Distribution of termites (Isoptera) throughout Namibia - environmental connections

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2. CHAPTER 1

Declaration

Declaration

I declare that this thesis is my own, unaided work and has not been submitted in any form for another degree of diploma at any university or institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text.

Juliane Zeidler

Date

Abstract

Termites contribute greatly to the functioning of ecosystems. As effective soil modifiers and transformers of energy they are of particular importance in arid systems, adding to soil fertility and energy flow. Loss of biodiversity is a world-wide concern and loss of termite genera, as well as changes in generic distribution and composition of termite communities, may impair ecosystem health. The question is whether climatic variability and/or changes in land-use affect termite communities. In this study, based on the data of the Namibian National Survey of Isoptera which was conducted between 1964 and 1968, the distributions of termite genera were mapped using a Geographic Information System. Distribution maps of generic richness, as well as of guilds based on feeding and nesting characteristics, have now been derived for Namibia using the above data. Distinct distribution patterns of individual genera as well as guilds are discernible. In order to ascertain whether termite community patterns would possibly alter in relation to climatic change, relationships between rainfall and the distribution of individual termite genera were established. It was found that individual genera show distinct associations with rainfall. Four genera recorded from Namibia show a negative association with increasing rainfall, while 22 genera are positively associated. Generic richness increased with increasing rainfall. The comparison of two rainfall models derived for the periods 1952-'67 and 1978-'93 shows that average rainfall in Namibia has declined over the past decades. The possible implications of such changes for termite distribution patterns are hypothesised. Continuous studies of termite ecology are important both scientifically and for the future welfare of arid ecosystems and human environments in Africa.

Acknowledgements

I want to thank my supervisors and mentors Shirley Hanrahan, Mary Seely and Mary Scholes for their guidance and generous support throughout this project.

Many of the skills and ideas I had for this study evolved during the class work module of the Resource Conservation Biology course at Wits. I want to thank all lectures involved for a most stimulating academic experience.

The data of the National Survey of the Isoptera (1963-68) were made available by the Plant Protection Research Institute, Agricultural Research Council, Pretoria, South Africa. G. Prinsloo and Vivienne Uis are to be thanked in particular for all their support.

Alois Rwiyegura assisted with the computerisation of this overwhelming set of data.

Climatic data were provided by the Weather Bureau Windhoek, Ministry of Transport and Communication, Namibia. Ben Strohbach, National Botanical Institute, Ministry of Agriculture, Water and Rural Development, provided the maps of vegetation types and vegetation cover in Namibia. Dorthe Holme, National Remote Sensing Centre, Ministry of Environment and Tourism, Namibia provided several GIS ARC/INFO maps which were not incorporated into this study.

At an early stage of my project I had the opportunity to discuss some of my ideas with termite experts and ecologists from around the world. I am particularly grateful to J. Anderson, University of Exeter, UK, for reading my proposal and providing insightful criticism. I have J. Holt, CSIRO, Townsville, Australia, D. Bignell, Queen Mary and Westfield College, London, UK and P. Eggleton, Natural History Museum, London, UK, to thank for their stimulating discussions and criticism. Pep Canadell and Dave Ward have advised throughout my project.

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Simon Mason from the Climatological Group at Wits advised me on my rainfall models.

Jacky Galpin, Department of Statistics and Actuarial Science, Wits, helped with some of the statistics. John Mansfield checked on the logistic regressions.

John Palett took on the daunting task of correcting a German lady's termite talk.

The Desert Research Foundation of Namibia, and particularly Mary Seely and Joh Henschel, have provided great support throughout my studies and this project.

I have to thank the Ministry of Environment and Tourism, Namibia, for permission to stay in the Namib-Naukluft Park.

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Foreword

Namibia, the most arid country in sub-Saharan Africa, depends strongly upon its natural resources. Agriculture is one of the largest income earners of the economy, directly supports many households. However, due to the harsh climatic conditions, characterised by low and variable rainfall, the country has a generally low and extremely variable carrying capacity. Increasing human pressure on the natural resources, aggravated by these conditions, make the environment susceptible to land degradation.

In 1994, following the Conference on Environment and Development (UNCED) held in Rio de Janeiro in 1992, Namibia signed the International Convention to Combat Desertification as well as the International Convention on Biodiversity, and dedicated itself to addressing these environmental issues on a nation-wide level. National programmes are now established which aim to implement the objectives of these conventions, incorporating research programmes on natural resource conservation. One of these, Namibia's Programme to Combat Desertification (NAPCOD), is a collaborative effort between the Ministry of Agriculture, Water and Rural Development, the Ministry of the Environment and Tourism and the Desert Research Foundation of Namibia. The programme takes a multifaceted approach to the issue, combining research on the biophysical and socio-economic aspects of desertification with research on policy constraints. It aims to translate scientific information into sound management policies which will contribute to the welfare of Namibians, and to broaden environmental awareness and understanding throughout the country.

Amongst the many topics that relate to natural resource conservation, the maintenance and management of healthy soil systems deserves particular attention. Soil fertility directly affects the productivity of agricultural systems, including crop and animal husbandry and forestry. It thus forms one of the main links to food security, economic yield and finally, rural development. It is in this context that soil biota are important to ecosystem functioning. As part of the research component of Namibia's Programme to Combat Desertification, the present MSc research aims to examine termite functional groups in Namibia and termite genera spatial distribution.

1. Introduction

1.1 Literature

1.1.1 The role of soil biota in ecosystems

Soil biota are recognised key actors in maintaining and improving soil characteristics such as nutrient status, organic matter stabilisation and water balance, and protecting against processes such as leaching and erosion (Lee & Wood, 1971; Anderson, 1988). Generally soil micro-, meso- and macrofauna modulate the chemical and physical attributes of soil through mechanical and physiological processes, ultimately contributing to soil fertility and ecosystem productivity. Some soil organisms impact such biogeochemical processes more than others (Anderson, 1994). The diversity and composition of soil biotic communities and their associated functions varies within and between ecosystems and may shift under changing land-use regimes (Swift & Anderson, 1993; Anderson, 1994). This is of particular relevance to desertification. Similarly, environmental fluctuations, induced for example by global climate change or pollution, may alter naturally established soil biotic structures (e.g. Whitford, 1992). Whether such impacts impair the functioning of the soil system needs to be critically assessed (e.g. Naeem *et al.*, 1994).

1.1.2 The role of termites in ecosystems

Termites are usually regarded as pests of crops, trees, and buildings, and farmers actively eliminate them from their fields and pastures (e.g. Hartwig, 1965; Wood *et al.*, 1980; Logan *et al.*, 1990; Logan, 1991; Logan, 1992). However, not all termite taxa have pest status, and in fact, termites are known to positively affect ecosystem productivity (e.g. Lee & Wood, 1971; Deshmukh, 1989; Whitford, 1991). Because of their interactions with their habitat, termites are often referred to as 'ecosystem engineers' because they change the availability of resources, by causing physical state changes in biotic and abiotic materials (Jones *et al.*, 1994). This is well demonstrated by Wood & Sands (1978) who summarise the role of termites in ecosystems. They distinguish two main categories of habitat modification caused by termites: (1) the alteration of soil and vegetation parameters through activities such as feeding, nesting and burrowing, and (2) their contribution to energy flows in ecosystems, related to the termites' production ecology. In the following paragraphs a review of the effects of termites on ecosystems is given, based on the more recent termite literature.

It has been suggested that termites play a major role as soil organisms in arid Namibian ecosystems, contributing to processes such as decomposition, particularly during dry periods when most other soil organisms are inactive (Crawford, 1981; Crawford *et al.*, 1993; Crawford & Seely, 1994). Drawing from studies that were conducted in semi-arid savannas in Nigeria, Kenya, Zimbabwe and South Africa, it can be anticipated that the biological, chemical and physical processes mediated by termites are also significant in these relatively dry African ecosystems (Wood & Sands, 1978; Deshmukh, 1989).

Termites affect soil physical parameters and process rates through, for example, the distribution and breakdown of soil organic matter, the alteration of soil nutrient composition and changes in soil texture. Studies on the composition of mound and gallery systems of various representatives of Macrotermitinae in semi-arid regions in Kenya (Arshad, 1981; Arshad, 1982; Bagine, 1984; Darlington, 1982), South Africa (Griffioen & O'Connor, 1990) and Zimbabwe (Watson, 1976) and *Trinervitermes* from South Africa (Laker *et al.*, 1982), for example, show that fine grained soil particles as well as exchangeable cations, nitrogen and occasionally organic carbon are accumulated in termite mounds. This suggests that important constituents contributing to soil fertility are amassed in termite structures. Griffioen and O'Connor (1990) also show that a distinct herbaceous flora is associated with the soils of termitaria. However, based on her studies carried out on the Macrotermitinae in Tanzania, Jones (1990) hypothesises that these termites contribute little to carbon, nitrogen and phosphorus accumulations in the soil. On the contrary, she suggests that soil organic matter is removed from soil and accumulated in termitaria, thereby reducing the organic matter content of dry tropical soils. A lack of organic matter dispersion through the soil would lead to high erodibility and poor nutrient- and water-holding capacities of soils, and thus to their impoverishment.

Summarising results from different publications addressing similar questions for the subterranean termite species *Gnathamitermes tubiformans* and *Amitermes* *wheeleri* in arid Northern American deserts, the most emphasised and measurable impacts of abundant termites were related to the translocation and fragmentation of organic matter (Whitford, 1991; MacKay *et al.*, 1994). Schaefer & Whitford (1981) as well as Parker *et al.* (1982) show that nitrogen increases in plots from which termites were excluded, and they interpret this as termites depleting soil nitrogen reserves. Elkins *et al.* (1986) found that water infiltration and retention capacities were improved through enrichment of organic matter in the soil, accumulation of fine grained soil particles such as clay, and better drainage due to extensive subterranean gallery systems. However, given the variety of functional groups in termites it can be expected that the nature and magnitude of their impacts are rather variable. Also are the complex interactions of termites, nutrients and water properties not easily separated, but exclusion of termites can definitely lead to changes in plant species composition and differences in vegetation performance (MacKay *et al.*, 1990). For example, an abundant annual grass species disappeared from treatment plots without termites. The phenology of several plant species was also negatively affected by the extinction of termites.

When trying to assess the impact of termites on ecosystems it is important to consider their role as primary consumers, secondary producers and as agents of transformation within the system. In African savannas total termite biomass can outnumber large mammal herbivore biomass (Wood & Sands, 1978; Gandar, 1982). For Nylsvley, a South African savanna system, it was calculated that large mammal biomass was 6kg/ha, while termite biomass constituted 10kg/ha.

The annual consumption per unit of biomass was 50% greater in the termites compared to the large mammals (Gandar, 1982; Deshmukh, 1989). Other studies do not provide such pronounced results but certainly underline the notion that termites are important consumers in various African ecosystems (e.g. Wood & Sands, 1978).

It needs to be considered that biomass and consumption rate do not necessarily reflect the relative significance of different species of termites in production ecology. The efficiency with which individual termite taxa fix and return energy and nutrients to the ecosystem is of great interest. As for other herbivores, it is not only the quantity of forage material that determines a taxon's contributions to energy and nutrient flow in the ecosystem, but also the quality of the herbage ingested and the efficiency at which it is digested and allocated (e.g. Bignell, 1994; Bignell & Eggleton, 1995; Wood, 1978; Brian, 1978).

Eggleton & Bignell (1995) warn that termites have high rates of species turnover across relatively short biogeographical distances and that taxonomic differences may radically alter ecological patterns. However, there is indeed a vigorous debate on whether species turnover at regional scales impairs the functioning of the ecosystem (Lawton *et al*, 1996; Lawton & Brown, 1993). Therefore comparisons of termite assemblages in different habitats across biogeographical regions need to be interpreted with caution.

1.1.3 Functional group concept

It is virtually impossible to assess each single termite species' significance in the functioning of an ecosystem. The functional group and guild concepts have been discussed in the literature by e.g. Simberloff & Dayon (1991) and the use of these terms remains often unclear and need closer definition. For this study the classification of taxa into broad and provisional functional groups seems to be a practical approach, allowing for a qualitative categorisation rather than a purely taxonomic one. Based on the concept that termites play a role in energy transfers in ecosystems, a classification into functional groups based on feeding characteristics seems to be justified. Feeding groups such as soil-, wood-, litter- and mixed-feeders as well as fungus-growers can be distinguished (e.g. Wood & Sands, 1978; Eggleton *et al.*, 1995). In order to fully assess the functional significance of termites in ecosystems, their impacts on soil properties should also be included. However, such a classification is complicated by the lack of knowledge particularly of the termite´s nutritional ecology.

The Macrotermitinae, the fungus growing termites, are generally found to be the most effective consuming and producing taxa occurring in Africa (Wood & Sands, 1978; Deshmukh, 1989). Whether they contribute to physical modification of the soil environment is yet to be determined. Most species are mainly mound-builders but a few also nest below-ground, particularly in the juvenile phase of the colony (Abe & Darlington, 1985). It could be hypothesised that hypogeal (subterranean) taxa are more important in the alteration of soil physical and chemical properties than epigeal (above-surface) termites. Their gallery and nesting systems, for example, extend over large areas and into great depth, forming drainage channels through the soil surface, improving the areation of soils as well as water infiltration (Anderson, 1988). However, which taxa are more important in maintaining ecosystem processes remains unclear. Clearly the impacts of individual termite taxa differ, and certain taxa or functional groups have more impact than others (e.g. Anderson, 1994).

1.1.4 Loss of biodiversity

Of major concern is that most ecosystems are currently experiencing a loss of biodiversity. This has primarily been attributed to human-related activities such as intensified land-use, pollution and global climate change, although the latter may also arise from natural climatic variability. One of the main discussions evolves around the question of whether the loss of particular species and/or a change in community composition disturbs or possibly interrupts crucial biogeochemical processes, possibly leading to an impoverishment of ecosystem functioning and performance (e.g. Naeem *et al.*, 1994). Considering the role of termites in ecosystems, it is most relevant to assess what environmental conditions determine their distribution, how different termite taxa react towards environmental change and what the consequences of such changes would be for ecosystem functioning.

1.1.5 Limitations of termite ecological studies

In order to assess changes in biotic communities, before and after data are required and long-term monitoring programmes need to be established. Studying termites is more labour-intensive than for most insect groups. Their diversity of habitats demands intensive sampling to reliably determine the taxon richness in an area. Ecological termite studies and field experiments are difficult to undertake, and the resulting data hard to interpret, because it is almost impossible to define exact limits of individual colonies. This also applies to measuring their impacts on ecosystems and to comparing results between biogeographic regions (Eggleton & Bignell, 1995).

1.1.6 The Namibian context

Termite research conducted in southern Africa to date lacks the functional context. However, some good inventory data on termite taxonomy and biogeographic distribution of single genera are available, which can be used in a more contemporary research context. The National Survey of the Isoptera of South Africa was initiated in 1958 and later expanded to neighbouring countries such as Namibia, Botswana, Zimbabwe and Mozambique. Under the auspices of the Agricultural Research Council of South Africa, termite taxonomists W.G.H. Coaton, J.L. Sheasby and collaborators sampled these regions thoroughly to assess the richness and distribution of termite taxa across southern Africa. The full collection represents one of the most intensive efforts of its kind in the world and numerous publications arose from these surveys. The study covered descriptions of new species and genera, some observational data on the natural history and biology of the resident taxa, as well as distribution maps.

These historic data can be used in various ways, underpinning current research efforts. Firstly, they can serve as a reference to the richness of genera about 30 years ago, which can be compared to what is found today, thus providing a valuable measure of change. Secondly, parameters determining the distribution of genera can be delineated through the re-analysis of these historic data in relation to environmental data, and models can be developed predicting distribution patterns today, to be confirmed in the future. Thirdly, the distribution data of taxonomic groups can be compiled for functional classes, providing a useful background for a qualitative interpretation of the biogeographic patterns.

The present MSc project aims to establish a baseline for a functionally orientated approach towards termite ecological research in Namibia. It forms the basis for a planned PhD study which will identify the properties of selected termite taxa that could be used as indicators for habitat condition assessment in Namibian rangelands, specifically addressing questions related to land-use change. The work presented in the following report is based on the National Survey of the Isoptera conducted throughout Namibia between 1963 and 1968. No additional data were collected. In chapter one the distribution data available for the individual termite genera is displayed and interpreted in a process orientated approach, grouping taxa according to feeding and nesting characteristics. Such a classification is based on extremely superficial field notes and data available from the literature. Chapter two investigates the relation of rainfall to the richness of termite genera and to their distribution. Predictions of change in termite distribution are made on the basis of alterations of rainfall patterns in Namibia.

1.2. Objectives & Key questions

(1) To investigate and re-analyse the data of the National Survey of the Isoptera (1964-68) with the following questions in mind.

(a) What is the spatial distribution pattern of termite generic richness in Namibia?

(b) What is the nature of the spatial distribution of termite functional guilds?

(2) To examine the relationship between the spatial distribution of termites and rainfall in Namibia.

(a) Have rainfall regimes over Namibia changed over a thirty year period?

(b) Is termite generic richness related to rainfall?

(c) Are there relationships between rainfall patterns and the distribution of individual termite genera?

2. Chapter 1

The Namibian National Survey of the Isoptera (1964-68) revisited

2.1 Introduction

Coaton & Sheasby (1972) published a thorough report on the National Survey of the Isoptera which was conducted throughout Namibia between 1964-68. In their publication detailed distribution maps of each of the 33 genera present are provided, as well as descriptions of their feeding and nesting habits. Some basic background information on the Namibian environment and its different ecosystems, in the form of vegetation, rainfall and topographic maps for example, are included in the report. The focus of the survey was to establish an inventory of termite taxa present in the area and to roughly assess their pest status. Since the resulting information was thorough and considered to be reliable (Ruelle, 1978), changes in genera/species distribution and composition in a spatial context can be assessed over the 30 year period. Relevant information from the historic data base can be extracted and, through subsequent sampling in future studies, such data can be compared to the situation today. There are some general draw-backs to the sixties' data, the most relevant being that only the presence of taxa were recorded, not their absence or abundance. It is particularly the lack of absence recording that diminishes the robustness of the distribution data. However, the database allows the determination of larger-scale biogeographic patterns of termite genera distribution, and by applying modern mapping tools, multi-dimensional display and analysis of the data are possible.

The primary objective of this chapter is to re-analyse the historic data from the National Survey of the Isoptera. Using a Geographic Information System, namely IDRISI for Windows (Clark University, 1995), maps composed of several layers of data were created, generating distribution maps such as of generic richness and functional groups. From these maps databases were derived and processed in a spreadsheet programme. Biological information was supplemented by a review of the Namibian termite literature and functional attributes, such as feeding and nesting habits are summarised for each termite genus present.

2.2. Methods

2.2.1 Spatial analysis of National Survey of the Isoptera (1964-68)

The original data of the National Survey of the Isoptera from Namibia collected by Coaton and collaborators were computerised in the scope of this study. All samples collected during the survey, running from September 1964 to May 1967 as well as data from two shorter-term sampling events conducted in 1967 and 1968, were included. Termite taxa presence was recorded by Coaton *et al.* along the public roads throughout Namibia in 16 km intervals and the geographic coordinates were noted down. In the present analysis termite genera occurrence is mapped on a quarter degree grid scale. Duplicate records for the same genus found at one grid square sampling point were summarised as "genus present". This resulted in a reduction of the total of 714 collecting stations to 483 quarter degree grid squares sampled. Three-thousand-five-hundered-ninty-two individual genus occurrence records were noted within the grid defining the borders of Namibia (11°45'E/16°45'S, 25°30'E/29°00'S), excluding the Caprivi Strip.

The termite presence data for each individual genus were imported from the database into the raster-based GIS IDRISI. In GISraster based geographical information of various factors can be overlayed, achieving a composite map of interactions. Thus to obtain for example the map of generic richness, all single genus maps were added in an overlay procedure. Maps on the distribution of individual termite genera, as well as of generic richness and feeding and nesting guilds were created in that manner, based on the original point data. A surface model predicting generic richness throughout Namibia was developed, assuming that termites were abundant throughout the country, thus a minimum of one genus would be present in each grid square. A nearest neighbourhood interpolation model was chosen to fit the data. For further analysis only the original point data were used. Graphs depicting the proportional presence of termite taxa and guilds in 483 quarter degree grid squares were derived off the maps and exported into a spreadsheet programme for visual display.

2.2.2 Assessment of functional attributes of termite genera occurring in Namibia

Information on functional attributes, i.e. feeding and nesting habits, of the Namibian termites were synthesised from the literature and used to classify all genera into functional groups.

2.3. Results

2.3.1 Distribution of generic richness

The composite map of termite generic richness based on the original data obtained from 483 sampling sites is displayed in Figure 2.1. The results of the descriptive statistical procedures are displayed in the associated histogram (Figure 2.3). From the histogram it is apparent that at all sampling sites a minimum of one termite genus was found. Six percent of all sampling squares were inhabited by a single genus only. Generic richness ranged from one to 19 genera, the maximum observed at a single location in the Okavango region in north-eastern Namibia. The mean number of genera present per grid square was seven. Visual examination of the original data map as well as of the interpolation model (Figure 2.2) suggest that generic richness was highest in northern Namibia. A declining gradient from north-eastern Namibia towards the south-western border is apparent. High generic richness was recorded in additional areas in northern Namibia, one being situated in the northern

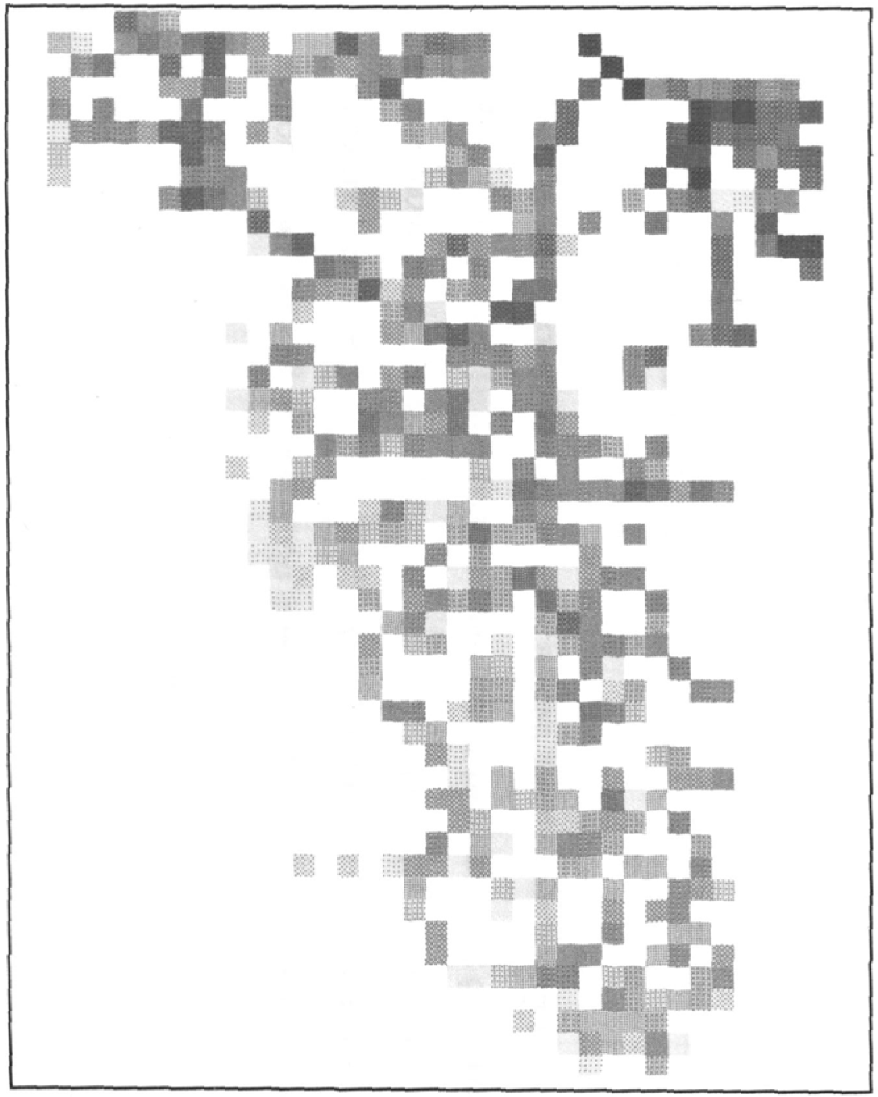


Figure 2.1: Termite genera richness within 483 sampling grids throughout Namibia. *Original data from theNational Survey of the Isoptera, conducted 1963-67 (Coaton & Sheasby, 1972). The grid cell carrying the higest number of genera is marked in red (19). The darkest green represents 18 genera. Presence of a single genus is indicated by a light yellow square. Numbers found increase with increasing green value.*

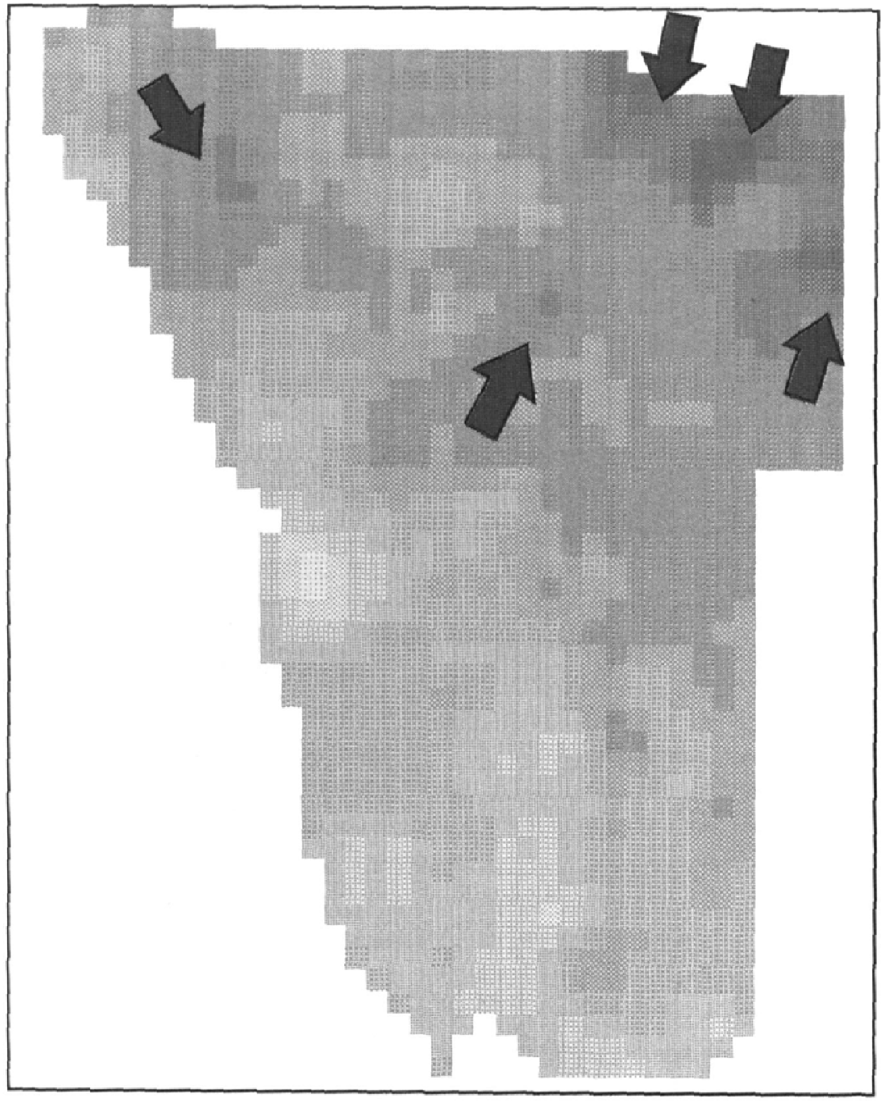


Figure 2.2: Surface interpolation model of termite genera richness. *The arrows indicate regions in darker green colour shading, being comparatively genera rich. Areas marked in yellow colour shading indicate low numbers of genera present.*

Kunene region, the others in north-western Otjozondjupa and south-eastern Oshikoto regions.

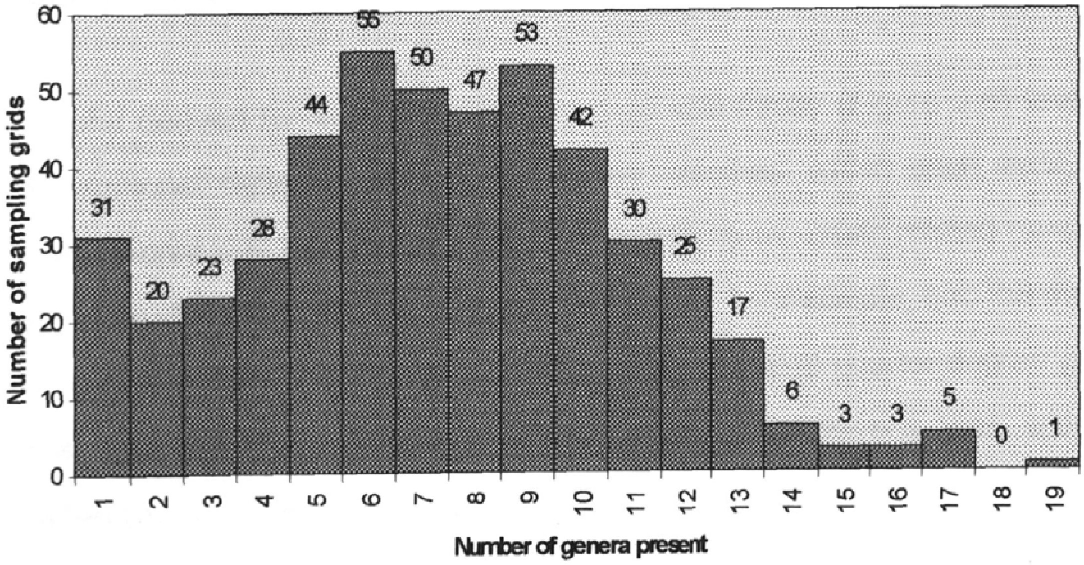


Figure 2.3: Number of genera recorded from 483 sampling grids from the National Survey of the Isoptera (1963-68).

2.3.2 Distribution patterns of taxonomic groups

Genera were not evenly distributed across the 483 sampling stations (Figure 2.3). On average seven genera were found per sampling grid. The absolute maximum recorded was 19. The graph in Figure 2.4 shows the proportional presence of each genus at all 483 sampling stations. Six genera were found at more than 50% of all sampling stations. The genus *Hodotermes* had the widest distribution, being present at 84.3% of the sampling sites, followed by *Amitermes* (70.2%), *Microcerotermes* (63.4%), *Psammotermes* (60%), *Trinervitermes* (54.2%) and *Odontotermes* (52.4%). In contrast, 14 genera were found at less than 5% of all sampling sites.

The graphs derived for sub-family (Figure 2.5) and family (Figure 2.6) levels reveal additional patterns. Among the 'lower' termites, within each family it was always only one genus that was more widespread, other related genera being of subsidiary importance. The Kalotermitinae, for example, had the most restricted distribution, being present at 35% of all sampled quarter degree grid squares. Of the four genera recorded, only *Epicalotermes* was widely distributed (33.5%), the remaining genera having only limited distribution. The Hodotermitidae include two genera, which, when combined, were present at an overwhelming 86% of all sampling grids. Here the genus *Hodotermes* made up for 84.3% of the records, representing the most widely distributed termite genus in Namibia. The related *Microhodotermes* was very limited in its range, being found in only 3.7% of the sampling area, and being restricted in its distribution to the south of Namibia. With an overall proportional distribution of 61%, the Rhinotermitidae, including its three sub-families and genera, were the third most widely distributed termite family. Again, one single genus, *Psammotermes*, was present throughout large areas (60%).

A very different pattern can be detected amongst the Termitidae, referred to as the 'higher' termites. This family is characterised by high generic richness, comprising 23 genera in four sub-families. Members of this family inhabited

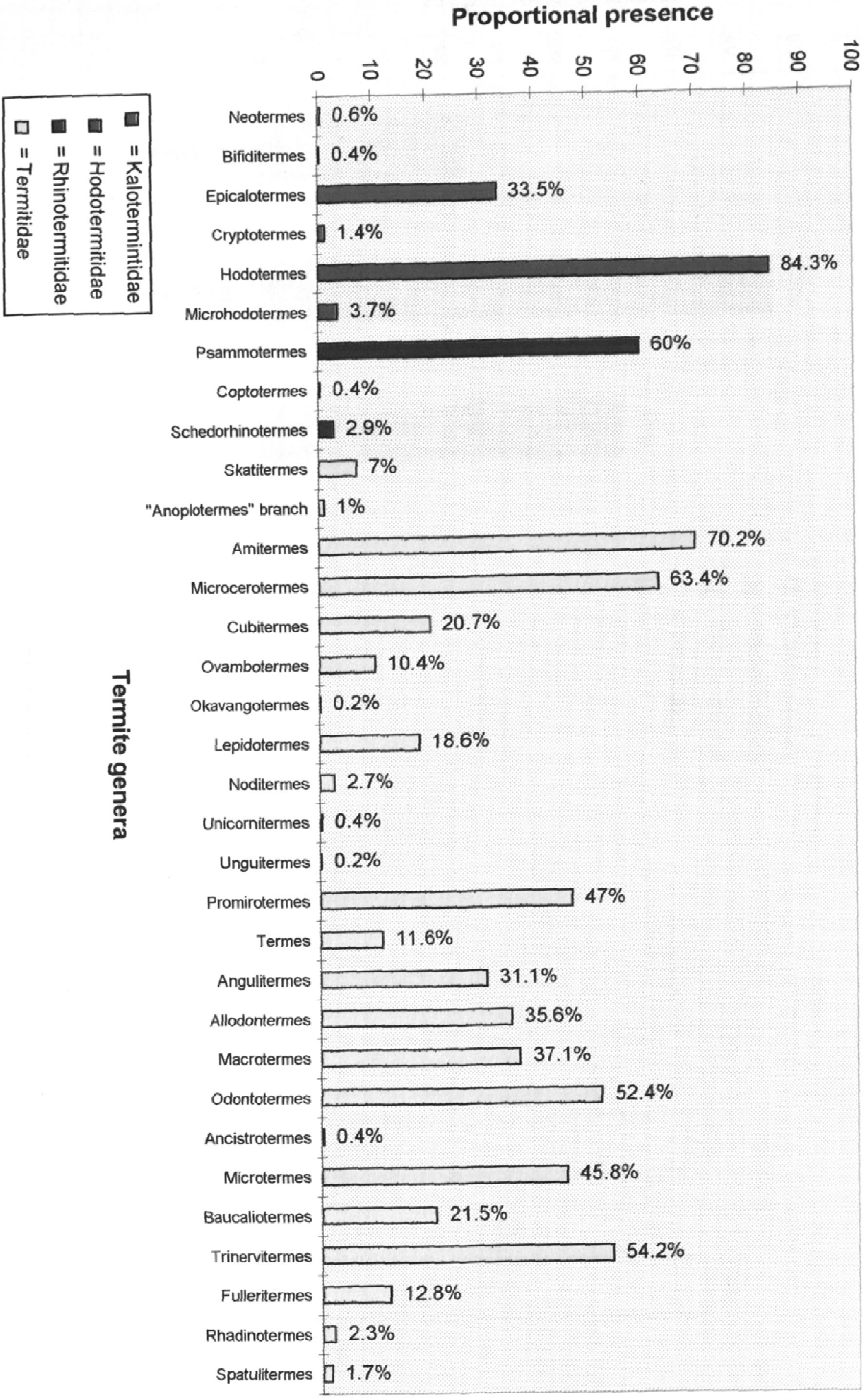


Figure 2.4: Distribution of **genera** among 483 sampling stations throughout Namibia. *Data from National Survey of the Isoptera, 1963-68.*

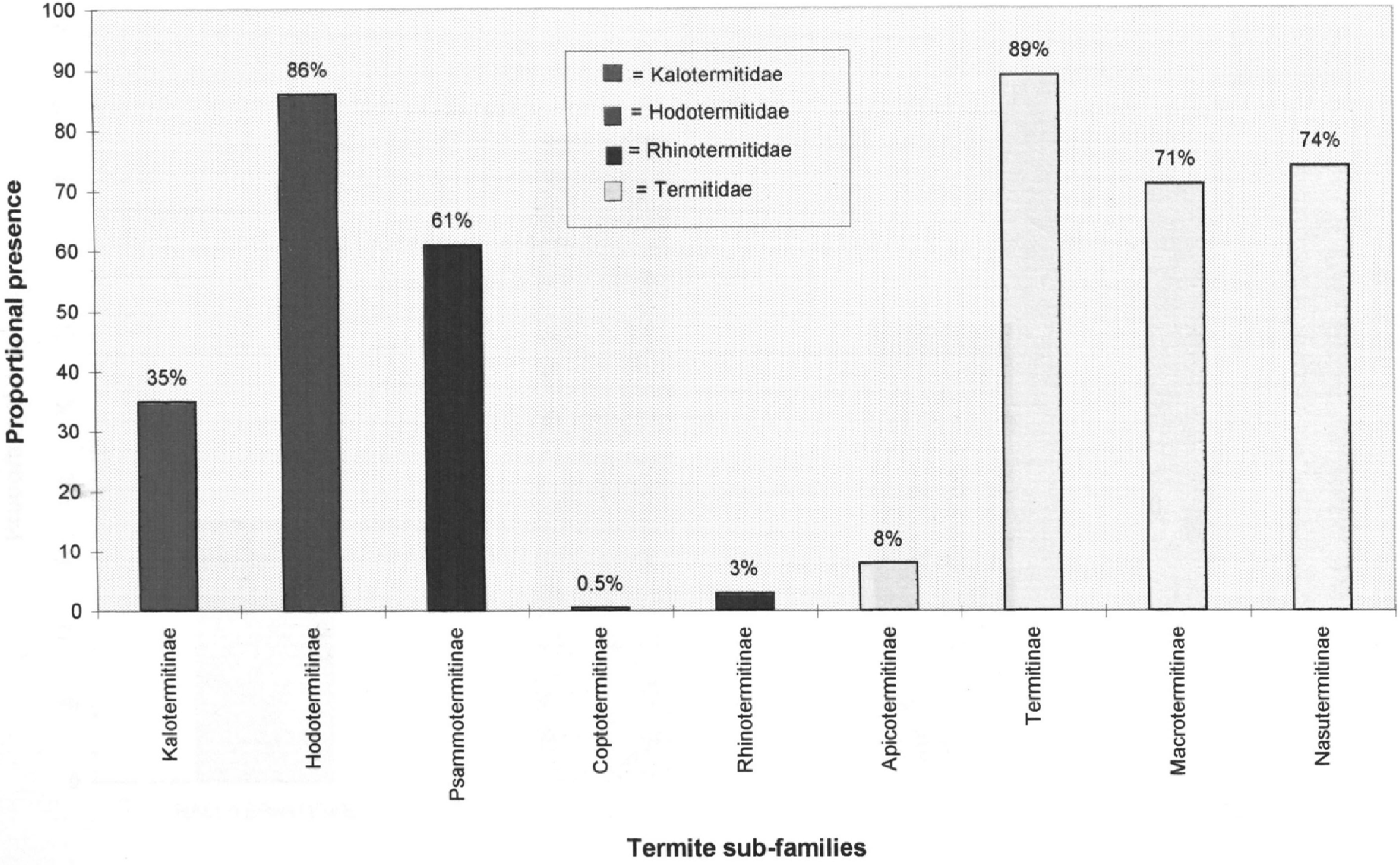


Figure 2.5: Distribution of **sub-families** among 483 sampling stations throughout Namibia. *Data from National Survey of the Isoptera, 1963-68. The color scheme indicates sub-families belonging to the same family.*

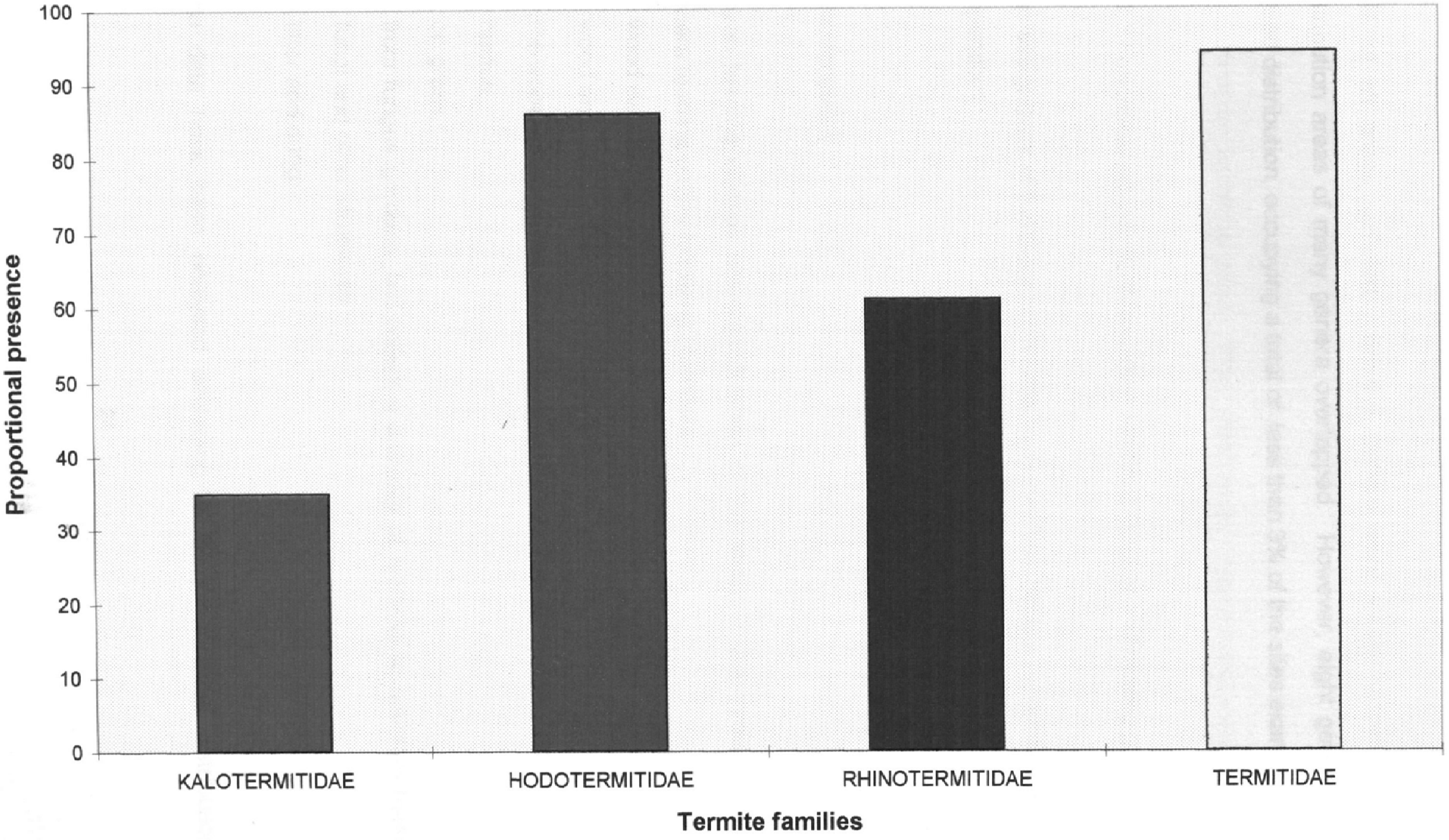


Figure 2.6: Distribution of **families** among 483 sampling stations throughout Namibia. *Data from National Survey of the Isoptera, 1963-68.*

94% of all areas sampled. Several genera were widely dispersed and distribution areas of many genera overlapped. However, eight genera had limited distribution, occupying a total of less than 3% of the sites examined.

2.3.3 *Functional attributes of Namibian termites: feeding and nesting groups*

The assignment of functional attributes to the various genera is represented in Appendix 1.

Feeding guilds

Seven feeding classes are distinguished in this study. These group termite genera feeding on the following materials

- wood exclusively,
- wood and litter,
- the wood/soil interface,
- humus,
- on grass,
- from fungus gardens, but collect a diversity of material to maintain these fungi and other structures
- litter and dung.

The data have been analysed according to the proportional distribution displayed in Figure 2.7 and are mapped directly in Figure 2.8.

Wood feeding termites were most restricted in their range, occurring at only 35.6 % of all sampling sites. Their distribution concentrated along a band reaching from north to south throughout central Namibia and in the north-east, but they are generally excluded from the Kalahari and Namib Deserts. In most places only one genus was present. The guild is primarily formed by the Kalotermitidae, but two representatives of the Rhinotermitidae, *Coptotermes* and *Schedorhinotermes*, also fall into this group. The **wood/soil interface feeders** showed a considerably higher proportional presence (54.9%). Usually only one species that was present in each grid square. In contrast, the **wood and litter feeding termites** were widely distributed throughout Namibia, being found at 92.3% of all sampling stations. Most members of this group belong to the 'higher' termites, the Termitidae, with the exception of *Psammotermes*. In most places more than one genus were recorded. This was particularly evident for the more arid regions towards the south of Namibia, where up to four genera were present per grid square.

Humus feeding termites accounted for a proportional distribution of only 40%, although this group has the highest number of genera, including eight members of the Termitidae. Their distribution was scattered throughout Namibia, with mainly one to occasionally two genera being present in a grid square. Generic richness as well as proportional presence were high in the north-eastern corner of Namibia, in the Kavango region. Here up to six genera occurred in one grid square. The **grass feeding guild**, with 89%

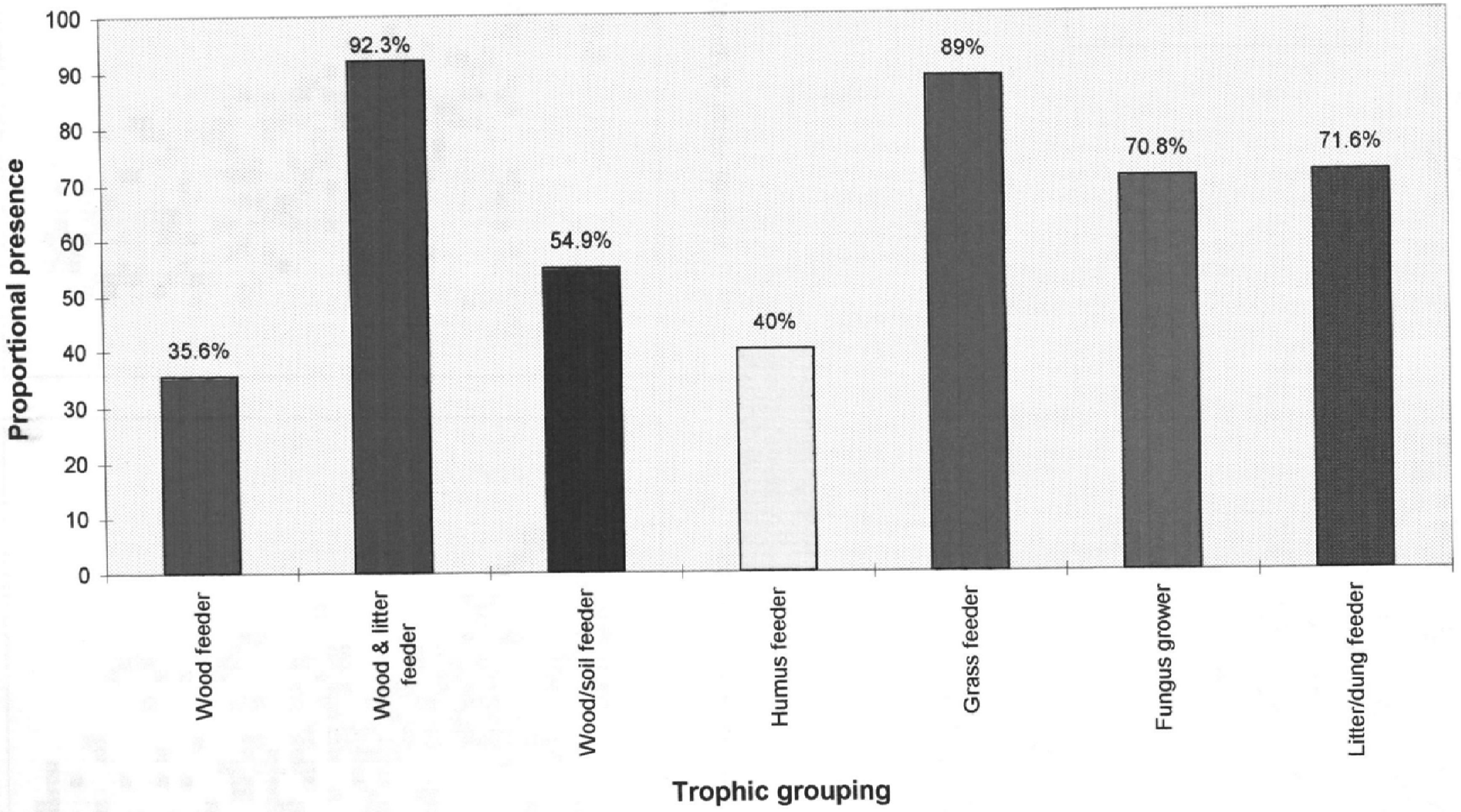


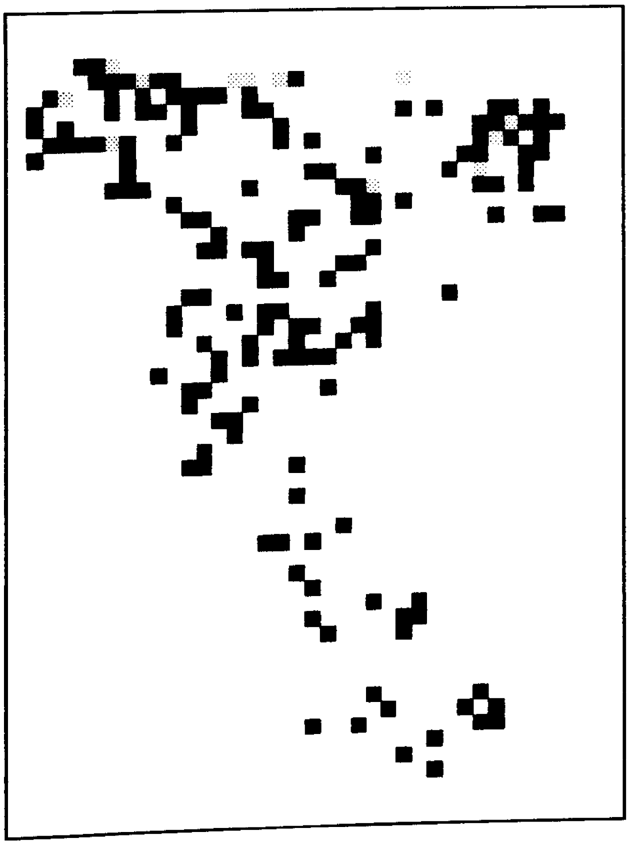
Figure 2.7: Distribution of **feeding guilds** among 483 sampling stations throughout Namibia. *Data from National Survey of the Isoptera 1963-68*

Figure 2.8: Distribution maps for the seven feeding guilds. *The color scheme indicates how many different genera were found in the respective grid square.*

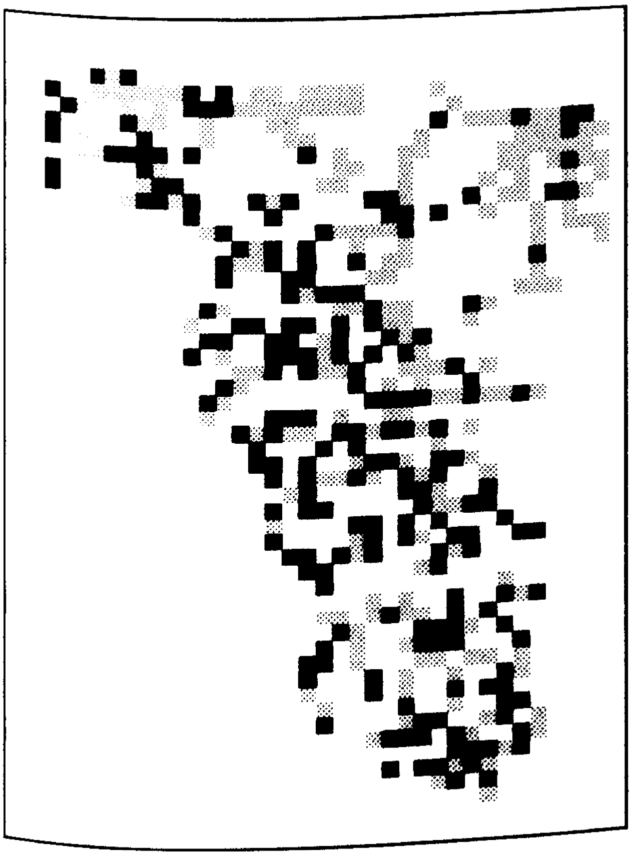
Legend:

■ = 1
□ = 2
■ = 3
▨ = 4
■ = 5
■ = 6

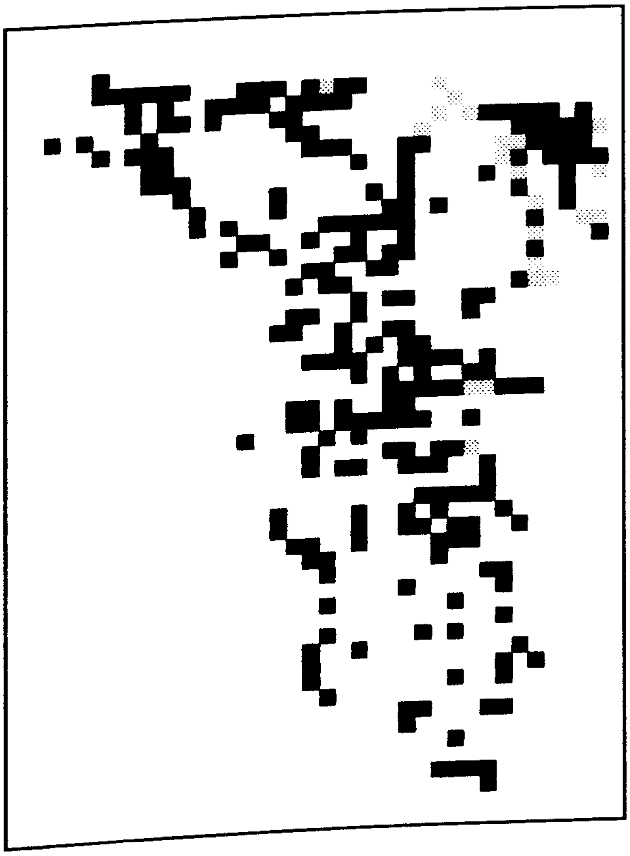
Wood feeder

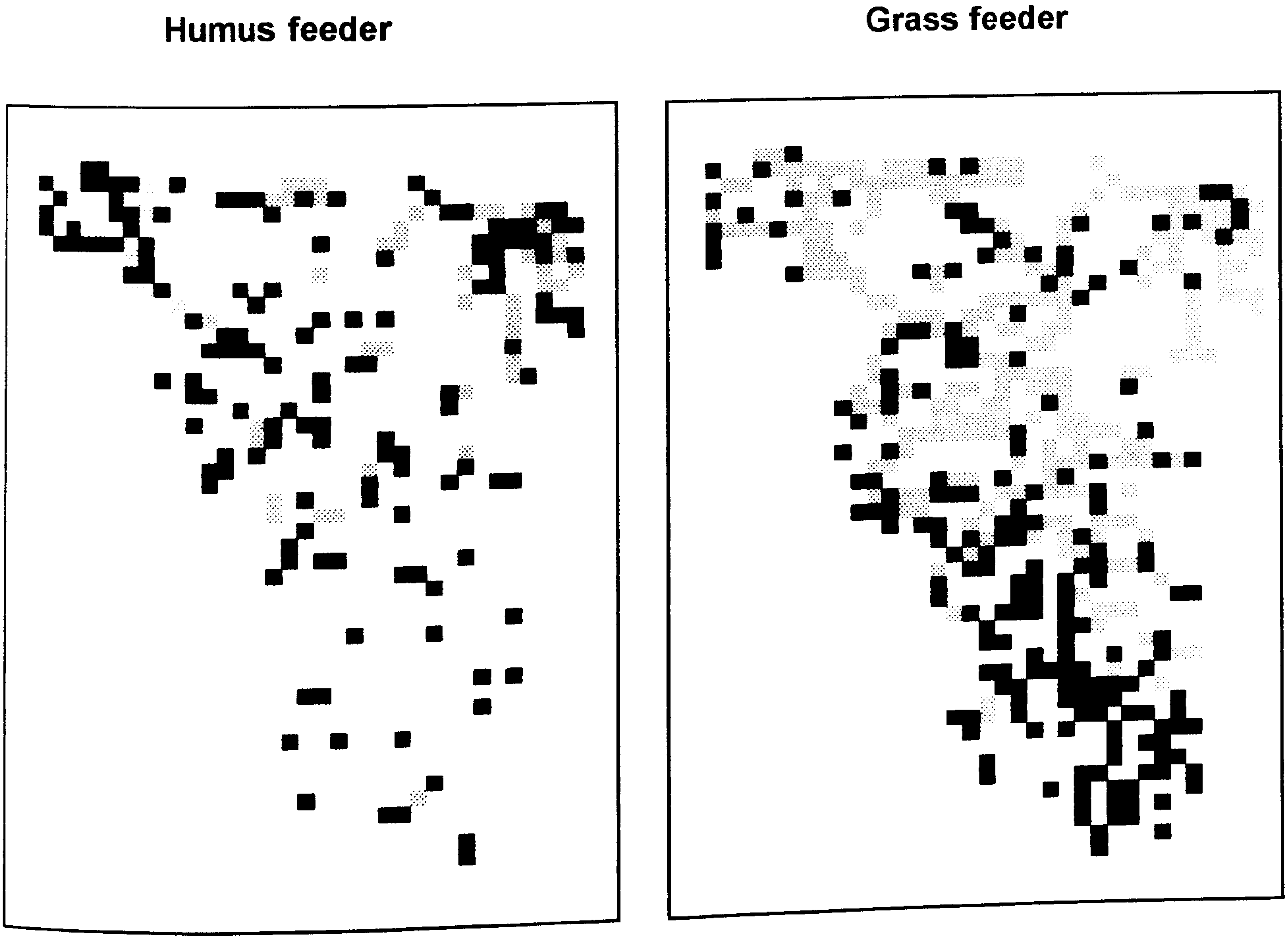


Wood- & litter feeder



Wood- & soil feeder





Fungus grower Litter & dung feeder

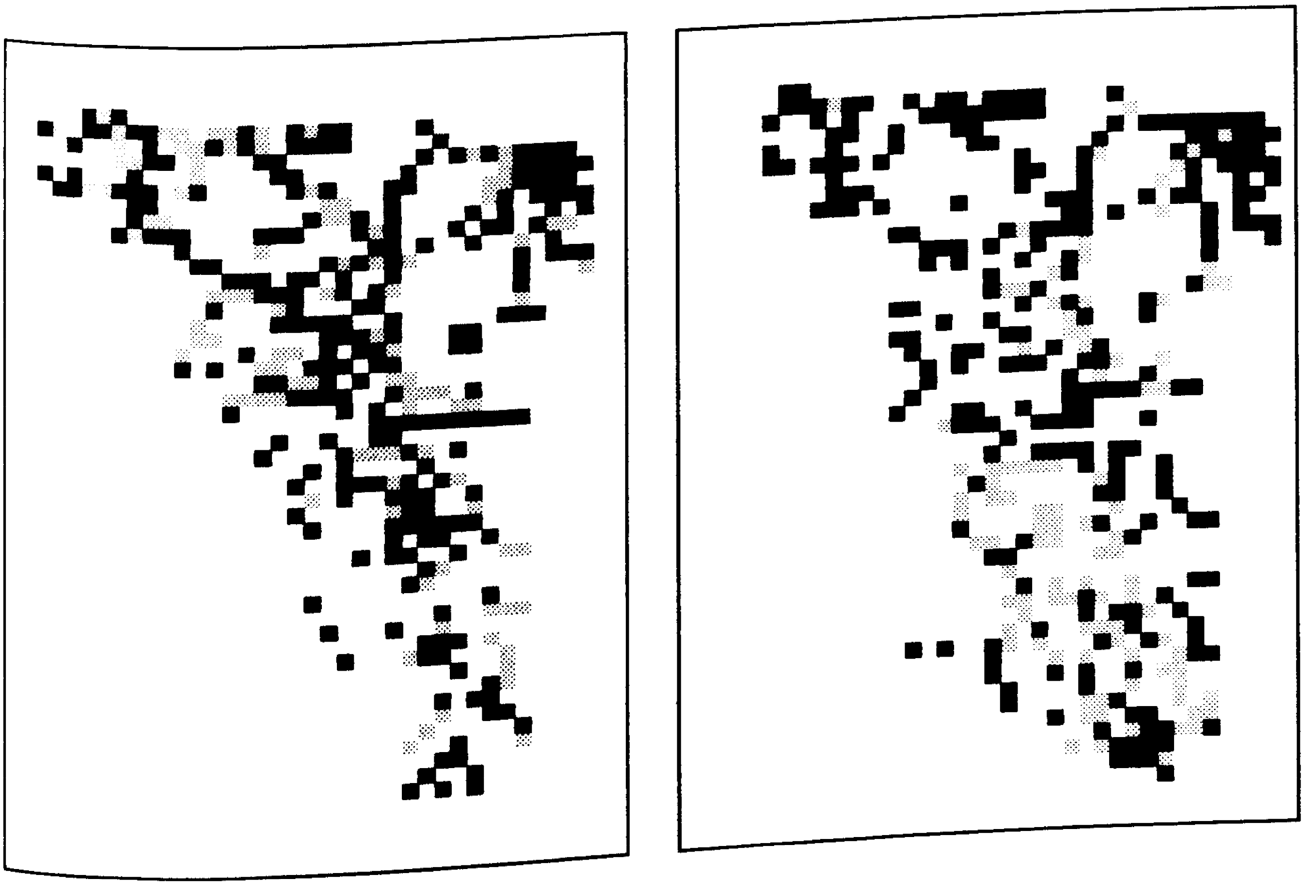


Figure 2.8 cont.

proportional presence was the second most widely distributed group. Only two genera fall within this class, namely *Hodotermes* and *Trinervitermes*, these two genera had similar distributions, except in southern areas of Namibia where *Trinervitermes* was excluded. All **fungus-growing termites** belong to the sub-family Macroterminae. The five genera which fall into this class occurred at 70.8% of all sampled areas, being relatively sparsely distributed in the more arid regions of Namibia, where only representatives of *Allodontermes* and *Microtermes* were found. *Odontotermes*, *Macrotermes* and *Ancistrotermes* were restricted to a more northerly range. Here often two to three fungus growing genera are found within the same grid square. The last feeding group to be considered is the **dung and litter feeders**, with an overall proportional distribution of 71.6%. Three genera, all from different sub-families, are grouped here. *Baucaliotermes* and *Microhodotermes* have their primary distribution in southern Namibia. *Skatitermes*, in contrast, only occurred in the north, inhabiting a very different area compared to the other two genera.

Nesting guilds

Three nesting guilds were defined (Figure 2.9),

- termites that build mounds (epigeal nesting structures),
- termites that are associated with arboreal structures, and
- termites that live in subterranean (hypogeal) constructions.

Data were analysed for nesting guilds in the same manner as for feeding groups (Figure2.10).

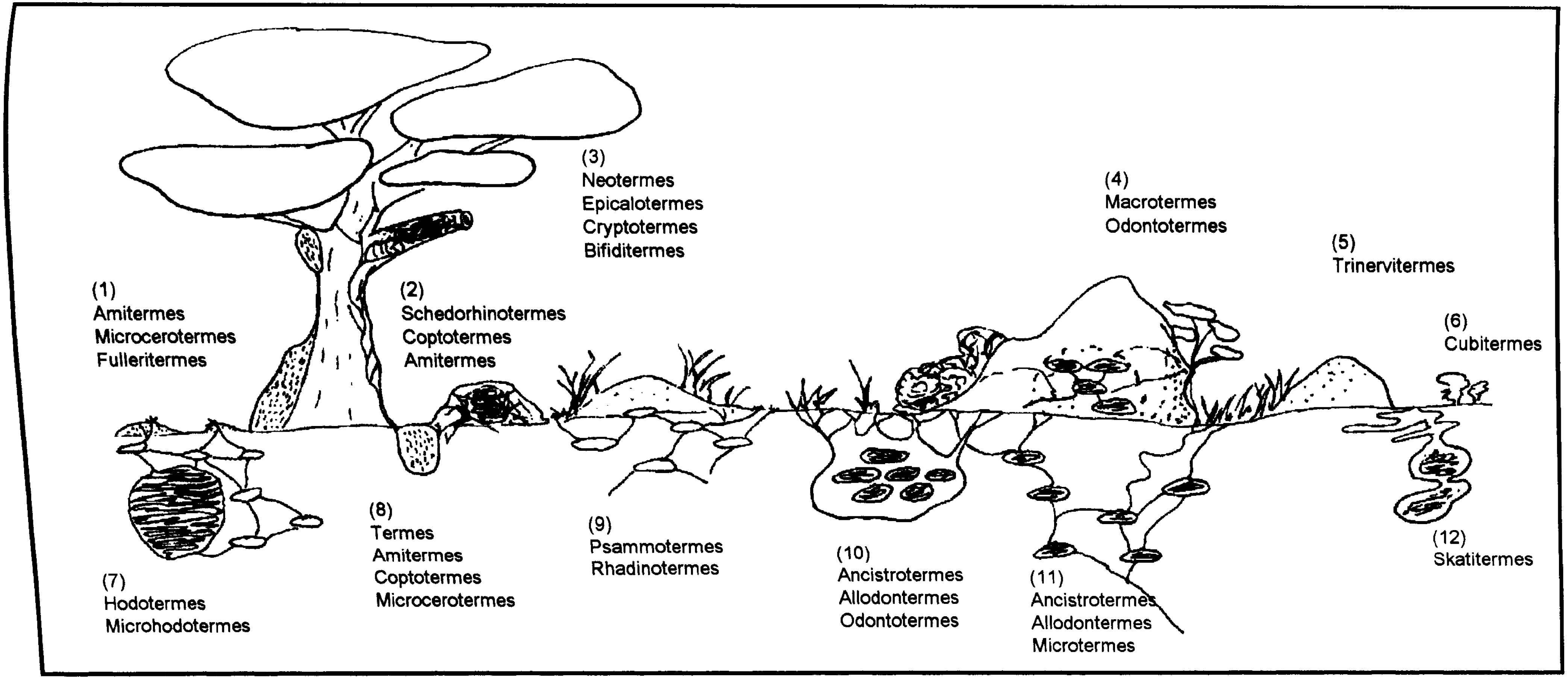


Figure 2.9: Main nesting structure and microhabitats inhabited by termite taxa occurring in Namibia. *Arboreal, epigeal and hypogeal nesting guilds are distinguished, separated into twelve categories. Some genera are named under several categories in this drawing. (1) Termites that attach their mounds to standing woody structures. Runways may be build throughout the canopy and on the ground. (2) Termites nesting within woody structures. (3) Termites nesting arboreal. They live entirely in (dead) woody structures and do not have contact with soils. (4) Fungus growing termites building large epigeal mounds. (5) and (6) Termites building smaller epigeal mound structures. (7) Termites building hypogeal nesting structures with large carton combs. (8) Termites building hypogeal structures with runways that may extend outside of epigeal wooden structures. (9) Termites maintaining extensive hypogeal gallery systems with many foraging and nesting chambers, often extending into epigeal mound structures. (10) Fungus growing termites that maintain hypogeal "mounds" housing the fungus combs. (11) Fungus growing termites maintaining extended hypogeal gallery systems with several dispersed fungus combs. (12) Termites building extended hypogeal combs.*

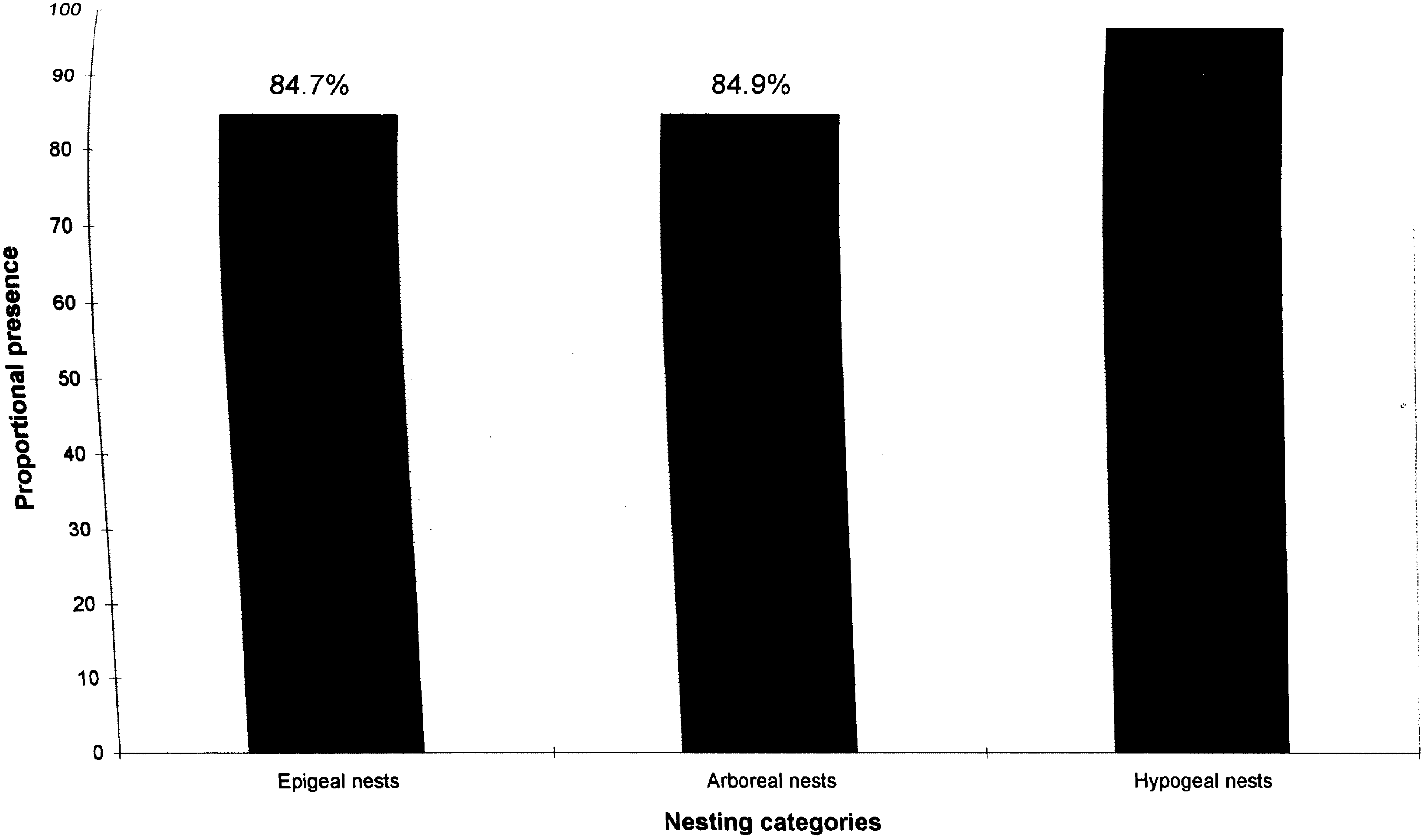


Figure 2.10: Distribution of **nesting guilds** among 483 sampling stations throughout Namibia. *Data from National Survey of the Isoptera 1963-68*

All three nesting strategies were widely distributed over Namibia. Epigeal and arboreal genera occurred in about 85% of all sampled areas, and hypogeal genera were found at 97,5% of all sites. Only five genera build mounds, whereas 16 genera live in subterranean nests.

2.4. Discussion

2.4.1 Reliability of the survey data

Sampling was conducted in a more or less arbitrary way, by researchers venturing out from a fixed point for a defined time period. Potential termite habitats were searched, but no standardised sampling methods were applied. It is possible that rare termite species, these living in more obscure places may have been neglected or underestimated. It has been suggested (Eggleton, pers. com.) that specifically subterranean, soil-feeding species would be under-represented by this sampling procedure. An additional drawback to the survey data is that seasonality as well as diurnality of termite activity were not fully accounted for, again underestimating termite generic richness as well as providing inaccurate distribution patterns. Again it is to be stressed that unfortunately no abundance data were collected. Taxonomic classification is reliable, although various taxonomic groups may be revised in future (Uis, pers. com.).

2.4.2 The higher taxon approach

Usually, species richness per unit area is used as a measure for conservation purposes. Gaston & Williams (1993) suggest that the number of higher taxa of biota present in an area is directly related to species richness. Eggleton *et al.* (1996) established such a relationship for termites, concluding that generic richness is indeed highly correlated with species richness. In their survey they used data from various ecosystems around the world. Data from drier ecosystems in Africa, e.g. from Sands (1965) working in the Northern Guinea savanna, Nigeria and from Lepage (1974) studying termites in the Sahel savanna, Senegal, suggest that (in relatively small study areas) 15 to 18 species can be found for 10 genera (Eggleton *et al.* 1996).

The data of the National Survey of the Ispotera has only been fully identified to the genera level. Extrapolating this value to Namibia, it could be expected that the 33 genera that occur represent 60 species. A similar estimate was put forward by Coaton & Sheasby (1972).

2.4.3 Spatial patterns of termite generic richness - environmental links

A gradient of declining termite generic richness extends from the north-eastern corner of Namibia (Okavango region) to the coastal south-west (see Appendix 6 for a map of political regions in Namibia). The north-easterly regions of Namibia have high species diversity, for termites as well as for a number of other invertebrates (Prinsloo, pers. com.). However, it is surprising that a fairly large area in north-western Namibia, namely in the northern Kunene region, as well as some smaller and fragmented areas in north-western Otjozondjupa and south-eastern Oshikoto regions, are 'hot spots' of termite generic richness, coinciding, for example, with the Joubert Mountain Range in Kaokoland (Kunene region) and the Otavi Mountain Range (Otjozondjupa region). What are the factors determining these patterns?

Vegetation, soil and climate are some of the factors which may influence such a zonation. Topography may be an additional factor because it may determine regional climatic conditions, primary productivity and vegetation types. Which environmental factors *ultimately* determine the observable pattern of termite generic richness and distribution may be difficult to identify. However, although only the relationship between rainfall and termite distribution has been analysed in more detail in this study (Chapter 2), some basic ideas concerning other environmental factors are discussed in order to establish their relevance. Maps showing vegetation types, vegetation cover and soil types occurring in Namibia are included in Appendices 2-4.

Bouillon (1970) indicates that the distribution of termite taxa is determined by vegetation type. It makes general sense that food availability, thus the type of vegetation present, strongly affects habitat suitability for termite taxa. This notion is discussed in the Namibian context below with the distribution patterns of feeding groups.

Vegetation cover reflects primary production. It can generally be expected that primary productivity is linked to rainfall, although soil fertility is an additional determinant (Bell, 1982; Scholes, 1990) (discussed in Chapter 2). Based on the energy-diversity concept (Currie, 1991), it can be expected that increasing species richness is linked to increasing primary productivity. Eggleton *et al.* (1994) have critizised this perception for termites on a global scale, however, in Africa the concept seems to hold.

The satellite image of Namibia (Appendix 3), taken in October 1994, provides a general picture of vegetation cover throughout the country. Although the picture is only a one-time snap-shot and not a good reflection of overall primary production, it clearly shows a gradient of vegetation cover at that time. Whether such a gradient generally exists across Namibia needs to be established.

The fact that the picture was taken at the end of the dry season may affect the perception of what is available. The seasonality of available food resources needs to be discussed, for instance, in the context of termite biology, since termite activity and population dynamics are often seasonal too (e.g. Braack, 1995; Ferrar, 1982; Ohiagu, 1979).

Soil characteristics have been shown to determine species presence on a regional scale (Whitford, 1996). Specific requirements for building material for the nesting structures is also of relevance, as well as the water-holding capacity of the soil. Whether the larger-scale distribution of soil types influences termite distribution patterns should be considered.

2.4.4 Distribution patterns of taxonomic groups

Looking again at the distribution patterns of the 33 genera (Figure 2.4) it is apparent that almost half of these genera are present at less than 5% of all sampling stations, which in addition are mostly situated in northern Namibia. It could be said that these genera are spatially less widely distributed, at least within the borders of Namibia. The fact that genera are spatially rare does not necessarily mean that they are rare in local or regional abundance. Unfortunately no measure of abundance is available. For example, the genus *Okavangotermes* was found at one location only, possibly indicating its overall rarity or poor sampling.

Six genera are widespread, occurring in more than half of all grid squares sampled. That their distribution extends across a number of extremely different ecosystems suggests that they are either generalists in their habitat requirements or that they are composed of a number of different species which differ in their needs. This needs to be carefully considered for any future work. Also, 'proportional presence' may give a skewed impression of a genus' commonness. The data for *Odontotermes*, for example, shows that this genus is present at 52% of all sites. Comparing its distribution to other Macrotermitinae reveals that in fact *Odontotermes* is present in most grid squares, but it is also revealing that a higher percentage of areas sampled fall within the boundaries of this particular genus' distribution range.

A look at the feeding group classification (see also below) reveals that

Amitermes, *Microcerotermes* and *Psammotermes* belong to the wood and litter feeding group, *Hodotermes* and *Trinervitermes* form the grass feeding guild and *Odontotermes* is the only fungus grower. The former two groups seem to provide the most flexible feeding strategy, which may guarantee food accessibility. Grass and litter resources are generally abundant throughout Namibia, even in true desert regions. As mentioned above, the data for *Odontotermes* do not give a good reflection of its widespread distribution throughout the country. In fact, *Microtermes* and *Allodontermes* seem to be more flexible in their habitat requirements than *Odontotermes*. The idea that some of the widely distributed genera are composed of several species is certainly true for e.g. *Trinervitermes*. Although identification to the species level is not available, it has been suggested that this genus may include up to seven species (Coaton & Sheasby, 1972; Uis, per. com.). However, *Hodotermes* and *Psammotermes* are represented by one single species each. These two taxa can therefore be considered to be true habitat generalists.

The classification into 'higher' and 'lower' termites is based on phylogenetic reasons, distinguishing two broad classes of 'older' ('lower') and 'younger' ('higher') clades of termites (Eggleton *et al.*, 1994). This systematic split also represents biological and habitat differences. The 'higher' termites apparently predominate in tropical forest systems as litter, wood and soil feeders. 'Lower' termites are generally found outside forests and are mostly wood feeders. The 'higher' termites are much more genus-rich than the 'lower' termites, a phenomenon ascribed by Eggleton *et al.* (1994) to the high cladogenetic adaptability of the relatively 'young' family to environmental change. This pattern also holds for the Namibian situation; however, the reasons for such a structuring need to be carefully considered.

2.4.5 Distribution patterns of functional guilds

Termites were classified into seven feeding guilds, based on information derived from a literature review (see Appendix 1) and from discussion with other termite researchers. However, information on the natural history of the individual genera is patchy and was derived from field observations made while collecting the specimens during the national survey. Although such observational information may be partially inaccurate, it was the best information available under the given circumstances.

Feeding guilds

Classification of the termites into feeding and nesting guilds show interesting results. Looking at the six most widespread genera first, it can be found that three of the feeding groups predominate in occurrence, considering their wide geographic distribution. The wood & litter, grass and fungus growing guilds are common throughout most the country. All other groups are restricted to particular areas, for example, the humus feeder to the far north east and the exclusive wood eater to the central and northern areas of the country. However, at this stage no conclusions can be drawn on the importance of these groups to ecosystem functioning and performance in Namibia.

The distribution of feeding groups is largely determined by food availability (Whitford, 1996). Presumably, decaying organic matter occurs primarily in north eastern Namibia, where primary productivity, and resulting organic matter inputs, are high. Consequently humus feeders can be expected to be restricted to such areas. However, it was found that one representative of this guild, *Lepidotermes*, occurred scattered into more arid regions, were decaying organics are largely absent. This could be attributed to the fact that adequate food resources were available spatially limited on a microhabitat level, or seasonally after the rains. It is also possible that this genus' diet is not restricted to humus only, but is complemented by other, less decayed material. Wood eating genera are only predicted from areas where woody plant species occur, thus their distribution in typical desert regions, such as the Namib and Kalahari Deserts which cover larger areas of Namibia, may be restricted to beds of ephemeral rivers and gullies. The fungus growing Macrotermitinae concentrate in the more humid areas in northern Namibia. The relative importance of fungus-growing Macrotermitinae increases as rainfall decreases (e.g. Deshmukh, 1989; Wood & Sands, 1978). This relationship is mainly based on biomass data, but it should certainly be considered in the present context. The Namibian data suggests that the occurrence of the Macrotermitinae may be linked to optimal rainfall conditions, which may differ for various genera (see also Chapter 2). The wide distribution of wood & litter feeders as well as grass feeders seems to be justified by the general abundance of grasses and shrubs throughout most ecosystems within

Namibia. Although such food sources may be ephemeral, so is the activity of termites. Termite activity is characterised by a strong seasonality, especially in more arid environments (e.g. Buxton, 1981). One feeding guild which has not been included in the classification system, but which may be of particular importance to Namibian ecosystems, is that of the root feeders. No reference to root-feeding genera has been made in the Namibia-related literature. Possibly such a group is not considered to be of relevance, and is included in other groupings. Possibly their significance has not been assessed, since below-ground systems are generally poorly accessible. However, it appears that genera such as *Trinervitermes* and *Psammotermes* survive on below-ground plant resources in the central Namib desert. *Psammotermes* colonies in the Namib desert, for example, are associated with *Stipagrostis* grass hummocks. Although the termites can be seen foraging on above-ground resources, including detritus, it is likely that sub-surface materials are attacked as well. These issues require further research.

Comparing the composition of feeding groups in Namibia with what is known from other more arid ecosystems in Africa, some parallels become apparent. Representatives of the same feeding groups are present in the northern Guinea savanna in Nigeria and in the Sahel savanna (Lepage, 1974; Sands, 1965; Wood & Sands, 1978). There termites feeding on living wood & fresh woody litter as well as on grass & herbaceous litter dominate the composition of termite communities. These groups are similar to the wood, litter and grass feeding classes distinguished in this study. However, soil feeders and termites foraging on decomposing wood are limited in their occurrence in those systems. It can be speculated that a similar underlying factor, namely food availability, leads to such a structuring in relatively arid systems.

Nesting guilds

Epigeal-nesting genera are mainly restricted to the northern, more mesic areas in Namibia. Only five genera fall into this group. One of these, *Baucaliotermes*, only occurs in the arid south of the country, apparently adapting to hot and dry climates. Hypogeal-nesting genera, on the other hand, are present at 97,5% of all study sites. Almost half of all genera belong to this category and distribution ranges shared by up to nine genera are no exception. Termites nesting below the surface are therefore the most common, at least in spatial distribution, in Namibian ecosystems. Presumably ambient conditions these are more stable and favourable than they are in above-ground structures.

3. Chapter 2: **Rainfall as a determinant of termite generic richness and biogeographic distribution.**

3.1. Introduction

In the preceding chapter the spatial distribution of termite taxa throughout Namibia has been described. The next step must be to analyse the underlying determinants of the observed patterns. Once such connections are established, it will be possible to estimate how environmental change, naturally- or human-induced, will affect termite generic richness, distribution and community structures. The implications of these changes in ecosystems can then be postulated by considering the functional attributes of the individual termite taxa.

In southern Africa, changes or at least variations in rainfall patterns have been observed over the past few decades (Tyson, 1981, 1993; Tyson & Dyer, 1975; Tyson & Lindesay, 1992). In Namibia, a long-term reduction of rainfall may lead to drought situations with severe implications for the immediate agricultural productivity. Very little is known about the longer-term effects on ecosystem productivity and stability which are, for instance, mediated through soil organisms. The main problem is that in order to gain an understanding of longer-term changes in community structure and composition of soil fauna, as well as of the direct causal links between these features and ecosystem productivity, long-term monitoring programmes need to be established. These are time consuming and results can only be expected after a long period. As an alternative, the data from the National Survey of the Isoptera conducted 30 years ago are available today, and they provide a good reference to termite biogeographic distribution throughout Namibia at that time. Further, scenarios of environmental change can be modelled on the termite data and future distributions or termite genera can be postulated. Such theoretically derived termite distributions would need to be tested, for example, by conducting a subsequent survey.

This chapter is composed of three parts. Firstly, average rainfall and variability surfaces for the time period of 1952 to 1967 are interpolated for Namibia, presenting the rainfall conditions prevailing roughly 15 years prior to the National Survey of the Isoptera. Termite colonies are known to reach an age of 15 to 20 years (e.g. Collins, 1981). Therefore it is assumed that most of the termite populations sampled during the survey developed under the climatic regime that is modelled. These data are then used to establish whether termite generic richness and distribution are related to rainfall parameters, and mathematic relationships between the two are established for each individual genus. A second rainfall model is derived for the arbitrary period of 1978 to 1993, again depicting a 15 year time span under which one generation of termite populations would have developed. Climatic data since 1993 is not as yet entirely accessible in Namibia. Therefore an earlier period was chosen for this project, which could be up-dated for future research. This more recent rainfall model is compared to the first in order to establish whether a change in rainfall patterns has occurred. The possible effects of such changes on termite generic richness and distribution are then postulated.

3.2. Methods

3.2.1 Rainfall

The rainfall data used is tabulated in Appendix 5. Also are the model derivations described in that section.

Generally average rainfall and rainfall variability were modelled from monthly rainfall data from climatic stations in Namibia for two time periods, namely (a) 1952-'67 and (b) 1978-'93. Rainfall variability was represented by the coefficient of variation calculated from the data. The data were imported into GIS IDRISI and a coherent rainfall surface for the region was calculated using a nearest neighbour interpolation on a quarter degree grid scale to be coherent with the scale that was used to map the termite data.

The rainfall data were grouped into five categories, each comprising approximately 20% of all stations. This arbitrary classification was chosen for statistical reasons, deriving classes of similar sampling size.

In order to test whether a significant change in rainfall patterns had occurred, the IDRISI derived images for the two time periods were compared by means of a cross-tabulation. In addition a two tailed, paired t-test was performed on the numerical data for the 483 quarter degree grid squares, corresponding with the scale on which the termite data were assessed. These data were derived from the generated surface model maps generated in IDRISI as described before and exported into a statistical computer package for further analyses (SAS, 1988).

3.2.2 *Termite generic richness & rainfall*

In order to examine the relationship between rainfall and termite generic richness in Namibia a regression analysis was performed.

An image with the rainfall data for the 483 sampling stations of the National Survey was obtained from the rainfall surface image for 1952-67 created in IDRISI (see above). A linear regression analysis between the two image files for rainfall (1952-67) and generic richness was carried out. Additionally, the image depicting generic richness throughout Namibia was analysed for autocorrelation and trend. All statistical analyses were performed with the in IDRISI available tools for spatial analyses.

3.2.3 *Individual termite genera & rainfall*

The distribution of each individual termite genus found in Namibia was mapped as a raster image in IDRISI. Data were recorded as presence/absence across the 483 sampling stations of the Survey. For further statistical analysis the data were exported into the statistical package SAS (SAS Institute, 1988).

Logistic regression analyses were performed between the termite genera and rainfall to establish the relationship between them.

3.3. Results

3.3.1 Rainfall

Figure 3.1 shows the ranges of the rainfall classes that were established. Five classes were distinguished, ranging from 0-651mm of rain. The data used to derive the rainfall models for the two time periods are provided in Appendix 5.

Examining the rainfall class images, basic characteristics of rainfall patterns in Namibia can be noticed. Rainfall patterns established for both time periods, (a) 1952-'67 and (b) 1978-'93, appear to be similar, but some significant differences can also be noticed. Generally rainfall in Namibia is low, with a maximum annual average of approximately 650 mm. More than half of the country receives less than 350 mm rainfall per year. There is a rainfall gradient over Namibia, with relatively high amounts falling in the north-eastern corner of the country, and the average decreasing gradually towards the south-west. Variability in rainfall (Figure 3.2) generally follows an inverse pattern, being low in the north-east and increasing towards the south-west.

Statistical comparison of the two rainfall models reveals that they are indeed significantly different (paired sample t-test, two-tailed, p=0.086). The results of

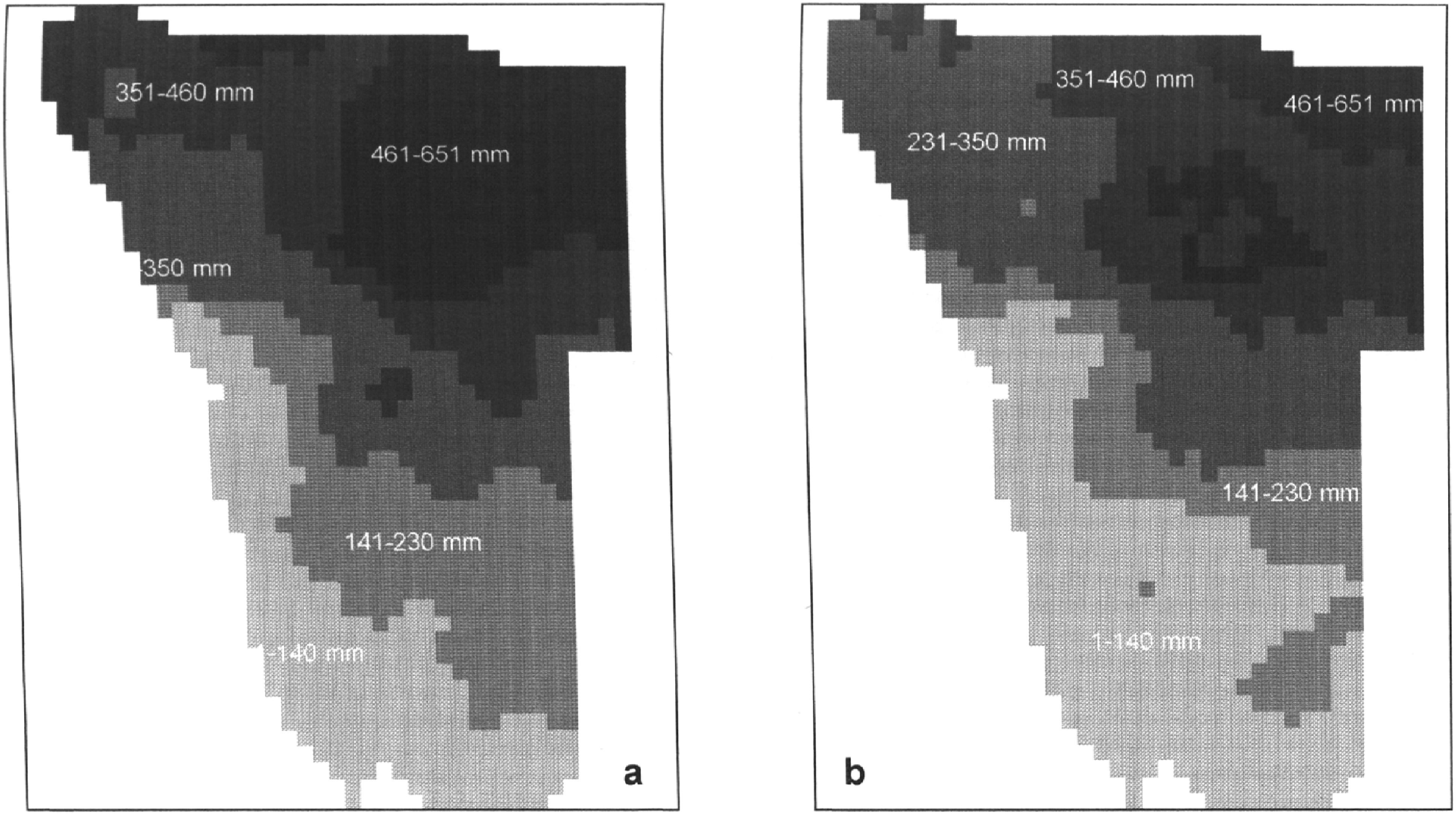


Figure 3.1: Average rainfall interpolation surface derived for (a) the period of 1952-'67 and (b) of 1978-'93. *Five rainfall classes are established.*

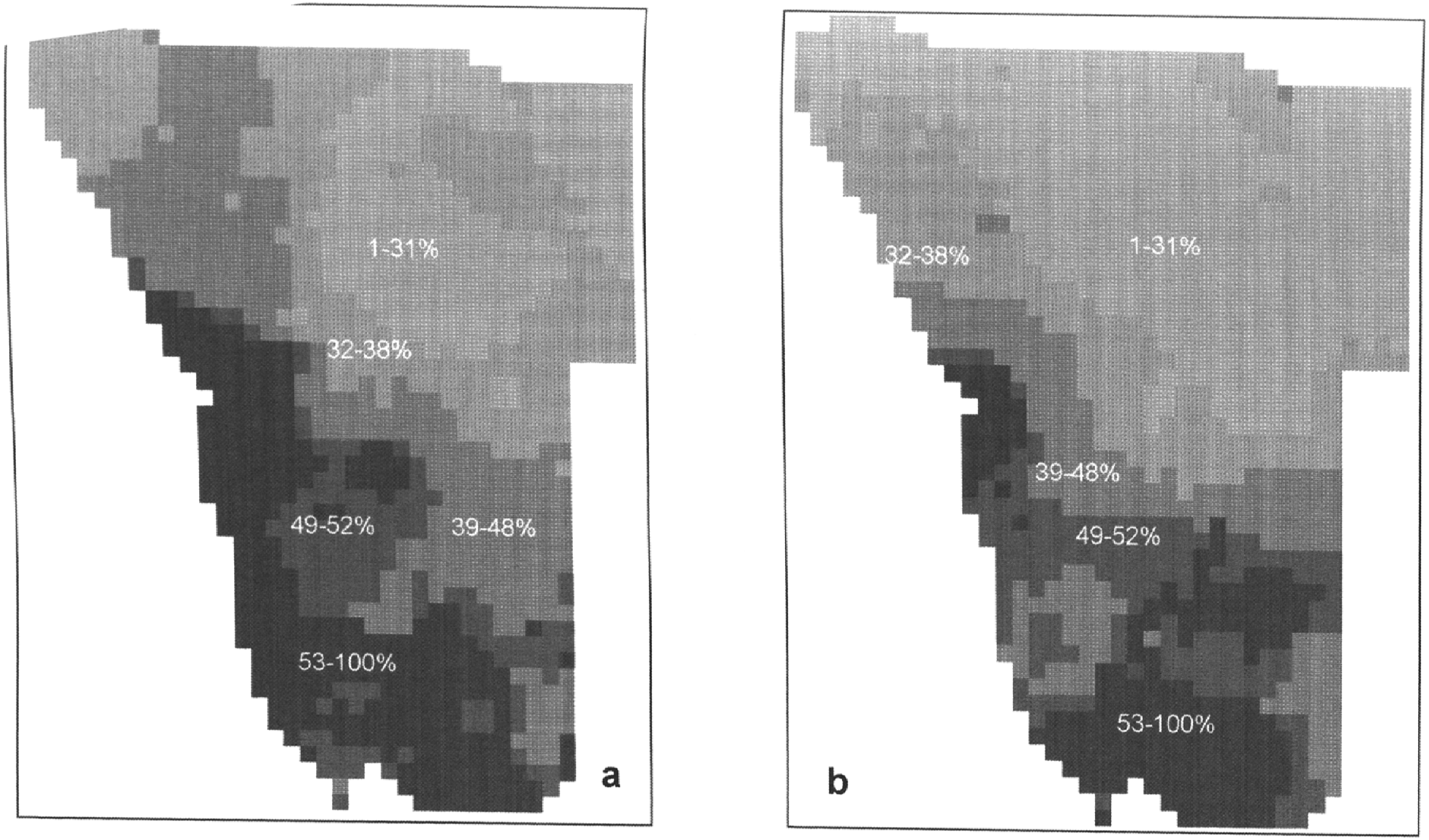


Figure 3.2: Coefficient of variation on the modelled rainfall data. *Five classes of percentage variability are established.*

the cross-tabulation (Table 3.1) performed on the rainfall class images clearly show that the number of pixels falling into each of the classes shifted significantly. For example, the high-rainfall area in Namibia, rainfall class 1 (461-651mm), declined overall in its spatial distribution. Class 2, with 351-460mm rainfall, diminished recognisably. Classes 3 and 5, ranging from 231 to 350 mm and 1 to 140 mm respectively, both increased in area covered. Class 4, with 141-230mm reaching towards the lower end, remained fairly similar in extent. Overall, the most pronounced declines and shifts in annual average precipitation were observed in northern Cunene, southern Okavango, eastern Otjozondjupa, north-eastern Omaheke and northern Karas/southern Hardap regions.

Table 3.1: Results from a cross-tabulation analysis performed to compare the rainfall class images based on average rainfall, derived for the time periods of (a) 1952-'67 and (b) 1978-'93. *Classes with higher average rainfall clearly 'lost area' over the past decades.*

Rainfall class	**Number of grid's 1960's**	**Number of grid's 1990's**	**Trend**
Class 1 (461-651 mm)	243	104	decrease
Class 2 (351-460 mm)	246	237	decrease
Class 3 (231-350 mm)	235	324	increase
Class 4 (141-230 mm)	236	162	decrease
Class 5 (1-140 mm)	241	365	increase

The results of the cross-tabulation carried out on the rainfall variability data are shown in Table 3.2. Classes 2, 3 and 5, ranging from 32% to 100% variability of rainfall, declined spatially. Class 4, representing 49% to 52% of variability, increased a little. However, it is class 5, comprising areas with a variability from 1-31%, that increased greatly in area covered. Thus variability of rainfall decreased in Namibia comparing the two selected time periods.

Table 3.2: Results from a cross-tabulation analysis performed to compare the rainfall variability class images derived for the time periods of (a) 1952-'67 and (b) 1978-'93. *The area under low rainfall variability is significantly greater during the latter time period.*

Coefficient class	**Number of grid's 1960's**	**Number of grid's 1990's**	**Trend**
Class 1 (1-31%)	230	472	increase
Class 2 (32-38%)	287	211	decrease
Class 3 (39-48%)	291	182	decrease
Class 4 (49-52%)	123	152	increase
Class 5 (53-100%)	261	175	decrease

3.3.2 Termite generic richness & rainfall

A linear relationship between generic richness and rainfall was established (R^2= 78.97%).

Spatial autocorrelation, thus spatial variation, occurs within the generic richness data set (Moran's I = 0.48 (Rook's case)). A pronounced environmental trend underlies these data. The trend was not removed since it was believed to be congruent to the prevailing rainfall gradient.

3.3.3 Termite genus distribution & rainfall

The results from the logistic regression analyses between individual termite genera and rainfall are summarised in Table 3.3. It indicates whether a significant relationship exists between rainfall and the presence of an individual termite genus. In cases where this is so, the nature of the relationship is described in more detail. A positive value indicates that one is more likely to find that particular termite genus under relatively higher rainfall regimes. A negative value predicts the opposite, namely a decrease of the termite genus' presence with increasing rainfall.

Overall, the distributions of seven genera (*Ancistrotermes, Bifiditermes, Coptotermes, Okavangotermes, Rhadinotermes, Unguitermes* and *Unicornitermes*) were not significantly determined by rainfall. However, these genera were generally sparsely distributed, and it is likely that no relationship to rainfall could be established because data were limited. Four genera, *Anguilitermes, Baucaliotermes, Microhodotermes, Psammotermes*, showed negative associations with rainfall, indicating that these genera have a preference for low rainfall conditions. However, *Angulitermes* and *Psammotermes* occur over wide rainfall ranges (from 100 to about 600 mm). The other two genera have limited distributions in arid climates, occurring under rainfall regimes ranging from 30 to 260 mm for *Baucaliotermes* and 30 to 140 mm for *Microhodotermes*. All remaining genera produced a positive correlation between their presence and average rainfall.

Table 3.3: Results of the logistic regression analysis done for each individual genus recorded from Namibia in relation to average rainfall at that time. *The range of rainfall under which each individual genus was found is recorded. Whether a significant relation could be detected and the form of the relationship is indicated by sig./+ for a positive correlation and by sig./- for a negative one.*

Genus	Rain (mm): range of occurrence	Intercept	Rain	Likelihood Logit	Significance pos./neg. relation
Allodontermes	120-650	-3.0210	0.007191	-259.643	sig./+
Amitermes	60-650	0.1142	0.002449	-289.068	sig./+
Ancistrotermes	480-520	-9.3519	0.009246	-13.409	n. sig
Angulitermes	100-580	0.3358	-0.003812	-284.409	sig./-
Anoplotermes	480-520	-7.9525	0.008299	-26.577	sig./+
Astaslotermes	360-650	-12.5307	0.016608	-19.430	sig./+
Baucaliotermes	30-260	2.2815	-0.015402	-162.925	sig./-
Bifiditermes	570-580	-17.7222	0.024491	-10.980	n. sig.
Coptotermes	460-580	-10.5351	0.011565	-12.933	n. sig.
Cryptotermes	310-620	-6.8284	0.006652	-35.341	sig./+
Cubitermes	240-650	-3.1680	0.005191	-224.356	sig./+
Epicalotermes	60-640	-1.5412	0.002632	-300.995	sig./+
Fulleritermes	380-650	-9.9936	0.018551	-104.609	sig./+
Hodotermes	30-650	0.9125	0.002608	-207.139	sig./+
Lepidotermes	90-620	-2.0052	0.002620	-231.786	sig./+
Macrotermes	160-640	-2.8390	0.006900	-266.381	sig./+
Microcerotermes	60-650	-0.6855	0.004090	-298.483	sig./+
Microhodotermes	30-140	0.9517	-0.024350	-53.559	sig./-
Microtermes	100-650	-1.7189	0.004853	-303.729	sig./+
Neotermes	570-620	-20.5231	0.030033	-13.424	sig./+
Noditermes	420-580	-8.9054	0.012210	-48.542	sig./+
Odontotermes	160-650	-3.1297	0.010553	-232.250	sig./+
Okavangotermes	580	-20.4817	0.027985	-6.935	n. sig.
Ovambotermes	430-650	-11.0800	0.019910	-90.241	sig./+
Promirotermes	80-650	-0.8590	0.002332	-327.932	sig./+
Psammotermes	30-650	1.8829	-0.004535	-299.950	sig./-
Rhadinotermes	260-500	-4.8241	0.003030	-53.187	n. sig.
Schedorhinotermes	310-590	-6.3104	0.007101	-58.377	sig./+
Skatitermes	290-650	-5.4134	0.007289	-108.192	sig./+
Spatulitermes	550-650	-18.1847	0.027960	-25.964	sig./+
Termes	290-650	-9.7113	0/017604	-102.600	sig./+
Trinervitermes	60-650	-2.3055	0.008131	-263.256	sig./+
Unguitermes	560	-15.8214	0.019932	-7.430	n. sig.
Unicornitermes	100-150	-2.3992	-0.016337	-12.772	n. sig.

The regression lines for all taxa showing a significant relationship between their distribution and rainfall are plotted in Figure 3.3. The seven genera which did not significantly correlate with rainfall are excluded from the diagram. The y-axis scaled from 0 to 1 represents the likelihood at which the presence of the genus can be expected.

It is obvious that individual termite genera react very differently to annual rainfall. Some genera such as *Microhodotermes* occur exclusively in low rainfall areas: its presence at 30 mm rainfall can be expected with a 60% likelihood. An annual increase of 10 mm of rain reduces the likelihood of its presence to 50%, while at 240 mm the correlation model predicts a 0% probability of finding this genus in the area. *Baucaliotermes* similarly shows a preference for drier climates but overall this genus survives higher rainfall conditions than *Microhodotermes*. In low rainfall (30 mm) areas it is predicted to occur with a probability of 90%. *Angulitermes* and *Psammotermes* generally occur over a much wider range of rainfall. The models predict that these genera appear under any of the rainfall conditions prevailing in Namibia (ranging from 30 - 650 mm), although both genera seem to prosper better under drier conditions. In such conditions *Psammotermes* is generally more likely to be found than *Angulitermes*. In areas with average rainfall below 420 mm *Psammotermes* can be found at a probability of 50 -90%.

The presence of several genera is triggered by a minimum amount of rainfall, above which the likelihood of their occurrence increases greatly. For genera such as *Spatulitermes*, *Neotermes* and *Astalotermes* the correlations predict

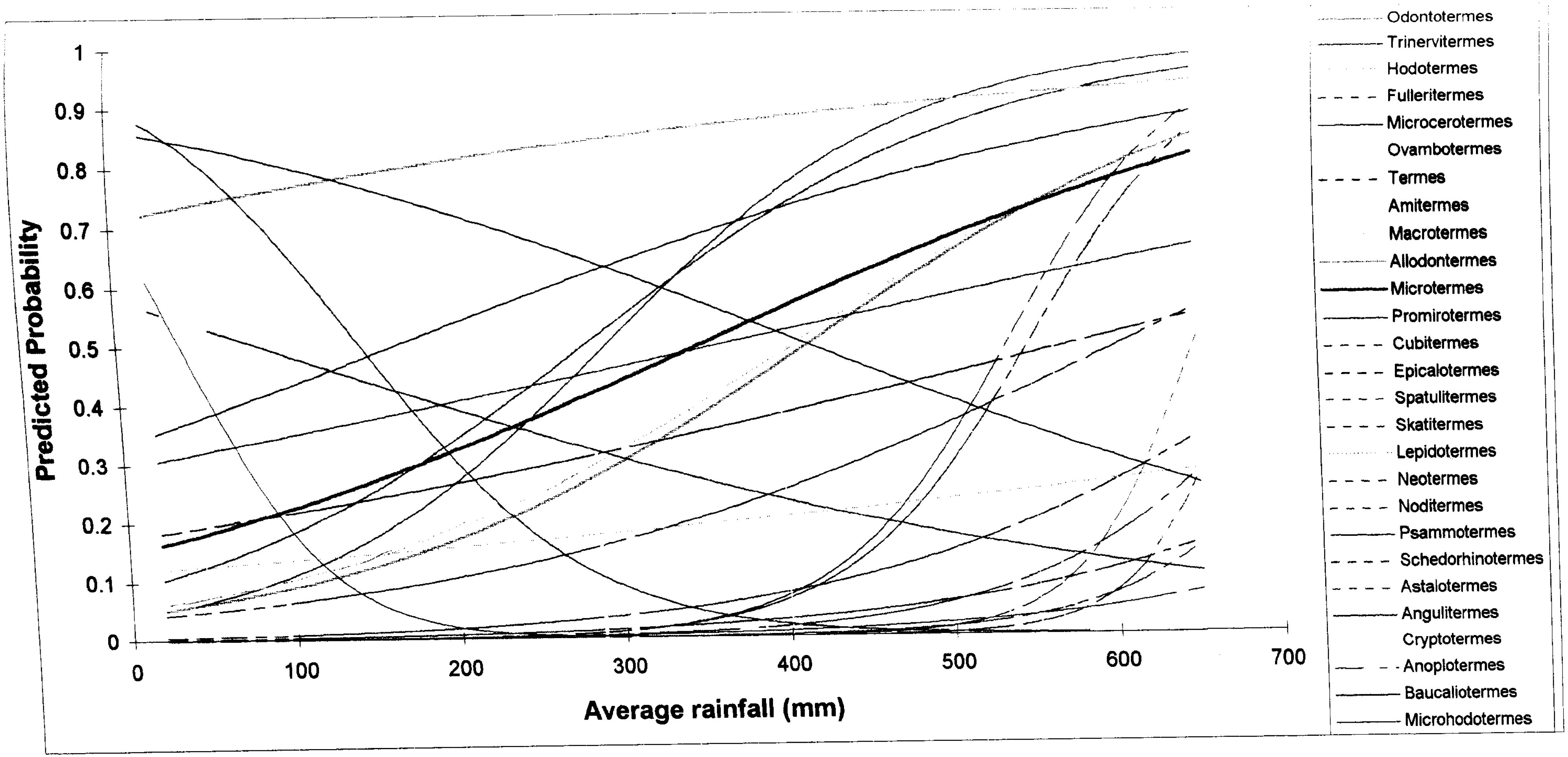


Figure 3.3: Logistic regressions of individual genera and average rainfall 1952-'67. *Genera showing significant correlations are displayed.*

their occurrence only at an average rainfall above 500 mm. At 650 mm *Spatulitermes*, for example, can be expected with a 50% likelihood. *Fulleritermes*, *Termes* and *Ovambotermes* are three genera that occur above a 300 mm rainfall limit. At approximately 550 mm these genera can be expected to occur with a 50% probability. Above 620 mm average rainfall their presence is predicted with a 85% likelihood.

Most other genera occur under much broader climatic conditions. Although the probability of finding such genera increases with increasing rainfall, they seem to be less bound to specific rainfall conditions. Genera such as *Hodotermes* and *Amitermes* are predicted with a probability greater than 50% under any rainfall conditions in Namibia. *Hodotermes*' appearance is even predicted at a likelihood of 72 -92 % under any such situation. *Microcerotermes* survives well under relatively low rainfall conditions, reaching the 50% probability level at 160 mm. The models of the remaining genera predict 50% likelihood of occurrence at greater than 280 mm average rainfall.

3.4. Discussion

3.4.1 *Average rainfall - not the full story*

The richness of termite genera is related to rainfall: it is lower in arid than in mesic ecosystems. However, vegetation characteristics may affect termite genera distribution more strongly than average rainfall per se (e.g. Bouillon, 1970; Whitford, 1992). Obviously, rainfall is directly linked to primary productivity (e.g. Bell, 1982), and vegetation types are associated with rainfall characteristics (e.g. Giess, 1971). Increased rainfall not only leads to higher primary productivity (e.g. Bell, 1982), but also increases species richness in vegetation (Currie, 1991; Currie & Paquin, 1987). This could mean a diversification of food resources available to termites, possibly generating more niches that could be occupied by a greater number of different termite genera. Thus rainfall may directly as well as indirectly influence the distribution of termite genera in Namibia. Consequently changes in rainfall patterns may not directly impact termites and their distribution, but it is rather changes in the vegetation that may lead to a quantitative as well as qualitative loss of forage material and to an alteration of microhabitat (Whitford, 1992). Rainfall may affect the abundance of termites more strongly than it affects generic richness (e.g. Whitford, 1996), an important point to be considered when assessing the role of individual taxa in ecosystems. Social insects such as termites can survive drastic changes of environmental conditions by retaining only a small number of colony members, particularly the reproductively active pair (e.g. Oster & Wilson, 1978). In this way they can bridge seasons of low resource availability, and it is only prolonged periods of unfavourable circumstances that may drive them from a system. In addition termites live in elaborate nesting structures which provide a thermally well buffered environment (Turner, 1993), thus contributing to their survival under variable environmental conditions.

It is likely that the seasonality of rainfall and consequently primary productivity is a primary determinant of termite distribution. Future investigations should also elaborate on a possible relationship between termite generic richness, genera distribution and the coefficient of variation, since rainfall variability may greatly affect spatial distribution patterns.

Generally it should be noted that the applied rainfall model is rather simplistic and was used with the specific goal to represent the rainfall conditions at specific locations over a defined time period. Other models could used in further investigations.

3.4.2 Changes of rainfall patterns in Namibia

Based on the model used differences in rainfall pattern between the periods of 1952-'67 and 1978-'93 are discernible, as shown by the data above. Whether these changes represent a long-term change or are merely coincidental remains questionable, and no conclusions can be drawn on whether they are the consequence of natural climatic variability or of global climate change. However, the fact is that the prevailing climatic conditions under which termite populations would have established themselves (15 years) are significantly different for the two arbitrary chosen time periods under investigation.

Overall, conditions in Namibia during the later time period were more arid compared to the earlier one, when the National Survey of the Isoptera was conducted. Surprisingly, at the same time variability of rainfall declined over large areas. As discussed above, social insect populations are relatively unaffected by shorter-term environmental fluctuations, but it might be very interesting to investigate whether rainfall variability affects termite populations.

3.4.3 *Single genus distribution - rainfall connections*

Different termite genera respond differently to the amount of rainfall. Most genera are positively associated with increasing rainfall, but the distribution of some seems to be correlated with more arid conditions. Genera that are relatively widespread in their distribution are obviously more flexible in their requirements and occur over a wider range of rainfall, although it is more than just rainfall that must be taken into consideration when assessing overall distribution patterns. If one considers the association of representatives of the various feeding groups established in Chapter 1, interesting correlation between feeding requirements and rainfall can be ascertained.

All members of the humus feeding guild, for example, show a positive association with increasing rainfall (*Okavangotermes* and *Unicornitermes* are excluded due to a lack of data). The models derived for *Fulleritermes*, *Ovambotermes*, *Spatulitermes* and *Noditermes* predict their occurrence where average rainfall is high, reaching a likelihood of 50% only where rainfall is greater than 500 mm. *Cubitermes* and *Lepidotermes* are predicted to occur in dry climates, and the probability of finding them increases with rainfall.

Examining the feeding links of the four genera that show a negative association to rainfall (*Angulitermes, Baucaliotermes, Microhodotermes & Psammotermes*) reveals that they belong to only two feeding guilds, the wood & litter and litter & dung feeders. Again, there is a very strong connection between food requirements and rainfall. Litter, dung and non-decayed wood are available resources in arid regions, and are possibly the main organic food resources in some areas such as the Namib desert dunes, where *Psammotermes* are abundant. It is also revealing that three of these four genera nest underground. Only one genus, *Baucaliotermes*, constructs epigeal mounds, which may be underlined by a subterranean gallery system. Possibly microclimatic conditions are more favourable below ground. An interesting aspect in the distribution of *Baucaliotermes* and *Microhodotermes* is that both these genera are restricted to the south of Namibia. Here, winter rainfall prevails, and environmental conditions not only differ in the seasonality of climate, but also in characteristics of vegetation, compared to Namibia's summer rainfall areas.

An interesting pattern can be observed between the models obtained for the fungus growing termites, which all display very similar curves (*Ancistrotermes* is excluded due to insufficient data). Macrotermitinae are predicted to occur over a wide range of rainfall conditions. The limit of a 50% likelihood of occurrence is reached between about 260 mm and 410 mm average rainfall. Elsewhere the distribution of Macrotermitinae is said to be related to decreasing rainfall (e.g. Wood & Sands, 1978; Deshmukh, 1989), but this does not agree with the data in this chapter. The findings of this research suggest that, in Namibia, the likelihood of occurrence of the Macrotermitinae increases to reach a maximum likelihood at approximately 600 to 700 mm of annual rain, which is where the curves for all fungus growing genera seem to level out.

For the grass feeding guild it can be stated that *Hodotermes* seems to be the most flexible and 'successful' genus, showing extremely high probabilities of occurrence under any of the climatic conditions prevailing in Namibia.

3.4.4 Changes of rainfall patterns: implications for termite genera distribution and ecosystem performance - a hypothesis

Aridification of climatic conditions in Namibia may lead to shifts in distribution of single termite genera. It is probably changes in vegetation brought on by a changed climate that determine whether termite genera expand or diminish their distribution ranges, or whether they will be driven out of a systems.

On the basis of the correlation between rainfall and termite distribution alone, a few genera could be extirpated due to changes in rainfall regimes. However, most termite genera are fairly flexible in the range of their rainfall requirements. The more vulnerable genera are those that are generally restricted in distribution and which depend on a narrow range of rainfall conditions at the upper end of the scale. These are primarily the 'rare' species with few records (see above). Examples are genera such as *Fulleritermes*, *Ovambotermes*, *Termes*, *Spatulitermes*, *Noditermes* and *Neotermes*, which predominately occur in the areas of rainfall class 1 with high precipitation (461-651mm). The area covered by this rainfall class is significantly smaller in 1978-'93 compared to the 1952-'67 period, thus reflecting a reduction of suitable habitat for these taxa. Other species with a high likelihood of occurrence in this rainfall class will possibly be present in patches only, occurring at a reduced probability. Generally it will be the genera that are adapted well to arid conditions that may extend their distribution ranges, such as *Microhodotermes*. The other three 'arid-adapted' genera (*Psammotermes*, *Angulitermes* and particularly *Baucaliotermes*) may be more common under the altered climatic conditions.

Summarising, it can be hypothesised that primarily those genera that live at the 'edges' of the extremes will be affected by aridification. Genera that require more mesic conditions will have their ranges limited, while genera preferring more arid conditions will expand their distribution. However, it must be emphasised that other environmental factors need to be considered when changes of distribution patterns are assessed. Various environmental determinants, as well as factors inherent to the termite's biology, act together and need to be considered as an entity to obtain a better picture of the consequences of environmental change on termite distribution.

4. Conclusions

It would be most desirable to establish how changes in termite genera or if possible species distribution and the overall composition of soil communities affects ecosystem processes and ecosystem health. Due to the lack of information on the functional significance of termites in Namibian ecosystems, reliable predictions cannot be made. Little is known about how termite populations and communities react to environmental change, induced, for example, by alterations of the global climate or land-use practices. The results herein form the first step in delineating possible associations with individual termite genera that could be used as indicators of ecosystem function (Angermeier & Karr, 1994; Karr *et al.*, 1986) in Namibia, by firstly establishing the possible correlations of the termites' spatial distribution and rainfall patterns. However, many questions remain unresolved. Future research needs to clarify what the implications of environmental change are for termite populations and communities, and to explore the functional significance of key taxa occurring in Namibia. A general weakness of termite studies is that population parameters and functional impacts on the ecosystem are extremely difficult to measure in the field. However, only studies performed under natural conditions can really elucidate some of the important questions that need to be addressed. In the Namibian context two main approaches can be envisaged.

Firstly, re-sampling of termite populations should be performed in order to establish whether a change in genera presence and composition has occurred over the past 30 years. Such a survey could be restricted to key areas in

Namibia which are important, for example, for agricultural use and agronomic outputs. Areas with different land-use histories could be sampled to test whether specific land-use affects termite populations. Many weaknesses or shortcomings were found in evaluating the data from the National Survey of the Isoptera. It is therefore necessary to improve on the sampling method. Techniques need to be developed that allow for a comparison of the data from different sampling sites, and a census of *all* termite taxa currently present in the area. It would be desirable to identify termites to full species level. It is essential to determine not only termite taxon richness but also abundance under given environmental conditions. This is absolutely crucial to assess the significance of termites in ecosystem processes. In the attempt to link termite data to environmental data it became apparent that the latter are often of poor quality. Rainfall data has been sampled erratically, and the scale of measurement of vegetation types, for example, is extremely coarse. The value of such data must be interpreted carefully. For future studies it seems therefore beneficial to also collect required environmental base data. Secondly, field experimental studies with a functional focus need to be put into place. They need to measure the effect of individual termite genera and populations on soil, vegetation and possibly fauna. This is particularly difficult. Some researchers have tried to study soil biota mediated processes in so-called microcosms, imitating the natural environment as well as possible under defined laboratory conditions. However, the consensus of researchers of soil biota is that results of such studies are of limited value in drawing conclusions for field conditions (Curry *et al.*, 1996). It remains a major challenge to develop robust field techniques for measuring process oriented parameters under natural conditions.

However, although such research seems to be very elaborate and intensive, its results can contribute to a better understanding of Namibian ecosystems and, ultimately, to the ratification of the Desertification and Biodiversity Conventions in Namibia.

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Appendix 1

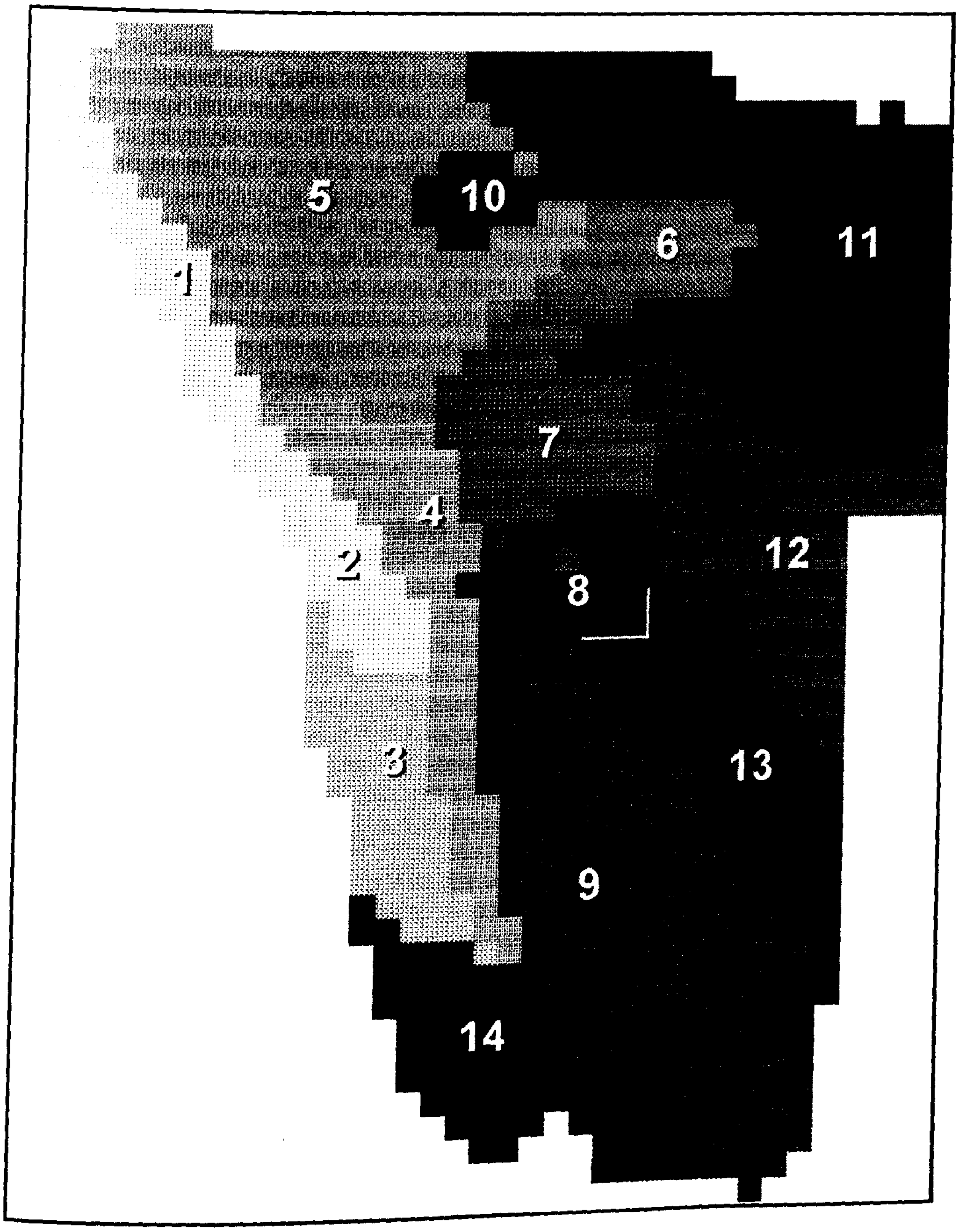
from the literature. Genera that are not idientified to species level are marked as 'n.f.i.'.

Taxon	Feeding group	Nesting group	Reference
KALOTERMITIDAE			
Kalotermitinae			
(1) Neotermes	wood feeder	arboreal	Coaton & Sheasby, 1972
(2) Bifiditermes	wood feeder	arboreal	Coaton & Sheasby, 1972, 1980
Bifiditermes sibayiensis Coaton			
(3) Epicalotermes (n.f.i.)	wood feeder	arboreal	Coaton & Sheasby, 1972
(4) Cryptotermes	wood feeder	arboreal	Coaton & Sheasby, 1972, 1979
Cryptotermes havilandi Sjöstedt			
HODOTERMITIDAE			
Hodotermitinae			
(5) Hodotermes	grass feeder	hypogeal	Coaton, 1958, 1981; Coaton & Sheasby, 1972, 1975b
Hodotermes mossambicus Hagen			
(6) Microhodotermes	litter/dung feeder	hypogeal	Coaton & Sheasby, 1972, 1974b
Microhodotermes viator Latreille			
RHINOTERMITIDAE			
Psammotermitinae			
(7) Psammotermes	wood & litter feeder	hypogeal	Coaton & Sheasby, 1972, 1973c
Psammotermes allocerus Desneux			

Taxon	Feeding group	Nesting group	Reference
Coptotermitinae			
(8) Coptotermes	wood feeder	arboreal	Coaton & Sheasby, 1972, 1976
Coptotermes amanii Sjöstedt			
Rhinotermitinae			
(9) Schedorhinotermes	wood feeder	arboreal	Coaton & Sheasby 1972, 1973b
Schedorhinotermes lamanianus Sjöstedt			
TERMITIDAE			
Apicotermitinae			
(10) Skatitermes	litter/dung feeder	hypogeal	Coaton, 1971; Coaton & Sheasby, 1972
Skatitermes psammophilus Coaton			
Skatitermes watti Coaton			
(11) "Anoplotermes" branch	wood/soil feeder	hypogeal	Coaton & Sheasby, 1972
Termitinae			
(12) Amitermes (n.f.i.)	wood & litter feeder	arboreal	Coaton & Sheasby, 1972
(13) Microcerotermes (n.f.i.)	wood & litter feeder	arboreal	Coaton & Sheasby, 1972
(14) Cubitermes (n.f.i.)	humus feeder	epigeal	Coaton & Sheasby, 1972
(15) Ovambotermes	humus feeder	arboreal	Coaton, 1971; Coaton & Sheasby, 1972
Ovambotermes sylvaticus Coaton			
(16) Okavangotermes	humus feeder	not known	Coaton, 1971; Coaton & Sheasby, 1972
Okavangotermes giessi Coaton			
(17) Lepidotermes (n.f.i.)	humus feeder	hypogeal	Coaton & Sheasby, 1972
(18) Noditermes (n.f.i.)	humus feeder	hypogeal	Coaton & Sheasby, 1972
(19) Unicornitermes	humus feeder	hypogeal	Coaton, 1971; Coaton & Sheasby, 1972
Unicornitermes gaerdesi Coaton			

Taxon	Feeding group	Nesting group	Reference
(20) Unguitermes	wood/soil feeder	arboreal	Coaton & Sheasby, 1972; Ruelle, 1973
Unguitermes unidentatus Ruelle			
(21) Promirotermes (n.f.i.)	wood/soil feeder	hypogeal	Coaton & Sheasby, 1972
(22) Termes (n.f.i.)	wood/soil feeder	hypogeal	Coaton & Sheasby, 1972, 1978
(23) Angulitermes (n.f.i.)	wood & litter feeder	hypogeal	Coaton & Sheasby, 1972
Macrotermitinae			
(24) Allodontermes	fungus grower	hypogeal	Coaton & Sheasby, 1972; Ruelle, 1979
Allodontermes rhodensiensis Sjöstedt			
Allodontermes schulzei Silvertry			
(25) Macrotermes	fungus grower	epigeal	Coaton & Sheasby, 1972; Ruelle, Coaton & Sheasby, 1975
Macrotermes subhyalinus Rambur			
Macrotermes vitlalatus Sjöstedt			
(26) Odontotermes (n.f.i.)	fungus grower	epigeal	Coaton & Sheasby, 1972
(27) Ancistrotermes	fungus grower	hypogeal	Coaton & Sheasby, 1972, 1975a
Ancistrotermes latinotus Holmgren			
(28) Microtermes(n.f.i.)	fungus grower	hypogeal	Coaton & Sheasby, 1972
Nasutermitinae			
(29) Baucaliotermes	litter/dung feeder	epigeal	Coaton & Sheasby, 1972, 1973a
Baucaliotermes hainesi Fuller			
(30) Trinervitermes (n.f.i.)	grass feeder	epigeal	Coaton & Sheasby, 1972
Trinervitermes dispar Sjöstedt			
Trinervitermes rapulum Sjöstedt			
Trinervitermes rhodesiensis Sjöstedt			
Trinervitermes trinervoides Sjöstedt			
(31) Fulleritermes	humus feeder	arboreal	Coaton & Sheasby, 1972, 1973d
Fulleritermes contractus Sjöstedt			
(32) Rhadinotermes	wood & litter feeder	hypogeal	Coaton & Sheasby, 1972, 1974a
Rhadinotermes coarctatus Sjöstedt			
(33) Spatulitermes	humus feeder	hypogeal	Coaton, 1971; Coaton & Sheasby, 1972
Spatulitermes coolingi Coaton			

Appendix 2

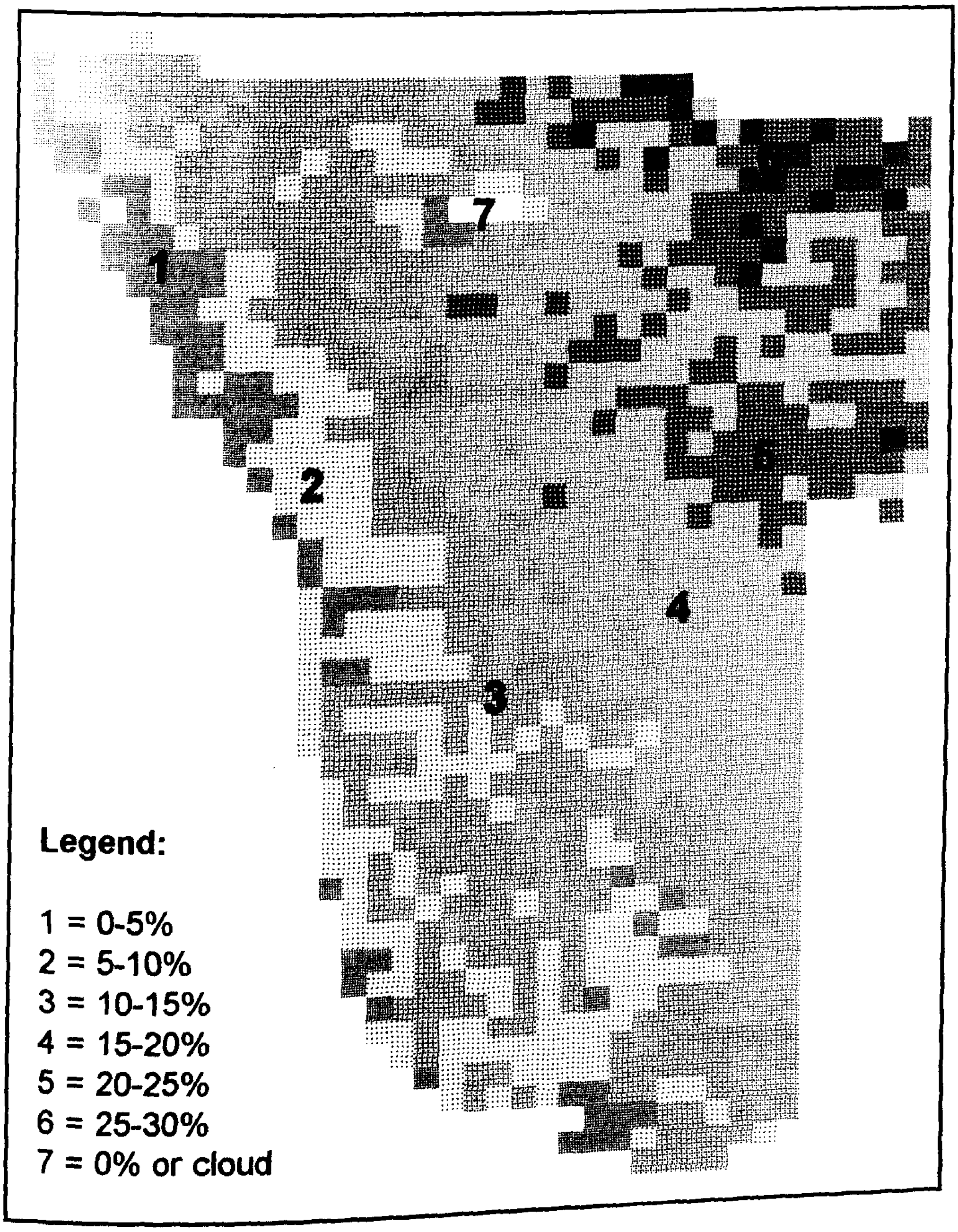


Legend:

1 = Northern Namib
2 = Central Namib
3 = Southern Namib
4 = Semi-desert and savanna transition
5 = Mopane savanna
6 = Mountain savanna and Karstveld
7 = Thornbush savana
8 = Highland savanna
9 = Dwarft shrub savanna
10 = Saline desert with dwarf savanna fringe
11 = Forest savanna and woodland
12 = Camelthorn savanna
13 = Mixed tree and shrub savanna
14 = Desert and succulent steppe

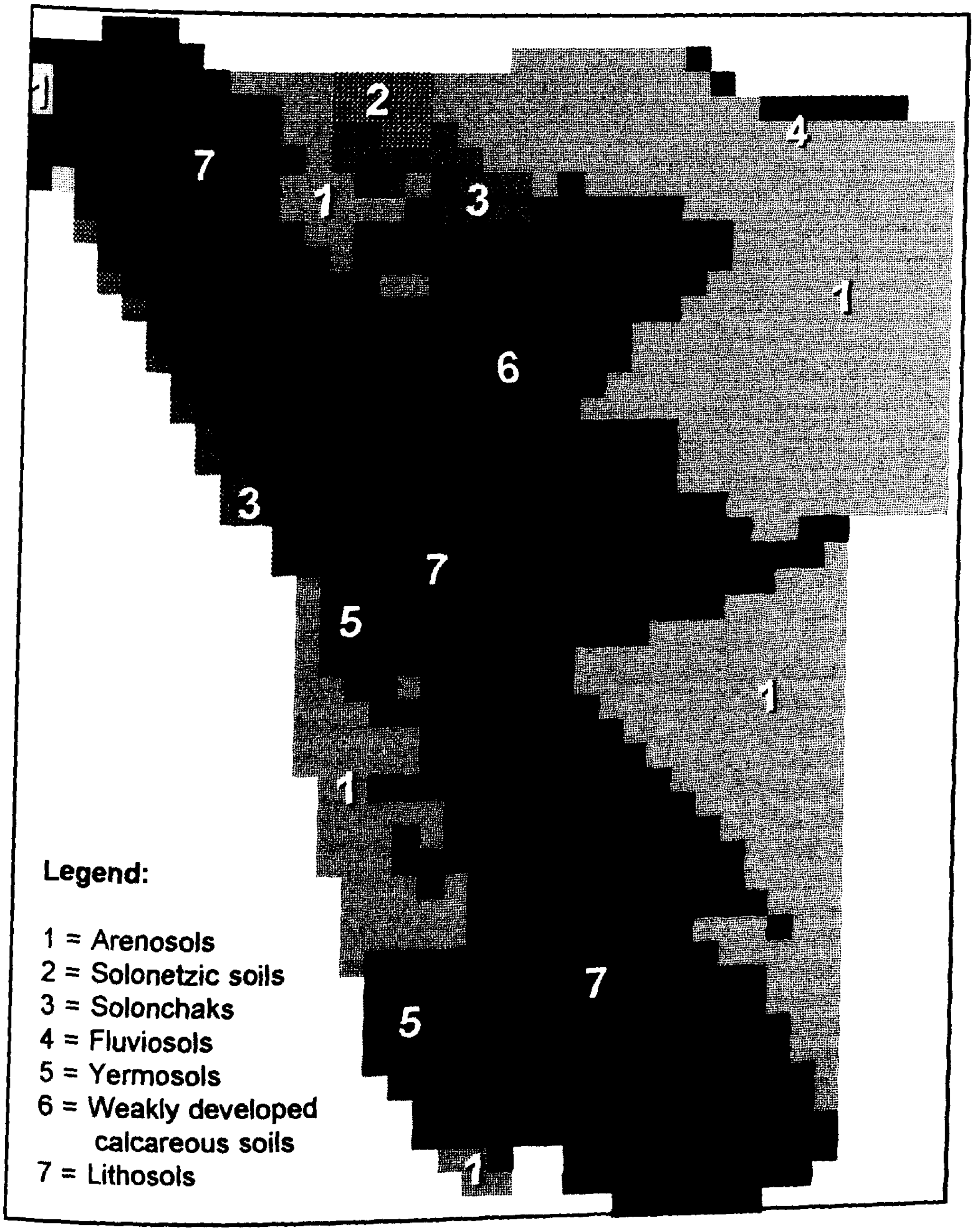
Appendix 2: Map of vegetation types in Namiba after Giess, 1971. Rasterised IDRISI image adapted from Strohbach, National Botanical Research Institute, Windhoek.

Appendix 3



Appendix 3: Estimated vegetation cover of Namibia for October 1994, derived from a NOAA image. Map modified from Strohbach et al., in prep..

Appendix 4



Appendix 4: Map of soiltypes in Namibia after *Heyne*, 1995. Processed and produced in the GIS IDRISI.

Appendix 5

Appendix 5: Rainfall data & Model derivation

Model derivation

- The raw data for annual average rainfall was provided by the Weather Bureau, Windhoek. Data for the two time periods of 1952-'67 and 1978-'93 were extracted for weather stations with a minimum of 12 years data records for each 15 year time period. 106 stations were included for 1952-'67 and 76 for 1978-93 (see raw data, black numbers). The mean, standard deviation and coefficient of variation were calculated for each station. Londitude and latitude were transformed to integer numbers.
- The annual means calculated by the Weather Bureau were checked for accuracy. It became apparent that the means were partially derived from data series with missing values. This could have serious implications for the validity of the derived mean. It was therefore decided to derive modelled data values for these locations by applying a surface interpolation available in the GIS IDRISI.
- Surfaces were interpolated for each individual rainfall year (April-March), excluding missing values as well as data which were thought to be unreliable (means derived from missing value data series).
- Modelled values from locations with missing data were read off the screen with the cursor (see raw data, red numbers). The mean, standard deviation and coefficient of variation were calculated for each station.
- The model data obtained for each location were tested against the original data by calculating Pearson's correlation coefficient between both data series.
- In cases were the correlation coefficient was above 0.5, the model was accepted. Only one data series, Swakopmund 1978-'93, showed an insufficient fit of the modelled data. In this case the original data was included in the final rainfall model.
- Average rainfall and coefficient of variation were modelled with the GIS IDRISI, using rainfall data adjusted for missing values. The obtained values were grouped into five rainfall classes (see Figure 3.1 and 3.2).

Rainfall data for 1952-'67

Station	Long	Lat	1952/53	1953/54	1954/55	1955/56	1956/57	1957/58	1958/59
Andara	21.47	-18.07	658.1	653.4	980.8	585.4	596.6	604	534.7
Aranos	19.12	-24.13	150.8	355.2	246.1	361.4	126.1	285.3	57.7
Aroab	19.65	-26.78	11.6	222.5	230.5	351.8	82	215.6	71.7
Aruab	16.58	-25.7	257.1	202.5	168	330	145.5	78.8	64.3
Aus	16.32	-26.68	172.4	136.1	34.6	72.8	17.2	72.5	70.7
Avonvrede	15.58	-19.3	254.7	796.9	276.3	374.9	261.7	374.4	179.8
Awagobital	17.87	-19.65	584.7	894.9	436	815.1	519.1	588.7	608
Bethanie	17.15	-26.05	170.7	177.6	146.6	184.7	83.8	56.8	52.6
Buitepos	19.95	-22.3	533	464.9	419	451.5	201.8	473.4	299.9
Bunja	19.35	-17.85	*649*	505.8	588	771.7	301.1	652.9	595.3
Choantsas	18.12	-18.87	418.5	753.6	564.3	720.7	446.6	454.5	308.5
Conradie	17.02	-19.08	462.6	919.8	519.5	669.2	489.7	660.2	475.3
Davignab	19.82	-27.53	101.1	145.1	298.2	310.3	87.4	163.6	61.6
Diaz Punt	15.1	-26.63	44	12.6	8	59	5.8	4.5	7.7
Duursdrift	18.97	-27.65	124.5	210.7	95	348	86.5	64	92.8
Elim	15.48	-17.72	364 354.4	808.8	356.1	407.3	395.1	436.1	207.7
Engela	15.87	-17.45	381.5	751.6	272.6	557.6	579.1	470.7	479.3
Erfdeel	19.97	-26.72	54.8	231.1	120.5	273.5	289 62.5	75.5	65.5
Excelsior	16.47	-26.2	207.5	165.1	98.7	282.4	172	33.9	31.2
Fairview	18.27	-19	545.6	703.8	482.3	855	486.7	568.1	*497* 397.3
Gababis	18.07	-19.97	338.3	530.8	483	712.4	296.3	527	410.2
Gaub	17.75	-19.45	669.3	898.4	794.6	855	672	682.5	609
Goabforte	17.18	-19.53	505.8	839.8	673	853.2	521.6	636.5	653.1
Gobabis	18.97	-22.47	447.2	622.6	517	391.7	365.4	403.6	153.8
Grenzland	17.23	-18.7	585.1	855.5	397.6	793.3	438.6	422.8	396.2
Grootfontein	18.1	-19.57	576.4	957.6	476.3	825.5	523.7	740.6	473.3
Hemeringshausen	16.85	-25.88	284	219.1	124.5	285	158.1	116	68.5
Hüttenhof	17.18	-19.48	536	948.4	666.1	919.3	599.4	655.8	541.7
Imperial	16.2	-19.88	350.4	752.2	390.1	442.4	431	517	229.5
Kamanjab	14.85	-19.63	256.8	550.1	265.3	402.5	321.6	279.7	156.4
Karasburg	18.75	-28.03	141.8	114.7	52.4	294	76.4	69.5	186.1
Katima Mulilo	24.25	-17.47	822.6	802.7	971.8	736.7	715.5	1464.1	591.7
Keetmanshoop T	18.13	-26.58	142.7	285.3	69.6	365.8	162.3	153.7	48.8
Keetmanshoop A	18.12	-26.53	149.6	235.7	73.9	380.3	113.5	193.8	69
Klifdrif	17	-26.53	94.5	201.5	51.5	191.5	55.5	61.5	29
Koes	19.15	-25.95	164.8	223.6	87.9	350.7	164.3	168.6	106.5
Konkiep	17.23	-26.75	135.5	205.3	22.5	363.5	48	*56*	20.3
Kuibis	16.85	-26.68	162	79.9	226.8	104.5	*129.6*	24	50.2
Lorelei	16.72	-27.07	145.5	118.5	70	148.3	47.7	65.3	34.3
Louwsvlei	19.8	-26.97	93.1	262.6	221.9	330.1	153.2	177.5	79.8
Manguams	16.88	-25.53	238.6	183.4	120.2	357.9	306.5	95.7	102.4
Maroelaboom	18.85	-19.27	404.6	639.8	426.9	739	452.9	619.8	425.9
Morgenson	19.37	-26.15	110.5	320.8	110	351.6	*352* 137	*149* 170	110.1
Nabas	19.57	-27.88	185.5	215.2	142	213.7	96.5	165.3	85.3
Nageib	17.58	-19.65	571.4	974.1	668.7	745.8	862.2	747.7	570.3
Namasvrede	19.53	-28.03	161.5	229.3	196	254.5	94.4	90	82.2
Namatanga	15.55	-19.08	*299*	*735* 403.1	388.6	413.5	392.7	329.6	219.3
Namutoni	16.97	-18.8	420.9	789.9	404	654.5	386.5	387.4	410.5
Naos	18.98	-27.2	131.6	421.7	142.5	424.6	79.7	150	83.5
Narugas	18.73	-28.12	*126*	*134*	56.7	385.6	89.3	60.9	100.7
Nkurenkuru	18.62	-17.62	733	731	578.1	753.8	586.2	831.4	*557* 222.8
Noahabeb	18.52	-27.65	80.1	188	109	286.6	*301*	116.2	120
Noibis	19.05	-27.87	123.2	213.6	86.7	321	78.2	151.6	86.
Nyangana	20.63	-18.02	657.7	747.2	699.2	634.1	586	737.2	623.6
Oase	17.85	-27.2	*132*	*237*	83.4	299.7	123.2	44.8	81
Ohopoho	13.08	-18.05	*300* 245.7	417.6	248	266.4	356.2	*358* 277.4	202.6
Okatana	15.72	-17.75	332.4	653.3	253.9	533.9	441.1	502.3	296.
Okaukuejo	15.92	-19.18	315.4	658.4	429.3	436.4	312.3	467.6	379.4
Omambonde	17.95	-20.05	459.6	514.5	419	653.2	373.4	448.8	*512* 284.8

t	1952/53	1953/54	1954/55	1955/56	1956/57	1957/58	1958/59	1959/60	1960/61	1962/63	1963/64
8.07	658.1	653.4	980.8	585.4	596.6	604	534.7	443.7	553.2	484.8	329.7
24.13	150.8	355.2	246.1	361.4	126.1	285.3	57.7	249.3	210.8	266.3	115.9
26.78	11.6	222.5	230.5	351.8	82	215.6	71.7	171	116.5	266.5	81.4
-25.7	257.1	202.5	168	330	145.5	78.8	64.3	75.7	147	285.5	98.1
26.68	172.4	136.1	34.6	72.8	17.2	72.5	70.7	165.9	57.7	163.6	148
-19.3	254.7	796.9	276.3	374.9	261.7	374.4	179.8	*268*	264.4	435.1	350.4
9.65	584.7	894.9	436	815.1	519.1	588.7	608	540.4	466.6	593.1	432
26.05	170.7	177.6	146.6	184.7	83.8	56.8	52.6	96.1	100.5	178.9	86
-22.3	533	464.9	419	451.5	201.8	473.4	299.9	431.6	203.1	161.9	256.8
17.85	*649*	505.8	588	771.7	301.1	652.9	595.3	343	426.2	323.2	314.8
18.87	418.5	753.6	564.3	720.7	446.6	454.5	308.5	405.8	389.3	546.3	319.9
19.08	462.6	919.8	519.5	669.2	489.7	660.2	475.3	414	415.9	724.7	473.7
27.53	101.1	145.1	298.2	310.3	87.4	163.6	61.6	162.7	168.8	196.5	63.5
26.63	44	12.6	8	59	5.8	4.5	7.7	19.6	20.8	32.8	36.8
27.65	124.5	210.7	95	348	86.5	64	92.8	137.5	125	172.5	60.5
17.72	364 354.4	808.8	356.1	407.3	395.1	436.1	207.7	317.9	267	573.4	346.6
17.45	381.5	751.6	272.6	557.6	579.1	470.7	479.3	417.5	463.6	607.2	441.8
26.72	54.8	231.1	120.5	273.5	289 62.5	75.5	65.5	122.5	138	*221* 124	38
-26.2	207.5	165.1	98.7	282.4	172	33.9	31.2	115.3	50.1	182.2	82.7
-19	545.6	703.8	482.3	855	486.7	568.1	*497* 397.3	391.3	379.7	*521*	62
19.97	338.3	530.8	483	712.4	296.3	527	410.2	410.5	364	441	299.8
19.45	669.3	898.4	794.6	855	672	682.5	609	582.3	669.5	647.3	445
19.53	505.8	839.8	673	853.2	521.6	636.5	653.1	575.8	527.5	861.2	374.9
22.47	447.2	622.6	517	391.7	365.4	403.6	153.8	367.8	198.2	426.6	282.4
-18.7	585.1	855.5	397.6	793.3	438.6	422.8	396.2	399.3	378.4	452.2	381.7
19.57	576.4	957.6	476.3	825.5	523.7	740.6	473.3	462.7	462.9	535.9	335.1
25.88	284	219.1	124.5	285	158.1	116	68.5	159.1	185.5	375.1	152
19.48	536	948.4	666.1	919.3	599.4	655.8	541.7	635.2	400.3	806.4	526
19.88	350.4	752.2	390.1	442.4	431	517	229.5	311.5	424.3	410	*319* 248.4
19.63	256.8	550.1	265.3	402.5	321.6	279.7	156.4	344.6	206.6	548	241.4
28.03	141.8	114.7	52.4	294	76.4	69.5	186.1	81.8	166.1	158.1	44.4
17.47	822.6	802.7	971.8	736.7	715.5	1464.1	591.7	641.7	673.8	844.8	493
26.58	142.7	285.3	69.6	365.8	162.3	153.7	48.8	57	137.1	170.8	65.6
26.53	149.6	235.7	73.9	380.3	113.5	193.8	69	93.8	147.3	159.5	57.6
26.53	94.5	201.5	51.5	191.5	55.5	61.5	29	22.7	52.7	79.7	*94* 13.5
25.95	164.8	223.6	87.9	350.7	164.3	168.6	106.5	112.7	160	123.8	136.5
26.75	135.5	205.3	22.5	363.5	48	*56*	20.3	78.4	100.7	148.5	82
26.68	162	79.9	226.8	104.5	*129.6*	24	50.2	35.5	43	66.1	105.1
27.07	145.5	118.5	70	148.3	47.7	65.3	34.3	117.9	36	*105* 168.7	134.4
26.97	93.1	262.6	221.9	330.1	153.2	177.5	79.8	110	118	188.1	134.7
25.53	238.6	183.4	120.2	357.9	306.5	95.7	102.4	177	128	296.1	112.9
19.27	404.6	639.8	426.9	739	452.9	619.8	425.9	426.5	361.8	365.5	294.3
26.15	110.5	320.8	110	351.6	*352* 137	*149* 170	110.1	*121*	*150*	185	61
27.88	185.5	215.2	142	213.7	96.5	165.3	85.3	79	*124* 120.4	219.2	71
19.65	571.4	974.1	668.7	745.8	862.2	747.7	570.3	492.1	509.6	641.4	471.5
28.03	161.5	229.3	196	254.5	94.4	90	82.2	113	117	165	82.2
19.08	*299*	*735* 403.1	388.6	413.5	392.7	329.6	219.3	282.9	179.9	278	277.2
-18.8	420.9	789.9	404	654.5	386.5	387.4	410.5	409	237	505.4	433.5
-27.2	131.6	421.7	142.5	424.6	79.7	150	83.5	166.7	196.5	318.5	93.5
28.12	*126*	*134*	56.7	385.6	89.3	60.9	100.7	67.6	139.5	101.3	34.7
17.62	733	731	578.1	753.8	586.2	831.4	*557* 222.8	479.7	475.9	751.5	650
27.65	80.1	188	109	286.6	*301*	116.2	120	167.5	247.5	159	44.5
27.87	123.2	213.6	86.7	321	78.2	151.6	86.1	131.7	161	150.8	53.9
18.02	657.7	747.2	699.2	634.1	586	737.2	623.6	456.5	578.6	555.8	455.9
-27.2	*132*	*237*	83.4	299.7	123.2	44.8	81	168.4	112	140.1	22.9
18.05	*300* 245.7	417.6	248	266.4	356.2	*358* 277.4	202.6	295.2	358.7	685.1	*303* 336.9
17.75	332.4	653.3	253.9	533.9	441.1	502.3	296.1	297	346	826.1	456
19.18	315.4	658.4	429.3	436.4	312.3	467.6	379.4	270.5	228.8	500.3	328.1
20.05	459.6	514.5	419	653.2	373.4	448.8	*512* 284.8	436.7	*423* 272.8	518.2	297.2
[illegible]	401.5	345.8	[illegible]	316	235.5	244.7	141.1	313.6	143.2	355.5	222.2

4	1964/65	1965/66	1966/67	1967/68	Mean	Stdv	Coeff.Var	*Mean*	*Stdv*	*Coeff.Var*	*Pearson's*
.7	311.9	709.5	558.5	651.5	571.26	156.68	27.43				
.9	162	125.6	245.3	206.2	208.39	85.84	41.19				
.4	181.2	93.4	180.3	228.5	168.06	87.08	51.81				
.1	116.5	332.5	223.7	148	173.92	88.81	51.07				
48	50.5	109	63.5	71	95.09	49.73	52.29				
.4	205.9	459.8	423.4	477	355.78	156.42	43.96	*350.29*	*152.7*	*43.59*	*1*
32	418.7	620.3	569	838.2	585.6	147.98	25.27				
86	103.6	61.5	209	139.5	121.13	51.03	42.13				
.8	111.2	280.8	383.7	379.3	333.31	125.93	37.78				
.8	256	380.4	611.5	919.5	493.74	192.33	38.95	*503.44*	*189.82*	*37.7*	*1*
.9	444.6	470.7	599	869.7	503.68	162.23	32.21				
.7	506	492.5	478.4	693.3	543.76	151.4	27.84				
.5	196.5	85.1	175.5	205	160.63	73.21	45.58				
.8	48.7	18.8	27.4	6.1	23.08	16.87	73.11				
.5	135	51.5	191	118	135.19	72.89	53.91				
.6	331.3	472.7	472.6	702.8	429.95	160.44	37.32	*425.83*	*155.88*	*36.61*	*1*
.8	536.5	592.5	535.8	1009	528.5	171.24	32.4				
38	199.3	73	277.5	156.7	138.74	79.38	57.21	*153.28*	*84.8*	*55.33*	*0.73*
2.7	89.8	78.3	138.8	127.2	119.61	69.05	57.73				
62	247	235.8	530	1007.2	490.97	247.81	50.47	*493.23*	*230.82*	*46.8*	*0.99*
.8	310	503	474.5	460.5	427.77	113.95	26.64				
45	468.5	537.1	597.7	985	658.42	160.61	24.39				
4.9	442.6	369.6	691.9	706	603.15	163.58	27.12				
2.4	364.9	389.7	496.9	391.9	382.48	115.34	30.16				
1.7	313.1	481	389.1	715	490.81	160.5	32.7				
5.1	330	696.9	519.1	833.7	572.94	184.98	32.29				
52	146.6	167.5	230	230	191.33	76.32	39.89				
26	438.6	445.2	512.4	622	600.01	173.12	28.85				
.4	301.8	406.4	414.8	608	419.69	130.06	30.99	*413.4*	*128.15*	*31*	*0.99*
1.4	268.2	536.2	308.5	348.7	329.91	121.47	36.82				
4.4	115.8	25	102.9	138.5	118.31	65.62	55.46				
93	269.2	557.2	611.9	821.2	722.6	259.38	35.9				
5.6	174.9	108.7	263.8	132	155.57	86.9	55.86				
7.6	129.3	90	189.8	121.5	147.39	79.21	53.74				
3.5	50.3	130	75.2	91.9	76.63	55.74	72.74	*85.97*	*51.09*	*59.43*	*0.89*
.5	132.5	108	148.7	174	163.89	66.42	40.52				
82	54.7	55	154.1	154	112.53	88.13	78.32	*109*	*86.31*	*79.18*	*1*
5.1	113.1	286	148.1	160.3	120.17	76.25	63.45	*120.76*	*73.71*	*61.03*	*1*
4.4	122.5	58	89.5	*147*	92.65	46.5	50.19	*92.06*	*42.88*	*46.58*	*0.94*
4.7	195.4	61.7	172.6	242.5	170.93	71.81	42.01				
2.9	108.3	116.3	313.7	115.5	180.76	90.68	50.17				
4.3	267	562.5	397	894.5	476.83	170.5	35.76	*477.75*	*169.81*	*35.54*	*1*
61	174	117	124.5	142	160.96	80.9	50.26	*169.91*	*90*	*52.97*	*0.79*
71	80.2	53	80	195	134.24	58.37	43.48	*134.46*	*58.32*	*43.37*	*1*
1.5	417.3	656.7	576	838	647.77	153.62	23.72				
2.2	124	57.5	147.7	142	137.28	54.67	39.83				
7.2	508	381.4	392 536.1	389.5	370.03	112.24	30.33	*377.33*	*137.98*	*36.57*	*0.74*
3.5	344.1	530.5	465	662 680	461.13	142.83	30.97	*460*	*141.05*	*30.66*	*1*
3.5	159.5	112.5	193	130	189.55	108.93	57.47				
4.7	73.6	109.9	85	81.4	108.05	84.64	78.33	*110.79*	*79.16*	*71.45*	*1*
50	491.7	751.5	784.8	803.5	630.15	168.59	26.75	*651.04*	*131.34*	*20.17*	*0.87*
4.5	139	112.3	146.5	95.5	141.25	62.65	44.35	*151.24*	*72.52*	*47.95*	*1*
3.9	195.1	91.9	133.8	148.4	140.46	64.31	45.79				
5.9	471.9	659.2	852.8	703.8	617.81	117.46	19.01				
2.9	135	70	199 211	58.3	117.67	72.48	61.6	*125.28*	*72.9*	*58.19*	*1*
6.9	310.7	247.9	406.9	466.8	335.26	119.01	35.5	*341.57*	*116.4*	*34.08*	*0.98*
456	444	551.6	385.1	683.8	456.3	162.17	35.54				
8.1	194.8	368.8	378.7	433.6	370.74	118.37	31.93				
7.2	320.2	355	459.5	509	418.33	102.9	24.6	*441.92*	*89.33*	*20.21*	*0.77*
2.2	228	251 381.5	316.2	394.3	278.91	85.72	30.73	*270.76*	*81.41*	*30.07*	*0.93*

Omajette	15.48	-21.03	300.3	367.5	281.5	274.6	235.2	195.3	83.6
Ombalantu	15.02	-17.52	343.6	812.6	494.5	675.3	577.9	339.5	1239.8
Ondangua	15.98	-17.9	315	679.8	276.1	476.5	343	443	392.4
Ondjou	14.82	-19.8	168.2	425.3	409.2	334.6	408.1	248.6	169
Ogandjera	15.08	-17.88	310.2	926.3	400.5	618	549.2	364.3	241.5
Onguma	17.1	-18.68	460.2	748.2	416	760.4	428.9	467.3	375.2
Oniipa	16.08	-17.95	828.4	313	433.5	344.8	424.4	378	257.7
Oranjemund	16.43	-28.57	82.7	79.1	61.5	84.1	15	48.1	28.2
Oshikuku	15.47	-17.07	372.6	849.4	443.4	459.7	510.7	567.1	184.5
Oshigambo	16.07	-17.82	352.4	892.3	288.4	360.5	429	478.2	260.8
Otavi	17.03	-19.63	442.5	726.6	506.5	827.9	613	567.8	515.3
Otjikondo	15.47	-19.88	424	642	438.2	296.6	336.7	265.7	275.6
Otjirukaku	17.98	-19.7	719.7	516.1	995.2	513.7	631.2	560.6	520.8
Otjitambi	15.18	-19.78	311.3	706.6	295.9	517.6	409	375.7	181.7
Otjituo	18.58	-19.07	*471*	746.9	344.5	752	482.6	505.6	525.9
Otjiwarongo	16.63	-20.45	532.3	770.1	508.7	602	355.3	462.6	476.8
Otjovasandu	15.87	-19.07	343.2	705	343.6	541.9	272.6	545.1	361.5
Philadelphia	17.43	-19.13	*538*	*870*	538.9	685.4	483.6	530.8	355.9
Prosit	15.8	-19.92	442.9	761.1	329.8	421.3	372	455.1	278.7
Rietfontein	17.77	-19.78	475.1	909.8	432.9	897.6	525.4	676.4	622.2
Rooiberg	16.8	-27.15	200.8	247.2	81.2	142.6	72.5	60.5	56.5
Rundu	19.77	-17.92	677.5	600.3	747.5	723.4	498	664.5	681.3
Sinclair	16.03	-25.72	167.8	83.5	18.6	230.3	185.6	86	118
Sissekab	17.2	-19.03	566.5	845.6	599.9	717.5	508.4	578.2	473.2
Soavis	17.13	-19.35	516.4	799.2	565.9	723.3	500.8	514.5	489.1
Springputz	19.37	-27.95	133.9	110.5	174	*242*	65.5	117	204.3
Streben	16.95	-19.45	422.6	883.5	510.5	665.9	426.5	608.6	779.8
Sus	18.4	-19.12	468.8	813.2	521	943.4	614	589	498.2
Swakopmund	14.52	-22.68	19.3	10.4	1.4	6.1	15.2	*20* 1.2	4.1
Swartkop	19.7	-27.08	142.4	277.5	213.4	238	90.1	146.3	84.1
Toggenburg	17.95	-19.48	526.9	842.1	542	*810*	491.8	676.5	497.9
Tondoro	18.78	-17.77	*668*	775.2	620.5	788.5	502.5	560.8	561.5
Tranental	19.55	-27.13	65.5	136.5	297.5	224.6	120.5	171	77
Tshandi	14.88	-17.92	*332* 279.2	764.3	401.6	555.6	592.8	327.3	328.4
Tsintsabis	17.95	-18.78	637	714.2	410.5	755.3	449.5	608.6	419.7
Tsumeb	17.72	-19.23	535.5	948.8	494.5	815.7	528.7	508.8	538
Ukamas	19.78	-28.03	*154*	421.2	135.5	202.2	125	109	12
Una	17.37	-20	312.9	652.5	464.7	636.8	471.1	543.3	571.5
Urieis Ekango	15.02	-19.73	301.4	597.6	280.2	258.6	320.1	283.3	115.2
Usakos	15.65	-21.98	238.1	220.8	142.7	202	240.3	76.1	20.5
Walvis Bay	14.05	-22.95	20.9	11.4	5	10.7	22.8	0.5	1.4
Warmbad	18.73	-28.45	44.1	127.9	33.3	324.1	103.7	59.1	46.8
Warmfontein	19.3	-27.1	91.2	309	196.5	306.9	218.8	277.8	107.5
Westfalenhof	16.4	-22.23	262.8	267.3	258.8	297.3	170.7	105.4	133.1
Wilderness	17.05	-23.68	281.6	435.1	170	412.2	*412*	234.7	114.7
Windhoek	17.1	-22.57	411.4	741.5	346.9	491.6	398.1	532.5	224

367.5	281.5	274.6	235.2	195.3	83.6	143.9	168.9
812.6	494.5	675.3	577.9	339.5	1239.8	473.5	382.5
679.8	276.1	476.5	343	443	392.4	272.5	326.8
425.3	409.2	334.6	408.1	248.6	169	200.8	257.3
926.3	400.5	618	549.2	364.3	241.5	327.8	293.3
748.2	416	760.4	428.9	467.3	375.2	533.2	361.4
313	433.5	344.8	424.4	378	257.7	259.9	281.4
79.1	61.5	84.1	15	48.1	28.2	53	14.8
849.4	443.4	459.7	510.7	567.1	184.5	307.8	365.7
892.3	288.4	360.5	429	478.2	260.8	328.9	366.5
726.6	506.5	827.9	613	567.8	515.3	454	463.5
642	438.2	296.6	336.7	265.7	275.6	164.3	317.1
516.1	995.2	513.7	631.2	560.6	520.8	460.4	*423*
706.6	295.9	517.6	409	375.7	181.7	254.8	240.3
746.9	344.5	752	482.6	505.6	525.9	364.5	307.8
770.1	508.7	602	355.3	462.6	476.8	350.1	431.4
705	343.6	541.9	272.6	545.1	361.5	307.4	309.8
870	538.9	685.4	483.6	530.8	355.9	354.6	414.4
761.1	329.8	421.3	372	455.1	278.7	252.6	369.1
909.8	432.9	897.6	525.4	676.4	622.2	472.2	*469* 380
247.2	81.2	142.6	72.5	60.5	56.5	112.7	93.5
600.3	747.5	723.4	498	664.5	681.3	521	549.8
83.5	18.6	230.3	185.6	86	118	84.5	85.5
845.6	599.9	717.5	508.4	578.2	473.2	344.8	486.4
799.2	565.9	723.3	500.8	514.5	489.1	366	443
110.5	174	*242*	65.5	117	204.3	102.3	118.5
883.5	510.5	665.9	426.5	608.6	779.8	465.5	420
813.2	521	943.4	614	589	498.2	409.9	471.8
10.4	1.4	6.1	15.2	*20* 1.2	4.1	9.3	3.4
277.5	213.4	238	90.1	146.3	84.1	101.4	157.3
842.1	542	*810*	491.8	676.5	497.9	595.4	444.6
775.2	620.5	788.5	502.5	560.8	561.5	488.6	458.4
136.5	297.5	224.6	120.5	171	77	107.4	130.5
764.3	401.6	555.6	592.8	327.3	328.4	316.1	304.9
714.2	410.5	755.3	449.5	608.6	419.7	429.9	255.7
948.8	494.5	815.7	528.7	508.8	538	612.1	557
421.2	135.5	202.2	125	109	12	145.5	122.5
652.5	464.7	636.8	471.1	543.3	571.5	399.8	364.1
597.6	280.2	258.6	320.1	283.3	115.2	241.9	148
220.8	142.7	202	240.3	76.1	20.5	81.1	116.3
11.4	5	10.7	22.8	0.5	1.4	1.2	22.9
127.9	33.3	324.1	103.7	59.1	46.8	79	143.1
309	196.5	306.9	218.8	277.8	107.5	137	205.6
267.3	258.8	297.3	170.7	105.4	133.1	137.7	221.2
435.1	170	412.2	*412*	234.7	114.7	97.1	120.1
741.5	346.9	491.6	398.1	532.5	224	220.7	203.4

395.7	186.7	163	21
629.3	291.6	425.7	383
657.6	394.4	370.8	417
496	*227*	208.8	388
520.3	320.8	251	333
472.8	454.8	386.5	41
404.2	394.1	411.2	34
70.2	69.2	45.7	4
665.4	438.9	397.4	535
606.3	411.2	369.5	359
692.2	499.6	501.8	458
429.8	169.1	289.3	483
746.2	331.4	332.4	679
592.8	195.9	433.4	450
414.3	350.6	280.8	542
502.1	423.4	469.6	490
478.5	332.9	287	412
614 461.5	401.8	173.8	541
474.1	323	329.6	356
522.2	434.7	327.2	499
100	118.3	84.6	96
466.2	358.2	317.6	628
214	84.5	78	2
576.5	429.4	419.1	507
542.6	377.1	348.3	471
68.1	59.4	*114* 52.2	46
487.3	349.5	428	4
522.7	304.5	303.5	3
30.8	4.5	5.5	27
232	34.9	179.4	63
542.9	357.8	289	674
559 479.4	464.2	481.6	535
158.6	38	177.9	67
709	288	336.4	438
462.4	379.2	424	530
509.1	324.9	386.4	575
138.5	21	106.5	84
530.5	382.1	372.3	4
433.8	225.1	257.6	570
367.1	74	122	135
13.5	25.7	5.6	9
98.2	31	47	*79* 31
162	62.5	157.5	9
439.1	222.8	217.5	292
358.7	93.6	183.1	1
633.2	354	344.9	346

168.9	395.7	186.7	163	212	390	301.7	234.39	103	43.94		
382.5	629.3	291.6	425.7	383.9	555.4	574	536.24	234.88	43.8		
326.8	657.6	394.4	370.8	417.3	339.8	542.5	405.29	129.37	31.92		
257.3	*496*	*227*	208.8	388.9	210.9	69.1	256.86	118.28	46.05	*269.94*	*125.7*
293.3	520.3	320.8	251	333.5	491.5	680.5	427.3	192.73	45.1		
361.4	472.8	454.8	386.5	419	507.1	579.9	482.12	123.36	25.59		
281.4	404.2	394.1	411.2	342	542	541	426.76	154.21	36.14		
14.8	70.2	69.2	45.7	46	33	14.7	51.36	24.73	48.16		
365.7	665.4	438.9	397.4	535.8	468.3	778.3	476.33	176.02	36.95		
366.5	606.3	411.2	369.5	359.1	357	678.7	428.4	165.36	38.6		
463.5	692.2	499.6	501.8	458.1	630.8	548.3	551.92	118.89	21.54		
317.1	429.8	169.1	289.3	483.2	325	624.8	353.03	146	41.36		
423	746.2	331.4	332.4	679.8	510.3	684.2	570.77	178.27	31.23	*561.54*	*176.1*
240.3	592.8	195.9	433.4	450.6	370.1	491.7	373.93	155.38	41.55		
307.8	414.3	350.6	280.8	542.8	473.5	672.1	470.31	157.06	33.4	*470.36*	*151.7*
431.4	502.1	423.4	469.6	490.2	492.9	636.7	481.87	126.89	26.33		
309.8	478.5	332.9	287	412.8	349.9	702.3	410.22	143.24	34.92		
414.4	*614* 461.5	401.8	173.8	541.7	394.3	699.8	458.52	137.66	30.02	*498.74*	*167.3*
369.1	474.1	323	329.6	356.6	501.5	595.9	403.68	138.41	34.29		
469 380	522.2	434.7	327.2	499.7	474.1	742	556.87	170.38	30.6	*562.43*	*165.6*
93.5	100	118.3	84.6	96.5	189.9	156.6	114.74	59.33	51.71		
549.8	466.2	358.2	317.6	628.6	713.4	760.9	592.79	133.75	22.56		
85.5	214	84.5	78	240	178.7	63.5	130.34	67.02	51.42		
486.4	576.5	429.4	419.1	507.1	506.2	675	535.27	133.98	25.03		
443	542.6	377.1	348.3	471.5	442.4	646.9	509.49	126.17	24.76		
118.5	68.1	59.4	*114* 52.2	46.1	51.9	127.3	101.82	46.54	45.71	*114.44*	*54.8*
420	487.3	349.5	428	432	385.6	721.5	521.24	161.85	31.05		
471.8	522.7	304.5	303.5	393	512.6	741.3	535.74	173.96	32.47		
3.4	30.8	4.5	5.5	27.6	10.5	44.3	13.26	12.2	91.99	*14.44*	*11.8*
157.3	232	34.9	179.4	63.5	159.6	174.5	151.52	67.24	44.38		
444.6	542.9	357.8	289	674.9	818.5	684.8	560.43	157.46	28.1	*576.03*	*164.4*
458.4	*559* 479.4	464.2	481.6	535.3	881.4	689.4	582.98	137.84	23.64	*593.27*	*13*
130.5	158.6	38	177.9	67.5	196.5	151	143.94	66.51	46.2		
304.9	709	288	336.4	438.9	260	716.5	435.43	173.43	39.83	*438.73*	*170.7*
255.7	462.4	379.2	424	530.2	495.9	878.8	510.04	168.13	32.96		
557	509.1	324.9	386.4	575.9	589.9	741.9	572.94	153.06	26.72		
122.5	138.5	21	106.5	84.5	111	142	132.49	92.61	69.9	*133.84*	*89.6*
364.1	530.5	382.1	372.3	448	504	544.4	466.69	111.34	23.86		
148	433.8	225.1	257.6	570.1	343.1	438.5	311.93	137.67	44.13		
116.3	367.1	74	122	135.5	155.5	152.7	149.35	88.23	59.08		
22.9	13.5	25.7	5.6	9.7	*46* 18	8.6	11.51	8.33	72.38	*13.26*	*11.9*
143.1	98.2	31	47	*79* 31.1	150.3	118	94.1	73.47	78.08	*97.09*	*71.6*
205.6	162	62.5	157.5	95	143	121	172.73	75.57	43.75		
221.2	439.1	222.8	217.5	292.2	255.3	238.1	230.72	80.29	34.8		
120.1	358.7	93.6	183.1	139	209.5	98.6	204.8	116.38	56.83	*217.75*	*123.*
203.4	633.2	354	344.9	346.9	331.1	410.8	390.3375	149.2697	38.24118		

12	390	301.7	234.39	103	43.94				
3.9	555.4	574	536.24	234.88	43.8				
7.3	339.8	542.5	405.29	129.37	31.92				
3.9	210.9	69.1	256.86	118.28	46.05	*269.94*	*125.75*	*46.58*	*1*
3.5	491.5	680.5	427.3	192.73	45.1				
19	507.1	579.9	482.12	123.36	25.59				
42	542	541	426.76	154.21	36.14				
46	33	14.7	51.36	24.73	48.16				
5.8	468.3	778.3	476.33	176.02	36.95				
9.1	357	678.7	428.4	165.36	38.6				
3.1	630.8	548.3	551.92	118.89	21.54				
3.2	325	624.8	353.03	146	41.36				
9.8	510.3	684.2	570.77	178.27	31.23	*561.54*	*176.14*	*31.37*	*1*
0.6	370.1	491.7	373.93	155.38	41.55				
2.8	473.5	672.1	470.31	157.06	33.4	*470.36*	*151.74*	*32.26*	*1*
0.2	492.9	636.7	481.87	126.89	26.33				
2.8	349.9	702.3	410.22	143.24	34.92				
1.7	394.3	699.8	458.52	137.66	30.02	*498.74*	*167.39*	*33.56*	*0.96*
6.6	501.5	595.9	403.68	138.41	34.29				
9.7	474.1	742	556.87	170.38	30.6	*562.43*	*165.61*	*29.45*	*0.99*
6.5	189.9	156.6	114.74	59.33	51.71				
8.6	713.4	760.9	592.79	133.75	22.56				
40	178.7	63.5	130.34	67.02	51.42				
7.1	506.2	675	535.27	133.98	25.03				
1.5	442.4	646.9	509.49	126.17	24.76				
6.1	51.9	127.3	101.82	46.54	45.71	*114.44*	*54.84*	*47.92*	*0.94*
32	385.6	721.5	521.24	161.85	31.05				
93	512.6	741.3	535.74	173.96	32.47				
7.6	10.5	44.3	13.26	12.2	91.99	*14.44*	*11.86*	*82.15*	*0.92*
3.5	159.6	174.5	151.52	67.24	44.38				
4.9	818.5	684.8	560.43	157.46	28.1	*576.03*	*164.42*	*28.54*	*1*
5.3	881.4	689.4	582.98	137.84	23.64	*593.27*	*132*	*22.25*	*0.99*
7.5	196.5	151	143.94	66.51	46.2				
8.9	260	716.5	435.43	173.43	39.83	*438.73*	*170.74*	*38.92*	*1*
0.2	495.9	878.8	510.04	168.13	32.96				
5.9	589.9	741.9	572.94	153.06	26.72				
4.5	111	142	132.49	92.61	69.9	*133.84*	*89.63*	*66.97*	*1*
48	504	544.4	466.69	111.34	23.86				
0.1	343.1	438.5	311.93	137.67	44.13				
5.5	155.5	152.7	149.35	88.23	59.08				
9.7	*46* 18	8.6	11.51	8.33	72.38	*13.26*	*11.94*	*90.08*	*0.82*
1.1	150.3	118	94.1	73.47	78.08	*97.09*	*71.69*	*73.83*	*0.99*
95	143	121	172.73	75.57	43.75				
2.2	255.3	238.1	230.72	80.29	34.8				
139	209.5	98.6	204.8	116.38	56.83	*217.75*	*123.79*	*56.85*	*1*
6.9	331.1	410.8	390.3375	149.2697	38.24118				

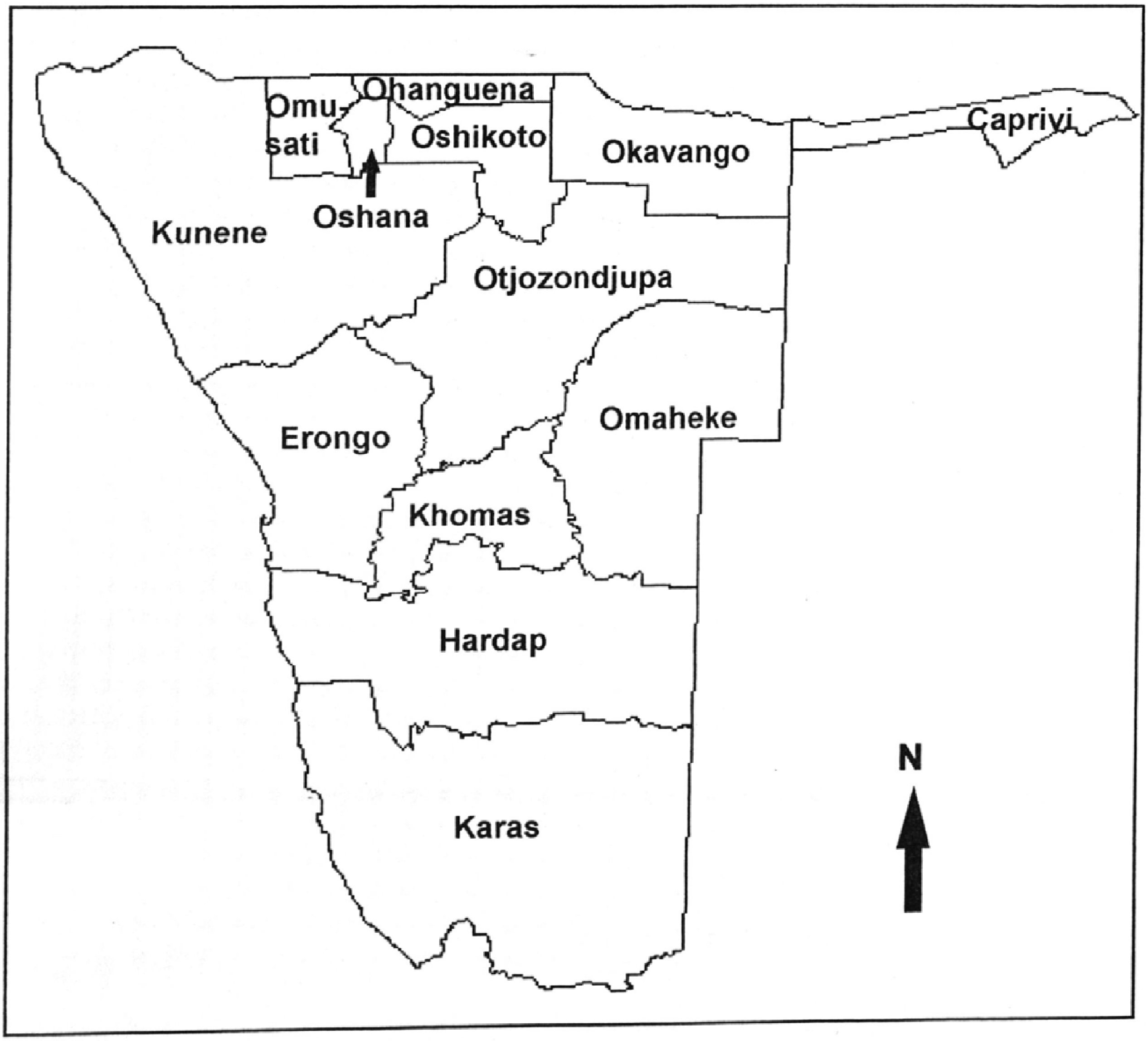
Rainfall data for 1978-'93

Station	Long	Lat	1978/79	1979/80	1980/81	1981/82	1982/83	1983/84	1984/85	1985/
Ai-Ais	17.05	-27.93	0	19	77 0	32.3	0	12.5	62.6	7
Andara	21.47	-18.07	389.3	485.1	928.1	518.1	407	483 540.6	563.3	53
Aranos	19.12	-24.13	260	140.8	94	31	76	208.5	156 97.5	8
Aruab	16.58	-25.7	96.5	154	65.5	138.5	99	246	109.2	17
Awagobital	17.87	-19.65	555.9	666.6	407	479	360	562	408	
Bethanie	17.15	-26.05	59	146.6	66	36	118	107	102	
Blanksdam	18.3	-27.78	70.5	99.6	51.5	33.5	167.7	130.1	100.7	29
Blinkoog	19.1	-27.63	90.2	123.7	142.8	51.1	45.6	144.2	98.6	12
Buitepos	19.95	-22.3	327.8	414.6	485.9	461.4	301	374.9	206.7	
Bunja	19.35	-17.85	589	550.8	623.3	451.5	385	535.4	446.8	54
Choantsas	18.12	-18.87	277	435.7	375.4	246.4	255	481.5	535.5	43
Davignab	19.82	-27.53	90.5	166.0	78.5	91.3	80.0	110.1	50.5	10
Excelsior	16.47	-26.2	115.7	78.5	42.9	56.7	71	92.6	113.4	12
Gababis	18.07	-19.97	342.5	582	411	476	401	388.2	409.9	39
Gaikos	18.4	-19.45	425	703	461.5	379.4	440	562.4	442.8	62
Goabforte	17.18	-19.53	604.2	559	433.4	543.1	426.8	594.8	392.7	50
Gobabis	18.97	-22.47	382.2	386.8	250.4	250	258	487.5	201	
Grootfontein	18.1	-19.57	372.7	681.5	408.8	545.8	357.6	597.6	390.5	54
Haremub	16.2	-25.6	164.5	184.6	67.8	68.5	73.6	175	137.8	21
Hemeringshausen	16.85	-25.88	118.3	155	14	21	49.8	138.5	65.8	
Hüttenhof	17.18	-19.48	593.1	634.4	479.9	521	389.9	606.9	531.5	45
Kamanjab	14.85	-19.63	269.8	199.4	71.5	199	172.1	247.8	286	
Karasburg	18.75	-28.03	119	140.1	123.5	42	110.5	114.5	79	
Keetmanshoop T	18.13	-26.58	105	187.6	85.2	35.1	88.6	134.8	220.5	20
Keetmanshoop A	18.12	-26.53	105.2	153.2	87.5	54.4	102.6	144.9	283.6	
Koes	19.15	-25.95	139	121.2	104.8	40.8	50	20.5	79.7	10
Koukuas	18.3	-18.92	459.5	550.5	382.5	395.3	340.5	613.5	458.2	5
Kuibis	16.85	-26.68	113.6	159.5	41	41	34.5	131.5	80.1	2
Louwsvlei	19.8	-26.97	114.9	174.2	58.5	87	110.6	94.7	103.9	
Lupala	19.08	-17.85	416.3	592.9	429.6	520 416.1	531	429	445	12
Manguams	16.88	-25.53	195.9	200.8	40.4	13.5	74.9	187.5	124	
Maroelaboom	18.85	-19.27	512.1	362.8	409.1	332.3	283	548.4	630.3	3
Mashara	20.15	-17.9	503.4	683.9	607.9	456.5	419.1	535.4	486.1	6
Morgenson	19.37	-26.15	117.3	156.6	111.5	100.3	82.2	120.1	130.2	2
Namasvrede	19.53	-28.03	91.9	146.8	69.1	85.6	29.5	59	74	1
Namatanga	15.55	-19.08	434.3	272.2	231.2	293.8	223.7	349.5	401.7	
Namutoni	16.97	-18.8	550.4	305.8	249.5	515.9	253.2	466.1	407.8	3
Naos	18.98	-27.2	117.4	302.9	149	100.4	49.8	319.8	127.5	1
Narugas	18.73	-28.12	52.4	174.46	69.8	41.3	42.2	64	50	
Nettleton	16.35	-19.92	396	383.4	181.7	381	331.6	374.8	301.7	4
Noahabeb	18.52	-27.65	95.5	190 180	69	57	88	163	109.5	3
Noibis	19.05	-27.87	84.6	144.2	90.8	44	61.5	128	76	2
Okatana	15.72	-17.75	440.9	465.5	281.4	413.5	329.1	658.3	507.7	4
Okaukuejo	15.92	-19.18	463.8	285.9	222.6	318	232.1	353.2	283.7	4
Ombalantu	15.02	-17.52	369	294.3	253.7	268.5	264.3	376.4	304.9	3
Ombika	15.95	-19.03	375.2	340.5	226 201.9	292 429	209.2	329.2	310.2	5
Ondjou	14.82	-19.8	225	257	46	137.5	85.5	280	196	3
Ongongo	15.3	-17.07	394.8	278.3	326	369.8	367.9	325.7	317.5	3
Oniipa	16.08	-17.95	489.5	411.9	241.6	398.5	314	591.4	572.2	3
Oranjemund	16.43	-28.57	22.2	21.3	79.2	118.4	52.1	115.9	45.5	
Oshikuku	15.47	-17.07	470.2	490.3	228.1	473.8	344.9	533.8	518.5	4
Otavi	17.03	-19.63	579.5	461	389.2	642.8	353.5	574.4	523.4	5
Otjirukaku	17.98	-19.7	482.3	938.5	416.3	1131.6	421.5	601.8	430.5	
Otjitambi	15.18	-19.78	263.1	322.3	131.2	219.5	242.6	254 265.9	309.5	
Otjituo	18.58	-19.07	349	535	357	286	229.8	339.2	357.5	611
Rishon	18.73	-27.3	135.9	234	154.5	105	105	170.5	98.5	3
Rundu	19.77	-17.92	476.4	438.7	546.6	429.3	435.9	422.2	735.7	6
Sendeling	15.1	-19.58	343.2	333.4	154.4	180.4	177	253	349.5	
Sissekab	17.2	-19.03	486.6	554.9	348.3	500.7	347.1	595.8	387.6	4
		-19.93	476.5	479.1	282	423.3	428.3	530.3	465.9	

88/89	1989/90	1990/91	1991/92	1992/93	Mean	Stdv	Coeff.Var	*Mean*	*Stdv*	*Coeff.Var*	Pearson'
83	16	51.7	13.5	43	35.22	32.48	92.21	*40.35*	*32.6*	*80.78*	0.8
1217.4	449	429.3	595.8	535.6	586.59	221.71	37.8	*570.77*	*219.76*	*38.5*	
219.4	217.6	338.4	160.4	*193* 154	152.2	84.11	55.26	*168.72*	*79.47*	*47.1*	0.8
273	148	96	60.6	190.5	145.79	61.99	42.52	*145.79*	*61.99*	*42.52*	
782.3	483.4	417.3	336.2	575.2	512.53	119.9	23.39	*512.53*	*119.9*	*23.39*	
174	54.2	81.2	32.5	113.1	100.27	47.03	46.9	*100.27*	*47.03*	*46.9*	
228.2	43.2	62.3	48	164.2	117.33	73.73	62.83				
390	113.3	175.6	182.6	*186* 54	129.13	83.31	64.52	*137.93*	*81.76*	*59.28*	0.9
349.5	133.5	380.9	215	217.1	313.18	104.18	33.27				
880.4	438.1	588.8	360.5	553.4	520.09	131.66	25.31	*520.09*	*131.66*	*25.31*	
652.5	328.5	452	343.7	422.2	391.69	111.69	28.51				
146.5	139.5	135.5	95.5	47.5	105.23	42.08	39.99				
184.3	54.1	91.1	25.4	144.4	97.88	43.87	44.82	*97.88*	*43.87*	*44.82*	
410.6	329	339.5	292.5	411.5	403.68	70.63	17.5	*403.68*	*70.63*	*17.5*	
634.6	447.7	426.5	479.1	321.7	475.04	88.48	18.63	*486.9*	*102.23*	*21*	
683.6	599.8	451.1	494	479.9	513.91	82.62	16.08				
331	302	429.8	333.7	299.3	334.08	85.19	25.5	*325.81*	*82.34*	*25.27*	
476.6	393.4	453.4	351.4	494.9	460.19	95.92	20.84				
263.6	61.1	84	90.4	99.7	132.71	61.53	46.36	*132.71*	*61.53*	*46.36*	
243	74	89.5	32.1	143	124.9	92.46	74.03	*124.9*	*92.46*	*74.03*	
519.1	632.3	475	392.2	440.7	506.84	84.34	16.64				
239.5	282	373.5	251	299	245.91	74.28	30.2				
164.6	120.3	49.5	108.5	113.8	113.55	59.56	52.45				
244	*63* 59.2	*75* 149.4	179.4	126	131.88	63.87	48.43	*132.85*	*67.94*	*51.14*	0.9
244.4	58.9	66.4	147.8	168.5	130.61	70.04	53.63	*135.77*	*70.39*	*51.84*	
210.7	78	114	60.6	91.5	122.84	81.35	66.23	*122.84*	*81.35*	*66.23*	
804.5	286	442	306	*399* 330.6	458.67	141.01	30.74	*463.23*	*137.64*	*29.71*	0.9
150.5	54	130.9	80.8	123.2	104.07	50.54	48.57				
248.5	106	196.5	88	148.5	127.77	59.98	46.95				
27 288	*402*	586.7	431.2	427.5	510.51	234.87	46.01	*555.91*	*226.04*	*40.66*	0.
154.5	145	67	67.9	130	130.39	63.43	48.65	*130.39*	*63.43*	*48.65*	
913.1	419.5	444.7	314.7	*354* 58	428.74	188.29	43.92	*448.47*	*160.05*	*35.69*	0.9
609.9	331	583.9	372.6	398.1	505.15	116.21	23.01				
292.1	147.4	224.4	114	*99* 126.3	156.27	60.4	38.65	*154.45*	*61.76*	*39.99*	0.9
215.6	63.5	123	128	89.7	101.79	48.6	47.75				
500	301	415	311.5	376.5	345.73	89.39	25.85				
636.2	437.4	380.7	368.8	428	404.31	107.02	26.47				
250	122.3	292.3	116.9	214.7	183.81	83.84	45.61				
135.5	9.5	68.5	64.7	79.1	81.66	54.97	67.31				
469.5	203	725.9	443	378.8	376	131.18	34.89				
166.6	90.6	123.5	*100* 101.4	199.8	135.57	70.17	51.76				
261	141.8	164.7	113.1	226	132.43	71.95	54.33				
542.2	351	604.4	411.2	330.5	427.07	113.78	26.64				
337.4	395.9	279.3	207.8	301.9	307.69	74.66	24.27	*307.69*	*74.66*	*24.27*	
468	201.5	190.3	200.5	216	261.92	81.13	30.97	*278.13*	*92.15*	*33.13*	
355.5	401.8	448.6	288.2	345.7	354.19	88.56	25	*346.66*	*84.71*	*24.44*	0.9
221	454.5	155	199.5	257.5	214.03	97.68	45.64				
460.6	381.71	532	288.2	341.4	356.39	67.54	18.95				
430	364.5	407.7	495.2	192.6	383.59	121.6	31.7				
49.5	61.5	29.1	65	32.5	58.44	30.55	52.27				
471.8	447.2	511.9	317.8	314.9	417.67	93.46	22.38				
707.3	451.7	476.5	363.1	337.4	478.47	114.82	24	*477.31*	*110.73*	*23.2*	
724.5	384	525.5	322.6	455.5	555.24	219.36	39.51				
362.9	278	343.1	*221* 56	222.5	244.86	87.22	35.62	*261.54*	*70.05*	*26.78*	0.8
524	276.5	468.3	331	356.5	355.89	104.84	29.46	*379.75*	*119.47*	*31.46*	0.6
363.5	117	148	132	187	183.43	98.91	53.92				
816.9	501.5	437.5	356.5	495.6	524.64	137.29	26.17				
330.5	328	277	196.5	221	263.49	77.58	29.44				
514.8	487.1	308.5	379.8	268.7	426.8	98.1	22.98				

/90	1990/91	1991/92	1992/93	Mean	Stdv	Coeff.Var	*Mean*	*Stdv*	*Coeff.Var*	Pearson's
16	51.7	13.5	43	35.22	32.48	92.21	40.35	32.6	80.78	0.81
449	429.3	595.8	535.6	586.59	221.71	37.8	570.77	219.76	38.5	1
17.6	338.4	160.4	193 154	152.2	84.11	55.26	168.72	79.47	47.1	0.88
148	96	60.6	190.5	145.79	61.99	42.52	145.79	61.99	42.52	1
83.4	417.3	336.2	575.2	512.53	119.9	23.39	512.53	119.9	23.39	1
54.2	81.2	32.5	113.1	100.27	47.03	46.9	100.27	47.03	46.9	1
43.2	62.3	48	164.2	117.33	73.73	62.83				
13.3	175.6	182.6	186 54	129.13	83.31	64.52	137.93	81.76	59.28	0.91
33.5	380.9	215	217.1	313.18	104.18	33.27				
38.1	588.8	360.5	553.4	520.09	131.66	25.31	520.09	131.66	25.31	1
28.5	452	343.7	422.2	391.69	111.69	28.51				
9.5	135.5	95.5	47.5	105.23	42.08	39.99				
54.1	91.1	25.4	144.4	97.88	43.87	44.82	97.88	43.87	44.82	1
329	339.5	292.5	411.5	403.68	70.63	17.5	403.68	70.63	17.5	1
47.7	426.5	479.1	321.7	475.04	88.48	18.63	486.9	102.23	21	1
99.8	451.1	494	479.9	513.91	82.62	16.08				
302	429.8	333.7	299.3	334.08	85.19	25.5	325.81	82.34	25.27	1
93.4	453.4	351.4	494.9	460.19	95.92	20.84				
1.1	84	90.4	99.7	132.71	61.53	46.36	132.71	61.53	46.36	1
74	89.5	32.1	143	124.9	92.46	74.03	124.9	92.46	74.03	1
2.3	475	392.2	440.7	506.84	84.34	16.64				
282	373.5	251	299	245.91	74.28	30.2				
20.3	49.5	108.5	113.8	113.55	59.56	52.45				
9.2	75 149.4	179.4	126	131.88	63.87	48.43	132.85	67.94	51.14	0.95
8.9	66.4	147.8	168.5	130.61	70.04	53.63	135.77	70.39	51.84	1
78	114	60.6	91.5	122.84	81.35	66.23	122.84	81.35	66.23	1
286	442	306	399 330.6	458.67	141.01	30.74	463.23	137.64	29.71	0.99
54	130.9	80.8	123.2	104.07	50.54	48.57				
106	196.5	88	148.5	127.77	59.98	46.95				
402	586.7	431.2	427.5	510.51	234.87	46.01	555.91	226.04	40.66	0.8
145	67	67.9	130	130.39	63.43	48.65	130.39	63.43	48.65	1
9.5	444.7	314.7	354 58	428.74	188.29	43.92	448.47	160.05	35.69	0.92
331	583.9	372.6	398.1	505.15	116.21	23.01				
7.4	224.4	114	99 126.3	156.27	60.4	38.65	154.45	61.76	39.99	0.99
3.5	123	128	89.7	101.79	48.6	47.75				
301	415	311.5	376.5	345.73	89.39	25.85				
7.4	380.7	368.8	428	404.31	107.02	26.47				
2.3	292.3	116.9	214.7	183.81	83.84	45.61				
9.5	68.5	64.7	79.1	81.66	54.97	67.31				
203	725.9	443	378.8	376	131.18	34.89				
0.6	123.5	100 101.4	199.8	135.57	70.17	51.76				
1.8	164.7	113.1	226	132.43	71.95	54.33				
351	604.4	411.2	330.5	427.07	113.78	26.64				
5.9	279.3	207.8	301.9	307.69	74.66	24.27	307.69	74.66	24.27	1
1.5	190.3	200.5	216	261.92	81.13	30.97	278.13	92.15	33.13	1
1.8	448.6	288.2	345.7	354.19	88.56	25	346.66	84.71	24.44	0.91
4.5	155	199.5	257.5	214.03	97.68	45.64				
.71	532	288.2	341.4	356.39	67.54	18.95				
4.5	407.7	495.2	192.6	383.59	121.6	31.7				
1.5	29.1	65	32.5	58.44	30.55	52.27				
7.2	511.9	317.8	314.9	417.67	93.46	22.38				
1.7	476.5	363.1	337.4	478.47	114.82	24	477.31	110.73	23.2	1
84	525.5	322.6	455.5	555.24	219.36	39.51				
78	343.1	221 56	222.5	244.86	87.22	35.62	261.54	70.05	26.78	0.86
.5	468.3	331	356.5	355.89	104.84	29.46	379.75	119.47	31.46	0.67
17	148	132	187	183.43	98.91	53.92				
1.5	437.5	356.5	495.6	524.64	137.29	26.17				

Appendix 6



Appendix 6: Regions in Namibia. Adapted after Dealie *et al.*, 1993.