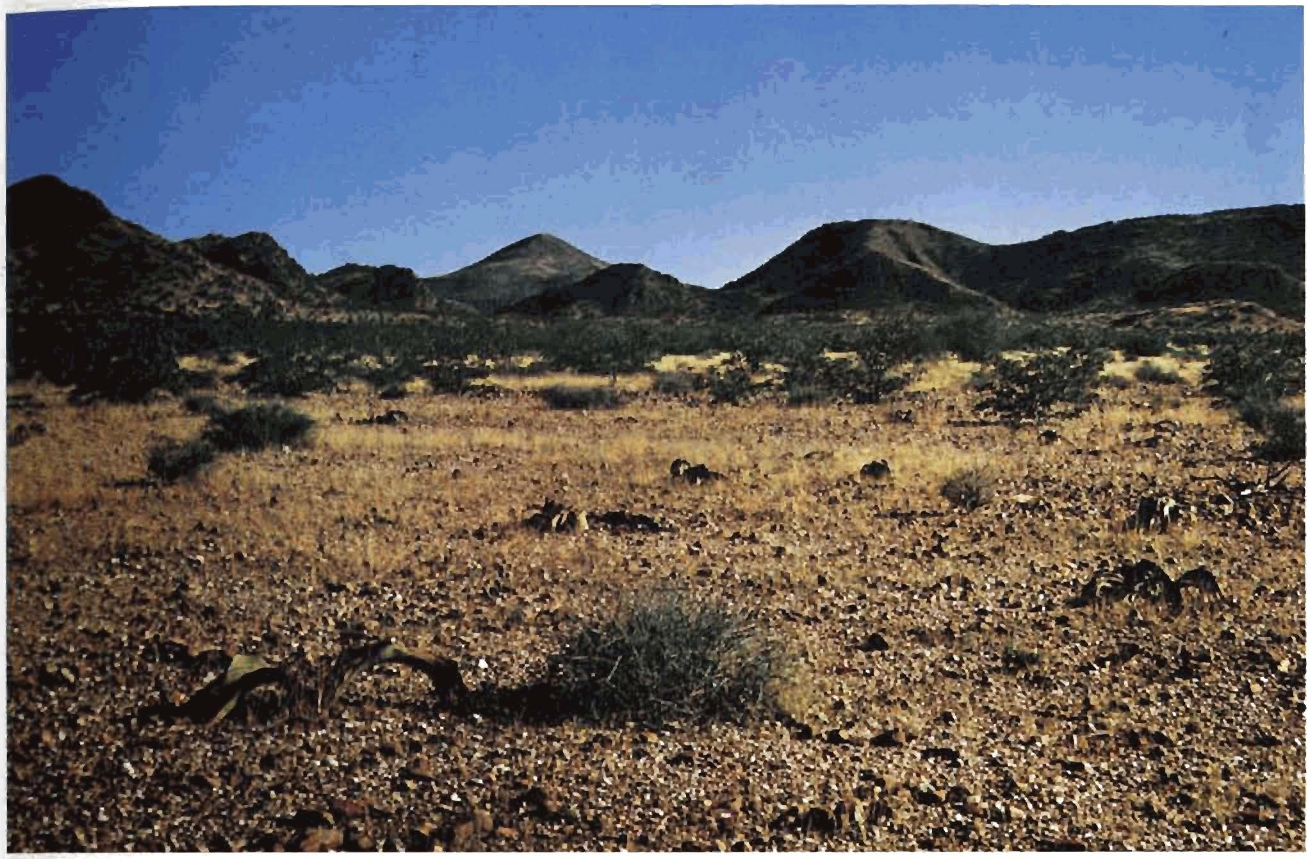

Plate 1. Vegetational aspect of the mopane savanna with *Colophospermum mopane* (*Caesalpiniaceae*). In the foreground several specimens of *Welwitschia mirabilis* (*Welwitschiaceae*) and *Cadaba aphylla* (*Capparaceae*) can be seen. The spaces between the trees is covered with grasses (*Stipagrostis hirtigluma, Eragrostis nindensis*).

Plate 2. Vegetational aspect of the grassland zone with great cover and species diversity of *Gramineae*. Several specimens of *Welwitschia mirabilis* can be seen.

Plate 3. Transition zone of grassland and full desert with a sparse cover of mainly *Stipagrostis* species. There are few herbaceous plant species (*Gisekia, Heliotropium, Monechma*) and *Welwitschia mirabilis*.

Plate 4. Aspect of a 'full desert' with *Welwitschia mirabilis* only.

Plate 5. Vegetational aspect of the coastal fog desert with *Welwitschia mirabilis* and many other succulent and evergreen dwarf shrubs (*Arthraerua leubnitziae*).