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Rain, fog and species richness in the Central Namib Desert in the exceptional rainy season of 1999/2000.

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Summary

In this paper, the exceptional rainfall in the rainy season of 1999/2000 is compared with low rainfall amounts of previous rainy season in the Central Namib Desert. Weekly rain and fog precipitation are set in relation to species diversity and diversity of growth forms which were monitored on 35 permanent sites over 4 successive years (1997-2000) along three coast to inland transects using a nested plot design with different plot sizes (1 m^2, 10 m^2, 100 m^2, 1000 m^2). Species response to rainfall was not homogenous but varied with respect to vegetation zone and coastal distance. Whereas near the coast no relationship between species diversity and rainfall amount was found, east of the major fog zone and with increasing distance to the coast rainfall correlated with species richness emphasising the steep climatic gradient evident in this desert. The influence of fog and rain is discussed separately for the different vegetation zones.

Zusammenfassung

Die ungewöhnlich hohen Niederschläge in der Regenzeit von 1999/2000 werden mit geringen Niederschlagsmengen vorheriger Regenzeiten verglichen. Sowohl die wöchentlichen Regen- und Nebelmengen als auch die jährlichen Niederschlagssummen werden in Beziehung zur Artendiversität und Diversität an Lebensformen gesetzt, die entlang von drei Küste-Inland-Transekten auf insgesamt 35 permanenten Aufnahmeflächen über vier aufeinander folgende Jahre (1997-2000) und mit Hilfe von ineinander geschachtelten Flächengrößen (1 m^2, 10 m^2, 100 m^2, 1000 m^2) untersucht wurden. Die Artendiversität folgte dabei nicht zwangsläufig der Regenmenge sondern variierte je nach Vegetationszone und Küstendistanz. Während in Küstennähe kein Zusammenhang zwischen Regenmenge und Artenvielfalt gefunden wurde, ließ sich östlich der Nebelzone und mit zunehmender Distanz vom Meer eine ansteigende Beziehung zwischen beiden feststellen, die die Bedeutung des steilen Klimagradienten in der Zentralen Namib unterstreicht. Der Einfluß von Regen und Nebel wird separat für die einzelnen Vegetationszonen diskutiert.

Keywords: exceptional rainfall, species response, species diversity, monitoring sites, Namib desert

Introduction

Deserts such as the Central Namib Desert are areas where precipitation is pulsed and shows a high unpredictability (Agnew 1997, Jürgens *et al.* 1997). It is only every 16-20 years that such rare rain pulses occur in the generally hyperarid Central Namib. However, in the rainy season of 1999/2000 exceptional high rainfall occurred in the Central Namib indicating such a rare rain pulse (or possibly the beginning of one lasting over several years). In contrast, in previous years the desert received considerably less rainfall than normal. Frequency of rainfall in the Central Namib is low and lies between less than 10 days and 10-20 days per year with a variability of over 80 % (van der Merwe 1983). Variability is inversely related to rainfall quantity and increases from the desert-savanna transition in the east towards the coast.

Next to rain, the other important source of water in the Central Namib is fog. Precipitation by fog is far more predictable than by rain and is recorded on more than half of the year in parts of the desert. Additionally, in the coastal areas water quantity precipitated by fog is considerably higher than by rain emphasising its great importance for the climate of the region (Goudie 1972; Hachfeld & Jürgens 2000; Henschel *et al.* 1998).

Both, rain and fog, contrast the extreme aridity evident in this desert and contribute to the existence and survival of plant species. Only rain, however, is capable to trigger germination and thus determines the establishment of any higher plant taxa. The spatial and temporal distribution of rain and fog form a steep climatic gradient which is, amongst others, responsible for the existence of a number of vegetation zones in the Central Namib (Hachfeld & Jürgens 2000). Generally, small or large rain pulses are considered to create an impressive variety of ephemeral plant species and thus species diversity emerging almost immediately after rainfall events (e.g. Aronson & Shmida 1992, Fernandes-Palacios 1992, Milton 1995, Seely 1978, Vidiella *et al.* 1999). However, with the Central Namib being one of the few fog driven deserts in the world exhibiting unique climatic conditions, the above statement might need some evaluation. Species responses to rare rain pulses in the Central Namib might - under the additional influence of fog and accompanying changes in environmental conditions - vary from that of normal and only rain-driven deserts.

In this paper, changes in species richness, composition and diversity due to the exceptional rainfall in the rainy season of 1999/2000 will be discussed in comparison to previous years with less rain than average. The influence of rain and fog is mainly analysed using a data set of a one year sequence of weekly fog and rain measurements along a coast to inland transect. Variability and potential of species richness in relation to rainfall is analysed using data on the monitoring of 35 permanent sites since 1997.

Study area

The Central Namib Desert forms the middle part of the hyperarid Namib Desert and stretches from north of the Great Dune Sea and Kuiseb River to the Huab River (Figure 1). The area dealt with in this paper comprises three coast to inland transects, where monitoring sites were placed and climatic measurements were carried out: the C 3 from Henties Bay to Uis, the B2 from Swakopmund to Usakos and the C14 from Walvisbay to the Kuiseb Canyon.

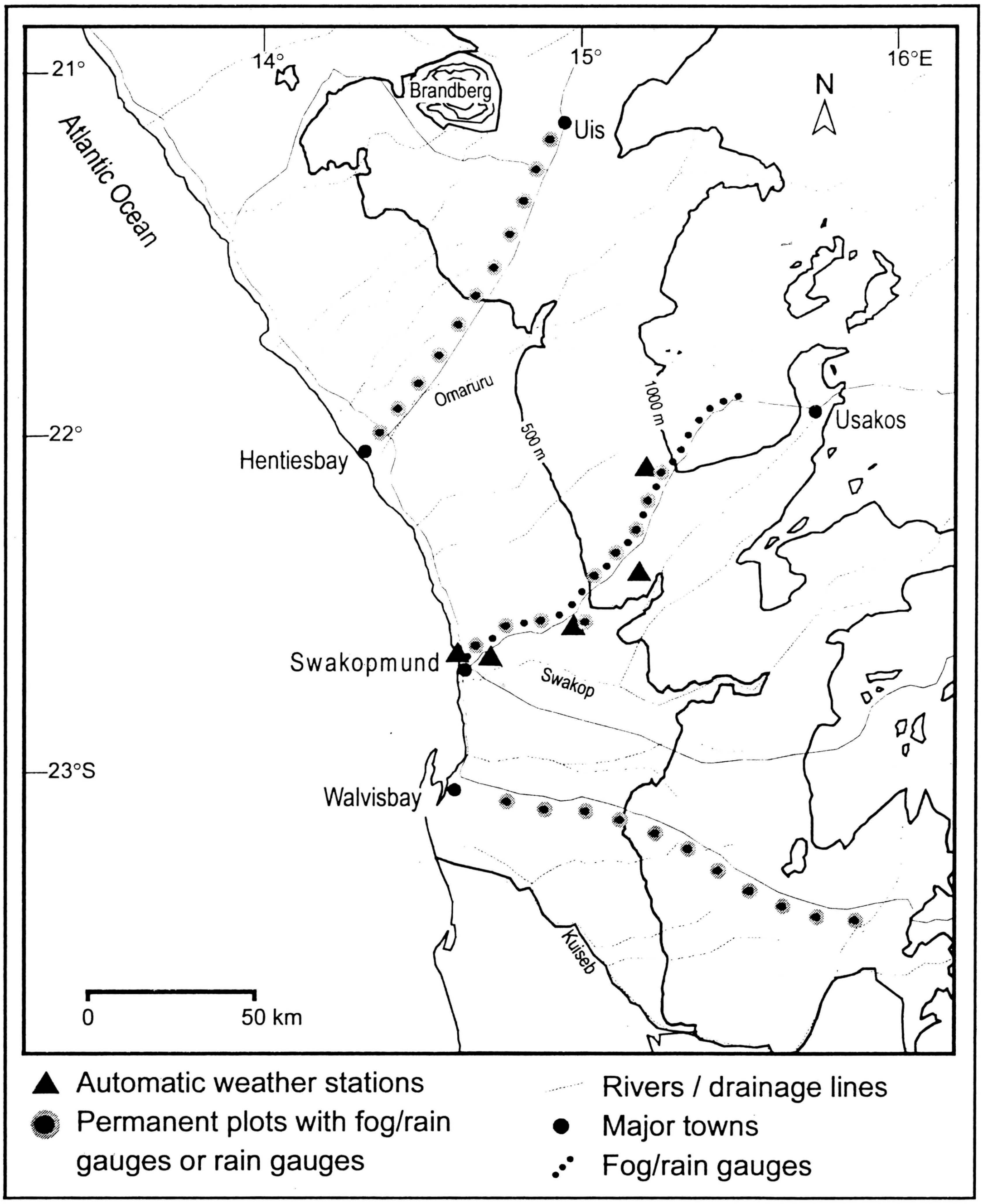

Figure 1: Map of the Central Namib Desert with position of automatic weather stations, fog/rain gauges and monitoring sites along 3 coast to inland transects.

Two major precipitation types, rain and fog, characterise the climate of the Central Namib. Here, three fog types can be differentiated: coastal or advective fog forming under a south westerly sea breeze, radiation fog which occurs only occasionally, and high fog. High fog, or Garua fog, is a low stratus and strato cumulus cloud sheet which develops below the inversion layer over the Atlantic Ocean at a height of 100-600 m. From there it penetrates inland and intercepts the land in the Namib interior (Lancaster *et al.* 1984; Olivier 1995). Whereas the frequency of fog decreases from west to east, frequency and amount of rain increase in the opposite direction. Generally, rain falls in form of convective summer storms which can move fairly far into the desert. Rainfall is normally highly erratic and localised. Mean annual rainfall in the west of the desert is about 23 mm yr^{-1} with a maximum received at the escarpment in the east (Goudie 1972). Whereas in the coastal regions climatic conditions are moderate with generally low air temperatures and high air humidity, in the mid part of the desert a zone with most harsh conditions exists: Here, daily frequency of maximum air temperatures and minimum air humidity is highest. These conditions are intensified by the fact that typically neither fog nor rain contribute valuable amounts of water to the vegetation. Further inland with increasing probability of rain air temperature is typically high and air humidity is low (Hachfeld & Jürgens 2000).

Topographically, the Central Namib Desert can be described as a weakly undulated and tilted plain. The vast plains are interrupted by few dry riverbeds (i.e. the Kuiseb, Swakop and Omaruru), various smaller drainage lines, single inselbergs as well as small granite outcrops and long-stretched dolerite ridges (Besler 1972, Spreitzer 1966). Near the coast gypsum crusts predominate but salt crusts also occur. Further inland crusts consist of limestone.

The flora of the Central Namib Desert comprises a total of about 415 plant species (Giess 1981) with a small number of endemics. The occurrence of many species is highly variable and dependent on rainfall. Species number, total canopy cover and composition of growth forms show a distinct pattern with respect to coastal distance and thus climatic conditions. Additionally, a number of vegetation zones can be differentiated which will be introduced also in this paper (Hachfeld & Jürgens 2000).

Methods

Climate

Along a coast to inland transect since 1995 five automatic weather stations have been placed in the following distances to the coast: 0 km, 12 km, 35 km, 56 km (Rössing Mine station), 92 km (Figure 1). Next to other climatic parameters total precipitation was measured in a 30 minute turn using rain gauges which were supplied with additional fog collectors similar to others used in this study. Precipitation measured included fog, fog-drizzle and rain with an accuracy of 0,1 mm.

Also along this transect a parallel series of 24 pairs of simple fog and rain gauges contributed weekly information on the small scale distribution of precipitation (Figure 1). The series starts in Swakopmund at 0 km (22°40'S, 14°33'E) and stretches to 120 km coastal distance (22°00'S, 15°20'E) with a distance of 5 km between each. A total of 54 weeks was measured in the rainy season of 1999/2000, i.e. from the beginning of May 1999 until the end of April 2000. Due to financial restrictions, in the dry season (June-December) measurements ended in 70 km coastal distance comprising data of a total of 27 weeks there. The construction of the gauges principally follows Schieferstein (1989): In an insulated 1-l bottle a plastic funnel (15 cm diameter) is inserted. The fog gauges are additionally supplied with a bunch of 45 stainless steel wires each with a length of 35 cm. Few drops of oil in the bottles prevent collected water from evaporating. The amount of fog collected was calculated by subtraction of the amount of water in the fog gauge by the amount of water collected in the rain gauge. For a better comparison of the data collected amounts in ml were transferred into mm with 25,45 ml equalling 1 mm of either fog or rain. The precipitation quantity collected in the rain gauges has to be differentiated in actual rain water and drizzle. As single rain events could be detected by analysis of the data of the weather stations placed along the same transect, the rest of the precipitation collected in the rain gauges falls to fog-drizzle.

On account of the highly localised rain events since 1998 a simple plastic rain gauge has been installed next to each monitoring site. A layer of 1 cm of oil was applied to prevent collected water from evaporating. At the beginning and the end of the rainy season (and if possible in between) gauges were emptied. After the exceptional rain event in March 2000 all rain gauges were emptied within two days.

Monitoring sites

Since 1997 along three coast to inland transects a total of 35 monitoring sites have been installed on plain habitats (Figure 1) with 10 km distance between two sites. Enough space was left next to the road to avoid any disturbance impact. South of the Swakop river, monitoring sites were placed along the C14 in the Namib Naukluft Park starting 20 km east of Walvis Bay up to 130 km inland. Monitoring sites along the middle transect begin in 10 km distance from Swakopmund and end shortly east of the beginning of the commercial farmland in 90 km coastal distance (Farm Vêrgenoeg). Along the C28 from Hentiesbay to Uis monitoring sites start only few hundred metres from the coast (in the following referred to as 0 km coastal distance) and end shortly before Uis in 110 km coastal distance. Sites were documented every year at possibly identical dates at the end of each rainy season. Here, data of 1997, 1998, 1999, and 2000 is presented.

Monitoring sites include a nested plot set-up following Whittaker (Shmida 1984) with plot sizes of 1 m^2, 10 m^2, 100 m^2 and 1000 m^2: Five 1 m^2 (1x1m) plots are placed within one 10 m^2 (2x5 m) plot. The 10 m^2 plot is nested in a 100 m^2 (10x10 m) plot which again is placed in a 1000 m^2 (20x50 m) plot. On each plot species number, number of individuals and cover in percent were documented to evaluate species diversity in relation to plot size. For the analysis the average of species number of the five 1 m^2 plots was used. Plant names follow Craven (1999).

Species were assigned to five different growth form types, i.e. forbs, grasses, small shrubs (up to 1 m in height), large shrubs (above 1 m in height) and geophytes. Diversity of growth forms was calculated for each site at the 1000 m^2 scale following the computation:

$$H' = -\sum p_i \ln p_i$$

Where: p_i is the proportion of total species in a 1000 m^2 plot within a single growth form category (Cody 1989, Cowling *et al.* 1994).

Results

Precipitation by rain and drizzle

Weekly measurements of precipitation show the temporal and spatial patterns of both, rain and fog, in the Central Namib Desert for the rainy season of 1999/2000 (Figures 2 and 3). Within this rainy season the Central Namib experienced between one to nine weeks of rainfall depending on coastal distance (Figure 2). The first rainfall of the season fell at the end of November (not considering the small amount of rain of the week 30.9.-7.10.99). In December rain clouds moved as far as 40 km coastal distance into the desert bringing rainfall of up to 1 mm to this area whereas slightly higher rainfall (2-5 mm) occurred in 65-95 km coastal distance increasing to 20-30 mm in 110-120 km coastal distance. After a dry January without any rain few small rain events were documented in February (weeks of 14.2.00 and 28.2.00) reaching as far as 90 km coastal distance into the desert. However, the extraordinary rain event occurred in the nights of the 24th and 25th of March, when already during the day a rain front moved into the Namib. In Swakopmund rainfall started on both days in the early morning hours. Whereas on the 24th of March 10 mm of rain fell within 7 hours (from 3-10:00), on the 25th of March 85 mm of rain fell within 3,5 hours only (from 5-8:30). Rainfall amounts measured after the exceptional rainfall event are shown in Figure 6.

Irrespective of this rare rain pulse which triggered the germination of several species, those climatic phenomena which occur with a high regularity and reliability – such as fog and fog-drizzle – form an important basis for the survival of plant individuals in the Central Namib. Fog-drizzle collected in the rain gauges occurred with a temporal concentration on the winter months from mid of May 1999 until the beginning of October 1999 (Figure 2). In February 2000, shortly before the heavy rain event, fog drizzle was also collected in the gauges. Weekly amounts typically did not exceed 0,1-1 mm. Only occasionally higher quantities were measured, i.e. in the week of the 30.9.-7.10.1999, when drizzle moved as far inland as 55 km coastal distance. Next to a temporal pattern weekly occurrence of fog-drizzle also showed a spatial pattern. Highest frequency of weeks with fog-drizzle was found within 0-30 km coastal distance, representing the coastal fog type (Figure 4). Here, on more than 34 weeks (63%, with n = 54 weeks) fog drizzle occurred. Highest weekly frequency was found in 5-20 km coastal distance (72-85%; coastal fog), whereas from 50 km coastal distance inland frequency decreased. This corresponds well with the eastern border of the major fog zone. The sudden decrease in the occurrence of fog-drizzle in 70 km coastal distance is partly due to a discontinuation in the measurements during the winter months but also reflects the decreasing fog quantities east of the major fog zone. Here, fog-drizzle occurred in 7-11 weeks (26-41%) of a total of 27 weeks measured.

Precipitation by fog

In contrast to fog-drizzle, fog collected in the fog gauges shows a more distinct spatial and temporal pattern which can be linked to different fog types, i.e. coastal fog and high fog/Garua fog. The temporal pattern shows a concentration of fog events in the dry season from the beginning of May 1999 until the end of October 1999. During the early rainy season fog frequency was lowest and only increased again in February 2000 with a peak at the end of the rainy season in April. Coastal fog occurred typically at the end of the rainy season, i.e. at the end of April 1999 (rainy season 1998/1999) and April 2000 (rainy season 1999/2000). The majority of fog was then measured in the vicinity to the coast up to 25 km coastal distance. In contrast, in June and from the end of July – October fog was mainly measured between 25/30 km to 50 km coastal distance, representing high fog/Garua fog. High fog only rarely reached further inland than 50 km from the coast indicated by the distinct break in the weekly occurrence of fog in Figure 3. How far fog is capable to reach inland in winter can not be stated as measurements stopped at 70 km coastal distance from May until December. In summer, however, fog did not penetrate further inland than 90-95 km. The number of weeks with fog measured (Figure 4) shows that surprisingly seldom fog was collected in the gauges in 0 km and 5 km coastal distance. Instead, fog-drizzle prevailed in this area which is due to the close vicinity to the coast with extremely high relative air humidity. In the coastal fog zone on 44-48 weeks of the year (81-89%) fog occurred typically comprising quantities below 2 mm/week. Only on 5-8 weeks of the year amounts of or above 2-5 mm/week were measured. The high fog zone showed not only a distinct eastern border with respect to the number of weeks with fog measured but also a change within the zone (Figure 4): Whereas from 30-40 km coastal distance high fog occurred about as often as coastal fog, in 45 km coastal distance a sudden decrease in frequency is evident. Instead, fog quantity here was higher comprising more weeks with fog amounts above 1mm/week and less weeks with fog amounts below 0,1 mm/week (Figure 2). East of 50 km coastal distance both, fog quantity as well as frequency of weeks with high fog (25-31 weeks), decreased. Mostly fog quantities from less than 0,1 mm to 1 mm/week were measured. No temporal pattern of fog occurrence was found in the area east of the major fog zone (in 50 km coastal distance) but a slight concentration

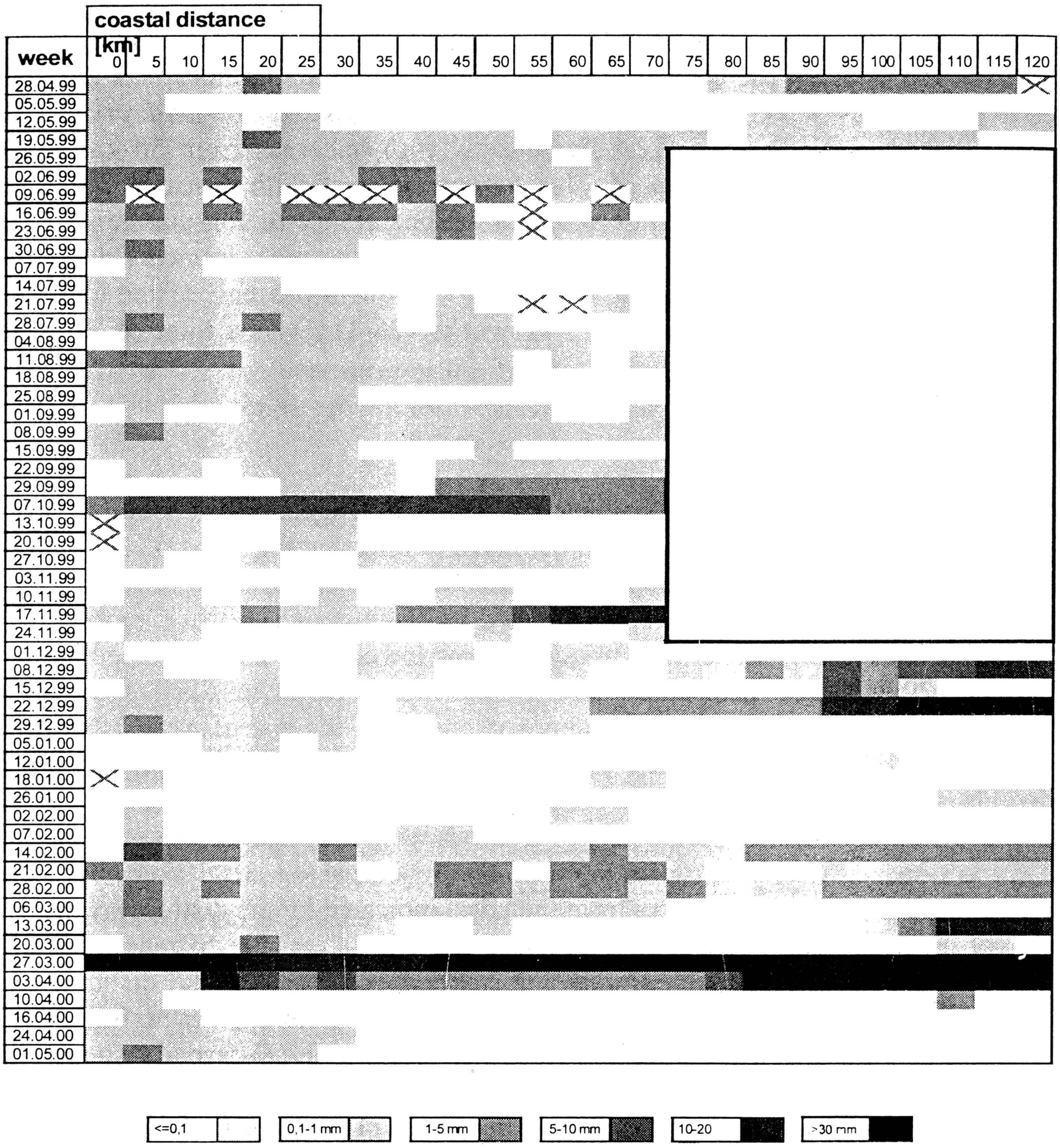

Figure 2: Weekly rain and drizzle measurements along the Swakopmund-Usakos Transect shown with respect to coastal distance for the period of May 1999 – April 2000. The box indicates a lack in the measuring period. Crosses symbolise weeks without data.

on winter, from the end of July – October was visible. Again, with respect to the lack in measurements during winter, part of the significant decrease in fog occurrence in 75 km coastal distance can be explained. However, generally this zone only occasionally receives fog.

Considering the total amount of fog (fog-drizzle and fog) it can be stated that fog is a greater source of water than fog-drizzle except for the direct vicinity to the coast from

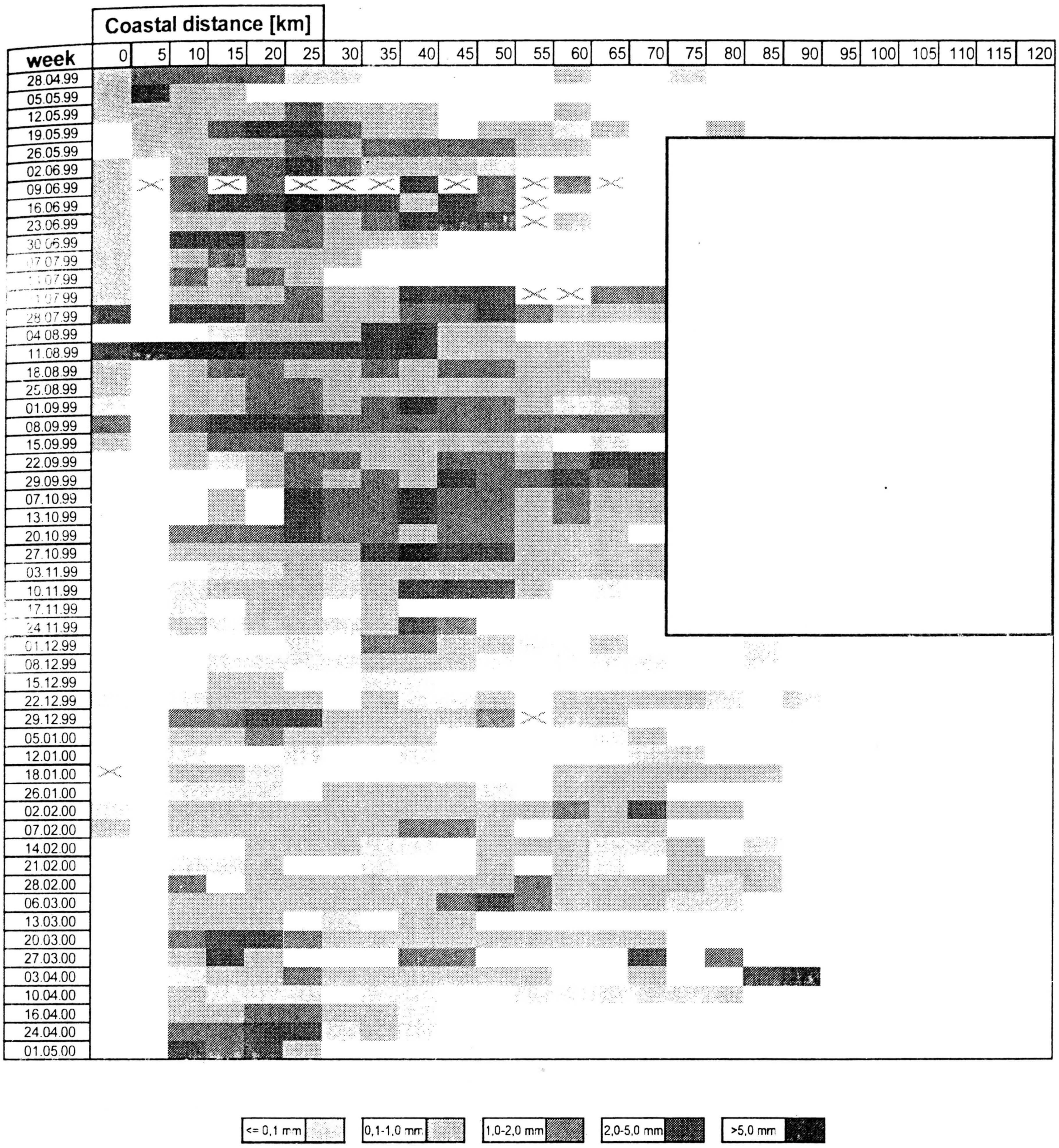

Figure 3: Weekly fog measurements along the Swakopmund-Usakos Transect shown with respect to coastal distance for the period May 1999 – April 2000. The box indicates a lack in the measuring period. Crosses symbolis weeks without data.

0-5 km coastal distance (Figure 5). Total fog amount with about 70 mm was maximum at 25 km and 30 km coastal distance where a transition zone between coastal and high fog exists (see also Hachfeld & Jürgens 2000). By coastal fog – not considering the area between 0-5 km but up to 25 km distance – the Central Namib received between 50-71 mm of water in the rainy season of 1999/2000. High fog comprising mainly the area from 25/30 km to 50 km coastal distance contributed only little less water (47-62 mm) to the landscape. Walter & Breckle (1990) state similar quantities of fog with a total of 40-50 mm/y^{-r} and fog quantities of typically less than 0,1 mm per fog event.

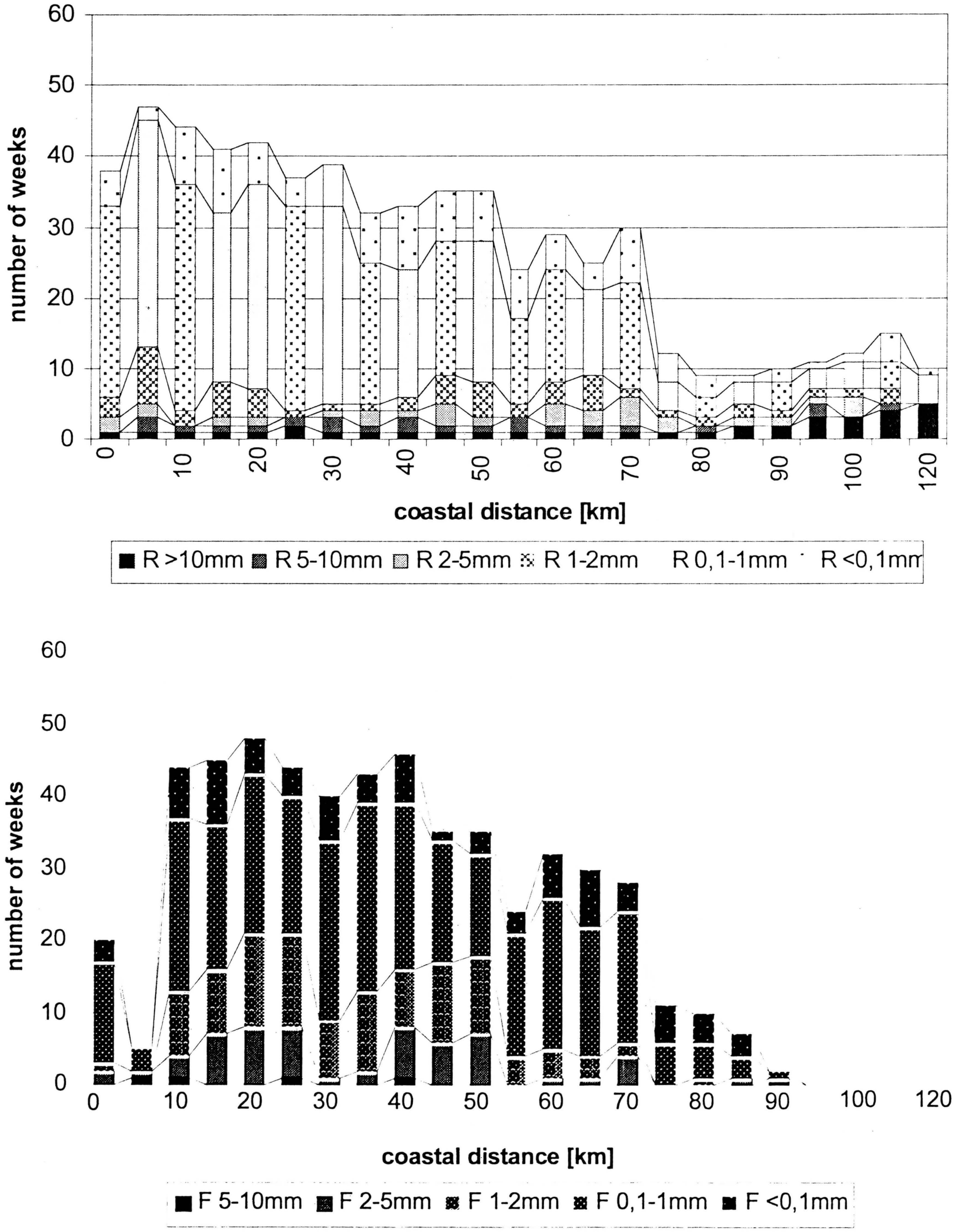

Figure 4: Number of weeks in which a) rain or drizzle occurred (top) and b) fog occurred differentiated in different precipitation amounts and shown with respect to coastal distance. Measuring period was May 1999 – April 2000.

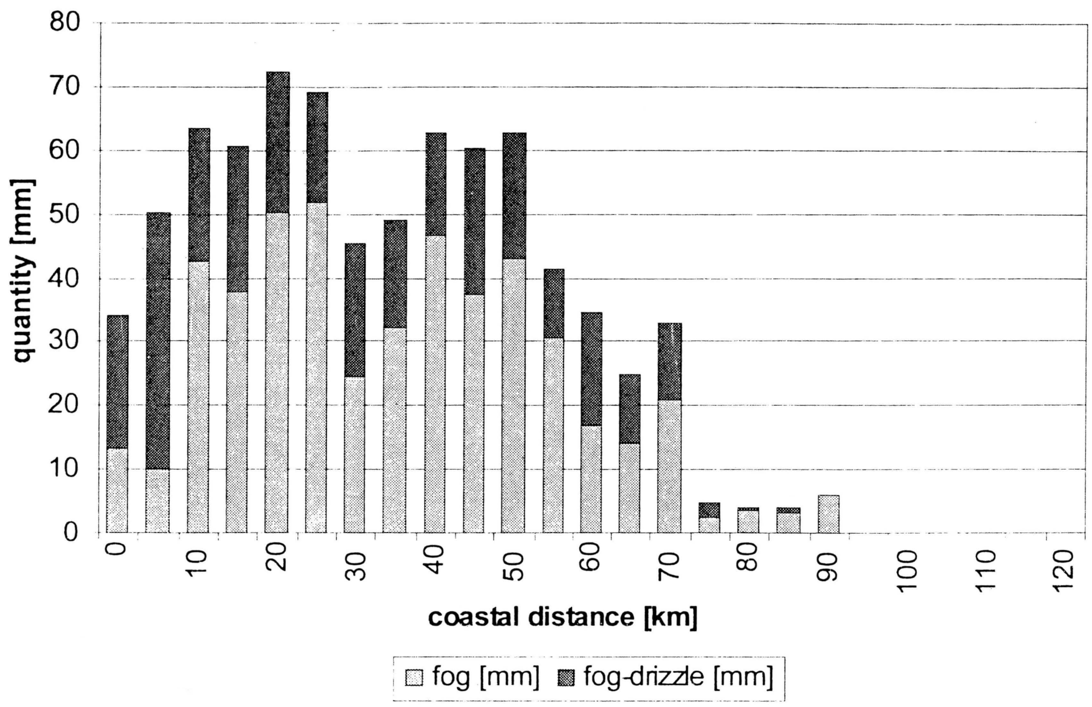

Figure 5: Total amount of fog in the Central Namib including fog and fog-drizzle for a transect from Swakopmund to Usakos for the period of May 1999 – April 2000.

Monthly precipitation amounts measured at the 5 automatic weather stations during the rainy seasons of 1997/1998, 1998/1999 and 1999/2000 emphasises the extraordinary rain pulse of this year in contrast to previous rainy seasons (Figure 7). At the stations in 0 km, 12 km, 35 km, and 56 km coastal distance monthly precipitation in the previous years was low with typically less than 20 mm/month. Considering that the three western-most stations (0, 12, 35 km's) also collected fog the comparatively high regularity in the occurrence as well as the quantity of monthly precipitation can be explained. Especially for the station at the coast a strong temporal concentration of precipitation during the winter months from May to October is evident which is not assigned to rain but to coastal fog. In contrast, at the station in 56 km coastal distance monthly precipitation was lower and no clear assignment to any period of the year was possible. Towards the transition to savanna in 92 km coastal distance higher rainfall occurred not only in 1999/2000 but also in January (80 mm) and March 1999 (57 mm). Generally, rainfall in this coastal distance shows a higher regularity from year to year.

Species richness and growth form diversity

In Figures 8-10, species richness along three coast to inland transects is shown for the years 1997-2000 comprising species numbers on different plot sizes and life form spectra differentiated in ephemeral species (grasses, forbs) and perennial species (small and large shrubs). A list of species found on each transect is shown in Table 1-3.

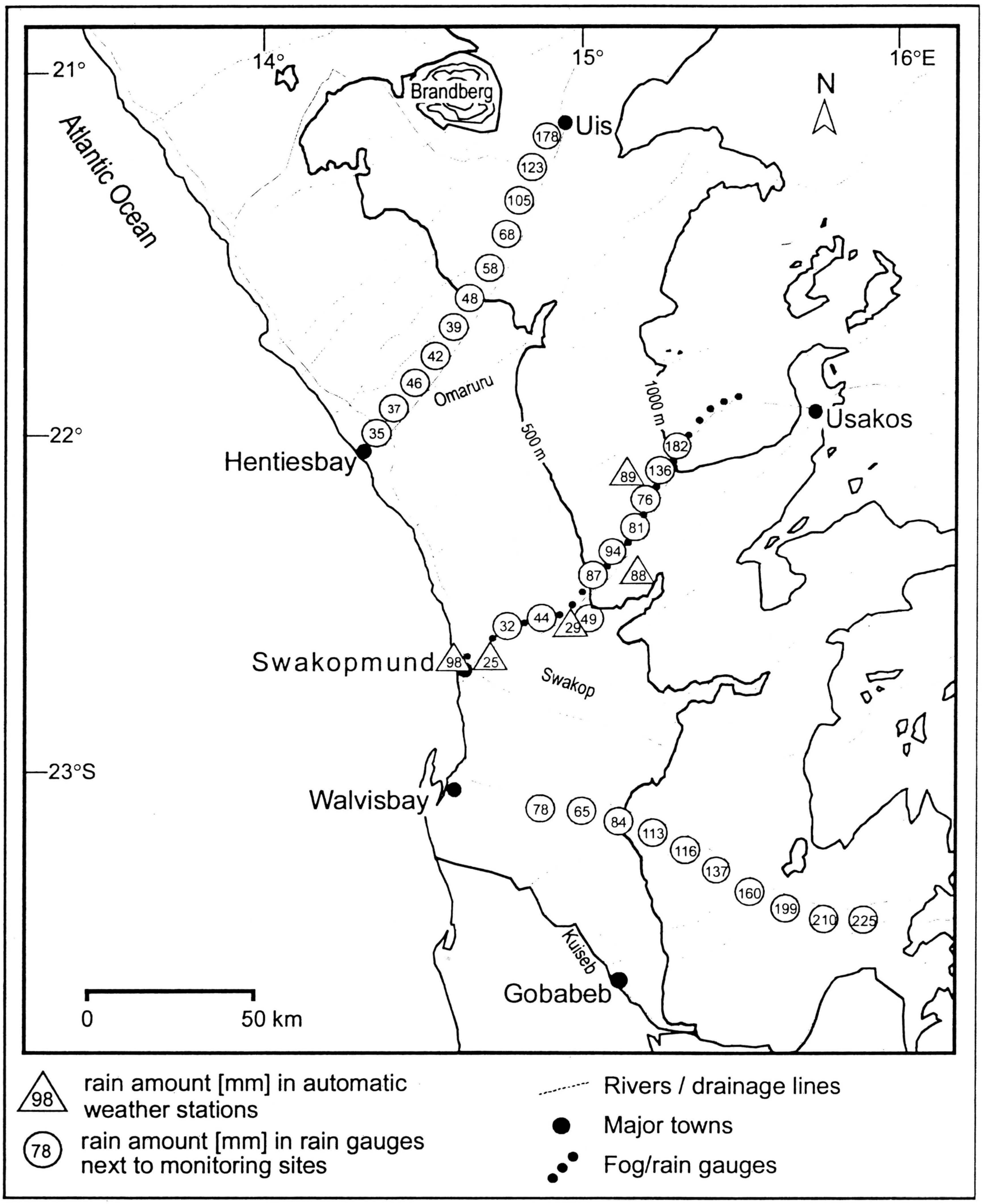

Figure 6: Precipitation amounts in the Central Namib Desert after the exceptional rainfall in March 2000 shown for the rain gauges and automatic weather stations along the three transects.

Namib-Naukluft Park Transect

Three major vegetation zones form the vegetation along this transect: the Lichen Zone represented by monitoring sites in 20 km and 30 km coastal distance dominated by lichens (not listed) and few perennial species; the Minimum Zone from 40-110 km

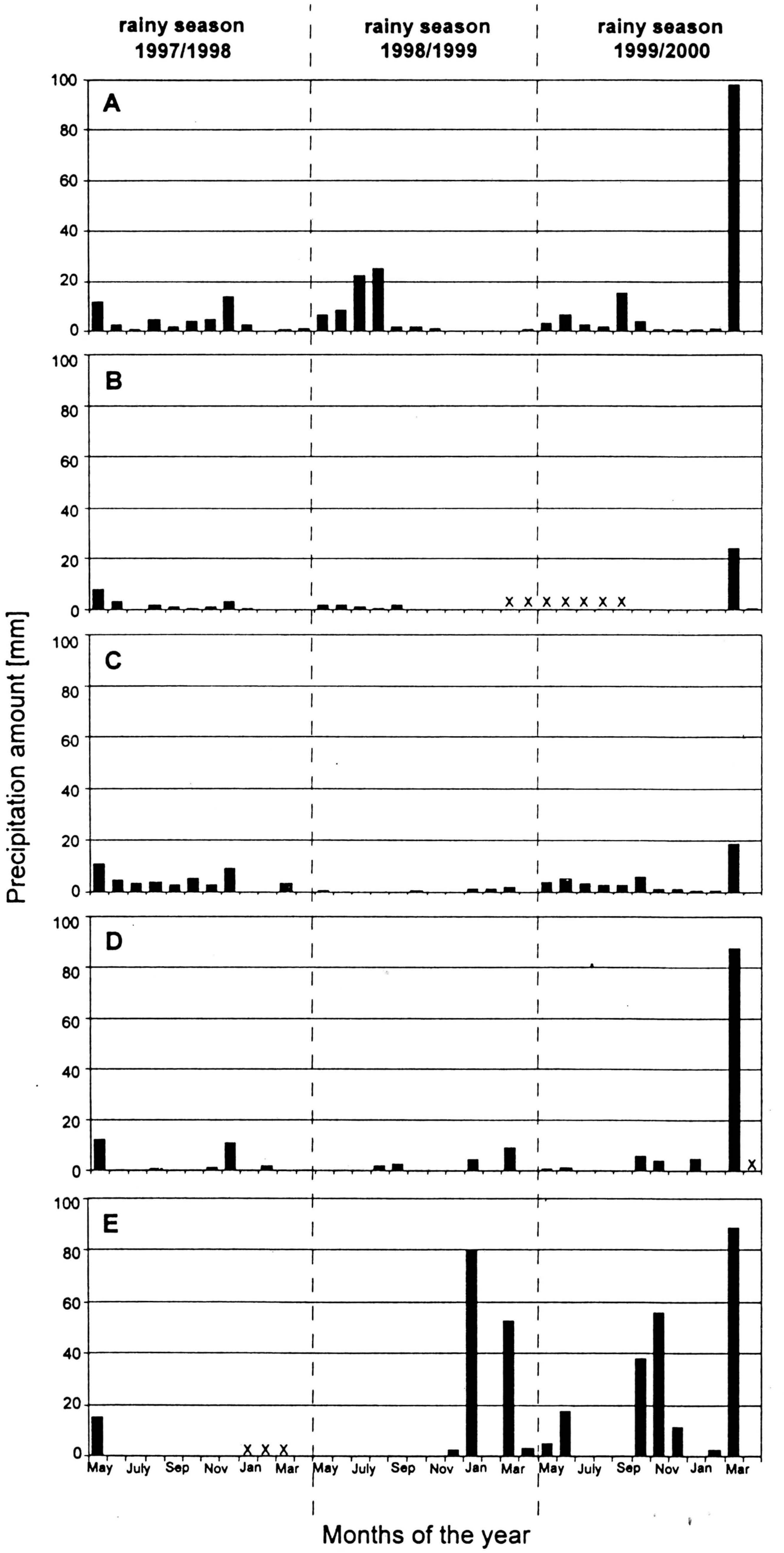

Figure 7: Total monthly precipitation measured at 5 automatic weather stations along a coast to inland transect for the rainy periods of 1997/98, 1998/99 and 1999/2000 in the following coastal distances: A: 0 km; B: 12 km; C: 35 km; D: 56 km; E: 92 km. Crosses symbolise months without data.

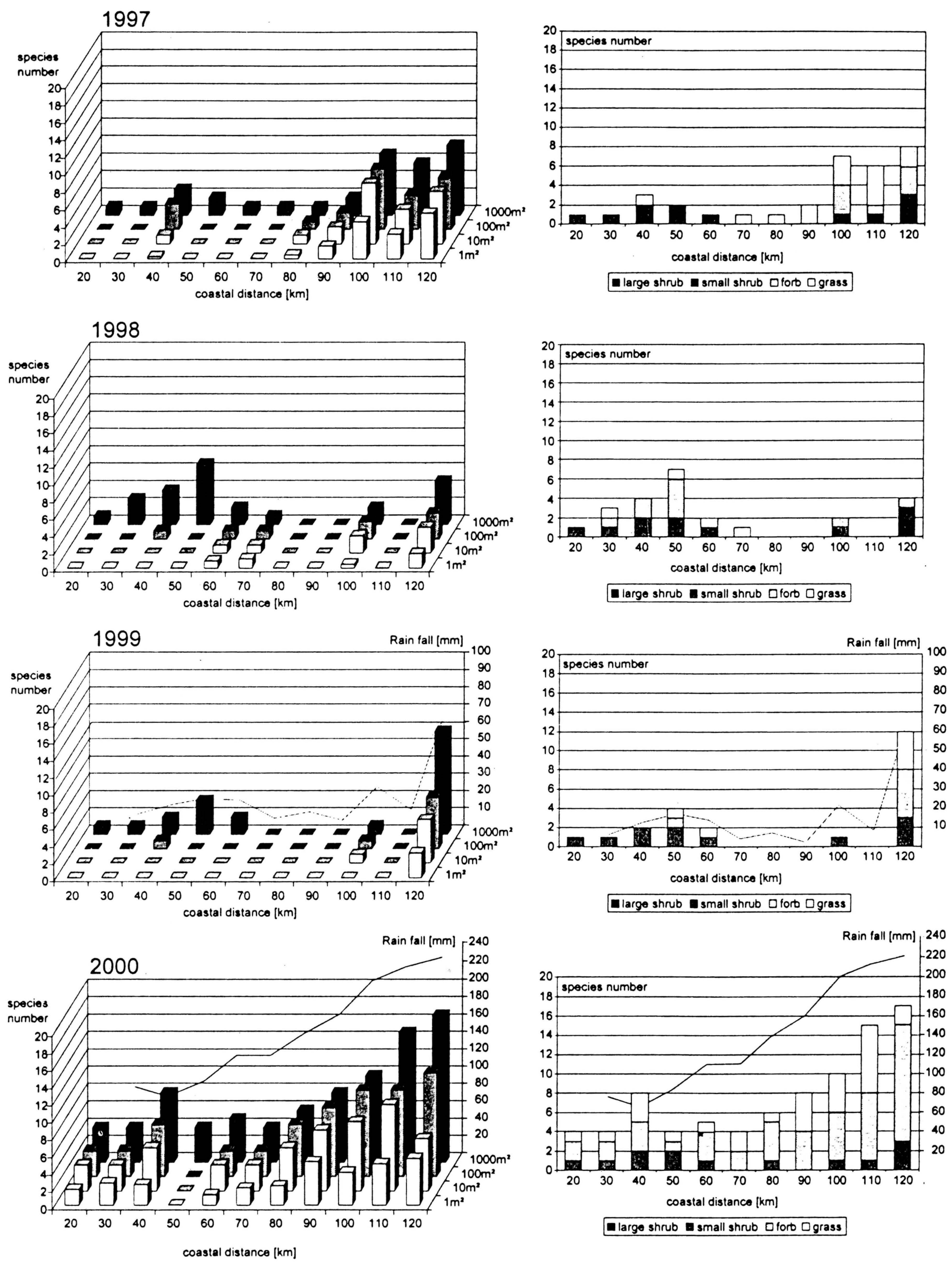

Figure 8: Left: Species number on plot sizes of 1 m², 10 m², 100 m² and 1000 m² shown with respect to coastal distance along the Namib-Naukluft Park Transect for the years 1997-2000. Right: Composition of life forms on the 1000 m² sites shown with respect to coastal distance along the Namib-Naukluft Park Transect for the years 1997-2000. Also shown is rainfall amount for 1999 and 2000 collected in rain gauges next to the plots.

coastal distance is characterised by a lack of perennial species (occasionally *Salsola* spec. occurs). It comprises a western part (40-50 km) corresponding with the end of the major fog zone and an eastern part (60-110 km). The *Calicorema capitata* Zone forms the inland part of the transect few kilometers west of the Kuiseb Canyon.

In years with low rainfall, 1997-1999, in the Lichen Zone no ephemeral species were found on the small plots sizing 1m^2, 10m^2 and 100 m^2 (Figure 8). Only in 1998, on the large plots (1000 m^2) two ephemeral species (*Stipagrostis subacaulis, Zygophyllum simplex*) were found together with the very scattered distributed shrubs *Arthraerua leubnitziae* and *Salsola* spec. After about 80 mm of rainfall in March 2000, in the nested plots of 1-100 m^2 only 1 grass and 1 forb germinated. The small increase in species number with plot size indicates an even and dense occurrence of ephemeral species after the rain event. Irrespective of the high rainfall in this zone total species richness per 1000 m^2 was with 4 species/1000 m^2 (3 ephemeral species) not as high as expected and almost as low as in previous years.

In the western part of the Minimum Zone (40-50 km coastal distance) a total of 6 ephemeral species were recorded in 1997-1999. Whereas in 1997 and 1999 only *Stipagrostis ciliata* and *Euphorbia phylloclada* occurred, in 1998 additionally 4 forbs germinated. However, total cover values were at a minimum with less than 0,1 %/1000 m^2. In 2000, due to 70-80 mm of rain species number (4-8 species/1000 m^2) as well as total cover (0,6-1,6 %) increased, but species response did not correlate with rainfall amount. This was especially true for the plot in 50 km coastal distance, where after 15 mm of rain in 1999 two ephemeral species (*Euphorbia phylloclada, Stipagrostis ciliata*) germinated, and irrespective of 80 mm of rain in 2000 only the same species were found showing only a little higher cover value of 0,41 % in comparison to 0,01 % in 1999. Species composition did not change much and comprised additionally only one *Stipagrostis* species (*Stipagrostis gonatostachys*) and one Fabaceae (*Lotononis* spec.).

The eastern part of the Minimum Zone reaches from 60-110 km coastal distance. Species richness from 1997-1999 was low (except for 100-110 km coastal distance in 1997) comprising only *Enneapogon desvauxii* and *Stipagrostis ciliata* with a cover of less than 0,1 %. No increase in species number with increase in plot size from 1 m^2 to 1000 m^2 took place. In 2000, species germination responded parallel to high rainfall amounts (115-210 mm) and species number increased with plot size: Whereas on 1 m_ 1-6 species were found, on 10 m^2 and 100 m^2 species richness was at 3-8 species and increased to 15 species (perennial and ephemeral taxa) for 1000 m^2. With much higher total cover values (7-21 %) in comparison to previous years *Stipagrostis ciliata* was dominant on all sites (Figure 14).

The *Calicorema capitata* Zone (plot in 120 km coastal distance), is characterised by shrubs such as *Calicorema capitata*, *Zygophyllum cylindrifolium* and occasionally *Adenolobus pechuelii*. In contrast to the other vegetation zones, in the *Calicorema capitata* Zone an increase in species number with plot size was found also in 1997-1999 showing especially a strong increase from 100 m^2 to 1000 m^2. This indicates a

Table 1: List of ephemeral species occurring in different vegetation zones along the Namib Naukluft Park Transect in the years from 1997-1999 and 2000.

NAMIB-NAUKLUFT PARK TRANSECT SPECIES NAME // VEGETATION ZONE	Lichen Zone 20-30 km		Minimum Zone				*Calicorema capitata* Zone 120 km	
			40-50 km		60-110 km			
FORBS	1997-1999	2000	1997-1999	2000	1997-1999	2000	1997-1999	2000
Aizoanthemum dinteri		X		X		X		
Aizoanthemum galenioides			X			X		
Aizoanthemum membrumconnectens						X		X
Anticharis ebracteata								X
Anticharis inflata								X
Cleome semitetrandra								X
Euphorbia glanduligera							X	X
Euphorbia phylloclada			X	X				
Geigeria alata						X		X
Geigeria ornativa								X
Gisekia africana var. *africana*					X	X	X	
Hermannia modesta						X		
Helichrysum roseo-niveum						X		
Heliotropium tubulosum			X	X				
Kohautia cynanchica								X
Limeum argute-carinatum					X	X	X	
Lotononis spec.				X				
Mollugo cerviana						X		
Monechma desertorum								X
Sesuvium sesuvioides			X	X				
Tephrosia dregeana var. *dregeana*						X		
Tribulus zeyheri					X	X	X	X
Zygophyllum simplex	X	X	X	X	X		X	X
GRASSES								
Enneapogon desvauxii					X	X	X	X
Eragrostis annulata						X		
Eragrostis nindensis					X	X		X
Stipagrostis ciliata			X	X	X	X		
Stipagrostis gonatostachys				X	X	X		
Stipagrostis hirtigluma ssp. *hirtigluma*						X	X	X
Stipagrostis obtusa					X	X	X	X
Stipagrostis subacaulis	X	X		X				
TOTAL	**2**	**3**	**6**	**9**	**9**	**18**	**8**	**15**

scattered distribution of ephemeral species with great distances between the individuals. Whereas in 1997-1999 ephemeral species number varied from 1-8 species/1000 m^2 (total of 3-11 species) in 2000, a total of 17 species/1000 m^2 was found comprising 11 forbs, 4 grass species and 3 shrubs. Total cover increased to 12 % in comparison to values from 2,9-5 % in the previous years. Species composition was very similar to the eastern Minimum Zone.

Hentiesbay – Uis Transect

Along the Hentiesbay-Uis transect the Lichen Zone stretches from the coast to 20 km inland comprising deep substrates of a former Omaruru riverbed. The adjacent Minimum Zone falls into a western part (30-50 km) and an eastern part up to 90 km coastal distance. Further inland (100 km) the *Calicorema capitata* Zone begins which changes into an *Euphorbia damarana* habitat in 110 km coastal distance.

In 1997-1999, species number in the coastal Lichen Zone was low and varied from 0-4 species/1 m^2 (*Aizoanthemum galenioides, Mesembryanthemum cryptantum, Stipagrostis subacaulis, Zygophyllum simplex*) and 0-6 species on 10 m^2 and 100m^2 comprising additionally *Aizoanthemum membrumconnectens, Sporobolus nebulosus* (Figure 9). Shrubs such as *Salsola nollothensis* and *Arthraerua leubnitziae* were very widely scattered and thus restricted to the 1000 m^2 plots where additionally only 0-9 ephemeral species were found (Table 2). However, as increase in species number with plot size was low not only in 1997-99 but also in 2000 after 40 mm of rain there is low potential in species richness in this zone (Figure 13). Moreover, total species richness with 9 species/1000 m^2 in the poor rainy seasons was the same as in the good rainy season (Table 2): In 1999, after rainfall of 21 mm in 10 km and 20 km coastal distance 5-7 ephemeral species germinated. After twice as much rainfall (± 40 mm) in March 2000 only the same number of ephemeral species was found. In contrast, total cover of ephemeral species in 2000 was more than twice as high as in 1999 (0,1 %-1,5 %) and cover reached values of 2-5,3 %.

The western part of the Minimum Zone is characterised by the occasional occurrence of the shrub *Arthraerua leubnitziae*. Again, from 1997-1999 almost no increase in species number with plot size was found and species richness was at 10 ephemeral species/1000 m^2 (Table 2). Quantity of germinated species on 1000 m^2 followed rainfall: Whereas rainfall of 15 mm (1999) triggered the germination of 2 grasses (*Stipagrostis ciliata, S. obtusa*) in 30 km coastal distance, after 21 mm of rain 40 km inland additionally 3 forbs (*Aizoanthemum membrumconnectens, Galenia papulosa, Zygophyllum simplex*) germinated. Instead, rainfall of 10 mm in 50 km coastal distance was not sufficient to trigger any germination. In 2000, rainfall in the western Minimum Zone was about as high as in the coastal Lichen Zone (40 mm): Whereas species richness was slightly higher (12 species/1000 m^2) and increased with plot size total cover values were lower (< 1 %) except for the plot in 50 km coastal distance.

The beginning of the eastern Minimum Zone corresponds with the end of the major fog zone and the occurrence of *Arthraerua leubnitziae*. As rainfall reached as far into the desert as 60 km (1997) and 80 km (1998) coastal distance up to 15 ephemeral species germinated on 1000 m^2. In contrast to western parts of the transect species number increased with plot size indicating a greater potential of richness in ephemeral species. Species composition in comparison to the Lichen Zone changed considerably comprising several species also present in the adjacent *Calicorema capitata* Zone (Table 2). Again, species richness corresponded well with rainfall:

Table 2: List of ephemeral species occurring in different vegetation zones along the Hentiesbay – Uis Transect in the years from 1997-1999 and 2000.

HENTIESBAY-UIS TRANSECT SPECIES NAME // VEGETATION ZONE	*Lichen* Zone 0-20 km		Minimum Zone 30-50 km		Minimum Zone 60-90 km		*Calicorema capitata + Euph. dama.* Zone 100-110 km	
FORBS	1997-1999	2000	1997-1999	2000	1997-1999	2000	1997-1999	2000
Aizoanthemum dinteri			X		X			
Aizoanthemum galenioides	X					X		
Aizoanthemum membrumconnectens	X	X	X	X	X	X		
Anticharis inflata				X	X	X	X	X
Blepharis grossa							X	X
Cleome angustifolia ssp. *diandra*								X
Cleome semitetrandra					X	X	X	X
Crotalaria podocarpa							X	X
Euphorbia glanduligera							X	X
Euphorbia phylloclada					X	X	X	X
Euphorbia prostrata						X		
Geigeria alata					X	X	X	X
Geigeria ornativa						X	X	X
Gisekia africana var. *africana*	X				X	X	X	X
Hermannia modesta					X	X	X	X
Hypertelis salsoloides		X						
Indigastrum argyroides					X	X	X	X
Kissenia capensis								X
Kohautia cynanchica				X	X	X		X
Limeum argute-carinatum			X	X	X	X		X
Lophiocarpus spec.							X	X
Lotononis spec.			X	X	X	X		X
Mesembryanthemum cryptanthum	X	X						
Mollugo cerviana	X	X		X		X		X
Monechma desertorum			X	X	X	X		
Monsonia umbellata								X
Sesbania cf. *macowaniana*								X
Sesuvium sesuvioides	X	X						
Tephrosia dregeana var. *dregeana*						X		
Trichodesma africana						X		
Zygophyllum simplex	X	X	X	X	X	X		X
GRASSES								
Aristida parvula					X	X		
Brachiaria glomerata				X	X			
Enneapogon desvauxii			X		X	X		X
Enneapogon scaber					X	X		X
Eragrostis annulata								X
Eragrostis nindensis							X	X
Oropetium capense						X		
Sporobolus nebulosus	X	X			X	X		
Stipagrostis ciliata			X	X	X	X	X	X
Stipagrostis hochstetteriana ssp. hochstett.								X

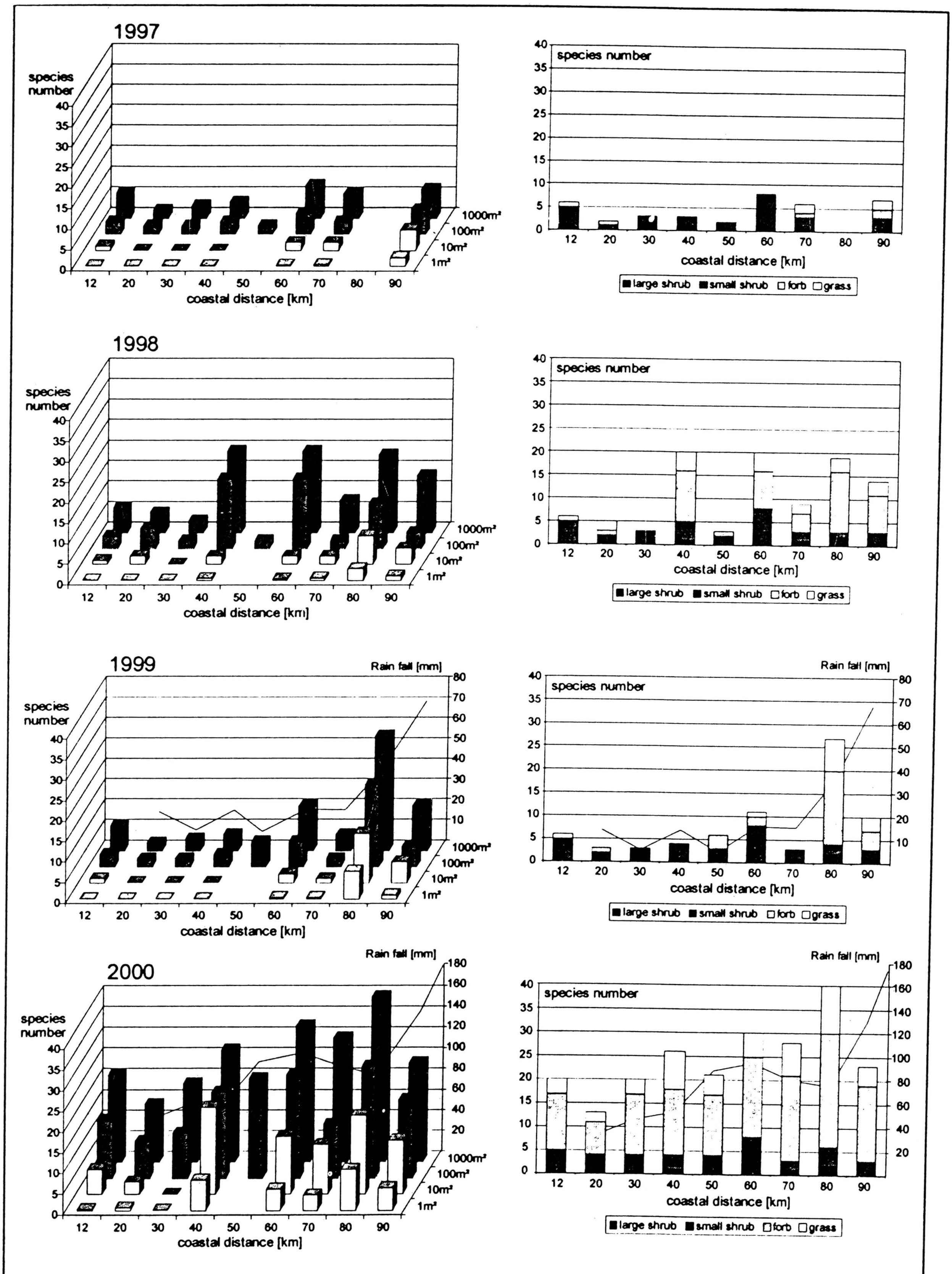

Figure 9: Left: Species number on plot sizes of 1 m², 10 m², 100 m² and 1000 m² shown with respect to coastal distance along the Hentiesbay Transect for the years 1997-2000. Right: Composition of life forms on the 1000 m² plots shown with respect to coastal distance along the Hentiesbay Transect for the years 1997-2000. Also shown is rainfall amount for 1999 and 2000 collected in rain gauges next to the plots.

Stipagrostis hirtigluma					X	X	X	X
Stipagrostis obtusa		X	X	X	X	X		
Stipagrostis subacaulis	X	X	X	X	X	X		
Stipagrostis uniplumis var. *intermedia*					X	X	X	X
TOTAL	**9**	**9**	**10**	**12**	**24**	**29**	**16**	**29**

Whereas in 1999 rainfall in 60-90 km coastal distance was with less than 10 mm not sufficient for the germination of any ephemeral species, in 2000, rainfall increased with coastal distance from 39 mm (60 km) to 105 mm (90 km) and led to the germination of various ephemeral species not only on 1000 m^2 (29 species) but also on 1 m^2 (5-9 species), 10 m^2 (5-14 species) and 100 m^2 (8-17 species). In contrast, from 1997-1999 24 species/1000 m^2 occurred. More forb than grass species germinated, but only in 80 km distance seedlings of one perennial species, *Zygophyllum cylindrifolium*, were found. Total cover varied strongly with respect to rainfall with values from 0,2-13 % and typically only one dominating grass species.

In the *Calicorema capitata* Zone and the *Euphorbia damarana* habitat rainfall is typically more regular. Consequently a higher number of perennial species occurs. In 100 km coastal distance on 1000 m^2 these are: *Calicorema capitata, Commiphora oblanceolata, C. saxicola, Euphorbia lignosa, Monechma genistifolium, Petalidium setosum, P. variabile,* and *Sarcocaulon salmoniflorum* (Figure 15). Other species found on the monitoring site in 110 km coastal distance are *Acacia reficiens, Adenolobus pechuelii* and *Euphorbia damarana*. Increase in species number with plot size was high indicating a high potential in species richness. Variation in species number from a very dry year (1999) to a year with good rainfall (2000) was also high comprising up to 28 ephemeral species in 100 km coastal distance. Total number of species found during 1997-1999 was 16 species/1000 m^2 and 29 species/1000 m^2 in 2000. Again, total cover varied with respect to rainfall with values between 1,7 % in a dry year (km 110, 1998) and 26 % after good rainfall (km 100, 2000). Whereas in 100 km coastal distance grass species were dominant (*Eragrostis nindensis, Stipagrostis ciliata, S. uniplumis* var. *intermedia*), on the *Euphorbia damarana* habitat forbs such as *Monsonia umbellata* and *Euphorbia phylloclada* dominated. In contrast to the other zones, species composition comprised also savanna taxa such as *Acacia reficiens, Monsonia umbellata, Sesbania* cf. *macowaniana, Eragrostis nindensis,* and *E. annulata.*

Swakopmund – Usakos Transect

The Lichen Zone of this transect ends in 20 km coastal distance. The adjacent Minimum Zone reaches in its western part from 30-50 km (major fog zone) and in its eastern part from 60-70 km coastal distance. The *Euphorbia damarana* Zone (80 km) is here combined with the *Calicorema capitata* Zone (90 km). Along this transect monitoring sites are not always placed within strictly plain habitats but occasionally include small drainage lines.

One monitoring site (12 km coastal distance) of the Lichen Zone is characterised by a small drainage line which supports additional water supply and thus a higher species richness (Figure 10). From 1997-1999 few ephemeral species occurred in the Lichen Zone: *Sporobolus nebulosus, Stipagrostis schaeferi, S. subacaulis* and *Zygophyllum simplex* with a minimum cover of 0,01%. Shrubs comprised spatially scattered individuals of *Arthraerua leubnitziae, Lycium tetrandrum, Sutera maxii, Tetragonia reduplicata*, and *Zygophyllum stapfii*. After about 40 mm of rain in March 2000 14 forbs and 4 grass species germinated on 1000 m^2 comprising a total cover of 2 %. Seedlings of all shrubs except for *Lycium tetrandrum* were found. Increase in species number with plot size was only visible after the good rainfall in 2000.

The end of the western Minimum Zone corresponds with the end of the *Arthraerua leubnitziae* Zone. Only little variation in species number and composition from 1997-1999 was found. One exception is the monitoring site in 40 km coastal distance characterised by micro habitat variations such as small drainage lines which form a suitable habitat for *Acacia reficiens* as well as for the germination of several ephemeral species after rainfall (e.g. 1998). Irrespective of this site only 2 ephemeral species (*Stipagrostis subacaulis, Zygophyllum simplex*) with a total cover below 0,1 % occurred in this zone from 1997-1999. In contrast, in 2000 germination of ephemeral species corresponded well with rainfall. Total species number rose from less than 5 species (0 ephemeral species) in 1997-1999 to 13-26 species/1000 m^2. The majority of ephemeral species were forbs. A strong increase in species number with plot size was found and total cover values raised to a maximum of 5,7 %. Species composition included species found in the Lichen Zone (e.g. *Stipagrostis subacaulis*) as well as species found in all vegetation zones (e.g. *Zygophyllum simplex*).

The eastern Minimum Zone comprises one plot (km 60) where *Acacia reficiens, Aloe asperifolia* and *Euphorbia giessi* occur on a very small drainage line. In 70 km coastal distance *Euphorbia damarana* as well as *Zygophyllum stapfii* form the major perennial species. Whereas in 1997 and 1999 only few ephemeral species germinated in 1998 rainfall was responsible for the occurrence of 9 forbs and 3 grass species. In 2000, after 80-90 mm of rainfall total species richness increased to 28-30 species/1000 m^2 with a majority of forbs. A strong increase in species number with plot size indicates once more a spatially variable occurrence of ephemeral species on 1000 m^2. Several seedlings of *Zygophyllum stapfii* but only few seedlings of *Euphorbia damarana* and none of other perennial species were found.

In the *Euphorbia damarana* Zone and the *Calicorema capitata* Zone rainfall is typically higher and more reliable. As ephemeral species were recorded in all four years no great difference in species richness between 1997-1999 (30 species/1000 m^2) and 2000 (40 species/1000 m^2) was found. Also, total number of ephemeral species was the same for 1997-1999 and 2000 with 35 species/1000 m^2 (Table 3). A strong relationship of rainfall with species richness was found for the plot in 80 km but not in 90 km coastal distance. In contrast, total cover values of the 1000 m^2 plots were highest in 90 km (31,2 %) but only 15,4 % in 80 km coastal distance. Species composition included widely distributed species such as *Zygophyllum simplex*, but

Table 3: List of ephemeral species occurring in different vegetation zones along the Swakopmund – Usakos Transect in the years from 1997-1999 and 2000.

SWAKOPMUND – USAKOS TRANSECT SPECIES NAME // VEGETATION ZONE	Lichen Zone 12+20 km		Minimum Zone 30-50 km		Minimum Zone 60-70 km		*Calicorema capitata + Euph. Dama.* Zone 80+90 km	
FORBS	1997-1999	2000	1997-1999	2000	1997-1999	2000	1997-1999	2000
Aizoanthemum dinteri				X				
Aizoanthemum membrumconnectens				X		X	X	
Anticharis inflata			X	X		X	X	X
Asteraceae spec.		X						
Blepharis grossa			X	X		X	X	X
Cleome carnosa			X	X	X	X		
Cleome angustifolia ssp. *diandra*							X	X
Cleome semitetrandra							X	X
Emilia marlothiana								X
Euphorbia glanduligera		X				X	X	X
Euphorbia phylloclada			X	X	X	X	X	X
Forsskaolea viridis							X	X
Galenia africana		X						
Galenia papulosa		X						
Gazania jurineifolia		X						
Geigeria alata							X	X
Geigeria ornativa					X	X	X	X
Gisekia africana var. *africana*					X	X	X	X
Heliotropium oliveranum		X						
Heliotropium tubulosum			X	X		X	X	X
Hermannia modesta			X	X		X	X	X
Indigastrum argyroides				X	X	X	X	X
Kissenia capensis						X	X	X
Kohautia cynanchica			X	X	X	X		X
Limeum argute-carinatum		X	X	X		X	X	X
Lotononis spec.		X		X	X	X	X	X
Mesembryanthemum cryptanthum		X						
Mollugo cerviana								X
Monechma desertorum			X	X		X		
Monsonia umbellata						X	X	X
Senecio engleranus		X						
Sesuvium sesuvioides		X	X	X	X	X		
Tephrosia dregeana var. *dregeana*		X		X		X		X
Tribulus zeyheri							X	X
Tripteris microcarpa ssp. *microcarpa*		X	X	X		X	X	X
Trichodesma africanum							X	X
Zygophyllum simplex		X	X	X	X	X	X	X
GRASSES								
Aristida parvula			X	X		X	X	X
Enneapogon desvauxii					X	X	X	X
Enneapogon scaber						X		X
Eragrostis nindensis							X	X
Sporobolus nebulosus	X	X		X				

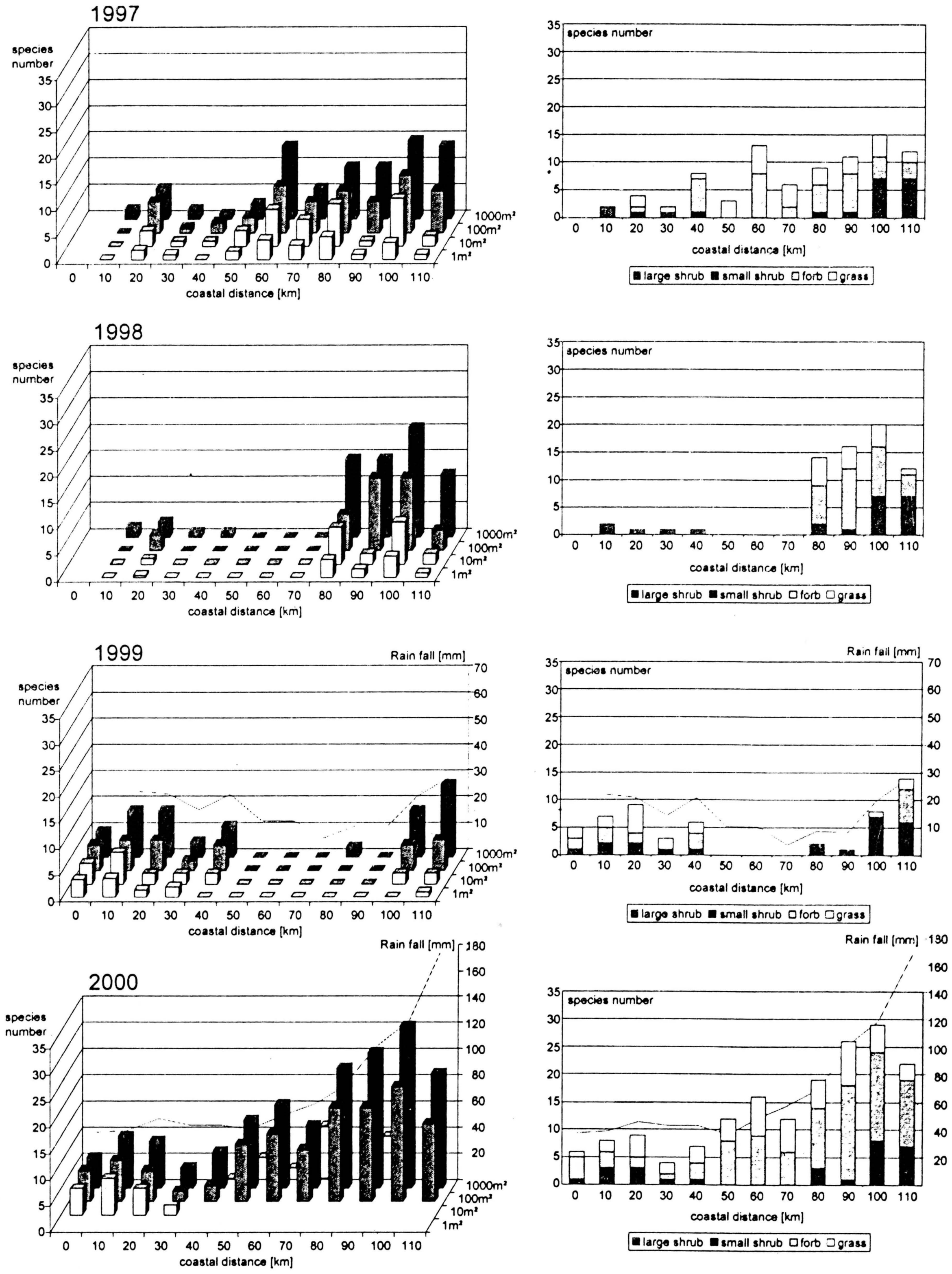

Figure 10: Left: Species number on plot sizes of 1 m², 10 m², 100 m² and 1000 m² shown with respect to coastal distance along the Swakopmund Transect for the years 1997-2000. Right: Composition of life forms on the 1000 m² plots shown with respect to coastal distance along the Swakopmund Transect for the years 1997-2000. Also shown is rainfall amount for 1999 and 2000 collected in rain gauges next to the plots.

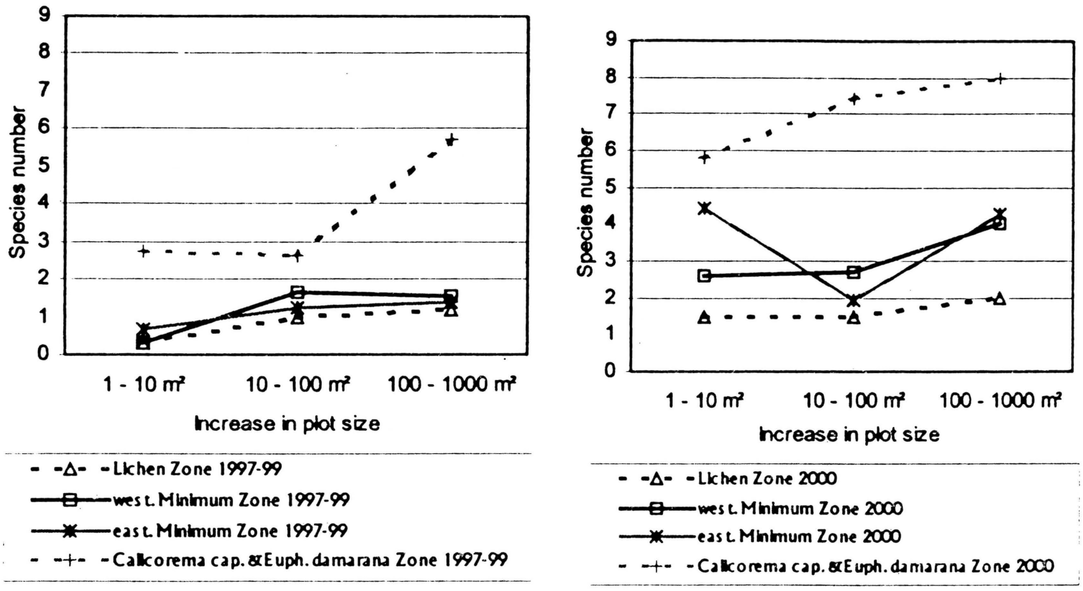

Figure 11: Average increase in species number with increase in plot size for the different vegetation zones calculated for all three transect. Left: the years 1997-1999, right: the year 2000.

of a similar growth form germinate and diversity of growth forms is in average little higher but shows less variation.

No correlation of species richness with rainfall was found. Moreover, species potential seemed to be limited irrespective of rainfall. Rainfall in 2000 was with 35-78 mm as high as it typically is in the eastern part of the desert, but species diversity was much lower. The Lichen Zone lies within the coastal fog zone (Figures 1-4) where on over 43 weeks of the past year fog was measured. Weekly fog contribution was typically less than 1 mm but total precipitation by fog in 1999/2000 was about as high as by rain. As coastal fog contains salt the germination of other than salt tolerant species may be limited and only few species namely leaf succulent species seem to be able to cope with such harsh environmental conditions.

Western Minimum Zone

The eastern border of the western Minimum Zone in 50 km coastal distance corresponds with the end of the *Arthraerua leubnitziae* Zone and the end of the major fog zone. Here, the transition between the dominance of both fog types, coastal fog and high fog, takes place. The potential of species richness per 1000 m^2 plot was higher than in the Lichen Zone and varied between 9-30 species/1000 m^2 with respect to the transect. In the Namib Naukluft Park species numbers were lowest. Overall potential in species richness over the past four years was 43 species/1000 m^2 comprising 11 grass species, 22 forbs and 10 shrubs. Similar to the Lichen Zone increase in species number with plot size was typically low, but increased after the good rainfall in 2000. Whereas from 1997-999 species numbers on 1 m^2 and 10 m^2

Stipagrostis ciliata		X	X	X	X	X	X	X
Stipagrostis hochstetteriana							X	X
Stipagrostis hirtigluma ssp. *hirtigluma*				X	X	X	X	X
Stipagrostis obtusa			X	X		X		X
Stipagrostis schaeferi	X	X		X		X	X	X
Stipagrostis subacaulis	X	X		X				
Stipagrostis uniplumis var. *intermedia*				X			X	X
TOTAL	3	18	15	25	12	28	30	35

also species that link to the savanna transition, e.g. *Eragrostis nindensis, Forsskaolea viridis, Monsonia umbellata* and *Trichodesma africana.*

Discussion

Irrespective of the high rainfall in the entire Central Namib Desert in March 2000 species response did not necessarily correlate with rainfall amount but showed variations with respect to vegetation zone and coastal distance. In the following, the different zones are discussed separately with respect to species richness, diversity of growth forms, rainfall, and fog.

Lichen Zone

The Lichen Zone stretches from the coast to 20-30 km inland. In the following, due to small scale habitat variations the monitoring site in 12 km coastal distance along the Swakopmund-Transect is excluded. The potential of species richness in the Lichen Zone is low: Depending on the transect but irrespective of rainfall richness of ephemeral species varied between 0-9/1000 m^2. Species composition over the past four years included a spectrum of 20 ephemeral species (5 grass species, 15 forbs) and 5 shrubs. Whereas some taxa were restricted to this zone, i.e. *Mesembryanthemum cryptanthum* and *Hypertelis salsoloides*, others were found in the entire study area (e.g. *Euphorbia glanduligera, Zygophyllum simplex*). Following the high rainfall in March 2000 next to ephemeral species also some perennial species germinated, i.e. *Arthraerua leubnitziae, Sutera maxii, Tetragonia reduplicata,* and *Zygophyllum stapfii.* Only rarely seedlings of *Salsola* spec. and none of *Lycium tetrandrum* were found. In contrast to the low potential in species richness, total cover was partly high with typically only one or two species contributing to this. The increase in species number with plot size was low with less than 2 species per plot size difference and hints to a generally low potential of alpha diversity in the Lichen Zone (Figure 11).

In the Lichen Zone the relationship between the diversity of growth forms and species richness (Figure 12) was significantly stronger in 1997-1999 than in 2000 indicating a community structure that is typically dominated by few perennial species but is possibly supplemented by ephemeral species after rainfall. Then, more species

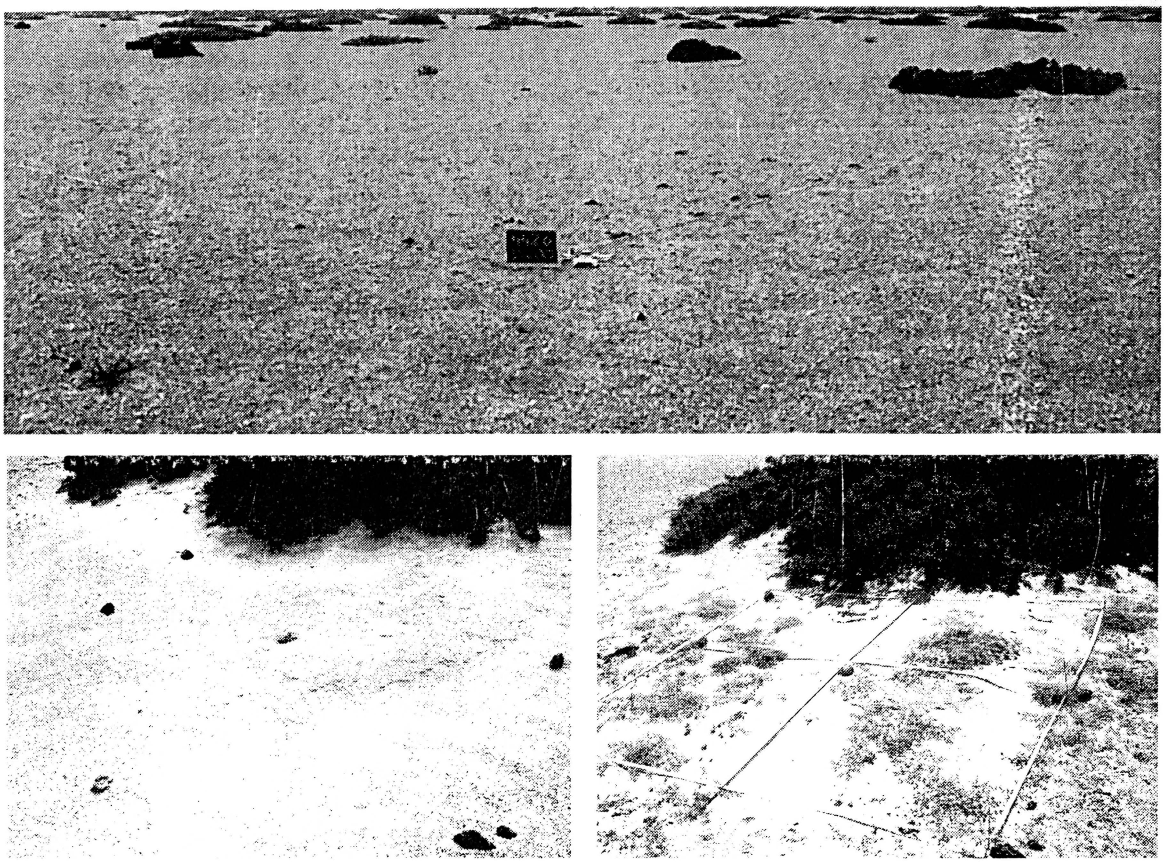

Figure 13: Top: Species richness in the Lichen Zone, here in 10km coastal distance along the Hentiesbay-Uis Transect stays low irrespective of rainfall amount. Whereas in the dry year 1998 no species were found (bottom left), after the high rainfall in 2000 (bottom right) only on the sand accumulations in the lee/wind shade (west) of the *Salsola nollothensis* shrubs a considerable number of individuals was able to germinate (i.e. *Zygophyllum stapfii, Aizoanthemum dinteri*).

were about as low as in the Lichen Zone (Figure 11) after the rainfall in 2000 increase in species number with respect to plot size was higher than in the Lichen Zone. This indicates not only a greater response of ephemeral species to rainfall but also a higher potential in richness of ephemeral species. The fact that increase in species number in 2000 was highest from 100-1000 m^2 emphasises the fact that the majority of species had a sporadic and scattered distribution but nevertheless added to the general diversity of this zone. Species composition showed an intermediate position between species found in the coastal fog zone and those found further east in the study area. As the Minimum Zone is characterised by a lack of rainfall and an extremely low vegetation cover by perennial species higher cover values were only due to single rain events and thus the germination of ephemeral species. After rainfall typically one grass species dominated with a cover of partly 10 %. Germination of

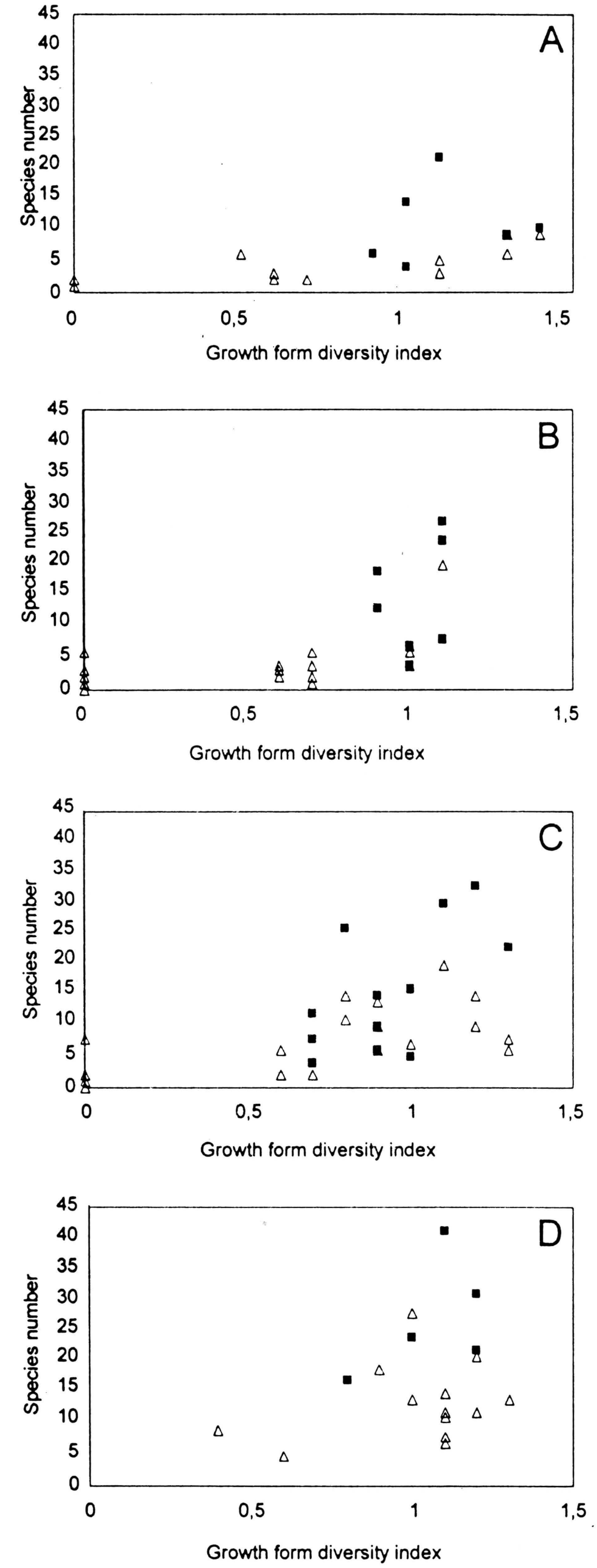

Figure 12: Index of growth form diversity in relation to species richness on the 1000 m² plots for the years 1997-1999 and 2000 in a) the Lichen Zone, b) western Minimum Zone, c) eastern Minimum Zone, and d) *Calicorema capitata* & *Euphorbia damarana* Zone.

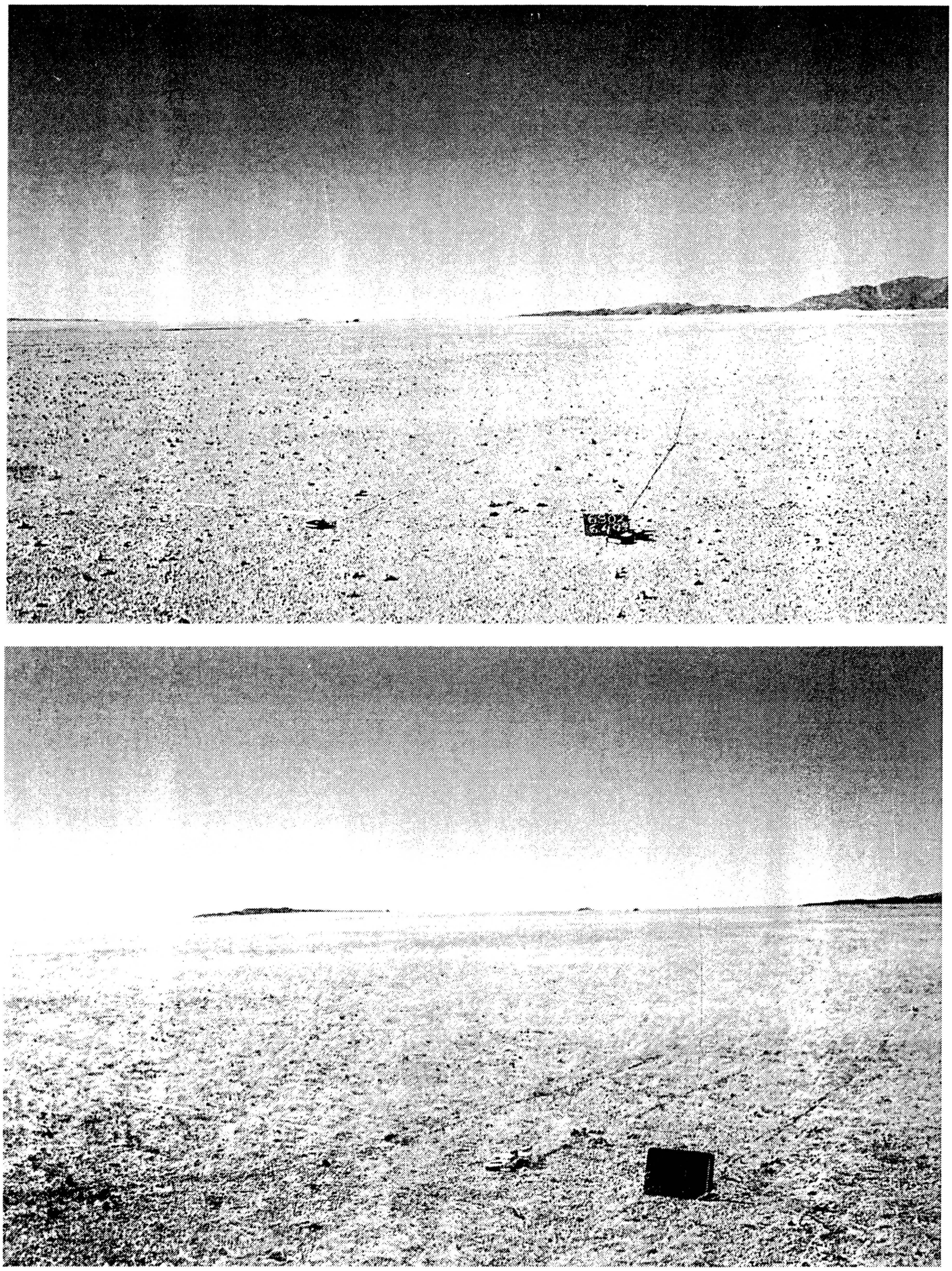

Figure 14: Species richness in the eastern Minimum Zone, here in 90 km coastal distance along the Namib Naukluft Park Transect is, (top) low in years with low rainfall (1997), but (bottom) can increase after sufficient rainfall (2000) with one species (*Stipagrostis ciliata)* being dominant in cover.

perennial species in 2000 was restricted to *Arthraerua leubnitziae, Hermbstaedtia spathuliformis* and *Zygophyllum stapfii*. No seedlings of other shrubs were found.

Diversity of growth forms (Figure 12) partly showed a dominance of one species only (diversity index is zero) but general tendency is equivalent to the Lichen Zone with a strong relationship between the diversity index and species richness for 1997-1999. Again, in 2000 higher species numbers did not cause an increase of the index but narrowed its variability.

In contrast to the Lichen Zone a weak relationship of species number with rainfall can be stated. No other factors seem to override the effect of rainfall even though correlation was not as strong as inland. In the rainy season of 1999/2000 rainfall in this zone was between 35-90 mm. Total precipitation by fog (fog and drizzle) was only little less with 45-61 mm. Fog occurred on 30-45 weeks of the year but as weekly amounts were typically 0,1-1 mm/week fog events could not trigger any germination of seedlings.

Eastern Minimum Zone

The eastern Minimum Zone begins with the end of the major fog zone in 60 km coastal distance. Along the Namib Naukluft Park Transect the eastern Minimum Zone is widest and stretches to 110 km inland, whereas along the Swakopmund- and Hentiesbay-Transect it ends 70 km and 90 km coastal distance. The potential of ephemeral species richness was higher than in the western Minimum Zone with 9-29 species/1000 m^2. Total species richness over the past four years was also higher with 56 species comprising 11 grass species, 30 forbs and 13 small and 2 large shrubs. From 1997-1999 average increase in species richness with plot size (Figure 11) was low with only 2 additional species found per plot size difference. Similar to the western Minimum Zone increase in species number was in average higher in 2000 but varied with respect to habitat conditions from site to site. The curvy shape in Figure 10 indicates that on one hand several species germinated showing a relatively high abundance and density responsible for the considerable increase in species number from 1-10 m^2. Other species on the other hand occurred very scattered and with large distances between the individuals such as perennial shrubs (*Zygophyllum cylindrifolium*) or geophytes. They were only found on the 1000 m^2 plots leading to the increase in species number there. Species composition was to a major extent similar to the *Calicorema capitata-* and *Euphrobia damarana* Zone. Whereas some ephemeral species such as *Stipagrostis subacaulis* were found in both, the major fog zone and this zone, other perennial species such as *Tetragonia reduplicata* were not found anymore. Similar to the western Minimum Zone, total cover varied extremely with respect to rainfall. Typically one grass species was dominant in cover even though forbs contributed most species. The very scattered occurrence of perennial species (the high number of 15 shrubs is mainly due to the monitoring site in 60 km coastal distance on the Swakopmund Transect) is probably responsible for a low germination rate of perennials. The only seedlings occasionally found were *Zygophyllum cylindrifolium*.

Similar to the western Minimum Zone, growth form diversity was partly zero and restricted to one growth form/1000 m^2 (Figure 12). A strong relationship between diversity of growth forms and species richness exists for 1997-1999 but not for 2000 when rainfall triggered the germination of mostly ephemeral taxa. Thus the diversity index stayed the same irrespective of the species number but variation was higher than in the western Minimum Zone.

A strong relationship was found between species richness and rainfall. In 2000, rainfall in this zone was 53-210 mm with an increase from west to east. Only if rainfall stayed below 10 mm (1999) no species germinated. As this part of the Minimum Zone lies east of the major fog zone only on 22-31 weeks of fog were recorded in 1999/2000 comprising weekly amounts of typically less than 1 mm and a total amount of 25-41 mm/year.

***Calicorema capitata* Zone & *Euphorbia damarana* Zone**

This zone marks the transition from the hyperarid part of the desert to the part with less harsh conditions for plant growth and survival. Here, rainfall is more regular with an average of 80-100 mm (van der Merwe 1983). Whereas along the Swakopmund Transect this part of the desert begins already in 80 km coastal distance, along the Hentiesbay Transect and Namib Naukluft Park Transect it begins in 120 km and 100 km coastal distance only. Potential in species richness is highest in comparison to the other zones: Between 8-35 ephemeral species were found on a 1000 m^2 plot. Total species richness over the past four years was about the same as in the eastern Minimum Zone and comprised 53 species/1000 m^2 including 10 grass species, 30 forbs, and 11 small and 2 large shrubs. However, in years with low as well as high rainfall a greater proportion of species showed a less scattered but more dense distribution and led to higher species numbers on the small plots of 1 m^2, 10 m^2 and 100 m^2. Generally, a strong increase was found between 10-100 m^2 where on average species number increased by 8 (Figure 11). The comparatively strong average increase in species number with plot size stresses the character of this zone as a transition from hyperarid to arid. Additionally, it shows once more that large but homogenous plot sizes are necessary in order to document species diversity in an arid landscape where species typically occur with extremely scattered distributions. Next to many species from hyperarid parts of the study area species composition also included some typical savanna taxa such as the shrubs *Boscia foetida* and *Acacia senegal*, the forbs *Forsskaolea viridis* and *Trichodesma africana*. In comparison to the other zones species cover was highest irrespective of variations between 1-35 %.

In contrast to the other vegetation zones diversity of growth forms in this part of the desert was always above zero, i.e. species composition always composed more than one growth form type (Figure 12). No relationship between diversity of growth forms and species richness was found in neither years, 1997-1999 or 2000. Moreover, diversity in growth forms occurred irrespective of species richness and thus rainfall amount.

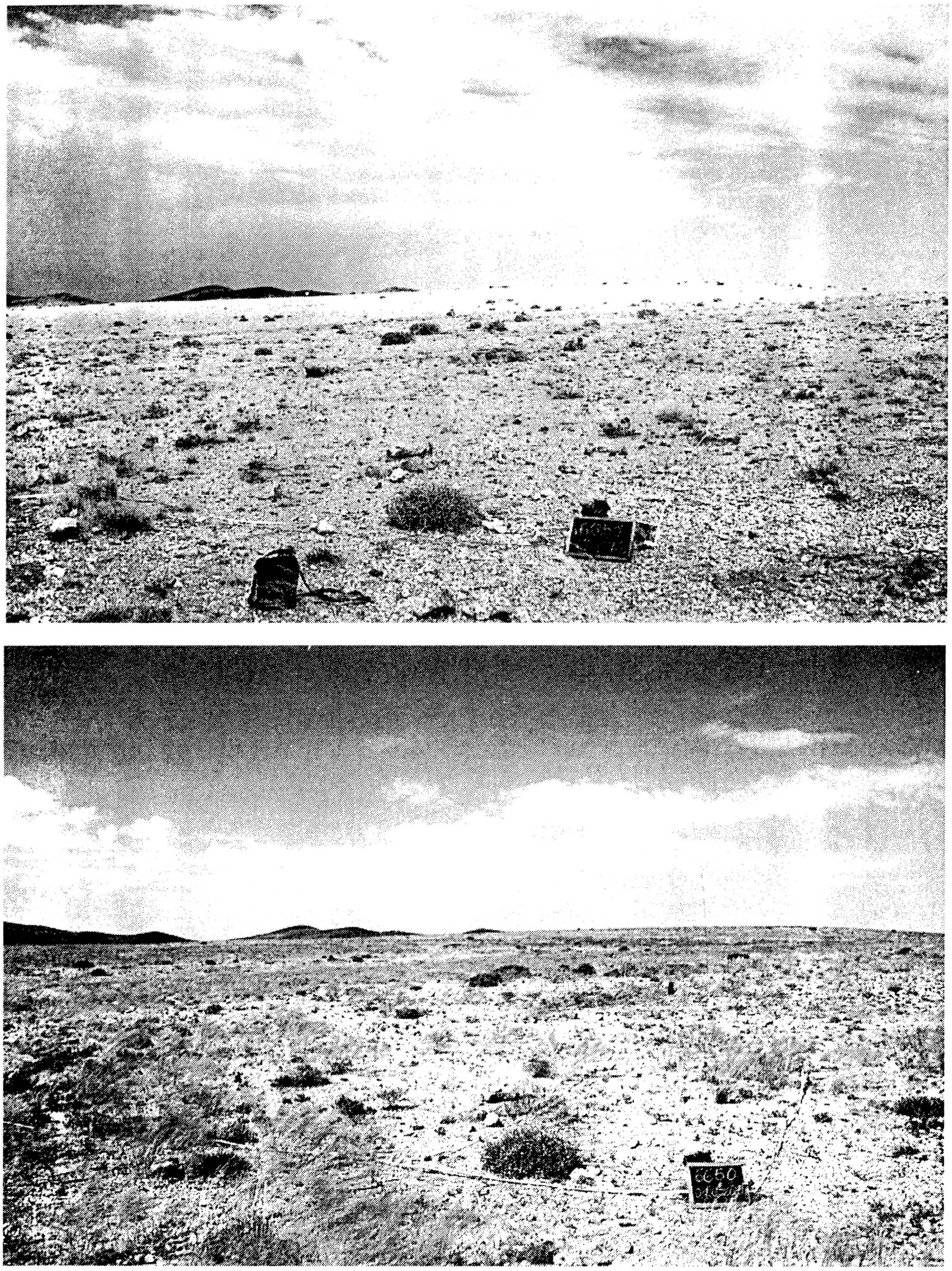

Figure 15: Species richness in the *Calicorema capitata* Zone, here in 100 km coastal distance along the Hentiesbay-Uis Transect, varies with respect to rainfall. However, perennial species always contribute to the diversity of this zone. Here, the vegetation is shown for the years 1998 (low rainfall) (top) and 2000 (high rainfall) (bottom).

the *Calicorema capitata* & *Euphorbia damarana* Zone indicates the transition to savanna. Here, climatic conditions are less harsh with a somewhat higher reliability of rainfall. Consequently, variation in species richness from year to year was less drastic and species composition comprises next to species with a wide distribution range also savanna taxa.

Summarizing it can be stated that in the fog driven Central Namib desert rare rain pulses do no necessarily evoke an impressive variety of ephemeral species as it is known from studies in other hyperarid to arid areas. Instead, species response to rainfall is also dependent on other factors such as fog frequency and amount and accompanying effects on climatic conditions.

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Correlation of species richness with rainfall is high in this part of the desert. Whereas rainfall reached amounts of 70-228 mm in the rainy season of 1999/2000 only rarely fog occurred which did not contribute valuable amounts of moisture to the vegetation.

Conclusions

Due to the strong rainfall of 100 mm in March 2000 in Swakopmund as well as in the entire study area the rainy season of 1999/2000 can be assigned to one of the rare rain pulses evident only once every one or two decades in the Central Namib Desert. In contrast, fog and fog-drizzle occurred with the typical high predictability and division in temporal and spatial patterns. High overall amounts of fog (including fog-drizzle) were related to two vegetation zones, i.e. the coastal fog zone corresponded with the Lichen Zone and the high fog zone was equivalent to the western Minimum Zone. Instead, the eastern Minimum Zone and the *Calicorema capitata* & *Euphorbia damarana* Zone are influenced by rainfall patterns only.

Species response to the rare rain pulse varied in the different vegetation zones irrespective of the overall high rainfall in the area. This indicates the influence of other factors next to rainfall on the species diversity, i.e. fog frequency and fog water contribution. In the Lichen Zone, correlation between rainfall and species richness was low and the exceptional rainfall rarely triggered the germination of any species. Next to ephemeral taxa able to cope with the environmental conditions near the coast, germination of species was restricted to perennial taxa (e.g. *Arthraerua leubnitziae*) which form the scattered shrub layer in the Lichen Zone anyhow. Monitoring of the future development of the seedlings will show whether or not the rain pulse of March 2000 was strong enough to ensure the establishment of a new generation of perennial species in this zone. Walter (1964) found for example that even though the heavy rainfalls in 1934 had triggered the germination of several seedlings of *Arthraerua leubnitziae* and *Zygophyllum stapfii* most of them had died already within the next few years. This is irrespective of the fact that the high regularity of fog is responsible for comparatively moderate climatic conditions near the coast and might help the plants to survive for a longer period. Species response in the western Minimum Zone was similar to the Lichen Zone. The relationship of species richness with rainfall was low but increased in 2000. Still influenced by fog (here high fog) species composition was rather related to the Lichen Zone than to the eastern Minimum Zone. This is probably due to the correspondence of the end of western Minimum Zone with the major fog zone which marks a significant change in species response to rainfall. In the eastern Minimum Zones as well as in the *Calicorema capitata* & *Euphorbia damarana* Zone variation in species richness, composition of growth forms and species diversity over the past four years was to a major extent related to variation in rainfall amount. In the rainy season of 1999/2000 species numbers increased in all plot sizes, but increase in species number from the poor rainy season to the good rainy season was also significantly higher. Whereas in the eastern Minimum Zone hyperarid climatic conditions are evident which link to the western parts of the desert with respect to species composition and low diversity of growth forms in dry years,

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