

TIME : Jan 85 - Aug 98



## Long-term growth patterns of *Welwitschia mirabilis*, a long-lived plant of the Namib Desert (including a bibliography)

Joh R. Henschel & Mary K. Seely

Desert Ecological Research Unit, Desert Research Foundation of Namibia, Gobabeb Training and Research Centre, P.O. Box 953, Walvis Bay, Namibia (E-mail: drfn@drfn.org.na)

**Key words:** Episodic events, Long-term ecological research, Namibia, Population dynamics, Seasonality, Sex ratio

### Abstract

Over the past 14 years, long-term ecological research (LTER) was conducted on the desert perennial, *Welwitschia mirabilis* (Gnetales: Welwitschiaceae), located in the Welwitschia Wash near Gobabeb in the Central Namib Desert. We measured leaf growth of 21 plants on a monthly basis and compared this with climatic data. The population structure as well as its spatial distribution was determined for 110 individuals. Growth rate was  $0.37 \text{ mm day}^{-1}$ , but varied 22-fold within individuals, fluctuating seasonally and varying between years. Seasonal patterns were correlated with air humidity, while annual differences were affected by rainfall. During three years, growth rate quadrupled following episodic rainfall events  $> 11 \text{ mm}$  during mid-summer. One natural recruitment event followed a 13-mm rainfall at the end of summer. Fog did not appear to influence growth patterns and germination. Plant location affected growth rate; plants growing on the low banks, or ledges, of the main drainage channel grew at a higher rate, responded better and longer to rainfall and had relatively larger leaves than plants in the main channel or its tributaries. This could be due to better water and nutrient conditions on the ledges than elsewhere. The population appears to be growing outwards, with the smallest (youngest?) plants highest. Sex ratio was male-biased and males grew larger than females. Our study, in conjunction with the extensive literature base on *Welwitschia*, published here in a bibliography comprising 297 papers, indicates the knowledge gaps and needs for further ecological studies, including the continuation of our LTER programme. This should elucidate the reproductive output, seed dispersal, recruitment, water availability, age structure, and ecological differences between the sexes, and long-term life history strategies. Such knowledge would contribute to desert ecology and improve the management strategies of this unique Namib Desert perennial.

### Introduction

Long-Term Ecological Research (LTER) is an invaluable approach to many questions that cannot be addressed or interpreted in the appropriate context by short-term studies (Henschel 1997). For instance, long-term studies are required to understand the ultimate factors affecting population dynamics of long-lived organisms. Brief, unpredictable, episodic events such as rainfall in arid regions can be of crucial importance in understanding the ecology of organisms or communities, but these events can best be captured by continuous, long-term monitoring. The ultimate aim

of LTER includes identifying the nature of important episodic events and of long-term processes as well as providing data for predictive modelling at large temporal scales. This may, *inter alia*, serve as indicator of long-term environmental changes. Conversely, an understanding of long-term patterns may be necessary to facilitate the maintenance of essential ecological processes.

An understanding of long-lived plants can provide such insight. The *Welwitschia*, *Welwitschia mirabilis* Hook.f. (Gnetales: Welwitschiaceae), which is renowned for its longevity (Herre 1961; Jürgens et al. 1997), could serve as a key example. This

16285

# DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)

## Combating Desertification

Printed on Wed 10 April 02 at 14:29:22

**NZABONIMPA, Abdallah**

Channel Africa Radio  
P O Box 91313  
AUCKLAND PARK  
Telephone (Work): 0117144198  
Fax: 0117142424  
E-Mail: nzabonimpaa@sabc.co.za

**O' FARRELL, Mr Patrick**

University Of Cape Town  
24 The Avenue  
WOODSTOCK 7925  
Telephone (Work): 4483675  
E-Mail: ofarrell@nbict.nbi.ac.za

**ODADA, Ms Catherine**

U N D P  
WINDHOEK  
NAMIBIA  
Telephone (Work): 09264612046232  
Fax: 09264612046203  
E-Mail: catherine.odada@undp.org

**OETTL, Noel**

E M G  
P O Box 13378  
Mowbray  
CAPE TOWN 8001  
Telephone (Work): 4882881  
E-Mail: dryland@global.co.za

**OGUNLOLU, Mr Olufemi Adebayo**

F R S C Kwara  
P O Box 2068  
Sapon  
ABEOKUTA OGUN 110221  
NIGERIA  
Telephone (Work): 0923208023076889  
E-Mail: femog2001@yahoo.com

**OKPARA, Mrs C. N.**

Nigerian Concerned Group For Environment, Population And  
57 Njiribeako Street  
P O Box 3122  
OWERRI  
NIGERIA  
Fax: 09234012610310  
E-Mail: n\_cogep\_d@usa.net

**OKPARA, Prof Enoch**

Nigerian Environmental Study / Action Team  
1 Oluokun Street  
Off Awolowo Avenue  
U I P O Box 22025  
IBADAN  
NIGERIA  
E-Mail: nestnig@nest.org.ng

**OLIVER, Mrs Ian**

Karoo Desert N B G  
P O Box 152  
WORCESTER  
Telephone (Work): 0233470785  
Fax: 0233428719  
E-Mail: karroid@intekom.ca.za

**ORLALE, Mr Martin**

Practical Skills Training Institute  
P.O. Box 57729  
NAIROBI 00100  
KENYA  
Telephone (Work): 09254272772360  
E-Mail: pinstitute@pinfosol.com

**OUESSAR, Mr Mohamed**

Researcher  
Institut Des Régions Arides (IRA)  
Ira, Route De Jorf Km22.5  
MÉDENINE 4119  
TUNISIA  
Telephone (Work): 0926165633005  
Fax: 0921675633006  
E-Mail: Ouessar.Mohamed@ira.rnrt.tn

**OYEBODE-ADESINA, Mr Adewale**

Timmey Nig.Ltd  
P O Box 28241  
IBADAN 200003  
NIGERIA  
Telephone (Work): 09232716548  
Fax: 09232413988  
E-Mail: shinedude2@yahoo.com

**PALMER, Anthony**

A R C - Range And Forest Institute  
P.O. Box 101  
GRAHAMSTOWN 6140  
Telephone (Work): 0466222638  
Fax: 0466222638  
E-Mail: t.palmer@ru.ac.za

**PANDO-MORENO, Ms Marisela**

Lecturer  
Universidad Autonoma De Nuevo Leon  
P O Box 41  
LINARES 67700  
MEXICO  
Telephone (Work): 095282124895  
Fax: 095282124251  
E-Mail: mpando55@hotmail.com

**PAUDYAL, Prof Dhanpati**

Inshured  
10 New Ban Pb6218  
KATHMANDU 6218  
NEPAL  
Telephone (Work): 099771487376  
Fax: 099771487376  
E-Mail: inshured@hotmail.com

evergreen plant differs in many respects from other desert plants and may therefore provide different insights into factors that govern desert ecology. Indeed, since its discovery in 1859 by Welwitsch and Baines, the *Welwitschia* has been considered a curiosity, with paradoxical characteristics and a challenge to botanists (Cooper-Driver 1994). It is important to know more about the ecology of this unusual plant and its satellite fauna in order to improve the management strategies of *Welwitschia* fields and to understand the *Welwitschia*'s importance in the Namib Desert ecosystem (Marsh 1987; Brinckman & von Willert 1987). Some of the following details indicate the kinds of questions that need to be addressed and provide a background to the present study.

The *Welwitschia* has only two large leaves (mean total leaf area  $\sim 1 \text{ m}^2$ , mean maximum leaf length = 85 cm, absolute maximum leaf length >250 cm), which grow continuously throughout the year at an average rate of  $0.2\text{--}0.8 \text{ mm day}^{-1}$  (Bornman et al. 1972; Walter & Breckle 1984; Brinckman & von Willert 1987; von Willert 1994). Growth rate may differ between years and between sites. The large leaves extend low over the hot desert surface, and it therefore appears somewhat surprising that it uses  $\text{C}_3$  metabolism, which requires it to open its many stomata during the day to take up  $\text{CO}_2$  (von Willert et al. 1982; Eller et al. 1983). Water transpiration rates are therefore usually high, amounting to about 1 litre per day for a medium-sized plant. Since there is no dormant season, a strong dependence on continuous water supplies is indicated. The plant itself does not appear to store enough water to sustain its high losses; its leaves contain only half the daily water requirements (Eller et al. 1983) and there are no bulbous roots (Kutschera et al. 1997).

Water may be obtained from fog absorbed through the stomata (Bornman et al. 1973), fog water run-off taken up with shallow hair roots below the leaves (Bornman et al. 1972; Kutschera et al. 1997), and ground water tapped with deep roots (Giess 1969; Bornman 1972; Eller et al. 1983; Kutschera et al. 1997a, b). Rainfall, on the other hand, is too rare and unpredictable for adult plants to depend on directly. An average of 2 mm rain and fog precipitation  $\text{day}^{-1}$  (730 mm per annum) would be required to sustain the plant's water consumption. This is 3 to  $\sim 100$  times the actual precipitation in this species' distribution area. Rain is, however, necessary to periodically top up ground water. It is also crucial for germination and seedling development (Butler 1975), but only certain types of rainfall patterns appear to be suitable for re-

cruitment (Bornman et al. 1972; van Jaarsveld 1990). Although females annually produce many seeds, recruitment events are rare (many years apart). The latter has been deduced by casual observations of the occurrence of different size cohorts (Walter 1971; Bornman 1972; Brinckman & von Willert 1987; von Willert 1994; Jürgens 1992; Jürgens et al. 1997).

During periods of extreme drought, the plant can keep its stomata closed to reduce water loss and uses carbon reserves from older leaf parts during photosynthesis (von Willert 1994; von Willert & Wagner-Douglas 1994; Herppich et al. 1996). Carbon reserves may explain the unusually large, live leaves of this desert plant (von Willert et al. 1982; Eller et al. 1983). In adverse conditions the plant can thus be kept in a continuously active state and grows despite the net carbon deficit. This should enable the plant to respond quickly when conditions improve, increasing its leaf growth rate in order to replenish the previous deficit. This suggested ability for quick response remains to be tested.

Here we report results obtained from an LTER programme on *Welwitschia* initiated by the Desert Ecological Research Unit at the beginning of 1985 and present a bibliography (Appendix), which forms part of the programme. By examining variations in the long-term pattern of plant growth, this study intends to elucidate possible factors that affect the long-term dynamics of this desert plant. Leaf growth of 21 *Welwitschias* was measured at monthly intervals and these results are compared with data on precipitation. Fog, rain, and run-off events that occurred during these 14 years enabled us to identify and characterise those that influence plant growth and recruitment. At the end of the study period, part of the local population, comprising 110 plants, was mapped and measured in order to examine patterns that may underlie population dynamics and distribution patterns. These analyses enable us to refine the questions, objectives and activities of the continuation of this LTER programme.

### Natural history

Although a great deal has been written about the morphology, development, ecophysiology, ecology, and distribution of *Welwitschia mirabilis* (297 papers; Appendix), many important aspects of the biology of this monogeneric and monospecific member of the family Welwitschiaceae are still inadequately understood or controversial. *Welwitschia* is endemic to the Cen-

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)**

Page: 8

**Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**MUSONDA, Mr Thomson C**

No Info At This Stage  
LUSAKA  
ZAMBIA

**MUTAMBA, Mr Emmanuel**

Team Director  
Green Living Movement  
P O Box 38254  
LUSAKA 10101  
ZAMBIA  
Telephone (Work): 0926096760966  
E-Mail: emutamba@yahoo.com

**MUWAYA, Mr Stephen**

M A A I F  
P O Box 102  
ENTEBBE  
UGANDA  
Telephone (Work): 0925641343696  
Fax: 0925641321255  
E-Mail: ccdnap@infocom.co.ug

**MWANZA, Regina**

P O Box 50266  
LUSAKA  
ZAMBIA

**NAKALE, Tufikifa**

D R F N  
NAMIBIA

**NANGOMA, Everhart**

No Info At This Stage  
BLANTYRE  
MALAWI  
Telephone (Work): 09266621348  
Fax: 09266621022  
E-Mail: umoyo@malawi.net

**NANTANGA, Komeini**

D R F N  
NAMIBIA

**NAWASEB, Gabes**

D R F N  
NAMIBIA

**NDITEZEUA, Mina**

D R F N  
NAMIBIA

**NDJITEZEUA, Asser**

Khoadi Lihôas Conservatory  
P. O Box 119  
KAMANJAB  
NAMIBIA  
Telephone (Work): 0926467333017  
Fax: 0926467333020

**NDLELA, Elmon**

Brot Für Die Welt / UNCCD Support Programme  
A C A T  
Eastern Cape  
E-Mail: des2002@gliese.de

**NJEAZAEH, Mr Jerome Akaning**

Associated Country Women Of The World (Acww)  
P. O. Box 446  
BUEA 0144  
CAMEROON  
Telephone (Work): 092377523264  
Fax: 092377523264  
E-Mail: nnangela@yahoo.com

**NOMTSHONGWANA, Mr Ngcali**

D E A T  
JOHANNESBURG

**NTANDO, Mr Simanga**

Yonge Nawe  
Covetry Cresent  
Jenden Building Office 13  
MBABANE  
SWAZILAND  
Telephone (Work): 092684041394  
Fax: 092684047710  
E-Mail: btmakama@yongenawe.rg.sz

**NUPPENAU, Prof Ernst-August**

Justus-Liebig-University  
Institut Fuer Agrarpolitik  
Senckenbergstrasse 3  
GIESSEN 35390  
GERMANY  
Telephone (Work): 09496419937022  
Fax: 09496419937029  
E-Mail: Ernst-August.Nuppenau@agr.uni-giessen.

**NYIKA, Walter Mugove**

Zimbabwe Institute Of Permaculture - S C O P E  
P O Box CY301  
Causeway  
HARARE  
ZIMBABWE  
Telephone (Work): 092634333812  
Fax: 092634333811  
E-Mail: scope@africaonline.co.zw

**NYIKAYARAMBA, Mr Charles Marcos**

Department Of Natural Resources  
P O Box 585  
MUTARE  
ZIMBABWE  
Telephone (Work): 092632062509  
Fax: 092632067098



tral and Northern Namib Desert, extending from the Kuiseb River in Namibia to the Nicolau River north of Namibe in Angola (Kers 1967; Giess 1969; Bornman 1978). It occurs in isolated populations, ranging from 2 to >1000 individuals.

Welwitschia is famous for its longevity. This is based on carbon dating of only two relatively small plants as being 500–600 years (Herre 1961) and 550 years old (stem diameter 18×55 cm; Jürgens et al. 1997). Photographs documenting little change of two medium-sized plants in 90 years also give the impression of great age (Massman 1976). Larger Welwitschias have been estimated to be 2000–3000 year old (Herre 1961; von Willert 1994; Bornman et al. 1972; Kutschera et al. 1997a), but this requires confirmation.

In some areas the Welwitschia is the dominant perennial vegetation present and may serve as source of food and water for various animals, including ungulates like oryx, rhino, and zebra (Moisel & Moll 1981; Brinckmann & von Willert 1987; Loutit et al. 1987; Seely personal observations), as well as microarthropods (Marsh 1987). It can withstand quite considerable degrees of herbivory and sandstorm abrasion, but is vulnerable to damage by people and is thus protected. In some populations, the roots are colonised by mycorrhiza (*Glomus* sp.) inoculated by grasses *Stipagrostis* spp. and *Cladoraphis* spp. (Jacobson et al. 1993). These symbiotic fungi may be important for nutrient cycling, but in some areas where the above-mentioned grasses are absent, Welwitschia appears to survive without mycorrhizae.

The two Welwitschia leaves continuously grow from monocotyledonous-type meristems at the margin of a corky stem (Rodin 1958a, b; Bornman 1977; von Willert 1993). Vitality recedes along the length of the leaves (Eller et al. 1983) and cells die at the tips after 1–10 years. Following earlier controversy, it is now established that the Welwitschia is a C<sub>3</sub> plant and there is no evidence of CAM and nocturnal CO<sub>2</sub> uptake (von Willert et al. 1982; Eller et al. 1983). The leaves bear 61–87 stomata mm<sup>-2</sup> that usually open by day, but can be regulated during hot hours in drought (von Willert 1994; von Willert & Wagner-Douglas 1994; Herppich et al. 1996). The leaves transpire water at 0.96 dm<sup>3</sup> m<sup>-2</sup> during the daytime hours and an average-sized plant therefore daily loses about 1 litre of water, about double the quantity available in the leaves at dawn (Walter 1936; Eller et al. 1983). The leaves have special water-conducting cells, called vessels, that allow high water transport effi-

ciency (Muhammad & Sattler 1982) that continuously replenish the transpired water at a rate of 25–32% per hour from storage in the sponge-like stem and roots. In drought, the osmotic potential of the leaves is –5.5 to –8.0 (Eller et al. 1983), compared to –3.2 to –3.4 after rain (Walter 1936).

The reputed dependence of Welwitschia on fog is controversial. Only 43% of the Welwitschia fields (Kers 1967) lie inside of the coastal fog belt (altitude <500 m above mean sea level; >50 mornings with stratus clouds that sometimes form fog; Olivier 1995). Nevertheless, Bornman et al. (1973) demonstrated that radio-actively labelled water can be absorbed and transported through the leaves. However, the stomata only open during the day-time hours (Eller et al. 1983) when fog at the study site is already lifting (Henschel et al. 1998). Furthermore, the stomata are not hydathode (Walter & Breckle 1984; Cooper-Driver 1994) and can thus only absorb little of the precipitated fog water by slow, passive diffusion. Bornman et al. (1972) and Kutschera et al. (1997a) found shallow hair roots below the leaves and suggested that these take up water that runs off the leaves during rain, fog and dew. This water pathway might benefit from the moderate micro-climate prevailing on and under the plant (Marsh 1990), due, in part, to efficient reflection of solar radiation and to evaporative cooling (Schulze et al. 1980; Eller et al. 1983; von Willert 1994). All forms of precipitation are, however, not nearly enough to satisfy the plant's high water requirements. It is therefore supposed that the main source is ground water (Eller et al. 1983) which is tapped with roots that go at least 1–3 m deep in a radius of up to 15 m around a plant (Giess 1969; Bornman 1972; Kutschera et al. 1997a, b). Dependence on ground water would explain the preferential occurrence of populations in washes or run-off depressions on the plains.

For seeds to germinate they require about 12.5 mm of rain and they need to soak for 3–21 days (Bornman et al. 1972; Cooper-Driver personal communication). The rapid growth of the roots of seedlings, initially 5–10 mm day<sup>-1</sup>, attaining 1 m after 8 months (Butler et al. 1973; Eller et al. 1983; von Willert 1994), enables them to follow receding moisture levels in the soil and eventually to reach the ground water. The root system may continue to grow in mature plants, probably extending during periods when the upper soil layer is wet (Kutschera et al. 1997a).

Reproduction is seasonal. Male flowers begin to develop in September–October and may attract pollinators by secreting a liquid attractant for insects

# DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)

Page: 7

## Combating Desertification

Printed on Wed 10 April 02 at 14:29:22

**MANSUR, Prof Shaban**TRIPOLI  
LIBYA**MCCLURE, Mr Beaumont**Bureau Of Land Management  
222 N. Central Avenue  
Phoenix  
ARIZONA 85004  
USATelephone (Work): 091602419430  
Fax: 091602417998  
E-Mail: beau\_mcclure@blm.gov**MHLANGA, Rose M**No Info At This Stage  
ZAMBIA**MITCHELL, Dr David**Wolverhampton University  
School Of Applied Sciences  
WOLVERHAMPTON WV11SB  
UKTelephone (Work): 091441902322173  
Fax: 091441902322680  
E-Mail: d.mitchell@wlv.ac.uk**MITEMBE, William**No Info At This Stage  
LILONGWE  
MALAWITelephone (Work): 09265771000  
Fax: 09265784268  
E-Mail: sadcfstu@malawi.net**MODISAOTSILE, Mr Modisaotsile K C**Ministry Of Agriculture  
Private Bag 003  
GABORONE  
BOTSWANATelephone (Work): 0926735510  
Fax: 09267307057  
E-Mail: mmodisoatsile@gov.bw**MOLAPO, Mr Jobo**Director  
S A D C Elms  
MASERU  
SWAZILAND**MONTOIRO, Mr Marcos**Associate External Relations Officer  
U N C C D Secretariat  
Martin Luther King Street 8  
BONN  
GERMANYTelephone (Work): 09492288152806  
Fax: 09492288152899  
E-Mail: mmontoiro@unccd.int**MOORE, Mr Franklin**U S A I D  
WASHINGTON  
USATelephone (Work): 092027121863  
E-Mail: fmoore@usaid.gov**MOSER, Petra**D R F N  
NAMIBIA**MOUAT, Dr David**Division Of Earth And Ecosystem Sciences  
Desert Research Institute  
2215 Raggio Parkway  
RENO NEVADA 89512  
USATelephone (Work): 097756737042  
Fax: 097756747557  
E-Mail: dmouat@dri.edu**MSANGI, Prof Josephine**Professor And Head Of Department  
University Of Namibia  
Private Bag 13301  
WINDHOEK 264  
NAMIBIATelephone (Work): 0926412063383  
Fax: 0926412063424  
E-Mail: jpmsangi@unam.na**MTHETHWA, Mr Doctor**

No Info At This Stage

**MUGUTI, Mr Edward Chege**Trace(K) Network  
P.O. Box 525  
EMBU 254(0)161  
KENYATelephone (Work): 0925416120120  
Fax: 0925416130165  
E-Mail: chegeh@yahoo.co.uk**MUKUTE, Mutizwa**Brot Für Die Welt / U N C C D Support Programme  
PELUM  
ZIMBABWE  
E-Mail: des2002@gliese.de**MULINDWA, Miss Aisha**Rwanda Desert Awareness Organisation  
B.P. 6215  
KIGALI 250  
RWANDATelephone (Work): 0925074506  
Fax: 09250570188  
E-Mail: aishamulinda@yahoo.com

(wasps, flies or ants; Marsh 1982; Carafa et al. 1989; Cooper-Driver 1994). Pollination occurs during November–January and seeds ripen during February–March. A female may produce 10 000–20 000 winged seeds (Bornman 1978; Bustard 1990), which appear to be dispersed by wind. Seeds are heavily infested with fungus *Aspergillus niger* (Bornman et al. 1972; van Jaarsveld 1992; Cooper-Driver, personal communication), apparently reducing viability to 0.1–10% (Bornman et al. 1972; Bustard 1990). These fungal spores may be transmitted by the bug, *Probergrothius sexpunctatis* (Heteroptera), that feeds on phloem tissue. The relationship of *A. niger* to precipitation may further complicate conditions affecting *Welwitschia* recruitment (Cooper-Driver, personal communication).

## Methods

Our study site is situated 14 km east of Gobabeb at the 'Welwitschia Wash' (23°38' S, 15°10' E) and 6 km west of the next population of *Welwitschias* in the Hope wash. The *Welwitschia* Wash is a ravine that runs down from the gravel plains of the Central Namib Desert past the #Aonin Village of Oswater towards the ephemeral Kuiseb River. The study area includes a 3–20 m wide ravine with a sandy channel, bordered by stony ledges. Other perennial plants are *Adenolobus pechuellii* (Kuntze) Torre & Hillc. (Fabaceae), *Orphanthera albida* Schinz (Asclepiadiaceae), *Sutera maxii* Hiern (Scrophulariaceae), *Euphorbia phylloclada* Boiss (Euphorbiaceae), and *Acacia erioloba* E. Meyer (Mimosoideae). The study period was January 1985 to August 1998 and is continuing. The only possible large herbivores of *Welwitschia* leaves present in the study area during the study period were springbok, *Antidorcas marsupialis* Zimmerman 1780, donkeys and horses, but there were no signs that they had fed on the plants.

*Welwitschia* leaf growth was measured at approximately monthly intervals (135 times in 164 months). A light scratch mark was made across a section of a particular leaf where it emerges from the stem and at the next visit the distance of this mark from the stem was measured ( $\pm 0.1$  mm) with callipers near the middle of the leaf width. Twenty plants were monitored, 10 females, 10 males, and a small male plant was included into the programme from 30 April 1993 onwards. Data years encompassed complete growth seasons, beginning on 1 September and ending on 31 August of the following calendar year and are referred

to by the 'year ending...', i.e., data years are 4 months earlier than calendar years. For calculations with annual data, 1985 was omitted, as it was an incomplete data year. Annual growth was calculated as follows:

$(\Sigma \text{growth measurements in a year} \times 365) / (\text{days between first and last measurement})$ .

In September–October 1998, *Welwitschias* occurring in the main wash, on its ledges, and in its nearby small side washes, comprising 110 individuals, were mapped and measured and sex was determined. Measurements were made of the following: stem height above ground; maximum and minimum diameter of the stem; meristem length for each leaf; length of the living and dead parts of the longest leaf; maximum diameter across the living part of the plant and the total diameter; number of leaf parts; distance from each individual to the nearest male and female plants; location in or next to the wash. Another 68 plants occurring in a large wash that joins the main wash half-way along its length as well as in more distant side washes and slopes were not measured, but sex was determined. A further 30 *Welwitschias* that occur in the vicinity of the *Welwitschia* Wash (Cooper-Driver personal communication) were not examined.

Climate was monitored continuously at Gobabeb with autographic recorders until 1993 and thereafter with data logger. Fog was measured by collecting runoff from a cylindrical mesh mounted on a rain gauge. Twice, rainfall at *Welwitschia* Wash appeared to exceed that recorded at Gobabeb. We estimate that at least 10 mm fell on 4 March 1993, and some 30 mm fell in a local shower on 13 December 1993 (when 7.8 mm was recorded at Gobabeb). The December 1993 shower caused runoff water to flow down the wash (K. Jacobson, personal communication) and was apparently the only occasion of runoff during the current study period. At other times, precipitation records of Gobabeb appeared to be applicable to the nearby *Welwitschia* Wash; both sites are located in the same climatic zone, intermediate between the western fog belt and the eastern Namib.

Analyses follow Zar (1996); means are given  $\pm$ SD. Unless otherwise stated significant differences are  $P < 0.05$ .

# DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)

Page: 6

## Combating Desertification

Printed on Wed 10 April 02 at 14:29:22

**KELLNER, Prof Klaus**

Potchefstroom University For C H E  
School Of Environmental Sciences And Development  
POTCHEFSTROOM 2520  
Telephone (Work): 0182992510  
Fax: 0182992370  
E-Mail: plbkk@puknet.puk.ac.za

**KHUMALO, Mr Luyanda T.**

No Info At This Stage  
MBABANE  
SWAZILAND  
Telephone (Work): 092684043858  
Fax: 092684044700  
E-Mail: lups@realnet.co.sz

**KIHAULE, Mr Joseph**

No Info At This Stage  
DAR ES SALAAM  
TANZANIA

**KLINTENBERG, Patrik**

D R F N  
NAMIBIA

**KOELLE, Ms Bettina**

Social Geographer  
Indigo Development Change  
P O Box 350  
NIEUWOUDTVILLE 8180  
Telephone (Work): 0272181148  
Fax: 0272181148  
E-Mail: bettina@indigo-dc.org

**KOMATI, Justine**

D R F N  
NAMIBIA

**KOOTJIE, Albertus**

D R F N  
NAMIBIA

**KRUGER, Bertus**

D R F N  
NAMIBIA

**KRÜGER, Prof Gert**

Potchefstroom University For C H E  
School Of Environmental Sciences And Development  
POTCHEFSTROOM 2520  
Telephone (Work): 0182992520  
Fax: 0182992503  
E-Mail: plbghik@puknet.puk.ac.za

**LANCASTER, Ms Judith**

Division Of Earth And Ecosystem Sciences  
Desert Research Institute  
2215 Raggio Parkway  
RENO NEVADA 89512  
USA  
Telephone (Work): 097756737300  
Fax: 097756747557  
E-Mail: judith@dri.edu

**LERATA, Mr Thabiso**

Ministry Of Environmental, Gender And Youth Affairs (E M P R)  
MASERU  
LESOTHO  
Telephone (Work): 09266314763  
Fax: 09266310506  
E-Mail: natenv@ilesotho.com

**LUNGU, Bazak Zakeyo**

Brot Für Die Welt / U N C C D Support Programme  
ZAMBIA  
E-Mail: des2002@gliese.de

**MACHARIA, Mr Peter**

Senior Research Officer  
Kenya Agricultural Research Institute / Kenya Soil Survey  
P.O. Box 14733  
NAIROBI  
KENYA  
Telephone (Work): 092542440903  
Fax: 092542443376  
E-Mail: kss@iconnect.co.ke

**MAJUVA, Rosaldina A C**

No Info At This Stage  
DAR ES SALAAM  
TANZANIA  
Telephone (Work): 0925522218005  
Fax: 0925522182240  
E-Mail: jet@africaonline.co.tz

**MANDAKH, Miss Nyamtseren**

Institute Of Geoecology Mongolian Academy Of Sciences  
Ulaanbaatar.Bruun Selbe - 13.  
ULAAABAATAR  
MONGOLIA  
Telephone (Work): 0997697411326620  
E-Mail: maaggi@yahoo.com

**MANGANDA, Ernest**

Focal Point  
CONGO  
E-Mail: Une adresse@yahoo.fr gratuite et en

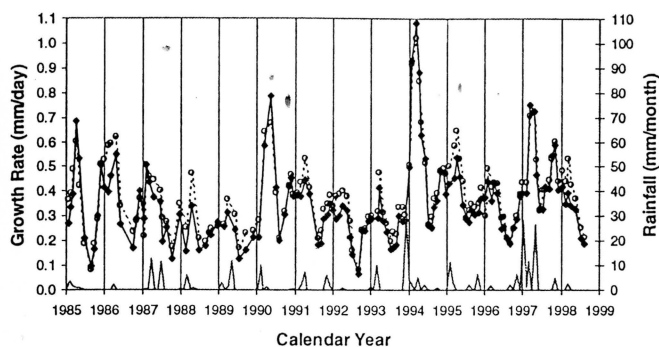


Figure 1. Monthly mean growth rate of *Welwitschia* females (diamond) and males (circle) (upper curves) and monthly rainfall totals (bottom spikes).

## Results

### Growth rate

Total leaf growth of individual *Welwitschia* plants over 13 years and 8 months was  $1780 \pm 407$  mm (range 1059–2416 mm) at an average rate of  $0.367 \pm 0.203$  mm day<sup>-1</sup> ( $0-1.597$  mm day<sup>-1</sup>;  $n = 2764$  measurements; note: the measurement of zero growth per month is a single outlier and growth was observed in all other cases). Average annual growth of individual plants was  $126.6 \pm 43.9$  mm (range 27.1–290.9 mm).

Growth rate fluctuated during each year, following a seasonal pattern, and varied between years (Figure 1). Individuals varied their monthly leaf growth rate by  $22 \pm 18$ -fold. Summer peak growth rate decreased successively during the first 5 years, then it increased in 1990, with peaks again declining over the following three years, then reaching a maximum peak in 1994, followed by two years of decline, an increase in 1997, and decrease in 1998. Some rain fell in each year (Figure 1), although it was usually  $<11$  mm event<sup>-1</sup>. Annual rainfall was  $16.2 \pm 16.9$  mm (range 2–70 mm).

The seasonal pattern was as follows. Normally, growth rate increased from September onwards and declined from April onwards, peaking in March and reaching a minimum in August (Figure 2). The amplitude of this annual trend was about double, i.e. in March growth was normally twice as high as in August (medians: 0.463 vs. 0.226), but could be as high as ten-fold. Absolute maximum growth rates were recorded during January and March, during that part of the season when the median growth rate was increasing (Figure 2). Monthly growth rate correlated with mean rainfall ( $r = 0.70$ ), but not with fog ( $r = -0.34$ ). Lagging by one or two months did not improve the correlations. It should, however, be noted that me-

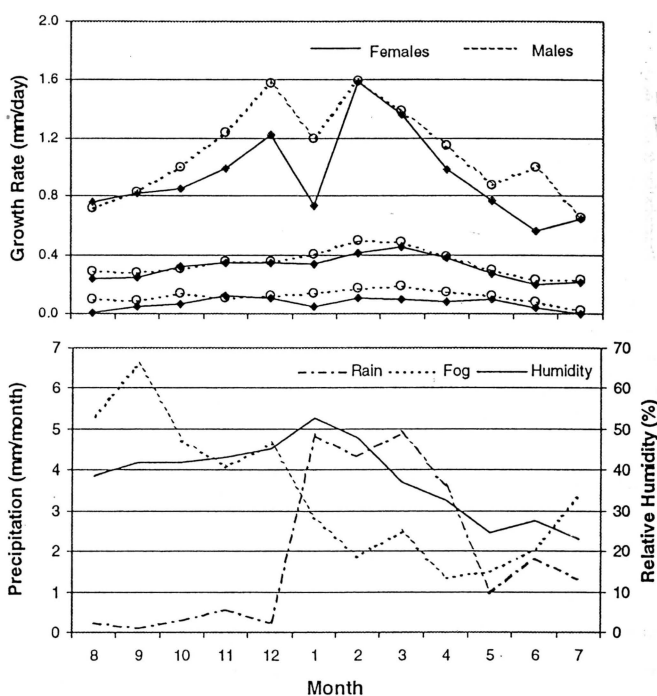


Figure 2. Maximum, median and minimum growth rate of female and male *Welwitschia* during the course of the year compared to mean monthly rainfall, fog and relative humidity.

dian rainfall was nil for all months, i.e. actual rainfall can therefore not explain the seasonal growth pattern, but that potential relative rainfall (as expressed by the mean) could play a role. Growth correlated best with relative air humidity, lagged by one or two months ( $r = 0.86-0.87$ ;  $p < 0.001$ ), although there was no relationship with no lag ( $r = 0.56$ ;  $p > 0.05$ ). Growth rate increased during all months when mean humidity was  $>35\%$  and declined when it was  $<35\%$  (Figure 2).

Annual change in growth ( $\text{growth}_{\text{year}(i+1)} - \text{growth}_{\text{year}(i)}$ ) of most individuals correlated well with each other, with 16 of 21 plants having similar annual growth patterns ( $r = 0.63-0.80$ ). One female (F8, in a side wash) did not correlate well with any other plants ( $r \leq -0.11-0.43$ ) and was even dissimilar in some cases. This female showed the least seasonal and annual change in growth of all individuals (maximum annual increase in growth rate of F8 vs. all others = 22 vs. 61–150 mm). F8 is thus excluded from further analyses, except where specifically referred to. Four other individuals were intermediate, with their growth patterns correlating well with 9–14 other individuals but poorly with the remainder. The five 'abnormal' plants (F0, F8, M5, M6, M10) had different years of peak growth compared to the other 16 'normal' plants and they also differed from each other (Table 1). These five plants were all in the upper part of the study area



**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)**

Page: 5

**Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**GUSTAFSSON, Sigi**D R F N  
NAMIBIA**GUSTAVO, Margareth**D R F N  
NAMIBIATelephone (Work): 0926461229855  
Fax: 0926461230172  
E-Mail: margarethg@drfn.org.na**HASSANE, Mr Moussa**Researcher In Forestry Agroforestry  
P O Box 429  
INRAN  
NIGER  
Telephone (Work): 09227740916**HAYWARD, Ntsiki****HENDRICKS, Howard**South African National Parks  
P O Box 110040  
Hadison Park  
KIMBERLEY 8306  
Telephone (Work): 0538325488  
Fax: 0538334543  
E-Mail: howardl@parks.sa.za**HESELMAN, Mr H****HOFFMAN, Prof Timm**Institute For Plant Conservation  
U C T  
RONDEBOSCH  
Telephone (Work): 6502440  
Fax: 6504046  
E-Mail: thoffman@botzoo.uct.ac.za**HUONGO, Mr Abias**J E A  
ANGOLA  
Telephone (Work): 0924423969547  
E-Mail: jea@angola.com**JAFARI, Dr Mohammad**Associate Professor  
University Of Tehran  
P O Box 14185/354  
Natural Resources College Of Tehran University  
KARAJ 37585-4314  
IRAN  
Telephone (Work): 09982612223044  
Fax: 09982261227765  
E-Mail: mjafari@chamran.ut.ac.ir**JAIN, Dr Kalpana**23, Jhiniret Ki Gali  
UDAIPUR 313001  
INDIATelephone (Work): 0991294525593  
Fax: 0991294529922  
E-Mail: ncjain@bppl.net.in**JONAS, Miss Zuziwe**University Of Cape Town  
47 Fumana Street Harare  
Khayelitsha  
CAPE TOWN 8000  
E-Mail: zjonas@botzoo**KALENGA, Mrs Lahja**D R F N  
P. O. Box 175  
Oshakati  
OSHAKATI 9000  
NAMIBIA  
Telephone (Work): 0926465221854**KALENTA,**D R F N  
NAMIBIA**KALLIPA, Mrs Wandile**Channel Africa Radio  
P O Box 91313  
AUCKLAND PARK  
Telephone (Work): 0117143759  
Fax: 0117144959  
E-Mail: kallipaw@channelafrica.org**KANOUTE, Mr Salif**S T P / C I G Q E  
B P 2357  
BAMA KO  
MALI  
Telephone (Work): 09223231074  
Fax: 09223235867**KARIMPOOR REIHAN, Dr Majid**Tehran University  
Iran Desert Research Center  
TEHRAN 31585  
IRAN  
Telephone (Work): 0998218958448  
Fax: 0998218965287  
E-Mail: karimpoor@chamran.ut.ac.ir**KASUSYA, Mr Pius**Resource Projects Kenya  
P O Box 59411  
NAIROBI  
KENYA  
Telephone (Work): 092542890595  
Fax: 092542890592  
E-Mail: iagi.rp@africaonline.co.ke

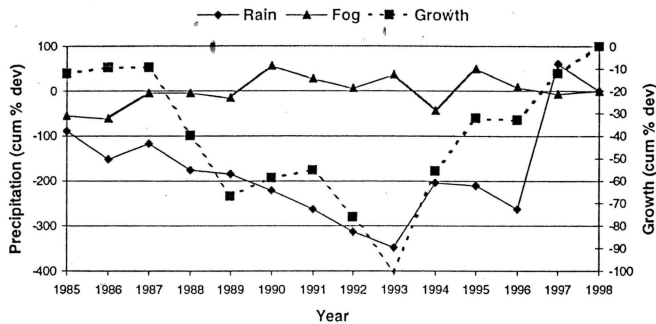


Figure 3. Cumulative percent deviation from the mean of rainfall, fog and of annual growth of *Welwitschia*.

and were located either in the middle of the main wash ( $n = 1$ ), or on its rocky ledges (2), or in side washes (2).

During the 14-year study period, most individuals showed three peaks in annual growth (Table 1). These were three or four years apart so that best autocorrelations were usually achieved with lags of 3–4 years in individual growth rates (3-year lag for 4 individuals, 4-year for 13), although even the best autocorrelations were relatively weak (only six were  $r > 0.5$ ). This gives a weak case for the occurrence of endogenous cycles.

Mean annual growth and change in growth did not correlate well with total annual rainfall ( $r^2 = 0.16$  and  $0.05$ , respectively) and fog ( $r^2 = 0.09$  and  $0.11$ ). However, when comparing the cumulative percent deviation from the mean of growth against that of rain, a good correlation is achieved ( $r = 0.82$ ; Figure 3), but there was no correlation with that of fog ( $r = -0.43$ ). There was a general decrease in growth (with minor deviations) before 1993 and a general increase thereafter. The maximum growth rates attained (up to  $1.6 \text{ mm day}^{-1}$ ) followed the December 1993 rainfall that had caused the wash to flood (Figure 1). This marked the turning point of the cumulative percent deviation of the growth curve (Figure 3). This prompts the conclusion that heavy rainfall (and runoff that may result in groundwater recharge) drives big changes in growth rate. Fog, which is relatively constant from season to season, does not appear to cause changes in growth.

In three years, 1990, 1994, and 1997, all plants showed an increase in annual change of growth rate ( $\text{growth}_{\text{year}(i+1)} - \text{growth}_{\text{year}(i)}$ ), i.e., in those years the change in annual growth was higher than the 13-year average (12 pairs of years), while in most other years the change in annual growth rate was below average. These three exceptionally high growth seasons

coincided with seasons during which  $>11.5 \text{ mm}$  rainfall events occurred during that part of the season when *Welwitschia* was approaching its 'normal' annual peak of growth rate, namely December–February (rainfalls were  $11.5 \text{ mm}$  on 11 February 1990,  $\sim 30 \text{ mm}$  on 13 December 1993, and  $26.6 \text{ mm}$  on 16 January 1997; Figure 1). The mean annual growth rate in these peak years was highly correlated with the amount of rainfall ( $r^2 = 0.88$ ). This correlation was good for 17 individuals ( $r^2 = 0.53$ – $0.99$ ) and poor for 3 ( $r^2 = 0.16$ – $0.37$ ). Hereafter we refer to this type of rain, i.e.,  $>11 \text{ mm}$  per event between December and February, as effective rain. Responses by the plants (change in growth rate much higher than in the same months of other years) was on average longer than 31 days after these rains, normally beginning after 35 days, peaking 59–64 days and remaining well above normal until 100–148 days after rain. After the flood of December 1993, a shortest response time of 19 days and maximum change in growth rate was recorded for a male and a female that respectively changed growth rate from  $0.43$  to  $0.89$  and from  $0.38$  to  $0.74 \text{ mm day}^{-1}$ .

Rainfall events at the end of the growth season, e.g., in March 1991 and March 1993, could still elicit a brief increase of growth during the same month (within 23 days), but did not affect the general growth pattern during that season (Figure 1). By contrast, annual growth rate did not change in relation to rainfall events of  $>11 \text{ mm}$  during winter (6 April 1987, 19 July 1987, 7 May 1989, and 24 May 1997).

Growth rate may differ slightly between sexes. Overall, males grew 1.104 times more than females (males vs. females:  $0.386 \pm 0.125$  vs.  $0.352 \pm 0.124 \text{ mm day}^{-1}$ ), but this was not significantly different ( $t$ -test,  $p > 0.05$ ). In the monthly measurements, growth of males and females was highly correlated ( $r > 0.955$ ), but male growth was usually higher than that of females (Figure 1). The difference was, however, significant in only 5 of 135 cases ( $t > 2.1$ ,  $df=18$ ,  $P < 0.05$ ). During months with exceptionally high growth rates (January to March of 1990, 1994, 1997), this trend was reversed, but not significant (U-test,  $p > 0.05$ ; Figure 1).

Vertical position across the wash (hereafter referred to as location) had a strong effect on growth rate. Mean annual growth of 10 plants that grew in the main wash ( $118 \pm 26 \text{ mm year}^{-1}$ ) was similar to that of 4 plants in side washes ( $106 \pm 20 \text{ mm year}^{-1}$ ;  $t = 0.81$ ,  $p > 0.05$ ), but 7 plants on the upper banks, or ledges, next to the main wash grew significantly more than in the main or side washes ( $150 \pm 20$ ,

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)**

Page: 4

Combating Desertification

Printed on Wed 10 April 02 at 14:29:22

**DIALLO, Mr Hama Arba**

BURKINA FASO

**ELFADL, Dr Mohamed**

Forestry Research Centre

P.O. Box 7089

Soba

KHARTOUM

SUDAN

Telephone (Work): 0924911787136

E-Mail: mohamed.elfadl@helsinki.fi

**EL GAMRI, Tarig**

Researcher

Environment And Natural Resources Research Institute

P O Box 6096

People Hall

KHARTOUM

SUDAN

Telephone (Work): 0924911475153

Fax: 0924911463416

E-Mail: tarig\_ncr@yahoo.com

**ESLER, Dr Karen**

University Of Stellenbosch

Private Bag X1

Matieland

STELLENBOSCH 7603

Telephone (Work): 8083063

Fax: 8083607

E-Mail: kje@sun.ac.za

**ESMAEIL ZADEH, Mr Hamid**

Tehran University

Faculty Of Natural Resources

KARAJ 31585

IRAN

Telephone (Work): 09982662232721

Fax: 09982612227765

E-Mail: hesmaely@yahoo.com

**FITTER, Dr Joern**

G T Z Office

P O Box 8016

WINDHOEK 061

NAMIBIA

Telephone (Work): 096461222447

Fax: 094661222427

E-Mail: fitter@iafrica.com.na

**FOX, Dr Dennis**

Associate Professor

C N R S

U M R Espace 6012 Cnrs

98 Blvd Ed Herriot

NICE 06800

FRANCE

Telephone (Work): 0933493375380

Fax: 0933493375430

E-Mail: fox@unice.fr

**GABES, Arnold**

D R F N

NAMIBIA

**GAMATHAM, Helen**

D R F N

NAMIBIA

**GASEB, Nickey**

D R F N

NAMIBIA

**GAUR, Dr Mahesh**

Head, Department Of Geography

S B K Government College

10/35 Chopasni Housing Board

JODHPUR 342000

INDIA

Telephone (Work): 0991291754406

Fax: 0991291438691

E-Mail: iemsd@satyam.net.in

**GEORGE, Kevin**

F O N S A G

GABORONE

BOTSWANA

Telephone (Work): 09267307506

E-Mail: fonsag@global.bw

**GLIESE, Jürgen**

Brot Für Die Welt / U N C C D Support Programme

Schifferstr 33a

FRANKFURT D-60594

GERMANY

Telephone (Work): 09496961993706

Fax: 09496961993707

E-Mail: des2002@gliese.de

**GOAGOSEB, Gabriel**

D R F N

NAMIBIA

**GOUWS, Ms Sarah**

Landscape Committee

D R F N

Postal Agency

PAULSHOEK 8221

Telephone (Work): 0275411055

Fax: 0276521356

**GURUNG, Mr Kumar**

Inshured

10 New Ban Pb6218

KATHMANDU 6218

NEPAL

Telephone (Work): 099771487376

Fax: 099771487376

E-Mail: inshured@hotmail.com

Table 1. Annual growth (mm) of leaves of 21 individual *Welwitschia* plants, designated 'F' for females and 'M' for males. Data years are 1 September to 31 August; 1985 was not a complete data year, and data were adjusted for the shorter period. Maximum stem diameter (cm) in 1998 and location (m = in main wash, l = ledge bordering main wash, s = side wash) are indicated. Annual rain and fog are in mm

Plant #	Stem	Loc	Year													
			1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
F0	79	m	106	71	89	67	86	117	84	81	91	168	101	120	123	102
F1	30	m	110	99	101	63	82	138	128	66	78	181	127	113	123	159
F4	86	m	95	73	83	60	56	127	80	66	67	178	130	90	142	109
F8	58	s	65	65	63	61	83	69	83	82	74	93	99	95	112	129
F13	105	l	138	160	175	121	105	158	180	137	127	213	243	165	188	154
F15	98	m	88	81	69	48	50	110	73	43	46	134	81	81	100	56
F17	83	m	131	152	166	74	75	137	149	86	85	218	138	121	168	130
F18	80	m	135	176	154	84	86	189	135	89	103	242	181	129	164	152
F19	30	m	135	125	139	76	121	134	154	124	115	205	163	156	211	158
F20	115	l	122	156	195	107	135	162	188	138	151	213	210	154	180	187
M2	57	s	113	96	136	98	81	109	102	95	98	160	134	119	167	136
M3	80	m	93	106	98	68	73	110	83	66	77	153	104	108	143	146
M5	74	s	82	86	94	70	92	97	96	77	85	109	106	97	141	113
M6	51	l	88	93	84	78	94	118	101	87	108	172	149	110	135	191
M7	63	l	77	127	137	100	104	137	138	132	113	178	171	157	177	187
M9	60	s	89	165	154	96	86	136	142	111	83	175	163	99	142	150
M10	165	l	106	179	128	91	97	143	159	119	112	165	185	164	133	140
M11	87	l	161	165	151	119	104	145	224	144	141	291	253	151	186	181
M12	94	l	138	260	162	136	130	199	170	113	96	221	220	137	142	127
M14	100	m	147	148	151	133	110	199	141	141	124	261	206	158	193	153
M16	10	m										116	103	103	139	115
Rain			7.0	2.0	12.9	23.8	16.3	11.5	10.9	9.2	4.5	21.4	15.4	18.6	70.0	3.0
Fog			22.7	19.6	47.4	47.3	41.7	77.0	63.5	52.9	67.5	27.5	74.2	53.7	46.6	49.4

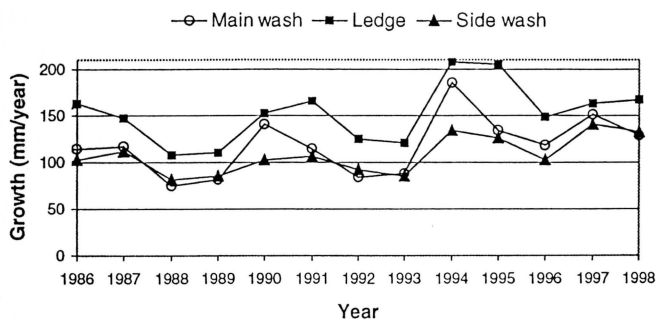


Figure 4. Mean annual growth rate of *Welwitschias* situated in the main wash ( $n = 10$ ), on its rocky ledges ( $n = 7$ ), or in side washes ( $n = 4$ ).

$t > 2.65$ ,  $p < 0.02$ ). During each year after 1989, ledge plants grew significantly more ( $t$ -test,  $p < 0.05$ ) than side-wash plants (Figure 4). They also grew significantly more ( $t$ -test,  $p < 0.05$ ) than main-wash plants during all years except 1987, 1990, 1994, and 1997 (Figure 4). The latter three years were ones

during which effective rain occurred. In such years, growth of plants in the main wash and on the ledges increased more than plants in side washes, but during the next season it had declined again to a similar rate as in the side-wash plants. Ledge plants continued to grow more than plants in main or side washes during the year following effective rain and then only did growth decline, albeit to a level still well above that of other plants. The sexes were not evenly distributed between the three locations, and most study females ( $n = 7$ ) were situated in the main wash, while half of the males ( $n = 5$ ) were on ledges (Table 1). Differences in location could contribute to differences between the sexes of the study plants.

There was poor correlation between stem size and growth ( $r = 0.29$ ;  $p > 0.05$ ) and this did not improve when comparing individuals of each sex or at one location. Plant size did not appear to have an effect on growth rate, e.g., M16 in the main wash was the

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)****Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**CLEMENTS, Mrs Amanda**

U.S. Bureau Of Land Management  
B L M Uncompohgre Field Office  
2505 South Townsend Avenue  
MONTROSE 81401  
USA  
Telephone (Work): 0919702405306  
Fax: 0919705405367  
E-Mail: amandaclements@montrose.net.

**CLOETE, Mr Eric**

D R F N  
P O Box 553  
SPRINGBOK 8240  
Telephone (Work): 0277122011  
Fax: 0277122174  
E-Mail: eric@intekom.co.za

**CLOETE, Helen**

D R F N

**CLOETE, Mr Mervin**

Landscape Committee  
Postal Agency  
PAULSHOEK 8221  
NAMIBIA  
Telephone (Work): 0275411055  
Fax: 0276521356

**COIRINI, Prof Ruben Omar**

Universidad Nacional De Cordoba  
San Juan 669 "20 De Junio"  
CORDOBA 5003  
ARGENTINA  
Telephone (Work): 09543514842399  
Fax: 095453514334118  
E-Mail: mam@agro.uncor.edu

**CONRADIE, Mr Wayne**

Rare Image  
Suite 1  
Private Bag X335  
CAPE TOWN 8000  
E-Mail: wphoto99

**CORJEUS, Mr John**

D R F N  
Postal Agency  
PAULSHOEK 8221  
Telephone (Work): 0275411055  
Fax: 0276521356

**DALL, Moizelle**

D R F N  
NAMIBIA

**DARKOH, M B K**

University Of Botswana  
Department Of Environmental Science  
University Of Botswana  
PrivateBag 0022  
GABARONE  
BOTSWANA  
Telephone (Work): 092673552526  
Fax: 09267318265  
E-Mail: darkohmb@mopipi.ub.bw

**DA SILVA BAIXO, Mr Eduardo Jorge**

No Info At This Stage  
MOPUTO  
MOZAMBIQUE  
Telephone (Work): 092581465843  
Fax: 092581465849  
E-Mail: Ihilario@teledata.mz

**DAUSAB, Rudolf**

D R F N  
NAMIBIA

**DAVIS, George**

D R F N

**DEFANG, Mr Pius**

Associated Country Women Of The World (Acww)  
P. O. Box 446  
BUEA 0144  
CAMEROON  
Telephone (Work): 092377523264  
Fax: 092373322366  
E-Mail: nnangela@yahoo.com

**DE KLERK, Mr Johannes Nicolaas**

Project Manager / Bush Encroachment  
Ministry Of Environment And Tourism  
P O BOX 5846  
Ausspannplatz  
WINDHOEK 26409  
NAMIBIA  
Telephone (Work): 0926461249015  
Fax: 0926461240339  
E-Mail: ndk@dea.met.gov.na

**DELEGATE 6,**

Brot Für Die Welt / U N C C D Support Programme  
ZIMBABWE  
E-Mail: des2002@gliese.de

**DEMBELE, Mr Moussa**

S T P - C I G Q E / Malie  
Bp 2357  
BAMA KO  
MALI  
Telephone (Work): 09223231074  
Fax: 09223235867  
E-Mail: stp@cefib.com



smallest study individual (stem diameter = 10 cm), but ranked 11th in terms of growth rate.

### *The population*

We counted 104 males and 71 females, which was significantly biased towards males ( $\chi^2 = 6.22$ ,  $df=1$ ,  $p < 0.02$ ). There were more larger males than females and the size distribution was significantly different (stem diameter of males vs. females: mean  $\pm$  SD:  $76 \pm 31$  vs.  $66 \pm 28$  cm; range: 10–165 vs. 18–124 cm;  $U_{\text{females}} = 1563$ ,  $U_{\text{males}} = 1125$ ,  $Z = 2.23$ ,  $p < 0.05$ ). Whereas 93.5% of the males had a stem diameter  $>40$  cm, this was true for only 72.1% of the females ( $\chi^2 = 9.05$ ,  $df=1$ ,  $p < 0.005$ ). The four largest plants were males, with the largest male having a stem diameter 30% greater than the largest female.

The wash can be divided into four different sections (Table 2, Figure 5). The uppermost section had two tributaries and these three parts together had the highest density of plants in the study area. In this section, the plants were significantly smaller than elsewhere ( $t$ -test,  $p < 0.01$ ). This was the only section where immature plants occurred ( $n = 3$ ). In the next section the walls of the ravine were steep and the ravine was narrow. *Welwitschia* density was low. This sector contained more large plants and there were fewer females than males. Density was again higher in the wide, sandy bed of Section 3 and declined in the steeper-sloping Section 4. Again, as in Section 2, there were more males than females. Size did not differ significantly between Sections 2–4.

Location may affect plant development. Throughout the study area, plants were significantly smaller in the side washes (stem diameter  $53 \pm 20$  cm,  $n = 35$ ) than in the main wash ( $74 \pm 30$  cm,  $n = 47$ ,  $t$ -test,  $p < 0.001$ ) and on the ledges ( $86 \pm 37$  cm,  $n = 27$ ,  $t$ -test,  $p < 0.001$ ). Based on our continuous growth rate data, we expected to find plants with relatively longer leaves on the ledges than elsewhere (one-tailed comparison). As leaf length was related to stem diameter (the latter being an index of plant size; maximum leaf length =  $37.6 + 0.674 \times$  stem diameter;  $r = 0.61$ ,  $p < 0.001$ ), we compared the regression slopes of ledge plants (slope = 1.102,  $n = 23$ ) against those in the main wash (0.537,  $n = 47$ ,  $t = 1.67$ ,  $p < 0.05$ ) and the side washes (0.500,  $n = 35$ ,  $t = 1.72$ ,  $p < 0.05$ ). Ledge plants had significantly longer leaves than other plants. There were more males than females in all locations (in the main wash, ledges, and side wash/slope respectively female:male ratios were: 18:27, 9:16 and

15:22), but these were not significantly different from parity ( $\chi^2$ -test).

Location may affect the development of saplings. We observed germination of 3 plants during 1987, after 12.9 mm rain fell on 6 April and 23.8 mm on 19 July. This was the only case when germination was observed. We observed that the upper layers of the soil retained the 1987 rain water for at least 6 months (see also Gut 1988). Eleven years after germinating, one plant on a ledge has grown much bigger (stem diameter: 6 cm, maximum leaf length: 43 cm) than the other two located in the main wash (stem: 2 and 2 cm, leaf: 27 and 14.5 cm). The last-mentioned short-leaved plant in the main wash appeared to be in bad condition with even the youngest parts of its leaves beginning to dehydrate.

### Discussion

Continuous monitoring of leaf growth on a long-term basis enabled us to elucidate possible factors causing variability in growth rate of a long-lived, evergreen plant over time, space and between sexes. The study period was long enough to cover episodic events that had significant effects, and the monitoring intervals were short enough to capture these. LTER thus revealed new information on a well-studied species as well as facilitating the identification of what constitutes episodic events. This may ultimately enable one to use *Welwitschia* as a yard-stick (e.g., by demographic modelling) for the occurrence of episodic events in a desert over very long periods of time (e.g., centuries).

The average growth rates of *Welwitschia* leaves ( $0.37 \text{ mm day}^{-1}$ ) measured by us compared well with previous measurements. Repeated measurements of leaf lengths at intervals of several years on the *Welwitschia* Plains (near Swakopmund) indicated that leaves grew at rates of  $0.2\text{--}0.5 \text{ mm day}^{-1}$  (Brinckman & von Willert 1987), while Walter & Breckle (1984) estimated  $0.23\text{--}0.82 \text{ mm day}^{-1}$ , and Bornman et al. (1972)  $0.38 \text{ mm day}^{-1}$ . At Brandberg (near the town of Uis) and Brandberg West, Brinckman & von Willert (1987) found growth rates of  $0.2\text{--}0.25 \text{ mm day}^{-1}$  in 1977–1981 compared to  $0.34\text{--}0.35 \text{ mm day}^{-1}$  during the subsequent period, 1981–1986, with higher local rainfall.

Our study provides monthly and annual resolution in growth rate determinations and enables quantitative analyses in relation to environmental factors.

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)**

Page: 2

**Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**ANDERSON, Ms Pippin**

University Of Cape Town  
24 The Avenue  
WOODSTOCK 7925  
Telephone (Work): 4483675  
E-Mail: panderson@botzoo.uct.za

**ARIBEB, Karl**

D R F N  
NAMIBIA

**ARIF, Mr Tanveer**

PAKISTAN

**AZARNIVAND, Mr Hossein**

University Of Tehran  
P O Box 14185/354  
Natural Resources College Of Tehran University  
KARAJ 37585-4314  
IRAN  
Telephone (Work): 09982612230497  
Fax: 09982261227765  
E-Mail: hazar@chamran.ut.ac.ir

**BADCOCK, Ms Jacqui**

Resident Representative  
U N D P  
NAMIBIA  
E-Mail: jacqui.badcock@undp.org

**BANK, Maria**

D R F N  
NAMIBIA

**BARAC, Miss Anuschka**

Student  
Potchefstroom University  
School Of Environmental Sciences And Development  
Potchefstroom  
POTCHEFSTROOM 2520  
Telephone (Work): 0182992499  
Fax: 0182992503  
E-Mail: plbasb@puknet.puk.ac.za

**BETHUNE, Ms Shirley**

National Co-Ordinator NAPCOD  
Directorate Environmental Affairs  
Private Bag 13306  
WINDHOEK  
NAMIBIA  
Telephone (Work): 0926461294015  
Fax: 0926461240339  
E-Mail: bethune@dea.mel.gov.na

**BEUKES, Adolf**

D R F N  
NAMIBIA

**BIELEK, Dr Pavol**

Director Of Institute  
Soil Science And Conservation Research Institution  
Gagarinova 10  
BRATISLAVA 82713  
SLOVAK REPUBLIC  
Telephone (Work): 09421743420866  
Fax: 09421743295487  
E-Mail: bielek@vupu.sk

**BOOIS, Salomon**

D R F N  
NAMIBIA

**BORJIGDKHAN, Mr Adiyasuren**

U N C C D Focal Point Of Mongolia Environmental Education And  
P O Box 752  
ULAANBAATAR  
MONGOLIA  
Telephone (Work): 0997611312458  
Fax: 0997611312320  
E-Mail: adyasurents@usa.net

**BOTES, Andre**

D R F N  
NAMIBIA

**BOTO, Mrs I.**

C T A  
Posbus 380  
WAGENINGEN 6700AJ  
NETHERLANDS  
Telephone (Work): 0931317467157  
Fax: 0931317460067  
E-Mail: boto@ccta.nl

**BRAHIMI, Mr Youssef**

PARIS  
FRANCE

**BRAND, Miss Nellie**

D R F N  
P O Box 20232  
WINDHOEK  
NAMIBIA  
Telephone (Work): 0926461229855  
Fax: 0926461230172

**CHIKWENYA, Musampa**

P O Box 450061  
MPIKA  
ZAMBIA  
Telephone (Work): 092604370387  
E-Mail: zaw@zamnet.co.zm

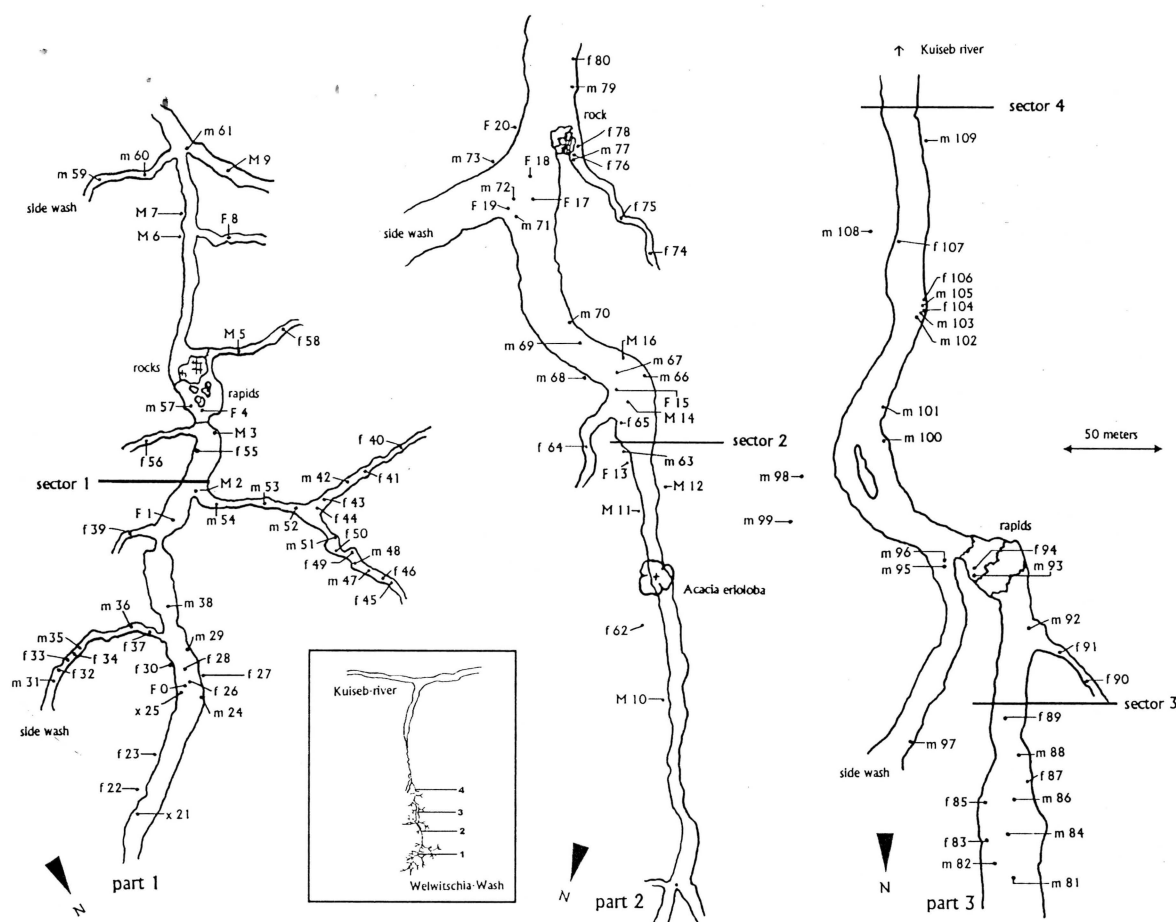


Figure 5. Map of main channel of Welwitschia Wash indicating the position of study plants (capital letter) and other Welwitschias (lower case), where 'F/f' denotes females and 'M/m' males.

Although *Welwitschia* grow continuously (bar one observation), an individual's monthly growth rate may vary about 22-fold while annual growth rates may vary 11-fold. Growth shows a definite seasonal cycle. It also differs between years, but there are no regular cycles over the course of several years.

Climatic factors appear to cause seasonal and annual changes in growth rates. Low relative humidity (mean monthly <35%) is correlated with slow growth between April and August. During this period dry berg winds (Föhn) prevail for 30–50% of the time (Lancaster et al. 1984). Bornman et al. (1973) and von Willert (1994) found that during berg wind conditions, *Welwitschia* vapour pressure deficits in the leaves were continuously high until the berg wind ceased. We observed that *Welwitschia* recovered its leaf growth during the moister part of the year, even without rainfall.

Fog does not appear to play a major role for *Welwitschia*. We found that the temporal distribution of fog differs from the growth patterns of *Welwitschia* both within each season and between seasons (Fig-

ures 2 and 3). The amount of fog-water precipitation on the low-lying leaves is probably slight compared to the plant's daily requirements of one litre of water per day (Eller et al. 1983). During one year, a metal model of 1 m<sup>2</sup> *Welwitschia* leaves at Gobabeb collected only 2.4 l of water, or 6.5 ml per day. A standard fog collector (upright 1 m<sup>2</sup> net) standing next to the model collected 16 times this quantity (Henschel et al. 1998). It is thus unlikely that *Welwitschia* leaves collect significant amounts of fog water.

By contrast, rainfall, or its influence on ground water, has a strong effect on *Welwitschia* growth. Three to six weeks after effective rains in mid-summer (>11 mm per event), growth rate increases up to double that of the same month in a dry year; 2–3 months after effective rain it can quadruple. The time for the first reaction of leaf growth after rain, 19–35 days, may be the time it takes rain water to sink to the roots. Overall degree of growth increase after effective rain depends on how much rain >11 mm falls during events. Mid-summer is the season when *Welwitschia* ordinarily increases its growth rate and rainfall merely

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)**

Page: 1

**Combating Desertification**

Printed on Wed 10 April 02 at 14:29:21

**ABISOYE, Dr V.**

Tropical Forest Network  
P.O. Box 38471  
Dugbe  
IBADAN 20001  
NIGERIA  
Telephone (Work): 09234712628  
Fax: 092348109051  
E-Mail: tfnnigeria95@yahoo.co.uk

**AJARU, Mr Ali Alias**

Mili Mil Paresh  
Kuja  
Amuria Country  
KATAKWI DISTRIK  
UGANDA  
Telephone (Work): 092564132004  
Fax: 0925641321010  
E-Mail: smuwaya@yahoo.com

**ABRAHAMS, Miss Natasha**

Student  
University Of Western Cape  
Botany Department  
Private Bag X17  
BELLVILLE 7535  
Telephone (Work): 9593783  
Fax: 9592266  
E-Mail: nabrahams@uwc.ac.za

**ALEX, Mr Lwakuba**

M A A I F  
P O Box 102  
ENTEBBE  
UGANDA  
Telephone (Work): 0925641320004  
Fax: 0925641321010  
E-Mail: smuwaya@yahoo.com

**ADESANYA, Mr Adekunle**

Alaaka Community Development Association  
P O Box 27040  
Agodi Post Office  
IBADAN 200003  
NIGERIA  
Telephone (Work): 0923422410842  
Fax: 0923422318400  
E-Mail: prince2002t@onebox.com

**ALLSOPP, Dr Nickey**

University Of The Western Cape / Botany Department  
ARC - Range & Forage Department  
Private Bag X17  
BELLVILLE 7535  
Telephone (Work): 9593373  
Fax: 9591376  
E-Mail: nallsopp@uwc.ac.za

**ADEYEMI, Prince**

Alaaka Community Development Association  
P O Box 27040  
Agodi Post Office  
IBADAN 200003  
NIGERIA  
Telephone (Work): 0923422410842  
Fax: 0923422318400  
E-Mail: prince2002t@onebox.com

**ALOJO, Mr Lawrence**

Alaaka Community Development Association  
P O Box 27040  
Agodi Post Office  
IBADAN 200003  
NIGERIA  
Telephone (Work): 0923422410842  
Fax: 0923422318400  
E-Mail: prince2002t@onebox.com

**ADISA-BALOGUN, Mrs I. A.**

Tropical Forest Network  
P.O. Box 38471  
Dugbe  
IBADAN 20001  
NIGERIA  
Telephone (Work): 09234712628  
Fax: 092348109051  
E-Mail: tfnnigeria95@yahoo.co.uk

**AMAAMBO, Otilie**

D R F N  
P O Box 1228  
Ondangwa  
OSHANA REGION  
NAMIBIA  
Telephone (Work): 0926465221854

**AHMADI, Dr Hassan**

University Of Tehran / Iran Desert Research Center  
P O Box 14185/354  
TEHRAN 37585-4314  
IRAN  
Telephone (Work): 09982612223044  
Fax: 09982612227765  
E-Mail: ghzehtab@chamran.ut.ac.ir

**AMOS, Mr D.G.**

Tropical Forest Network  
P.O. Box 38471  
Dugbe  
IBADAN 20001  
NIGERIA  
Telephone (Work): 09234712628  
Fax: 092348109051  
E-Mail: tfnnigeria95@yahoo.co.uk

Table 2. Welwitschia distribution, density, size and sex ratio in various sections of the Welwitschia Wash (Figure 5).

Section	Description	Length (m)	Distance (m)	Plants N	Density N/100 m	Stem $x \pm SD$	Stem range	Females: males
1	Shallow, 2 tributaries	120	320	37	11.6	48 $\pm$ 22	2–100	15:19
2	Ravine deepens and narrows	370	500	20	4.0	75 $\pm$ 34	22–165	6:14
3	Broad sandy base, sloping rocky walls	260	340	33	9.7	83 $\pm$ 31	10–160	15:18
4	Slope downwards, steep banks	300	420	20	4.8	82 $\pm$ 25	40–150	6:14
Total		1050	1580	110	7.0	69 $\pm$ 32	2–165	42:65

accelerates this. By contrast, rain has little effect on adult plants during their usual season of declining growth (March–August).

Availability of surface water late in the season may, however, be important for recruitment, as our observations of germination after rainfall in April 1987 indicate. Walter (1936), Walter & Breckle (1984), and von Willert (1994) previously suggested that heavy rains, such as the 1934–1935 events (> 100 mm), may be crucial for recruitment. After such extreme events, the surface layers of the soil may remain wet for a long time, allowing the seeds to soak before germination and sustaining the seedlings until their roots have penetrated to groundwater. Germination and establishment that we observed as a response to a less extreme late-season rain may be explained, as follows. During April–September the soil surface layers are cool (10 °C less at 10 cm depth than during summer; Lancaster et al. 1984) and can thus retain water for longer (Gut 1988). Furthermore, soon after the seeds are produced and disperse from their parent plant in March/April, many may still be viable; later, most seem to be lost to fungi (Bornman et al. 1972; Cooper-Driver, personal communication).

Location affects growth and development of Welwitschia. Von Willert (1994) found higher leaf water potential and leaf growth rates in plants occurring in drainage lines compared to those occurring outside them. In the Welwitschia Wash, we found that ledges elevated about 1 m above the bed of the main channel sustained the highest growth rates. There, plants were affected for longer by rainfall and had larger leaves than plants in the main channel, higher up the banks, or in side washes. Ledge plants may benefit from ground water in the main channel as well as

seepage towards it from the sides. Furthermore, flood water may perhaps cause damage to plants situated in the main channel and may wash away nutrient-bearing debris that accumulates under plants and enriches the soil under Welwitschias (Abrams et al. 1997). Ledge plants avoid damage and may retain nutrients while benefiting from a better supply of water.

Many plants in the upper section of the wash are smaller and probably younger than the plants elsewhere (Table 2; Figure 5). It thus appears that the winged seeds disperse uphill, probably borne by southerly winds. The population may be growing outwards, possibly due to the availability of more ground water or gradual soil formation by mycorrhiza-bearing grasses (Jacobson et al. 1993; Jacobson 1997). Outward seed dispersal could occasionally lead to exchange of seeds with the population in the Hope wash, situated 6 km from Welwitschia Wash but the ability for long-distance dispersal remains to be demonstrated. Outward expansion could also be occurring on a larger scale. Populations on the eastern margin of the Namib have a greater proportion of young plants than the western populations and the latter could be relict patches left after a wetter phase (Jürgens 1992). Great longevity and endurance may allow the western populations to persist despite rare recruitment events. Factors such as inter-specific competition, fungus, herbivory, damage by humans, and fire may, however, limit the eastern Welwitschias despite their possibly higher recruitment potential.

Sex ratio was male-biased throughout Welwitschia Wash (Table 2). To examine whether this is a more general phenomenon, we compared our data with data from other populations. In a sample of Welwitschias that we examined in April 1999 along a 16 km long



# DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)

Page: 12

## Combating Desertification

Printed on Wed 10 April 02 at 14:29:22

---

**WARD, Viv**

D R F N  
NAMIBIA

**ZVINGADZA, Mr Sheppard**

Zero Regional Environment Organization  
P O Box 5338  
HARARE  
ZIMBABWE  
Telephone (Work): 09263791333  
Fax: 09263791333  
E-Mail: zero@mweb.co.zw

**WEIK, Mr Jörg**

G T Z  
P. O Box  
AMMAN 11118  
JORDAN  
Telephone (Work): 092625359726  
Fax: 096265156457  
E-Mail: jweik@go.com.jo

**WEISS, Mr Eckehard**

G T Z  
P O Box 5180  
ESCHBORN 65726  
GERMANY  
Telephone (Work): 09496196791912  
E-Mail: eckehard.weiss@gtz.de

**WERNER, Wolfgang**

D R F N  
NAMIBIA

**WILCKE, Mrs Angelika**

Entwicklung And Laendlicher Raum/Agriculture And Rural  
Eschborner Landstrasse 122  
FRANKFURT 60489  
GERMANY  
Telephone (Work): 09496924788465  
Fax: 09496924788481  
E-Mail: A.Wilcke@DLG-Frankfurt.de

**WOEHL, Dr Helmut**

D R F N  
GERMANY

**WOLF, Katherine**

D R F N  
NAMIBIA  
E-Mail: katherinew@drfn.org.na

**ZEHTABIAN, Dr Gholam Reza**

Associate Professor  
University Of Tehran  
P O Box 14185/354  
Natural Resources College Of Tehran University  
KARAJ 31585/4314  
IRAN  
Telephone (Work): 0998261222044  
Fax: 0998261222765  
E-Mail: ghzehtab@chamran.ut.ac.ir

transect in the upper Messum Wash (running west of Brandberg), male bias was significant (males:females = 253:195;  $\chi^2 = 7.51$ ;  $p = 0.0061$ ). This was, however, variable along the length of the transect. When divided into groups of approximately 100 plants, the uppermost group was male-biased ( $p = 0.0072$ ; these were the edge of the population), the next group non-biased, followed by a male-biased ( $p = 0.0048$ ), and another non-biased group. Cooper-Driver (personal communication) documented male bias at Welwitschia Wash (125:80;  $\chi^2 = 9.88$ ,  $p = 0.0017$ ) and Brandberg (368:311;  $\chi^2 = 4.78$ ,  $p = 0.029$ ), but found no bias at Welwitschia Plains, Springbokwasser and Petrified Forest (near Khorixas). A map of the Welwitschia Plain population (Brinckman & von Willert 1987) shows no sex-ratio bias (114:101;  $\chi^2 = 0.79$ ,  $p = 0.38$ ). Female-biased sex ratio has not been recorded anywhere. Possible environmental or genetic causes for differences in Welwitschia sex ratios at different sites and different locations within sites should be examined (e.g., Freeman et al. 1976; Charnov & Bull 1977; Wallace & Rundel 1979; Waser 1994). For instance, age determination could reveal whether males survive longer.

Although much has been published on Welwitschia (Appendix), our study indicates that many important ecological questions remain unanswered. This unusual desert plant warrants further study and we are planning to continue the current long-term monitoring at our small local population. This LTER programme will provide data to relate lifetime recruitment to life history of this long-lived organism. In addition to measuring leaf growth and comparing this to microclimatic conditions prevailing in the Welwitschia Wash, we intend to monitor annual seed production (e.g., by counting cones, measuring cone size and weighing a sample of seeds), as well as measuring changes in stem and leaf sizes in the whole population at intervals of several years.

Our study highlights the need for better data on the Welwitschia's sources of water, including the mechanisms of how rain and run-off affects the soil moisture dynamics at different levels. This can be achieved by mapping ground water and tracing isotopic markers in it. Furthermore, analyses of age distribution, seed dispersal and sex ratio are crucial for an understanding of Welwitschia recruitment, population dynamics, and their relationships to environmental changes. Indeed, Welwitschia may enable a study of the occurrence of episodic events and environmental changes in recent centuries or millenia, which should make it an in-

valuable tool for LTER. This information would, in turn, improve understanding of arid lands in southern Africa besides facilitating the management of this unique Namib Desert plant.

### Acknowledgements

The Ministry of Environment and Tourism granted permission for this study to be conducted in the Namib-Naukluft Park. Numerous assistants helped in the field, with Christine Hänel, Linda Malan, Vilho Mtuleni and Juliane Zeidler conducting most of the monthly measurements of leaf growth. Axel Jakob, Mirjam Müller, Markus Oetjens and Alex Ölinger mapped and measured most of the population in Welwitschia Wash and drew the map. Inge Henschel assisted in compiling the bibliography. Edith Böhme, Gillian Cooper-Driver, Bill Hamilton, Kathy Jacobson, Rudy Jocqué, Norbert Jürgens, Sue Milton, Mark Robertson, Dieter von Willert and Juliane Zeidler provided valuable information and commented on previous drafts of the manuscript.

### References

- Abrams, M. M., Jacobson, P. J., Jacobson, K. M. & Seely, M. K. 1997. Survey of soil chemical properties across a landscape in the Namib Desert. *J. Arid Environ.* 35: 29–38.
- Bornman, C. H. 1972. *Welwitschia mirabilis*: paradox of the Namib Desert. *Endeavour* 31 (113): 95–99.
- Bornman, C. H. 1977. *Welwitschia mirabilis*: structural and functional anomalies. *Madoqua* (II) 10: 21–31.
- Bornman, C. H. 1978. *Welwitschia*: paradox of a parched paradise. C. Struik Publishers, Cape Town.
- Bornman, C. H., Botha, C. E. J. & Nash, L. J. 1973. *Welwitschia mirabilis*: observations on movement of water and assimilates under Föhn and fog conditions. *Madoqua* (II) 2: 25–31.
- Bornman, C. H., Elsworth, J. A., Butler, V. & Botha, C. E. J. 1972. *Welwitschia mirabilis*: observations on general habit, seed, seedling and leaf characteristics. *Madoqua* (II) 1: 53–66.
- Brinckmann, E. & von Willert, D. J. 1987. Injury and recovery of *Welwitschia mirabilis*. *Dinteria* 19: 69–76.
- Bustard, L. 1990. The ugliest plant of the world: the story of *Welwitschia mirabilis*. *Kew Magazine* 7: 85–90.
- Butler, V. 1975. Ultrastructure of the germinating *Welwitschia mirabilis* seed. Ph.D. Thesis, University of Natal, Pietermaritzburg, South Africa.
- Butler, V., Bornman, C. H. & Evert, R. F. 1973. *Welwitschia mirabilis*: Vascularization of a one-year-old seedling. *Bot. Gazette* 134: 63–73.
- Carafa, A. M., Napolitano, G. & D'Acunzo, A. 1989. *Welwitschia mirabilis* Hook.: una strana pianta del deserto della Namibia. *Natura e Montagna* 36: 17–20.
- Charnov, E. L. & Bull, J. 1977. When is sex environmentally determined? *Nature*, London 266: 828–830.

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)****Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**SHUUYA, Aili**

D R F N  
P O Box 939  
Oshakati  
OSHANA REGION  
NAMIBIA  
Telephone (Work): 0926465221854

**SIMULUMBE, Lumba**

No Info At This Stage  
ZAMBIA

**SMAEIL ZADEH, Mr Hamid**

M S C Student  
University Of Tehran / Faculty Of Natural Resources  
P O Box 14185/354  
TEHRAN 37585-4314  
IRAN  
Telephone (Work): 09982612223044  
Fax: 09982261227765  
E-Mail: hamidzaazusa@yahoo.com

**SMITH, Lorraine**

Posagentskap  
PAULSHOEK 8221  
Telephone (Work): 5411048  
Fax: 5411037  
E-Mail: eric@intekom.co.za

**SMITH, Maria**

D R F N

**STRAUSS, Mr Riaan**

Potchefstroom University For C H E  
School Of Environmental Sciences And Development  
POTCHEFSTROOM 2520  
Telephone (Work): 0182992502  
Fax: 0182992503  
E-Mail: greenpalms2000@yahoo.com

**SUKATI, Sicelo**

Brot Für Die Welt / U N C C D Support Programme  
SWAZILAND  
E-Mail: des2002@gliese.de

**TAFIRA, Ms Lubinda**

No Info At This Stage  
ZAMBIA  
Telephone (Work): 09601225514  
E-Mail: zaw@zamnet.co.zm

**THABETHE, Mr Mbana Peter**

Department Of Agriculture  
Private Bag X9071  
ERMELO 2350  
Telephone (Work): 0178192076  
Fax: 0178192072  
E-Mail: petert@ermagri1.agric.za

**THANISEB, Allie**

D R F N  
NAMIBIA

**THATCHER, Theresa**

D R F N  
NAMIBIA

**TJITEKULU, Joseph**

D R F N  
NAMIBIA

**TORRICO, Mr Jose****TREMBLAY, Ms Michelle**

Canadian International Development Agency  
200 Promenade Du Portage  
HULL K1A0G4  
CANADA  
Telephone (Work): 0918199945397  
Fax: 0918199970602  
E-Mail: michelle\_tremblay@acdi-cida.gc.ca

**TSEHLO, Mr Moshe**

No Info At This Stage  
LESOTHO  
Telephone (Work): 09266317205  
Fax: 09266310412  
E-Mail: lecongo@lecongo.org.ls

**TUFFY, Nakali**

D R F N  
NAMIBIA

**VAN HAVEREN, Dr Bruce**

U. S. Bureau Of Land Management  
P O Box 25047, Dfc Building 50,  
Lakewood  
COLORADO 80225  
USA  
Telephone (Work): 0913032360161  
Fax: 0913036707828  
E-Mail: bvanhave@jeffco.k12.co.us

**VOIGT, Mrs Werner**

Karoo Desert N B G  
P O Box 152  
WORCESTER  
Telephone (Work): 0233470785  
Fax: 0233428719

**VOS, Ms Petro**

C S I R  
P O Box 395  
PRETORIA 0001  
Telephone (Work): 0123367919  
Fax: 0123261488  
E-Mail: pvos@csir.co.za

- Cooper-Driver, G. A. 1994. *Welwitschia mirabilis* - a dream come true. *Arnoldia* 54 (2): 2-10.
- Eller, B. M., von Willert, D. J., Brinckmann, E. & Baasch, R. 1983. Ecophysiological studies on *Welwitschia mirabilis* in the Namib desert. *South Afr. J. Bot.* 2: 209-223.
- Freeman, D. C., Klikoff, L. G. & Harper, K. T. 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193: 597-599.
- Giess, W. 1969. *Welwitschia mirabilis* Hook. fil. *Dinteria* 3: 3-55.
- Gut, S. 1988. Untersuchungen zum Feuchtehaushalt in den Dünen der zentralen Namib (Namibia/Südwestafrika). M.Sc. Thesis, University of Zürich, Switzerland.
- Henschel, J. R. 1998. International research cooperation with the Desert Research Foundation of Namibia (DRFN) benefits the natural environment in Namibia. Pp. 401-406. In: Alexander von Humboldt Foundation (ed.), *Wissenschaftleraustausch und Entwicklungszusammenarbeit vor der Jahrtausendwende: Bestandaufnahme, Probleme und Perspektiven*. Nomos, Baden-Baden, Germany.
- Henschel, J. R., Mtuleni, V., Gruntkowski, N., Seely, M. K. & Shanyengana, S. E. 1998. Namifog: Namibian Application of Fog-Collecting Systems, Phase I: Evaluation of Fog-Water Harvesting. Occasional Paper No.8, Desert Research Foundation of Namibia, Gobabeb, 62 pp.
- Herppich, W. B., Flach, B. M.-T., von Willert, D. J. & Herppich, M. 1996. Field investigations of photosynthetic activity, gas exchange and water potential at different leaf ages in *Welwitschia mirabilis* during a severe drought. *Flora* 191: 59-66.
- Herre, H. 1961. The age of *Welwitschia bainesii* (Hook. f) Carr.: C14 research. *J. South Afr. Bot.* 27: 139-140.
- Jacobson, K. M. 1997. Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. *J. Arid Environ.* 35: 59-75.
- Jacobson, K. M., Jacobson, P. J. & Miller, O. K. 1993. The mycorrhizal status of *Welwitschia mirabilis*. *Mycorrhiza* 3: 13-17.
- Jürgens, N. 1993. Namib - die afrikanische Wüste der lebenden Wasserspeicher. *Uni Hamburg Forschung* 27: 68-76.
- Jürgens, N., Burke, A., Seely, M. K., & Jacobson, K. M. 1997. Desert. Pp. 189-214. In: Cowling, R. M., Richardson, D. M. & Pierce, S. M. (eds), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Kers, L. E. 1967. The distribution of *Welwitschia mirabilis* Hook.f. *Svensk Botanisk Tidskrift* 61: 97-125.
- Kutschera, L., Lichtenegger, E., Sobotik, M. & Haas, D. 1997a. Die Wurzel, das neue Organ, ihre Bedeutung für das Leben von *Welwitschia mirabilis* und anderer Arten der Namib sowie von Arten angrenzender Gebiete, mit Erklärungen des geotropen Wachstums der Pflanzen. *Pflanzensoziologisches Institut, Klagenfurt, Austria*, 94 pp.
- Kutschera Mitter, L., Lichtenegger, E., Sobotik, M. & Haas, D. 1997b. Die Wurzel - Hilfe für das Überleben von *Welwitschia mirabilis* und anderer Arten der Namib. *Palmengarten Frankfurt/Main* 61(1): 31-40.
- Lancaster, J., Lancaster, N. & Seely, M. K. 1984. Climate of the central Namib Desert. *Madoqua* 14: 5-61.
- Loutit, B. D., Louw, G. N. & Seely, M. K. 1987. First approximation of food preference and the chemical composition of the diet of the desert-dwelling black rhinoceros, *Diceros bicornis* L. *Madoqua* 15: 35-41.
- Marsh, B. 1982. An ecological study of *Welwitschia mirabilis* and its satellite fauna. *Namib Bull.* 4: 3-4.
- Marsh, B. A. 1987. Micro-arthropods associated with *Welwitschia mirabilis* in the Namib Desert. *South Afr. J. Zoology* 22: 89-96.
- Marsh, B. A. 1990. The microenvironment associated with *Welwitschia mirabilis* in the Namib desert. Pp. 149-153. In: Seely, M.K. (ed.), *Namib ecology: 25 years of Namib research*. Transvaal Museum 7, Pretoria.
- Massmann, U. 1976. *Welwitschia*: nach 90 Jahren. *Namib und Meer* 7: 45-46.
- Moisel, A. & Moll, E. J. 1981. A Braun-Blanquet survey of the vegetation of the Welwitschia Plain. *Dinteria* 15: 3-11.
- Muhammad, A. F. & Sattler, R. 1982. Vessel structure of *Gnetum* and the origin of angiosperms. *Am. J. Bot.* 69: 1004-1021.
- Olivier, J. 1995. Spatial distribution of fog in the Namib. *J. Arid Environ.* 29: 129-138.
- Rodin, R.. 1958a. Leaf anatomy of *Welwitschia*. I. Early development of the leaf. *Am. J. Bot.* 45: 91-95.
- Rodin, R. J. 1958b. Leaf anatomy of *Welwitschia*. II. A study of mature leaves. *Am. J. Bot.* 45: 96-103.
- Schulze, E.-D., Eller, B. M., Thomas, D. A., von Willert, D. J. & Brinckmann, E. 1980. Leaf temperatures and energy balance of *Welwitschia mirabilis* in its natural habitat. *Oecologia* 44: 258-262.
- van Jaarsveld, E. 1990. The cultivation and care of *Welwitschia mirabilis*, the extraordinary caudiciform from the Namib desert. *Aloe* 27 (3): 69-82.
- van Jaarsveld, E. 1992. *Welwitschia mirabilis* in cultivation at Kirstenbosch. *Veld & Flora* 12: 119-121.
- von Willert, D. J. 1993. Can *Welwitschia mirabilis* have more than only two foliage leaves? *South Afr. J. Bot.* 59: 639-640.
- von Willert, D. J. 1994. *Welwitschia mirabilis* Hook. fil. - das Überlebenswunder der Namibwüste. *Naturwissenschaften* 81: 430-442.
- von Willert, D. J., Eller, B. M., Brinckmann, E. & Baasch, R. 1982. CO<sub>2</sub> gas exchange and transpiration of *Welwitschia mirabilis* Hook. fil. in the central Namib desert. *Oecologia* 55: 21-29.
- von Willert, D. J., Eller, B. M., Werger, M. J. A., Brinckmann, E. & Ihlenfeldt, H. H. 1992. Life strategies of succulents in deserts with special reference to the Namib Desert. Cambridge University Press, Cambridge.
- von Willert, D. J. & Wagner-Douglas, U. 1994. Water relations, CO<sub>2</sub> exchange, water use efficiency and growth of *Welwitschia mirabilis* Hook. fil. in three contrasting habitats of the Namib Desert. *Botanica Acta* 107: 291-299.
- Wallace, C. S. & Rundel, P. W. 1979. Sexual dimorphism and resource allocation in male and female shrubs of *Simmondsia chinensis*. *Oecologia* 44: 34-39.
- Walter, H. 1936. Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika) unter Auswertung der Aufzeichnungen des Dr. G. Boss (Swakopmund). *Jahrbuch Wissenschaftlichen Botanik* 84: 58-221.
- Walter, H. 1971. The ecology of *Welwitschia mirabilis*. Pp. 369-374. In: *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh, 539 pp.
- Walter, H. & Breckle, S.-W. 1984. Die Überganszone mit *Welwitschia*. Pp. 290-298. In: *Spezielle Ökologie der tropischen und subtropischen Zonen* Vol. 2. G. Fischer Verlag, Stuttgart.
- Waser, N. M. 1984. Sex ratio variation in populations of a dioecious desert perennial, *Simmondsia chinensis*. *Oikos* 42: 343-348.
- Zar, J. H. 1996. *Biostatistical analysis*. 3rd edition, Prentice-Hall, Upper Saddle River, New Jersey.

**DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)****Combating Desertification**

Printed on Wed 10 April 02 at 14:29:22

**PAXTON, Ms Midori**

U N D P  
WINDHOEK  
NAMIBIA  
Telephone (Work): 09264612046232  
Fax: 09264612046203  
E-Mail: midori.paxton@undp.org

**PELLANT, Mr Mike**

Bureau Of Land Management  
1687 S. Vinnell Way  
Boise  
IDAHO 83709  
USA  
Telephone (Work): 0912083733823  
Fax: 0912083733805  
E-Mail: mike\_pellant@blm.gov

**PENNY, Ms Roben**

D R F N  
Woodbine  
Essex Road  
KALK BAY  
Telephone (Work): 7881285  
E-Mail: robenpen@jaywalk.com

**PHILANDER, Angy**

D R F N

**PRINZ, Aubrey**

D R F N  
NAMIBIA

**RAJI, Dr B. A.**

Ahmadu Bello University  
Department Of Soil Science  
Faculty Of Agriculture/Institute For Agricultural Research  
P.M.B. 1044  
ZARIA 0023469  
NIGERIA  
Telephone (Work): 0923469551607  
E-Mail: cndciar@inet-global.com

**RETHMAN, Dr Norman**

University Of Pretoria  
Department Of Plant Production And Soil Sciences  
PRETORIA 0002  
Telephone (Work): 0124203225  
Fax: 0124204120  
E-Mail: nrETHMAN@postino.up.ac.za

**ROGGE, Jo**

D R F N  
NAMIBIA

**SAIDE, Mr Eusebio**

Coterra  
Rua Henrique De Sousa  
No 45.  
MOPUTO  
MOZAMBIQUE  
Telephone (Work): 092581308866  
Fax: 092581308866  
E-Mail: eusibio2001@yahoo.com

**SALOMO, Mr C A**

D R F N

**SASS, Ms M**

D R F N

**SCHLYTER, Dr Peter**

Stockholm University  
Se-10691  
STOCKHOLM  
SWEDEN  
Telephone (Work): 094686747822  
E-Mail: peter.schlyter@natueo.su.se

**SECK, Dr Emmanuel**

Endatm  
B P 3370, 54 Rue Carnot Dakar  
DAKAR  
SENEGAL  
Telephone (Work): 092218222496  
Fax: 092218217495  
E-Mail: energy2@enda.sn

**SEELY, Dr Mary**

D R F N  
P O BOX 20232  
WINDHOEK  
NAMIBIA  
Telephone (Work): 0926461229855  
Fax: 0926461230172  
E-Mail: mseely@drfn.org.na

**SHIKONGO, Mr Sem**

No Info At This Stage  
NAMIBIA

**SHOKO, Mr Mzondiwa**

P O Box Cy385  
Causeway  
HARARA  
ZIMBABWE  
Telephone (Work): 092634705671  
Fax: 092634793123  
E-Mail: zpn143@mweb.co.zw