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

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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 $\mathrm{mm.day^{-1}}$, 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 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 282 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 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 ~ 1 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 0.2-0.8 $mm.day^{-1}$ (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 C_3 metabolism, which requires it to open its many stomata during the day to take up 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.day^{-1} (730 mm per annum) would be required to sustain the plant's water consumption. This is 3 to ~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 recruitment (Bornman *et al.* 1972; van Jaarsveld 1990). Although females annually produce many seeds, recruitment events are rare (many years apart). The latter has been deducėd 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. 19*83). 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* (282 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 Central 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 18x55 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 pers.obs.), as well as micro-arthropods (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_3 plant and there is no evidence of CAM and nocturnal CO_2 uptake (von Willert *et al.* 1982; Eller *et al.* 1983). The leaves bear 61-87 $stomata.mm^{-2}$ 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 $dm^3.m^{-2}$ 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 efficiency (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 pers.comm.). The rapid growth of the roots of seedlings, initially 5-10 $mm.day^{-1}$, 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 (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 10000-20000 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, pers.comm.), 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, pers.comm.).

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), *Orthanthera 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 (±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:
(Σgrowth measurements in a year x 365)/(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 pers.comm.) were not examined.

Climate was monitored continuously at Gobabeb with autographic recorders until 1993 and thereafter with data logger. Fog was measured by collecting run-off 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, pers.comm.) 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 ±SD. Unless otherwise stated significant differences are $P<0.05$.

Results

Growth Rate

Total leaf growth of individual Welwitschia plants over 13 years and 8 months was 1780±407 mm (range 1059-2416 mm) at an average rate of 0.367±0.203 mm.day^{-1} (0-1.597 mm.day^{-1}; 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±43.9 mm (range 27.1-290.9 mm).

Growth rate fluctuated during each year, following a seasonal pattern, and varied between years (Fig.1). Individuals varied their monthly leaf growth rate by 22±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 (Fig.1), although it was usually <11 mm.event^{-1}. Annual rainfall was 16.2±16.9 mm (range 2-70 mm).

Figure 1

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 (Fig.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 (Fig.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 median 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% (Fig.2).

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

Table 1

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; Fig.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 mm.day^{-1}) followed the December 1993 rainfall that had caused the wash to flood (Fig.1). This marked the turning point of the cumulative percent deviation of the growth curve (Fig.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.

Figure 3

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 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 mm on 11 February 1990, ~30 mm on 13 December 1993, and 26.6 mm on 16 January 1997; Fig.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 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 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 (Fig.1). By contrast, annual growth rate did not change in relation to rainfall events of >11 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±0.125 vs. 0.352±0.124 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 (Fig.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, $p>0.05$; Fig.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±26 mm.year^{-1}) was similar to that of 4 plants in side washes (106±20 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±20, $t>2.65$, $p<0.02$). During each year after 1989, ledge plants grew significantly more (t-test, $p<0.05$) than side-wash plants (Fig.4). They also grew significantly more (t-test, $p<0.05$) than main-wash plants during all years except 1987, 1990, 1994, and 1997 (Fig. 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.

Figure 4

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 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 ($X^2=6.22$, 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±SD: 76±31 vs. 66±28 cm; range: 10-165 vs. 18-124 cm; $U_{females}=1563$, $U_{males}=1125$, $Z=2.23$,

$p<0.05$). Whereas 93.5% of the males had a stem diameter >40 cm, this was true for only 72.1% of the females ($X^2=9.05$, 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, Fig.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.

Figure 5

Table 2

Location may affect plant development. Throughout the study area, plants were significantly smaller in the side washes (stem diameter 53±20 cm, n=35) than in the main wash (74±30 cm, n=47, t-test, $p<0.001$) and on the ledges (86±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 x 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 (X^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 others 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 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 0.2-0.5 mm.day^{-1} (Brinckman & von Willert 1987), while Walter & Breckle (1984) estimated 0.23-0.82 mm.day^{-1}, and Bornman *et al.* (1972) 0.38 mm.day^{-1}. At Brandberg (near the town of Uis) and Brandberg West, Brinckman & von Willert (1987) found growth rates of 0.2-0.25 mm.day^{-1} in 1977-1981 compared to 0.34-0.35 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. 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.2 & 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^2 Welwitschia leaves at Gobabeb collected only 2.4 litres of water, or 6.5 ml per day. A standard fog collector (upright 1-m^2 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 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 1934/35 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, pers.comm.).

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; Fig.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 transect in the upper Messum Wash (running west of Brandberg), male bias was significant (males:females = 253:195; X^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 (pers.comm.) documented male bias at Welwitschia Wash (125:80; X^2=9.88, p=0.0017) and Brandberg (368:311; X^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; X^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 invaluable 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.

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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.

			Year													
Plant #	Stem	Loc	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

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

Section	description	length (m)	distance (m)	plants N	density N/100m	stem x±SD	stem range	females : males
1	shallow, 2 tributaries	120	320	37	11.6	48±22	2-100	15:19
2	ravine deepens & narrows	370	500	20	4.0	75±34	22-165	6:14
3	broad sandy base, sloping rocky walls	260	340	33	9.7	83±31	10-160	15:18
4	slope downwards, steep banks	300	420	20	4.8	82±25	40-150	6:14
Total		1050	1580	110	7.0	69±32	2-165	42:65

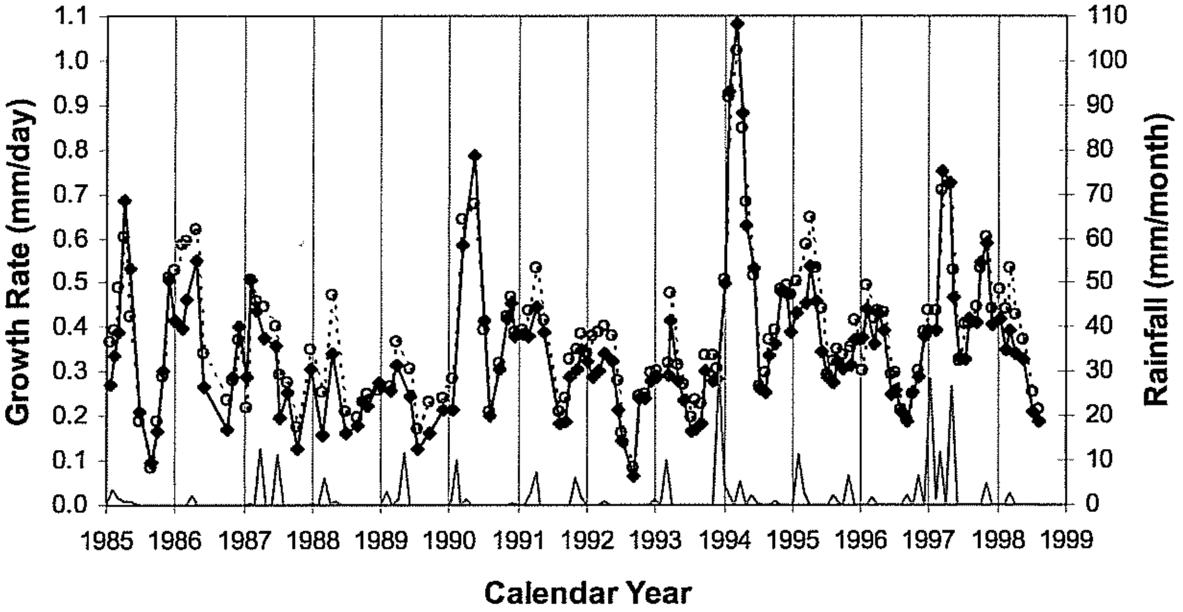
Figure 1: Monthly mean growth rate of Welwitschia females (diamond) and males (circle) (upper curves) and monthly rainfall totals (bottom spikes).

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.

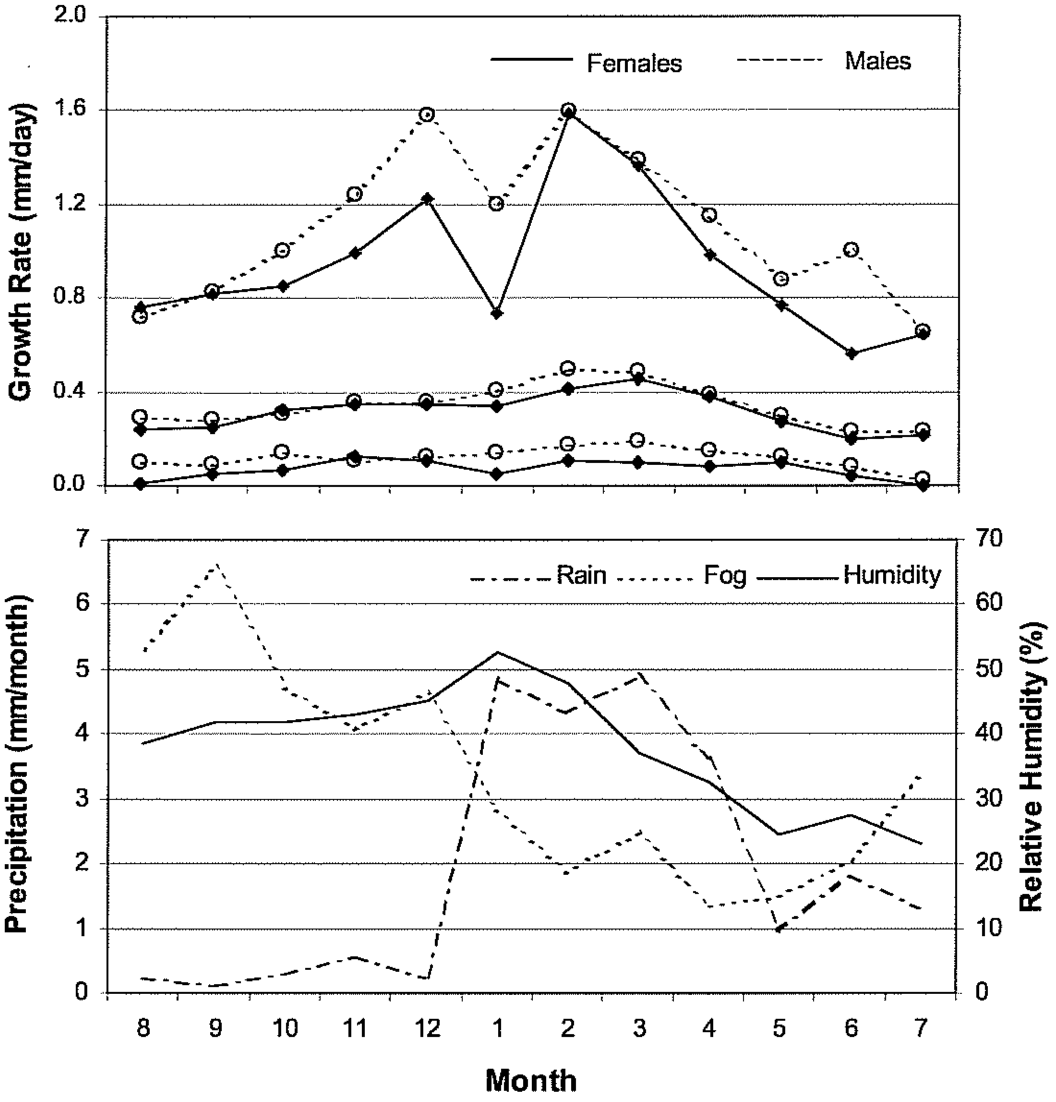
Figure 3: Cumulative percent deviation from the mean of rainfall, fog and of annual growth of Welwitschia.

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).

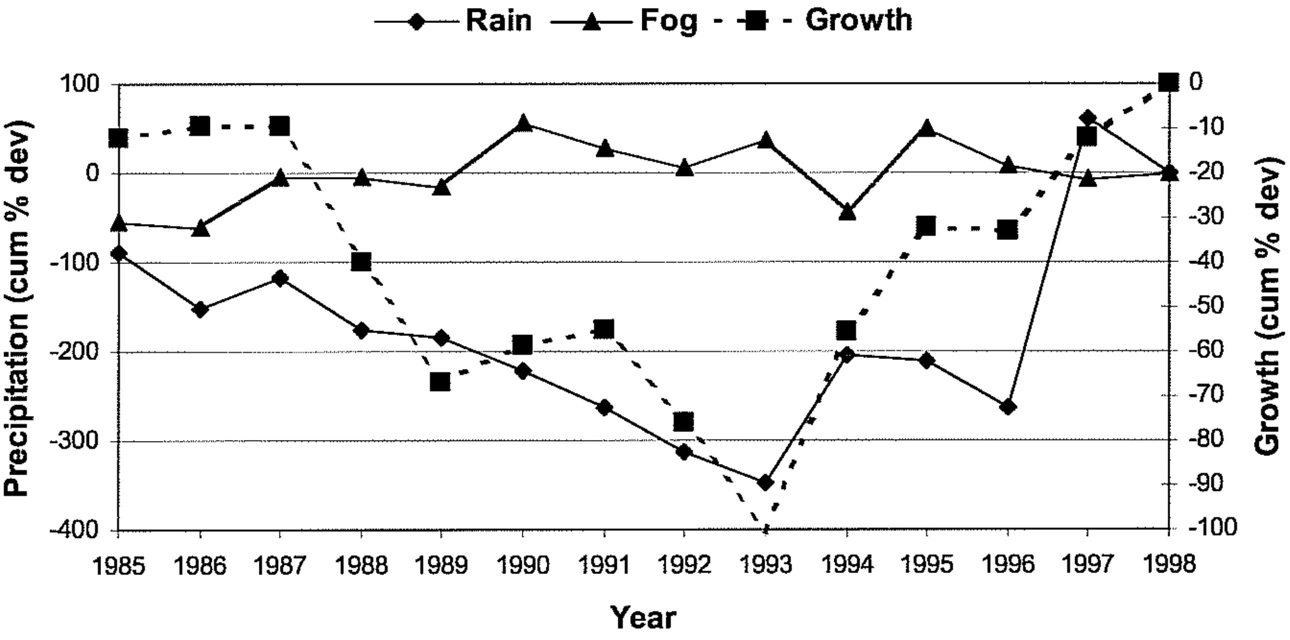
Figure 5: Map of main channel of Welwitschia Wash indicating the position of study plants (capital letter) and other Welwitschias (lower case), where "F/f" denotes females and "M/m" males.



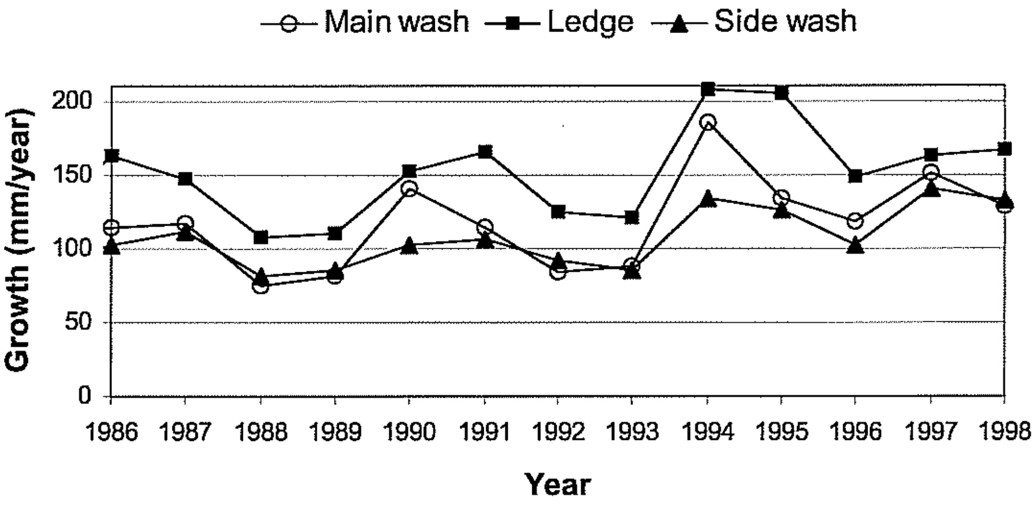
Henschel & Seely: Figure 1



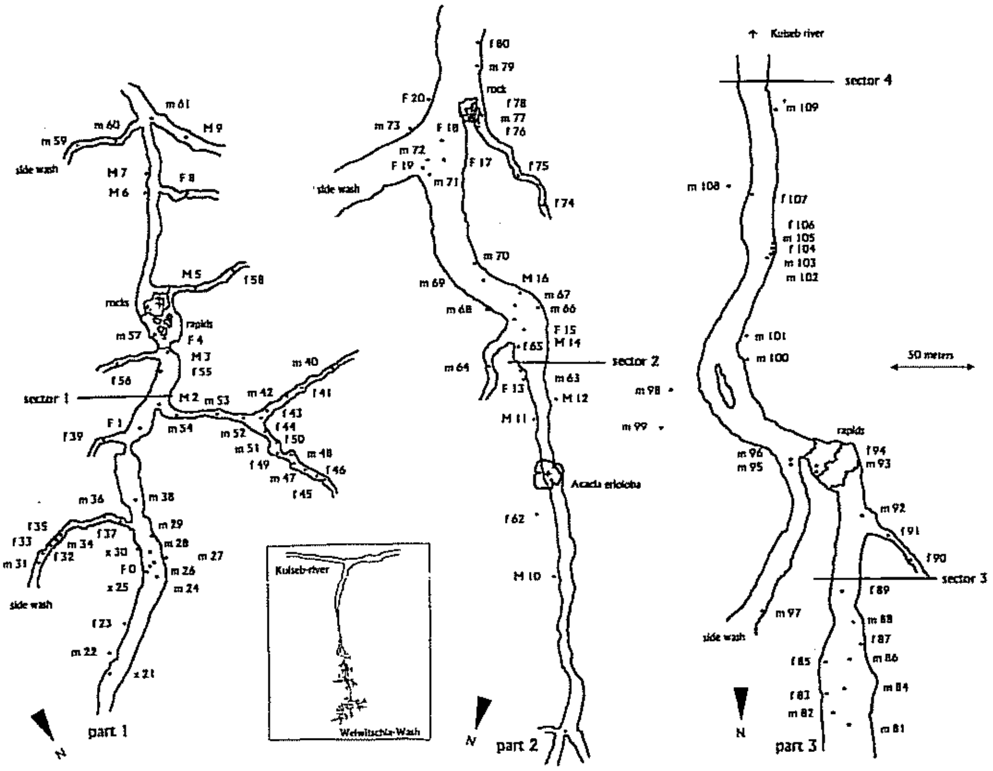
Henschel & Seely: Figure 2



Henschel & Seely: Figure 3



Henschel & Seely: Figure 4



Henschel & Seely: Figure 5

Appendix

Bibliography *Welwitschia mirabilis* J.D.Hooker

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