Population Dynamics and Sustainable Harvesting of the Medicinal Plant *Harpagophytum procumbens* in Namibia

Results of the R+D Project 800 86 005

Marianne Strohbach
Dave Cole

Federal Agency for Nature Conservation

BfN – Skripten 203

2007

Population Dynamics and Sustainable Harvesting of the Medicinal Plant *Harpagophytum procumbens* in Namibia

Results of the R+D Project 800 86 005

Marianne Strohbach
Dave Cole

Federal Agency for Nature Conservation

Cover picture: Harvesting Devil's Claw on the monitoring sites at Ben Hur (M. STROHBACH, April 2005)

For more information contact: Marianne Strohbach
P.O. Box 1669
Swakopmund
Namibia
E-mail: marstr@iway.na

This publication is included in the literature database "***DNL-online***" (www.dnl-online.de)

BfN-Skripten are not available in book trade.

Publisher: Bundesamt für Naturschutz (BfN)
Federal Agency for Nature Conservation
Konstantinstrasse 110
53179 Bonn, Germany
URL: http://www.bfn.de

Printed by the printing office of the Federal Ministry of Environment, Nature Conservation and Nuclear Safety.

Printed on 100% recycled paper.

Bonn, Germany 2007

Contents

List of Tables

List of Figures

Abbreviations

DC Devils' Claw *(Harpagophytum procumbens)*, called 'Kamagu' by the harvesters
SHDC Sustainably Harvested Devils' Claw Project
NDCSA National Devils' Claw Situation Analysis

Acknowledgements

This study would not have been possible without the contributions of numerous individuals representing a wide range of stakeholders. It is not feasible to acknowledge each and every individual, but we gratefully acknowledge the following contributors in particular:

- The German Federal Agency for Nature Conservation for funding this study;
- the Devil's Claw harvesters on the farms Vergenoeg and at the Tjaka Ben Hur complex, for their support and sharing of knowledge of different aspects of Devil's Claw. The study would have been incomplete without their contributions. We are particularly grateful to Fritz Kamti at Vergenoeg, the late Arnold Makabanyane and the late Agnes Auchas at Tjaka Ben Hur, and Mbazo Motlhaping, the Sustainably Harvested Devil's Claw Project Liaison Officer;
- Pierre Du Plessis, Cyril Lombard, James Leith and Michel Mallet of CRIAA SA-DC, for their contributions of current information on Devil's Claw;
- Ezekeil Kwembeya and Barbara Curtis for their constructive comments on the manuscript;
- The Namibian Ministry of Environment and Tourism for providing Devil's Claw export data, and the members of the Namibian Devil's Claw Working Group for their support.

"All research and management by outsiders must remember that their activities come and go, but food security – land and resource surety – is a long-term, life and death issue for rural peoples"

MARY HOSKINS 1990 in CUNNINGHAM 2001

1. Introduction

The harvesting of, and trade in various natural products has increased significantly over the last decade and the market is estimated to be worth in excess of U$ 50 billion annually. This increase has partially been the result of a need of rural communities, particularly in developing countries to, on the one hand generate additional or supplement much needed income and on the other hand and an increase in demand of plants, primarily those with medicinal values, in developed countries. In many instances, this has made an important contribution to improved livelihoods of the primary producers, often being rural communities, although there are cases where this has been to the contrary. While this increase in demand has brought about greater opportunities for primary producers, it has also vastly increased the pressures on the sustainability of these resources. The focus on sustainable utilisation has not only been because of concerns for the resource itself but also the desire to see the continued long-term benefit of the primary producers from the trade.

Threats to medicinal plants are similar to those threatening biodiversity in general – one of the most serious ones being over-harvesting. In addition, customary practices that traditionally regulated the use of natural resources are easily undermined by current socio-economic forces (HAMILTON 2004). Medicinal plants are material resources, which are related to healthcare, livelihood security and financial income. A loss of these plants – often due to short-term economic pressures – will create the most acute problems for the rural poor who rely on these plants growing in their vicinity for healthcare and income.

Recommendations for the conservation of medicinal plants include, amongst others, an understanding of the medicinal plant trade. Imperative to the survival of the species, however, is the gaining of scientific information on the population dynamics and the variables influencing these dynamics, as well as the development of scientifically based sustainable harvesting practices (CUNNINGHAM 2001, HAMILTON 2004). Work by conservationists on medicinal plants should be undertaken with people who own, manage or make use of the species, which requires the conservationist to also have an appreciation of the economics and social structures of the communities involved (HAMILTON 2004).

Storage tubers of *Harpagophytum procumbens*, widely known as Devil's Claw, have been used for their medicinal properties since ancient times by some southern African indigenous people (WATT AND BREYER-BRANDWIJK 1962). This knowledge was transferred to the modern pharmaceutical industry during the mid 20th century. Many subsequent studies, including some clinical trials, have verified the efficacy of this remedy in treating rheumatoid arthritis and similar conditions, which again established a steady and increasing trade in dried Devil's Claw storage tubers (GRUENWALD 2002). Up to today, most of the harvesting is conducted by rural people, with between 10 000 and 15 000 harvesters relying on sales of dried tubers as their only source of income (COLE AND LOMBARD 2000). These high levels of trade raised concerns over the potential over-exploitation of the plant.

Studies on the ecology and harvesting impact of Devil's Claw were conducted in Botswana during the 1980s (BURGHOUTS 1985, HULZEBOS 1987). Results of these studies were used as guidelines for the annual quota-system used by the SHDC Project, which aimed at ensuring a fair price to harvesters if the resource is harvested in a sustainable manner. However, already during the early stages of the SHDC project it became apparent that the applicability of the Botswana Devil's Claw studies to Namibian circumstances, where the bulk of annually traded Devil's Claw originates, was extremely limited (personal observations). This was confirmed by observation from NOTT (1986), who recorded much higher tuber yields for plants in Namibia than were observed during the studies in Botswana.

The need for this study to be undertaken arose because of a dramatic increase in export figures during 1998 and 1999 and corresponding concerns regarding the possible over-utilisation of Devil's Claw in Namibia. Further concerns regarding the sustainability of the Devil's Claw industry were also highlighted at an international forum when, in April 2000, at the (CITES) eleventh Conference of Parties (CoP 11) held in Gigiri (Kenya), Germany proposed that *Harpagophytum* species be listed on Appendix II.

Efforts to address this were limited by the lack of scientific data regarding the population and ecology of the plant as well as the impact of harvesting on the population status. There was therefore an urgent need to generate more information so that informed decisions could be made that would improve the management of the resource at all levels. This study has made an important contribution towards this.

The objectives of the study focussed on three main aspects:

- To investigate the influence of highly variable annual rainfall on Devil's Claw populations and the impact of harvesting thereon
- To develop a simple and reliable method to establish an annual Devil's Claw harvesting quota for potential harvesting areas
- To establish a sustainable harvesting method and make recommendations for more effective management of Devil's Claw

The approach adopted in this study is based on the incorporation of a combination of local (traditional) knowledge and scientific research. In this regard, the input from harvesters experience was crucial.

2. Background

2.1 Devil's Claw

Devil's Claw grows mainly in the Kalahari sands of Namibia, Botswana, South Africa, Angola, and to a lesser extent in Zambia, Zimbabwe and Mozambique. The Kalahari is largely covered by relatively dense savanna vegetation adapted to the prevailing semi-arid climate with frequent periods of droughts. Long-term annual rainfall averages vary from 150 to 400 mm, most of which falls during the summer months December to April (AEZ 2001).

Devil's Claw comprises two species: *Harpagophytum procumbens* (BURCH.) DC. EX MEISN. (with two sub-species, *procumbens* and *transvaalense* IHLENF. & H. HARTMANN) and *H. zeyheri* DECNE. (with three sub-species, *zeyheri, sublobatum* (ENGLER) IHLENF. & H. HARTMANN and *schijffii* IHLENF. & H. HARTMANN*)* (IHLENFELDT AND HARTMANN 1970). *Harpagophytum* is a geophyte with prostrate stems that sprout in late spring (September to November) from a primary tuber, and die back at the onset of the first cold fronts (May to June). The primary tuber extends into a deep taproot, with lateral, often horizontally growing thick secondary roots. These secondary roots develop a chain of tubers, usually between 4 cm and 40 cm long. These secondary storage tubers contain the highest concentrations of secondary compounds, including Harpagoside, and are harvested for their analgesic and anti-inflammatory properties (IHLENFELDT AND HARTMANN 1970). The plant is easily recognised by its large tube-shaped pink to dark mauve (sometimes white) flowers.

The vernacular name Devil's Claw is derived from the sharp recurved hooks protruding off the fruit. The fruit is dispersed by animals, and it may take several years for all seeds to be released from the hard fruiting body (personal observations). Seeds from one fruit may have variable degrees of inherent dormancy, but may remain viable for up to 70 years (ERNST *et al.* 1988). New cohorts of seedlings can be observed after large rainfall events, but further seedling establishment will depend on the temperature and rainfall regime after that initial large rainfall (personal observation).

Devil's Claw was listed in 1977 as a protected species under the Nature Conservation Ordinance of 1975 in Namibia. In terms of this ordinance, permits are required to harvest and export Devil's Claw. It is also protected through similar legislation in both Botswana and South Africa.

2.2 Traditional knowledge

The indigenous inhabitants of southern Africa, mainly the San, have made use of the tubers of this plant for medicinal purposes for centuries. Ethno-medicinal uses have been recorded mostly for digestive disorders, fever, as general analgesic, sores, ulcers and boils (WATT AND BREYER-BRANDWIJK 1962, VAN WYK *et al.* 1997). Even today, it is widely used by rural communities – mostly as an analgesic, for digestive disorders and as a general health tonic. Its medicinal value for the treatment of rheumatism and arthritis type ailments has only been recognised by "western medicine" during the last 50 years. G.H. Mehnert, an early bioprospector, exported some dried Devil's Claw tubers to Germany, where they were first studied at the University of Jena in the 1950s. By 1962, the Namibian company, Harpago (Pty) Ltd, started exporting Devil's Claw tubers in larger quantities to the German company Erwin Hagen Naturheilmittel GmbH (WEGENER 2000).

2.3 Trade

The first major commercial exports of Devil's Claw began in the 1960s, however export figures are available from the time the resource was regulated. Since the early 1990s, the international market demand has steadily increased, with total exports from Namibia, Botswana, and South Africa reaching a peak of nearly 1100 tonnes in 2002 (Table 1). Namibia is responsible for 95% of the supply of Devil's Claw.

Table 1: Total range state Devil's Claw exports (in kg) from 1992 - 2004, based on export data from Namibia, Botswana and South Africa (reproduced from STEWART & COLE 2005)

Year	Namibia	Botswana	South Africa	Total Exports
1992		10,719		10,719
1993		3,278		3,278
1994		24,437		24,437
1995	284,409	45,633		330,042
1996	313,652			313,652
1997	251,091	5,493		256,584
1998	613,336	501		613,837
1999	604,335	2,050	6,936	613,321
2000	379,740		341	380,081
2001	726,333	33,506	31,112	790,951
2002	1,018,616	29,608	20,619	1068,843
2003	457,485	3,084	4,500	465,069
2004	283,142	42,025		325,167
Total (kg)	**4,932,139**	**200,334**	**63,508**	**5,195,981**

The majority of the dried *Harpagophytum* tubers are exported to Germany and France. In 2001, *H. procumbens* had become the third-most-frequently used medicinal plant in Germany, with sales of approximately 30M Euro (based on mono-preparations and pharmacy sales). The industry showed a growth of 113% between 1999 and 2000, and an additional 59% between 2000 and 2001. The percentage of prescriptions for the treatment of arthritis and for back and joint pain increased from 40% in 2000 to 60% in 2001. *Harpagophytum* extracts accounted for approximately 74% of the treatments for rheumatism (GRUENWALD 2002).

In 2003, 57 *Harpagophytum procumbens* medicines licensed for the German pharmaceutical market were produced by 46 different companies (KATHE *et al.* 2003). The increase in demand for Devil's Claw can be attributed to an increase in the number of people suffering from arthritis and other locomotive disorders, well-substantiated clinical and other research data, the demonstrated effectiveness and safety of Devil's Claw products, and intensified marketing initiatives by product manufacturers (GRUENWALD 2002).

Despite the increasing export figures, positive market trends, and popularity of *Harpagophytum* (between 1998 and 2002) the demand for Devil's Claw has declined considerably over the last 2 years (2003 and 2004, see Table 1).

The reasons for the decline are complex and include several factors. One of these factors was the proposed listing of Devil's Claw in Appendix II by the Convention of International Trade in Endangered Species (CITES) in April 2000. During 2000, the export figures dropped and may have been due to the negative message sent to the market. At the beginning of 2004, Devil's Claw and a number of other natural products were removed from the German Medical Aid list (prescription drug insurance). By mid-2004, the sales of herbal medicines in Germany (including Devil's Claw) decreased by 50%. While the market is expected to recover, it is doubtful that demand will reach previous levels (J. GRUENWALD, pers. comm.).

A decline in exports may also be due to stockpiling by some buyers that has resulted in lower demand and reduced prices, which has been exacerbated by a lack of a concerted and coordinated marketing effort by the range states and exporters and may be responsible for a sporadic market. The demand for Devil's Claw is not altogether consistent and volumes purchased from an exporter by the same buyer can fluctuate considerably from year to year. This causes uncertainty and has a negative impact on the whole supply chain resulting in neither harvesters being able to plan what amounts to produce nor exporters being able to plan intake quantities.

The Devil's Claw industry in the range states is without a credible representative organisation of stakeholders. The largest part of the existing trade in the region is conducted through informal markets characterised by low harvester prices, low levels of value-adding and low overall levels of benefits achieved from large volumes of material. A characteristic of the Devil's Claw trade is that relationships between buyers and exporters are not stable. Export data clearly show that buyers change suppliers on a regular basis and it is known that such changes can occur without notice or explanation to former suppliers.

2.4 Harvesters

Thousands of harvesters and their families from Namibia, Botswana and South Africa rely on wild collection as a primary or sole cash income. The exact number of harvesters is not known but estimates have put this figure at 10 000. Most harvesters come from the poorest sections of society, many of them living in remote rural areas. The importance of this income to household food security should thus not be underestimated.

The unfavourable circumstances of harvesters are exacerbated by the general livelihood insecurity of a large number of them who are, as a result, more vulnerable to exploitation. The way harvesters are organised and the benefits they receive directly determines the manner of harvesting practice, i.e. whether it is done in a sustainable manner or not.

Despite mounting evidence to suggest that improved benefit sharing for harvesters makes a significant contribution to improved resource management and hence conservation at a local level, harvesters receive only 1% - 2% of the value of the trade (COLE AND DU PLESSIS 2001).

2.5 Population studies

Studies of population dynamics, including observations on age-specific (or size-specific) growth rates, reproductive effort, general phenology, mortality and germination rates are of ever-increasing importance for understanding populations to ensure that they are effectively managed and hence conserved (WERNER AND CASWELL 1977; GELDENHUYS AND VAN DER MERWE 1988; HEGAZY 1992). Some authors (e.g. HARPER AND WHITE 1974) determine population behaviour on two levels: changes in the number of plants and changes in the number of shoots per plant. The latter approach is not often used as a measure of population variability, but rather it is presented as plant phenology, which strongly influences population dynamics. For the purposes of this report, a population is defined as the sum of the individuals of a species, differing in their age and vitality state in given area (ROBATNOV 1985). Further, for this study we define occurrences of Devil's Claw plants as distinct populations if they are separated by discontinuities of at least one kilometre (KEITH 2000) or, due to possible differences in land management systems, if they are separated by artificial discontinuities such as roads or permanent fences.

Populations respond to both their outer environment and their internal state (WERNER & CASWELL 1977). The internal state of a population is a function of the biological age of the plants making up the population. Several authors (e.g. LEFKOVITCH 1965, WERNER AND CASWELL 1977, GATSUK *et al.* 1980) have demonstrated that in population studies, better predictive results are obtained by using plant size – related to age state or biological age – rather than actual age, which is difficult to determine for long-lived plants, especially perennial herbs.

Age states are successive periods within the ontogeny of plants, based on the rise and extinction of the reproductive function and on certain species-specific juvenile and adult characteristics (GATSUK *et al.* 1980). Age states were first defined by ROBATNOV (1985) for perennial herbaceous plants, but various fieldworkers have demonstrated the applicability of these definitions to short-lived annuals as well as long-lived woody plants (e.g. GATSUK *et al.* 1980).

The age states defined by ROBATNOV (1985) can be summarised as follows:

Ontogenic period	***Age state***	***Symbol***
I. Latent	1. Seed	**se**
II. Virginile period (from germination to generative shoot formation)	2. Seedlings 3. Juveniles 4. Immatures 5. Mature virginile	**pl** **j** **im** **v**
III. Generative period (reproduction by seed)	6. Young 7. Mature 8. Old	**g1** **g2** **g3**
IV. Senile period (when plants lose their ability to reproduce by seeds)	9. Senile	**s**

3. Materials and Methods

3.1 Study design and implementation

The following provides an overview of the sequence of activities of this study:

Initial identification of general problem – possible overexploitation of Devil's Claw, 2000

▼

Selection of SHDC project sites for fieldwork
The selection criteria were: familiarity with the local harvesting communities, their socio-economic situation; known harvesting histories of Devil's Claw populations; and their prior knowledge of the study components.

▼

Extensive information gathering from local communities through the SHDC project ►	Pre-site collection of information relative to the issue	Collection of relevant studies within the range states of Devil's Claw ◄

▼

Scoping research 2001 to 2005 to determine:

- nature of population dynamics and changes therein
- determination of major factors influencing population dynamics – harvesting, rainfall, grazing
- sustainable harvesting techniques

▼

Constant interaction with the communities by involving them in the research work and exchanging information with them

▼

Analysis of observed trends and the incorporation thereof into improved guidelines on sustainable harvesting

▼

Feedback to stakeholders, including traders, conservation agencies and policy-makers

3.2 Study area

The study area is located in the Omaheke Region of Namibia (Figure 1) which is approximately 85, 000 km^2 in size. The Omaheke area is often referred to as the Sandveld (LESER 1972) and is covered to a large extent by loose, weakly to unstructured aeolian sands of the Kalahari, which cover an underlying calcic horizon at varying depths. The sands themselves are described as either yellow to brown or red quartz sands. The Omaheke is culturally and ethnically a very diverse region with a population of in excess of 52 000, of which the majority are rurally based.

The specific research sites were located on two farms, Vergenoeg and Ben Hur, in the Omaheke Region. These two farms are part of the Sustainably Harvested Devil's Claw Project (SHDC). (See 3.3 below) Vergenoeg is a communal farm close to the Botswana border, while Ben Hur is part of a larger group of communal farms located about 50 km south of Gobabis (Figure 1).

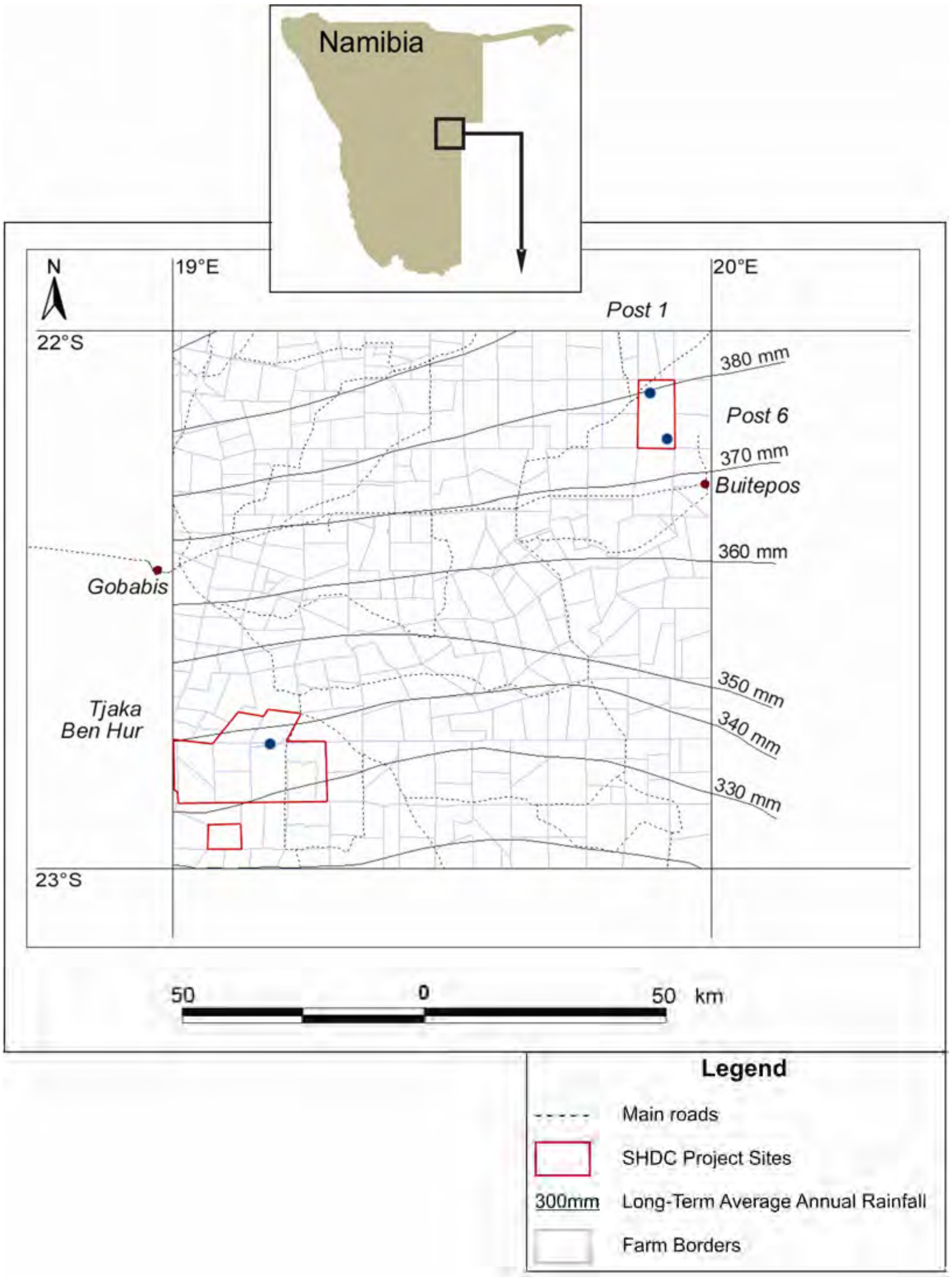


Figure 1: Location of the study area and study sites in Namibia. GIS files adapted from NARIS (AEZ 2001)

Long-term average annual rainfall gradients change from about 340 mm at Ben Hur to 380 mm at Vergenoeg Post 1. Rainfall events occur predominantly in summer with occasional early rains in October and November, the bulk of the rainfall between December and March, and occasional late rainfalls up to May (LESER 1972; AEZ 2001). Considerable inter-annual differences in rainfall are common, while the distribution of effective rainfall events over the rainfall season can be just as variable (LESER 1972; observations during the project).

3.2.1 Vergenoeg

At Vergenoeg the soils are predominantly deep, yellow to brown, coarse ferralic Arenosols of the Namibian soil type KSd1 (Figure 2, AEZ 2001). These sands are excessively drained, and very limited runoff occurs only in areas surrounding small depressions or *Omuramba* systems within the sandy plains. Vergenoeg Post 1 is a typical site on a raised sandy plain, while Vergenoeg Post 6 is a typical site in a small localised depression within a sandy plain. The depressions often have a more favourable water retention capacity, which makes moisture available to plants for a slightly longer period after sufficient rains. In addition, mineral and nutrient content is usually higher in the depressions as these accumulate from surrounding areas. This facilitates a short seasonal burst of dense herbaceous vegetation that then becomes a focal point for animals in search of grazing. It is therefore common that despite more favourable conditions, these depressions are greatly disturbed due to overgrazing and excessive trampling (LESER 1972). The absence of a persistent herb layer is the most likely reason for sometimes very high densities of Devil's Claw being found here (IHLENFELDT AND HARTMANN 1970).

Vegetation at Vergenoeg Post 1 is dominated by very low to 3 m high shrubs, mostly *Acacia luederitzii*, *A. mellifera* subsp. *detinens* and *Dichrostachys cinerea*. An increase of these shrubs from an initial 15% to almost 40% was observed during the study, which necessitated clearing of the monitoring sites in 2004 and 2005 to enable monitoring of Devil's Claw to continue. The herb layer is sparse and highly variable. Dominant grasses include *Eragrostis porosa* (annual) and *Aristida congesta* (weak perennial). On the fenced site the highly palatable perennial grasses *Antephora pubescens*, *Brachiaria nigropedata* and *Stipagrostis uniplumis* managed to get re-established during the course of the study.

At Vergenoeg Post 6, the vegetation consists of occasional low *Acacia* trees with a few *Grewia flava* and *Ozoroa paniculosa* shrubs. The herb layer is highly variable and in general short-lived. After the fencing off of one monitoring site, parts of the site were invaded by the perennial creeper *Senna italica*. In the following years the perennial grass *Stipagrostis uniplumis* could re-establish itself, accompanied by a strong layer of annual grasses and annual creepers, the latter mostly *Ipomoea* species. This dense herb layer out-competed not only *Senna italica* but also Devil's Claw in the course of the study.

3.2.2 Ben Hur

At Ben Hur the soils are predominantly shallower and finer-grained, reddish ferralic Arenosols of the Namibia soil type KSa1 (Figure 2, LESER 1972, AEZ 2001). The finer particle size ensures a slightly higher water retention capacity than at Vergenoeg Post 1, but soils are still excessively drained.

The vegetation at Ben Hur is dominated by low *Acacia erioloba* trees, as well as *Acacia hebeclada* subsp *hebeclada* shrubs. Initially, the site had a good layer of the perennial grass *Stipagrostis uniplumis*. Although canopy cover of this grass was up to 60%, basal cover was much less, enabling Devil's Claw to easily expand between the grass tufts. Gradually this grass layer became decimated by animals, most notably during low rainfall seasons. The grass layer was initially followed by a very dense layer of creepers, mainly *Acanthosicyos naudinianus* and *Ipomoea* species, which were strong but short-lived competitors of Devil's Claw. However, this layer was also decimated, leaving only a sparse herb layer towards the end of the study.

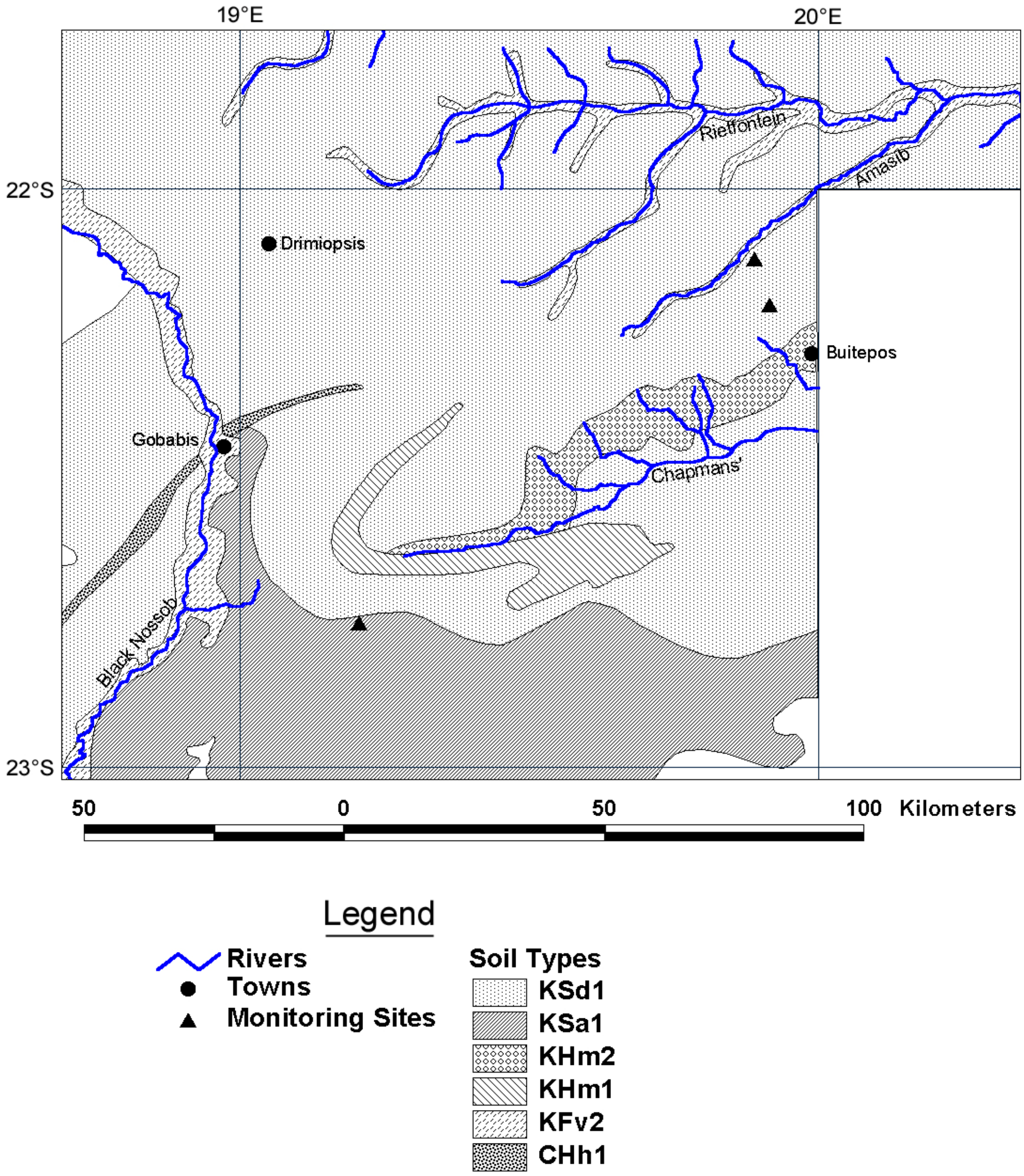


Figure 2: Soil types of the study area. Map adapted from the NARIS GIS files (AEZ 2001).
A full description of the soil types is given in the glossary.

3.3 The Sustainably Harvested Devil's Claw project

The Devil's Claw harvesters who participate in the SHDC project are among the most marginalised people in Namibia. They have limited skills in negotiating and bargaining. While concerted efforts were made to secure their input and to incorporate them into the design of the project, the initial benefit-sharing arrangements had to be made on behalf of harvesters by service NGOs. The arrangements contained in the SHDC project are fluid and evolving, however, and it is envisaged that harvesters will increasingly articulate their own priorities and expectations as they develop their organisational capacity and become more confident regarding their rights and powers as resource users (COLE & DU PLESSIS 2001).

Devil's Claw has been established in the world market for decades, but before the SHDC project very little thought had gone into sharing benefits with harvesters. In fact, as discussed above, the growth of the industry had been based on extremely exploitative relations of production and trade. Into this situation the SHDC project introduced a simple model for benefit-sharing arrangements, based on the insight that there is a growing congruence of interests linking ethical consumerism in the North to sustainable resource use and socio-economic equity in the South, and that the proper role of the trade under these circumstances is to link producers to consumers in a way that gives everyone what they want (COLE AND DU PLESSIS 2001).

A straightforward description of the SHDC project would be:

Donors fund a service NGO (CRIAA SA-DC) to activate and organise groups of registered harvesters. Harvesters engage in an exchange of knowledge about sustainable resource use and voluntarily adopt sustainable resource management practices that they have helped to formulate. Harvesters are assisted by pre- and post-harvest ecological surveys to set sustainable harvesting quotas, and to monitor compliance with sustainable harvesting techniques. They elect a co-ordinator and/or record-keeper and are assisted with simple processing technology such as knives, drying racks, scales, record-books, clean new bags and storage facilities, and with extension/liaison services and the securing of group harvesting permits.

The product is certified "Organic" by the Soil Association (Britain). The Soil Association Standards for Wild Crafted products is attached as Appendix I. When a group of harvesters has a full load of dried tubers, they contact the exporter directly or through the SHDC extension worker. The exporter collects the load and pays cash on the spot. In return for pre-financing, collating and transporting, the exporter makes a fair profit. An agreement between the exporter and CRIAA SA-DC (on behalf of the harvesters) to purchase the all Devil's Claw product and relevant benefit-sharing mechanisms are in place.

3.4 Sampling design

The data for the study were collected from the three sites, Vergenoeg Post 1 and -Post 6 and Ben Hur (see 3.2.1 and 3.2.2). The sites consisted of two monitoring areas, each measuring 10m x 30m. One site was fenced with diamond mesh to exclude all grazers. Each pair of sites had a rainfall gauge, from which daily rainfall figures were recorded by local community members throughout the rainfall season.

In March 2001, when plants were showing optimal growth for that season, all sites were subdivided into 1 x 1 m subsections, each plant per subsection was numbered and mapped, and the diameter of the widest part of the primary tuber was measured, taking care not to damage the plant. This exercise was repeated in April 2005 to record primary tuber growth and population growth rates. It was often necessary to very carefully excavate an entire subsection to a depth of about 40 cm to locate tubers of plants that had not surfaced in 2005. In most cases the intact tuber or the remnants of a tuber was found. This thorough investigation was necessary to account for dormancy. The population growth rates could have been underestimated by simply taking emergence as an indication of surviving plants (see also SHEFFERSON *et al.* 2001).

To be able to better compare the distribution of tuber sizes within populations with different harvesting histories, in March 2001 transects were placed through Devil's Claw populations at Kleinkamp and Resiesbaan close to Ben Hur, and at Vergenoeg Opstal close to Vergenoeg Post 1, with additional transects placed at Vergenoeg Posts 1 and 6. Along each transect the diameter of the primary tuber of each plant was measured, until a minimum of 200 plants had been measured.

From October 2001, monthly visits were undertaken to the sites for general observation of plant emergence, flowering, vigour and die-back. In the growing season following the mapping of all plants, it was noted that some plants had not surfaced by March (2002), thus, it was decided to mark 30 randomly selected plants with an iron marker on each site for future phenological monitoring. This data was collected during monthly inspections from mid-December to mid-May, until 2004. The parameters recorded were:

i. plant diameter;
ii. number of primary branches (the multiplication of these two parameters gives a relative estimate of plant spread or surface cover);
iii. number of flowers;
iv. number of immature fruit;
v. number of mature / fully ripened fruit; and
vi. vigour of plant – emerging, growing well, dying back and entering its dormant phase, or not emerged at all so far during the season.

It was realised that these observations did not record the full scope of phenological events, especially flowering intensity, but they still give a good idea of the timing and duration of some such events. In addition, these records indicated how rainfall variability may affect the overall magnitude of phenological events. A close evaluation of phenological traits for different tuber sizes also enabled a better definition of tuber size classes (as originally defined by LELOUP 1984) into age states (GATSUK *et al*. 1980), which in turn enabled a better description of population structure and population growth rate.

The only population parameter that was weakly recorded due to the nature of the study design was germination rates, as seedlings can emerge from November to March but can be too short-lived to have been noticed. 'New' plants could only be detected during the re-survey of the 1 x 1 m subsections of each site during 2005.

3.5 Soil physical and chemical properties

Soil samples were collected at each site from 20 cm below the surface as the upper soil layer is regularly disturbed, and the lower soil layer is more representative of the soils from which the Devil's Claw plants derive their nutrients and water.

All analyses were carried out by the Agricultural Laboratory of the Ministry of Agriculture, Water and Forestry in Windhoek. Samples were prepared by drying at low temperatures. Available phosphorous was determined using the Olsen method, while available K, Mg and Ca was extracted with 1M ammonium acetate at pH 7 and determined by atomic absorption spectroscopy. Texture analysis was done by sieving with a 53-micron sieve and the pipette method. Organic carbon was determined with the Walkley-Black method. The pH (H_2O) was measured with a 1:2, 5 soil/water suspension, which was also used to measure electrical conductivity as an indication of soluble salt content. Total N content was determined with Kjeldahl acid digestion. All methods are based on ROWELL (1998).

3.6 Harvesting

Harvesting frequency and selection of plants to be harvested was based on the input of experienced harvesters who were involved in the SHDC Project. According to them, a plant could be re-harvested every second year (provided the primary tuber is not disturbed), thus, the selected plants were harvested after a one-year rest period. It must be added that the initial years of the SHDC Project coincided with 3 successive good to above average rainfall seasons (METEOROLOGICAL OFFICE, WINDHOEK). Plants to be harvested were selected using the initial tuber diameter measurements as a guideline, with the harvesters confirming that the selections were large enough. Care was also taken to space the plants widely enough to prevent any confusion of below-surface secondary tubers, this being the main reason for so few plants being selected at the Vergenoeg Post 6 sites, which had the highest initial Devil's Claw plant densities.

The specific manner by which harvesting was done was left up to the community harvesters and simply observed, while the number and size as well as total tuber weight for each harvested plant was recorded.

At Ben Hur, harvesters were predominantly female. Their harvesting technique started with a gradual careful loosening of the top layer of soil from about 20 cm of the primary tuber, working in a semicircle around and away from the plant (the remainder of the plant was left untouched). Loosened sand was removed by hand, while a spade was used only afterwards to refill the holes. Large storage tubers could usually be located within the upper 50 cm of the soil. Deeper tubers were pursued only if it could be seen from the root thickness that another tuber could be attached deeper down. This harvesting technique is relatively slow, but damage to harvested storage tubers was minimal and the primary tuber remained entirely undisturbed.

Harvesters at Vergenoeg were predominantly male. At Vergenoeg Post 1, a digging stick was used to loosen the upper soil and locate the storage tubers closest to the plant, then a spade was used very skilfully to loosen and move larger volumes of sand as secondary roots were traced away from the plant. All storage tubers off a plant were harvested to a depth of 100-120 cm. Occasionally the lower storage tubers were situated relatively closely to the primary tuber and root, which not only disturbed the primary tuber, but in some cases also damaged the primary root.

The soil at Vergenoeg Post 6 tends to become relatively hard, most notably when dry, rendering the use of a digging stick rather ineffectual. Our harvester used a spade to carefully clear away the topsoil layer around the plant until he reached the primary tuber. Then, as far as possible by hand, he carefully excavated the primary tuber to where it narrowed into the taproot, and traced the storage tubers from the primary tuber using the spade to loosen and move sand. Due to the effort required to get the spade into the soil, storage tubers were often damaged, and occasionally taproots were severed if they were close to the storage tubers. Our harvester did not dig deeper than 45 cm because the plants need all tubers deeper down to be able to re-sprout the following year.

The harvesters at Post 6 usually restrict their harvesting activities to the sandier soils around this harder depression. The site was nevertheless chosen because it resembles the *Omuramba* systems in the remainder of the communal Kalahari areas from which large amounts of Devil's Claw are harvested each year.

3.7 Estimates of population densities

The central question in the determination of annual harvesting quotas of any resource is, "How much resource, measured by the number of individuals, is available to be sustainably harvested?"

Determining density by counting individuals is always the most accurate method, but it is impossible to count all individuals in a population. As defined by MUELLER-DOMBOIS AND ELLENBERG (1974), density measurement in quadrants relates to the counting of individuals per unit area. Counting is done in small quadrants placed several times into the plant community or population. Later, the sum of the individuals is calculated for the total area sampled by means of the quadrants, with the result expressed as species density per area unit.

Straightforward quadrants, however, pose a problem because a regular distribution of individuals within a population is extremely rare. Rather, populations tend to have a random or aggregated distribution (PIELOU 1960; URBANSKA 1992). In the case of Devil's Claw, distribution within a population is almost exclusively aggregated (personal observation), this being an important factor to take into account when sampling such a population. Several survey methods have been developed specifically for sampling plant density, of which basic distance methods (e.g. Nearest-Neighbour), angle-order estimating methods (e.g. Point-Centred Quarter and Wandering Quarter), as well as the Variable Area Transect (VAT) method are the most commonly used (ENGEMAN *et al.* 1994).

Basic distance estimators measure the distance form randomly placed sample points either to the closest plant, or from a chosen plant to its closest plant neighbour (COTTAM AND CURTIS 1956). However, these methods have been found to give unreliable results in aggregated populations (ENGEMAN *et al.* 1994). Angle-order methods have been adapted specifically to deal with the problem of aggregated populations: the area around a random point is divided into four quarters and the distance to the nearest individual in every quarter is measured (BARBOUR *et al.* 1998). Although this method is considered the most accurate (ENGEMAN *et al.* 1994), trials in the field have shown it to be extremely time-consuming and cumbersome, especially when working with and in between different strata of vegetation (personal observation).

PARKER (1979) developed the VAT estimator, which is a combination of distance and quadrant methods. The quadrant size has to be related to the size and spacing of individual plants – it is difficult to accurately count individuals in too large a plot. Further, how many individuals are counted within a quadrant is almost entirely a matter of judgement: species falling on the quadrant border may be included or excluded. It can thus be understood that more important than quadrant size is quadrant shape – many ecologists have shown that rectangular quadrants are most effective for density measurement (MUELLER-DOMBOIS AND ELLENBERG 1974). Hence, PARKER (1979) used a fixed-width (strip) transect to be investigated from a random point until a pre-determined number of individuals are encountered.

ENGEMAN *et al.* (1994) ranked the VAT method as the second most satisfactorily accurate method for determining densities. This slight compromise in accuracy is justified as this method has proven to be very rapid and easy to apply in the field, and can be easily taught to laymen, e.g. community members, while its straightforward nature ensures a low scope for error in sampling.

For the very dense, yet small populations of Devil's Claw studied in Omaheke, we adjusted this method to start the transect where the plants start occurring, continue in a straight line and stop counting when individuals are no longer observed (STROHBACH 2003), referred to as Transect Method 1. HACHFELD (2003) has used a similar method by placing fixed-length transects randomly over an area of 1 km^2 for the low population densities often encountered on commercial farmland, referred to as Transect Method 2. To account for the problem of inclusion/exclusion of individual plants encountered on the "borders" of the transect, communities were given a 1.80 m long stick to use as a guide to survey the 2 m wide strip. Only plants with their centres, i.e. point of primary tuber and stem, under the stick were included in the count as standard.

These methods to determine plant density have been developed in the course of the SHDC project, were replicated in the Namibian National Devil's Claw Situation Analysis (NNDCSA) (STROHBACH 2003), and have been found to be appropriate and easily implemented at various levels.

3.8 Statistical analysis

The statistical analysis of the study data was restricted to calculation of arithmetic means, absolute minimum and maximum values of a data set as well as percentages. It was regarded as more important to display some trends within the complexity of the relatively small dataset and to present them in a manner understandable for those who are unfamiliar with statistical analysis.

4. Results

4.1 Rainfall

The study area received average to above average rainfall during the years 1998 to 2000. This is based on meteorological data from Gobabis (METEOROLOGICAL OFFICE, WINDHOEK), which could differ to some degree from actual rainfall at the study sites. Another drawback of this data is that amounts supplied are from January to December, rather than from October to May, which would coincide with the growing season. Throughout the results presented here, a rainfall- or growing season is demarcated with two years – indicating that measurements are from October-year 1 to May-year 2.

Our sites were only selected in January 2001, so for the rainfall season 2000/2001, we have an incomplete rainfall record. However, as the bulk of annual rainfall in Namibia is only recorded from January onwards, the amounts recorded can still be regarded indicative of an average rainfall year. The following two seasons were below average, while at Vergenoeg Post 1 rains improved again in 2004 and 2005 (Table 2). As can be seen from later results, plant growth is not as dependent on absolute amount of rainfall as it is on the correct timing of rainfall events, which can be indicated by the cumulative rainfall for each season as a percentage of the long-term average annual rainfall (Figures 3-5). Plants seem to adapt to the general rainfall regimes of their areas.

Table 2: Seasonal rainfall in mm and percentage of long-term annual average rainfall as recorded at the different sites for the duration of the project

Season	Vergenoeg Post 1		Vergenoeg Post 6		Ben Hur	
2001	376	99%	296	80%	327	96%
2001/2002	322	85%	293	79%	320	94%
2002/2003	307	81%	252	68%	250	74%
2003/2004	474	125%	371	100%	274	81%
2004/2005	460	121%	325	88%	203	60%

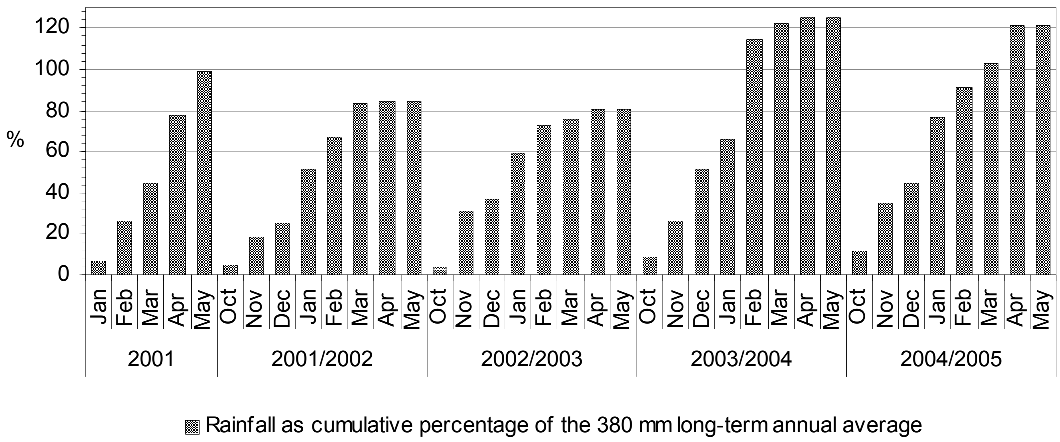


Figure 3: Annual cumulative rainfall for each season at Vergenoeg Post 1

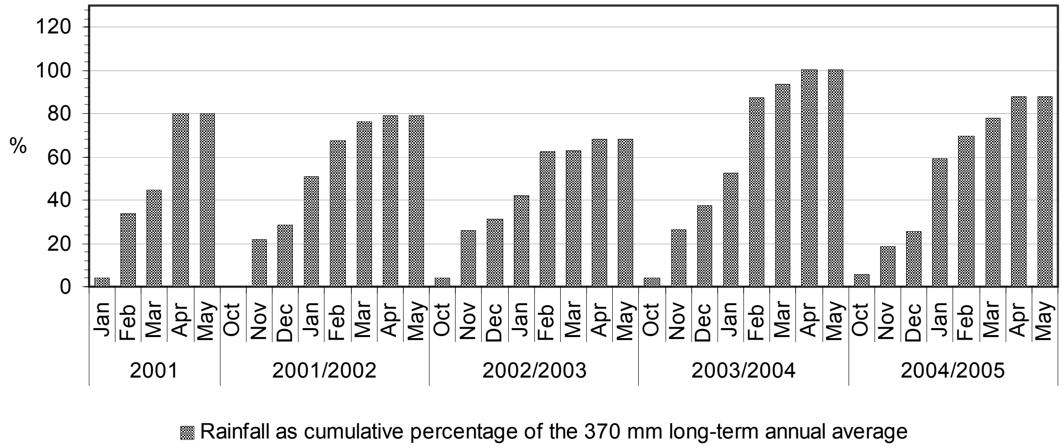


Figure 4: Annual cumulative rainfall for each season at Vergenoeg Post 6

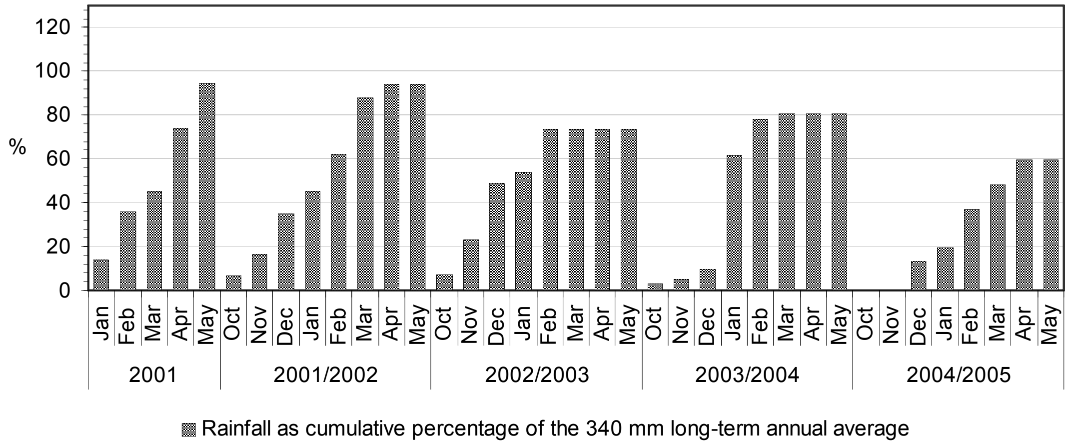


Figure 5: Annual cumulative rainfall for each season at Ben Hur

4.2 Soil analysis

Organic matter content for all three sites was very low. As this is the basis for soil organisms to live on and convert litter to available nutrients, it can be deducted that these sands also have very little soil organisms present, which was evident from the almost absent soil development. At the Vergenoeg sites pH was low enough (<6) to limit the availability of available N and P, as well as Ca and Mg, to plants (BARBOUR *et al*. 1999). These are all elements essential for the growth and photosynthesis of plants. P is important to the development of fruit, and limitations of P in the soil have been associated with high abortion rates of inflorescences and young fruit in some savanna species of the Kalahari (TOLSMA *et al*. 1987). The overall low N concentrations may contribute to a limited competitive ability of DC compared with shrubs that often have an underground symbiosis with nitrogen-fixing bacteria, enabling their much faster growth rates that in turn enable shrubs to become highly invasive (TOLSMA *et al.* 1987). Vergenoeg Post 1 soils probably have the lowest water retention capacity due to their very low content of fine silt and clay particles (which are highest at Ben Hur). At Vergenoeg Post 6, however, the higher electrical conductivity indicated that soil particles may bind strongly to available water, thus rainfall events need to be larger relative to the other sites to enable plants to take up that water. The results of the various soil analyses are presented in Table 3.

Table 3: Results of the soil analyses for the three sites

Site	pH H_2O	ECw µS/cm	Organic Carbon	P ppm	K ppm	Ca ppm	Mg ppm	Na ppm	N %	Sand %	Silt %	Clay %
Vergenoeg Post 1	5.75	16	0.340	0.91	332	38	26	5	0.007	96.7	1.8	1.4
Vergenoeg Post 6	5.49	118	0.303	3.79	133	212	58	18	0.034	94.9	2.7	2.4
Ben Hur	6.49	17	0.316	0.96	70	198	56	10	0.016	94.4	3.5	2.1

4.3 Phenology

In accordance with IHLENFELDT AND HARTMANN (1970), plants emerged after early rains between October and November, with most plants already showing strong growth by mid-December (Figures 9-14). Occasionally plants only emerged in January or February (Tables 4-6). It was also common for some plants not to emerge at all for an entire season, but to resprout again the following season. The season 2002/2003 was noteworthy: It had relatively good rains up to December, then a long dry period from mid-December to late January. Many plants were scorched in January, particularly at Vergenoeg, which caused some plants to die back and only re-emerge after late rains in April and May (Tables 4-6). Several of these plants were found dead in 2005.

Irregular resprouting and dying back patterns were common on the Vergenoeg Post 6 sites. On the fenced site, plants did not show much spread between the dense herbs – only being able to increase their spread late in the growing season when most annual herbs had died off (Figure 11). Here herbs had increased from a very sparse cover in 2001 (Figures 6 and 7) to almost 80% (Figure 8) during the peak growing season in subsequent years. Very high continued grazing on the unfenced site saw plants regularly eaten off to a 2 cm remaining stump from the primary shoots (Figure 12).

Usually plants started dying back relatively quickly from mid-May onwards, with only dead, barely recognisable shoots still visible above ground.

Flowering intensity was highest in December and January, also explaining why plants were more sensitive to desiccation effects during this time. If rainfalls from mid-December to late January were very poor, flowering ceased. Plants would flower again later, but with much less vigour. March was usually the last month of flowering (Tables 4-6); new buds formed in April were also often found aborted without having opened.

Likewise, immature fruit would already start forming in December, some ripening as early as February, with the bulk of the fruit only ripening in March and April. Stresses such as longer dry periods or intense competition from herbs and shrubs would result in many of the immature fruit being aborted – the largest f these found aborted was already fully grown. Of all the flowers counted, only a small portion formed immature fruit, of which even less ripened (Table 7).

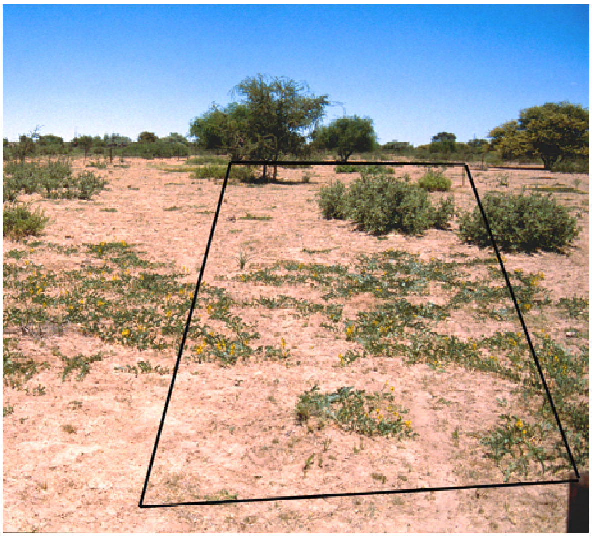


Figure 6: The fenced site at Vergenoeg Post 6 just prior to fencing in January 2001, approximate outline indicated. Note the sparse vegetation cover (STROHBACH 2001).

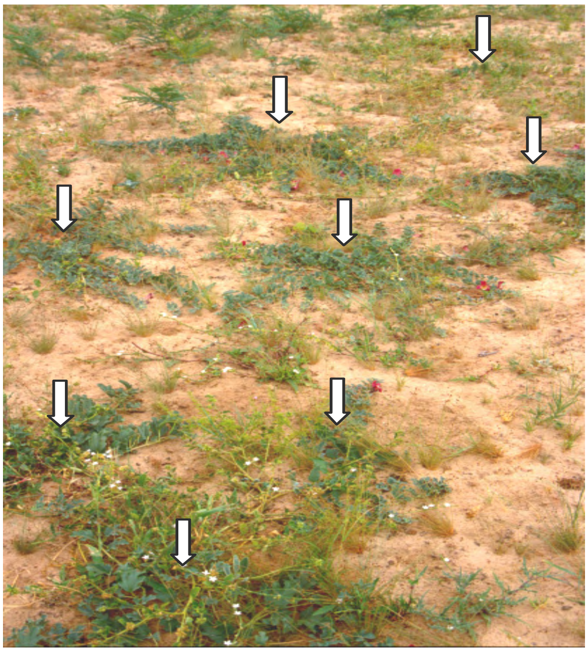


Figure 7: Close-up of the same site in March 2001 after sufficient rains – note the still sparse herb layer and the high density of *Harpagophytum* (STROHBACH 2001).

Figure 8: Fenced site at Vergenoeg Post 6 during the rainy season 2002. Note the dense and high herb layer that developed in the absence of grazing (STROHBACH 2002).

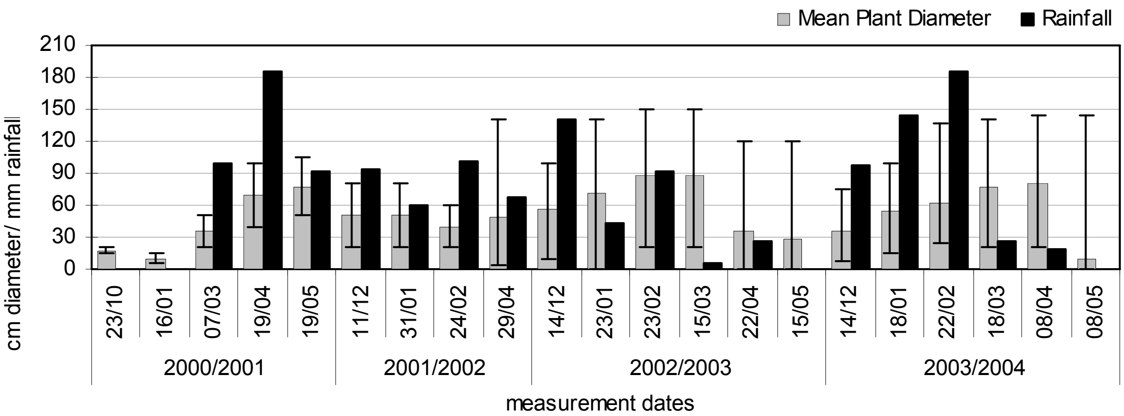


Figure 9: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Vergenoeg Post 1 Fenced Site. Rainfall shown here for December includes rainfall from October.

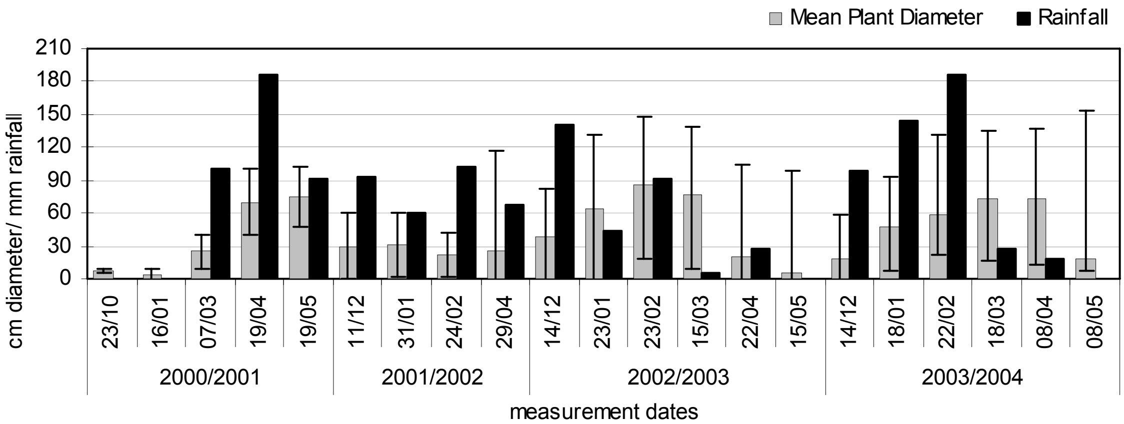


Figure 10: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Vergenoeg Post 1 Unfenced Site. Rainfall shown here for December includes rainfall from October.

Table 4: Phenology of DC plants at Vergenoeg Post 1 for the seasons 2002/2003 and 2003/2004. Numbers indicate number of plants.

	Post 1 Fenced Site												Post 1 Unfenced Site											
	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04
Emerging	1	1			8	4							2				2	12	1					
Growing	27	26	28	22	12	7	28	28	28	28	28		23	26	27	17	12	3	13	14	14	14	15	
Dying Back		1		6	6	17						28				10	13	12						15
Not Emerged	2	2	2	2	2	2	2	2	2	2	2	2	5	4	3	3	3	3	16	16	16	16	15	15
Flowers	34	4	3				12	12	7	10	2		23	3	12				12	13	4	13		
minimum	6	2	2				2	1	2	2	2		4	1	1				4	1	2	12		
maximum	102	5	8				32	38	16	24	2		52	6	39				28	40	6	14		
Immature Fruit	3	1	5	3			4	9					1	2	7					4	1			
minimum	1	1	1	1			2	1					1	1	1					1	1			
maximum	5	2	14	7			5	21					1	9	28					9	1			
Mature Fruit			1	1	2	2				1	1	1			2	3	3	3			1	1	1	1
minimum			1	1	1	1				1	1	1			1	1	1	1			1	1	1	1
maximum			3	3	2	2				2	2	2			6	6	6	6			1	1	1	1

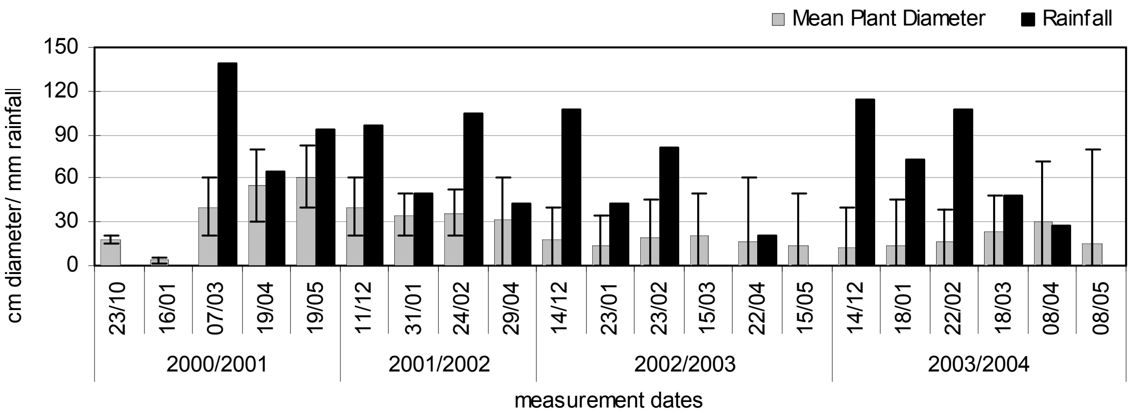


Figure 11: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Vergenoeg Post 6 Fenced Site. Rainfall shown here for December includes rainfall from October.

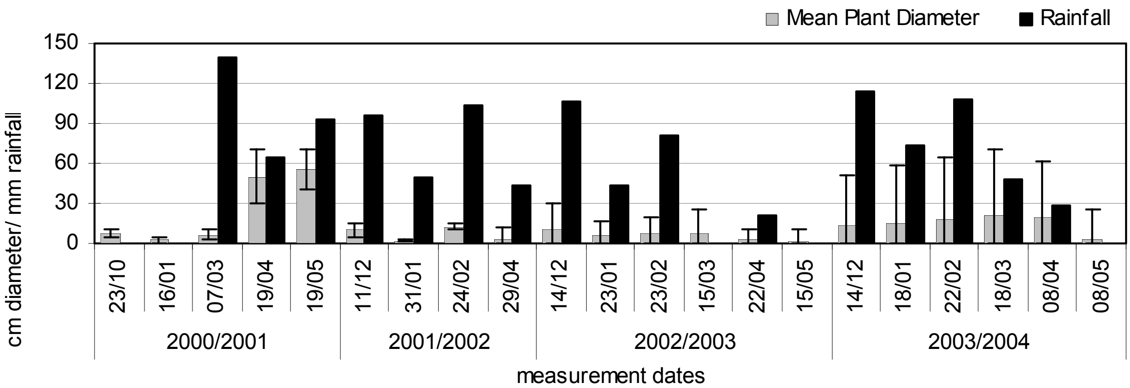


Figure 12: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Vergenoeg Post 6 Unfenced Site. Rainfall shown here for December includes rainfall from October.

Table 5: Phenology of DC plants at Vergenoeg Post 6 for the seasons 2002/2003 and 2003/2004. Numbers indicate number of plants.

	Post 6 Fenced Site												**Post 6 Unfenced Site**											
	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04
Emerging	5		4				4			1			10	2	1		2	2	4				1	
Growing	23	22	22	27	20	13	22	25	24	24	27	11	15	24	22	23	16	7	15	18	19	16	16	6
Dying Back		6	2	1	8	15		1	2	2		16		2	5	5	10	19		2	1	4	4	15
Not Emerged	2	2	2	2	2	2	4	4	3	3	3	3	5	2	2	2	2	2	11	10	10	10	9	9
Flowers	8	2	5				6	9		6			1	2	4	1			14	12		7		
Minimum	4	2	2				2	8		6			1	2	1	1			4	4		2		
Maximum	17	2	8				12	10		6			2	2	7	1			34	26		14		
Immature Fruit	3		3	2	2		2												4					
Minimum	2		3	1	2		1												1					
Maximum	5		3	2	2		6												6					
Mature Fruit																								
Minimum																								
Maximum																								

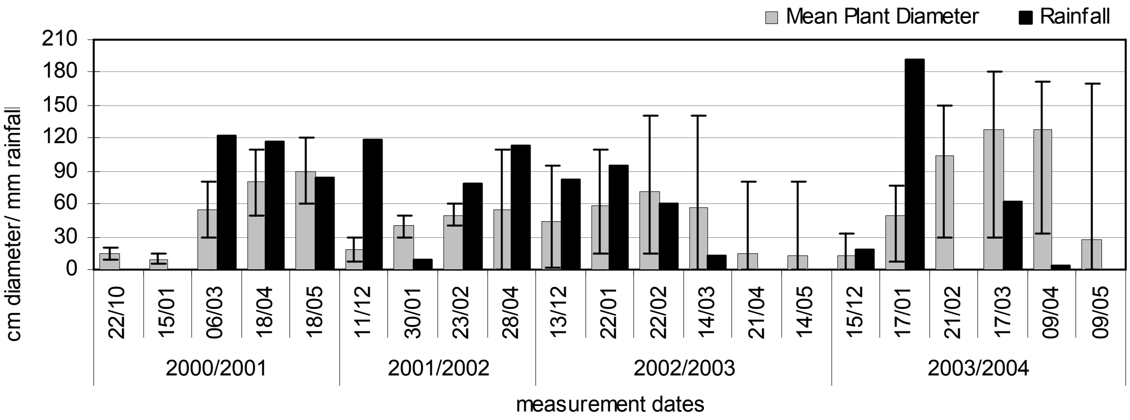


Figure 13: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Ben Hur Fenced Site. Rainfall shown here for December includes rainfall from October.

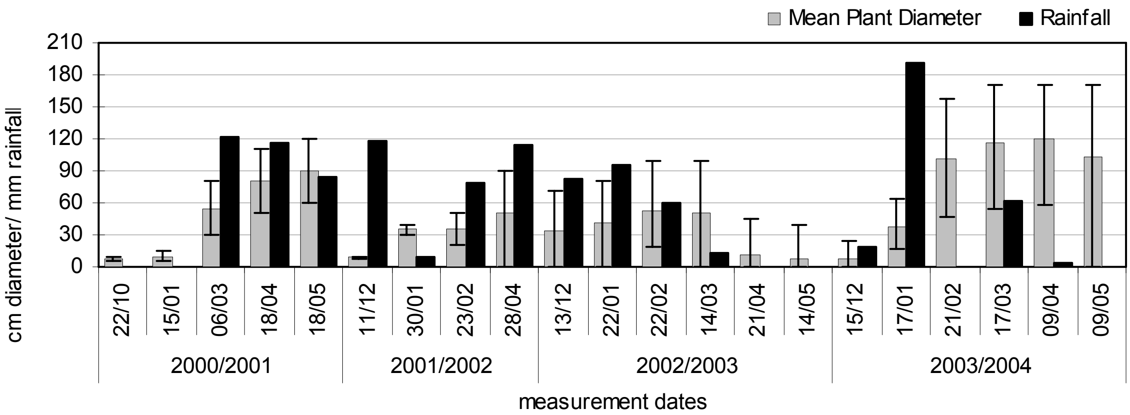


Figure 14: Growth rates – mean with absolute maximum and minimum – of DC plants throughout the seasons at the Ben Hur Unfenced Site. Rainfall shown here for December includes rainfall from October.

Table 6: Phenology of DC plants at Ben Hur for the seasons 2002/2003 and 2003/2004. Numbers indicate number of plants.

	Ben Hur Fenced Site												**Ben Hur Unfenced Site**											
	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04	Dec-02	Jan-03	Feb-03	Mar-03	Apr-03	May-03	Dec-03	Jan-04	Feb-04	Mar-04	Apr-04	May-04
Emerging	3				13	3	3						1				9	6	4					
Growing	27	30	30	14	8	16	24	30	30	30	30		28	29	30	22	11	14	23	30	30	30	30	5
Dying Back				16	9	11						30				8	10	10						25
Not Emerged							3						1	1					3					
Flowers	35	5	4				10	26	33	5			24	9	4	1			10	17	34	9	2	
minimum	3	1	1				2	1	2	2			2	1	1	1			2	2	2	2	2	
maximum	65	10	8				28	75	92	12			51	20	8	1			20	62	89	24	2	
Immature Fruit		4	4	2			6	4	10	4	2			6	5	2			3	4	18	5	1	
minimum		1	1	1			1	1	2	1	1			1	1	1			1	1	1	1	1	
maximum		12	8	4			15	9	48	13	2			15	16	4			7	12	51	14	1	
Mature Fruit			2	2	2	2			4	9	11	11			2	1	1	1			5	9	12	11
minimum			1	1	1	1			1	1	1	1			1	1	1	1			1	1	1	1
maximum			6	5	5	5			12	38	45	45			2	2	2	2			23	36	49	49

Table 7: The sums of all flowers, immature fruit, and mature fruit counted on the 30 marked plants on each monitoring site for two seasons

	2002/2003			2003/2004		
	Flowers	Immature Fruit	Mature Fruit	Flowers	Immature Fruit	Mature Fruit
Vergenoeg Post 1 Fenced	898	95	15	535	94	5
Vergenoeg Post 1 Unfenced	609	103	26	247	29	2
Vergenoeg Post 6 Fenced	137	24	0	72	12	0
Vergenoeg Post 6 Unfenced	18	0	0	158	7	0
Ben Hur Fenced	835	59	19	1632	285	263
Ben Hur Unfenced	863	128	9	1774	598	342

4.4 Age states

The ability of DC plants to produce fruit and secondary storage tubers, as well as primary tuber diameter and its rates of increase, were used as the most important criteria in defining age states. In addition, we looked at the increase of below-ground storage tubers to determine when a plant should have sufficient accumulated reserves to tolerate harvesting, without losing its ability to increase its primary tuber size (which we regarded as an indication of the plant's overall fitness).

The mortalities recorded during the second tuber diameter survey on all sites in 2005, showed that plants with an initial tuber diameter < 2.3 cm had the highest mortality rates, but those surviving showed the highest rate in tuber diameter increase (Figure 15). When looking at sexual reproduction, it was found that by April 2002, no plants with an original tuber size < 1.5 cm had produced any fruit, and had probably only produced very few flowers, if any.

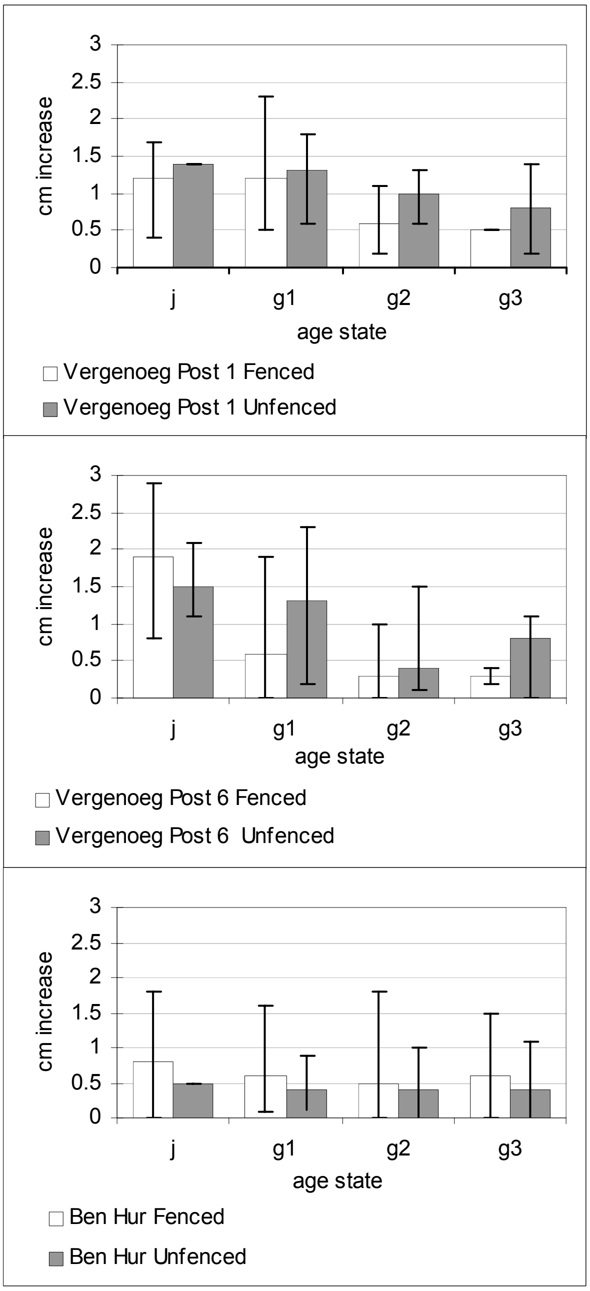
Harvesters consider plants with less than 400 g to 500 g of fresh storage tubers as not worthwhile harvesting, as it takes quite a considerable effort to dig out and locate these storage tubers. When all marked plants on each site were harvested in 2005, we found that mainly plants with a tuber diameter >2.4 cm were capable of producing such minimum harvestable quantities of storage tuber. Noteworthy here was the higher fitness of the >2.4 cm plants compared with the high mortality rates of the < 2.3 cm plants. We thus assumed that a plant with a tuber diameter of < 2.3 cm will probably re-invest more of it's assimilates into primary tuber growth rather than producing an extensive system of secondary storage tubers. It may also be that these plants simply do not have enough accumulated storage yet to be able to afford a harvesting loss, and will also take much longer to regenerate and grow bigger after harvesting, explaining the shift in age state distributions in frequently harvested populations (see section 4.5).

Plants with an initial tuber diameter > 2.4 cm had a very variable rate of increase, and generally showed high levels of shoot production and high levels of flowering and fruiting, compared with the smaller plants. However, it was observed that mortality rate of tubers >3.5 cm was generally higher than the age state class just below that. This coincided with an observed tendency of decreasing primary tuber diameter, most often in the >3.5 cm tubers, and close inspection often revealed that these tubers were starting to rot inside and plants were probably dying. Based on these observations, age states as opposed to the size classes (LELOUP 1984), were defined (Table 8).

The definition of these age states enabled a better interpretation of the population structure of DC plants at different sites with different harvesting histories (Figure 16 A-D), while also enabling the construction of life tables (Figures 17 and 19-23).

Table 8: The definition of Age States for *Harpagophytum procumbens*

Symbol	Age State	Description
se	Seed	Released from the fruit capsule over a period of 2 to 3 years, with variable levels of dormancy within the same seed-batch (ERNST *et al.*)
pl	Seedling	**Primary tuber diameter 0.1 to 0.5 cm**, calendar age less than one year, usually only one primary shoot, less than 30 cm long, no flowering. Seedlings may show a very rapid growth rate under favourable conditions, but may also only persist for several months
j	Juvenile	**Primary tuber diameter 0.6 to 1.4 cm**, calendar age one (to two) years. Juvenile plants do not flower but can exhibit vigorous shoot growth. Assimilates are used to increase the primary tuber diameter, while secondary tuber production is absent or only minimal
g1	Young reproductive plant	**Primary tuber diameter 1.5 to 2.3 cm**, calendar age estimated to be two to five years. Flowering and fruiting is limited, but shoot growth very strong. Assimilates are still mainly used for primary tuber growth, but secondary storage tubers are being formed, the latter mostly smaller than 1 cm in diameter, weighing less than 100 g
g2	Mature reproductive plant	**Primary tuber diameter 2.4 to 3.4 cm**. Calendar age estimated at three to ten years, but may be much younger under very favourable conditions (e.g. dry land cultivation). Shoot production, flowering and fruiting rates as at their optimal level. Assimilates are first used for the production of large amounts of flowers and the development of fruit, as fruit ripen assimilates are replenished and added to the storage tubers. The latter is very variable, but most plants are capable of producing at least 400 to 500 g under favourable conditions. The increase in primary tuber diameter becomes much slower compared with the smaller age states.
g3	Old reproductive plant	**Primary tuber diameter 3.5 cm and more.** Calendar age estimated to be from five or six years upwards. Tuber diameters of up to 6.5 cm were observed, but in general, plants with a primary tuber diameter above 5 cm are very rare. Shoot production, flowering and fruiting levels are optimal. Assimilates are first used for the production of flowers and fruit, then replenished and accumulated in the storage tubers. Plants that are harvested for the first time often have a storage tuber yield above 1kg, while healthy plants are generally able to regenerate at least 400 g of new storage tubers over a period of 4 years after harvesting. Many of these tubers are gnarled and woody to some extent.
s	Senile plants	**Primary tuber diameter in the range of 2 cm and more.** Calendar age difficult to estimate. These plants have a reduced shoot production, and flowering vigour strongly decreases. It is difficult to identify such plants from above-ground plant parts – they also have a tendency not to emerge for an entire season. The primary tubers very often exhibit extensive damage to their outer layers – either due to insects (worms or woolly aphids) or due to rotting. Even the storage tubers start shrivelling and start rotting from the inside. Several remnants of the outer woody layers of dead primary tubers were found during the 2005 tuber assessment.



Vergenoeg Post 1 Fenced Site

Mean increase in primary tuber diameter:	0.98 cm
Mode of increase in primary tuber diameter:	0.5 cm
Maximum primary tuber increase measured:	2.3 cm
Minimum primary tuber increase measured:	- 0.4 cm

Vergenoeg Post 1 Unfenced Site

Mean increase in primary tuber diameter:	1.04 cm
Mode of increase in primary tuber diameter:	1.5 cm
Maximum primary tuber increase measured:	1.8 cm
Minimum primary tuber increase measured:	- 0.2 cm

Vergenoeg Post 6 Fenced Site

Mean increase in primary tuber diameter:	0.25 cm
Mode of increase in primary tuber diameter:	- 0.1 cm
Maximum primary tuber increase measured:	2.9 cm
Minimum primary tuber increase measured:	- 2.0 cm

Vergenoeg Post 6 Unfenced Site

Mean increase in primary tuber diameter:	0.62 cm
Mode of increase in primary tuber diameter:	0.3 cm
Maximum primary tuber increase measured:	2.3 cm
Minimum primary tuber increase measured:	- 0.4 cm

Ben Hur Fenced Site

Mean increase in primary tuber diameter:	0.56 cm
Mode of increase in primary tuber diameter:	0.4 cm
Maximum primary tuber increase measured:	1.8 cm
Minimum primary tuber increase measured:	-0.6 cm

Ben Hur Unfenced Site

Mean increase in primary tuber diameter:	0.22 cm
Mode of increase in primary tuber diameter:	0.2 cm
Maximum primary tuber increase measured:	1.1 cm
Minimum primary tuber increase measured:	-1.4 cm

Figure 15: The average increase in primary tuber size for the 2001 age states, also indicating the absolute minimum and maximum increase rates observed.

From Figure 15, we deduced that age state depends on the overall external pressures, including habitat, grazing and harvesting on the plant. A juvenile may progress to age state g2 within one year under suitable conditions, whereas plants from age state g2 that are harvested too early or frequently, may never reach age state g3. In addition, we summarised the percentage of all plants on the sites that, over the 5 years, showed no change in age state, an increase or decrease, or actually died. A decrease in primary tuber diameter had not been recorded before, and we were surprised at how many plants did show this decrease. Hence, we divided these figures into fenced and unfenced sites, and compared shifts in age state of all plants with those of plants that were harvested (Table 9). The observed patterns of Table 9 are elaborated on in more detail in the following sections. What is clear from Table 9, however, is that weak plants that do become senile are much more likely to die if continuously grazed than plants protected from grazing and able to replenish their storage through producing more leaf area. This is in line with ROBATNOV (1985), who found that senile plants are influenced the most by environmental conditions. Under favourable conditions, such plants may persist for a longer period, under unfavourable conditions they will most likely die. Some authors (e.g. HARPER AND WHITE 1974, ROBATNOV 1985) have found that in geophytic species as well as perennial herbs, the juvenile period is usually extended considerably if environmental conditions remain unfavourable. Comparing growth rates of DC plants only, juveniles had the highest growth rates, contradictory to findings of these two authors. However, DC seedlings and juveniles have a slow growth rate compared with other species of semi-arid environments (ERNST *et al*. 1988). This is in accordance with GRIME AND HUNT (1975), who found that even under optimal growing conditions, plants that produce and depend on a swollen taproot or tuberous root system had the slowest growth rates. In addition, these plants had poorly developed permanent above-ground structures as most assimilates were allocated to below-ground reserve build up. This should enable plants to survive stress periods better when little or no growth is possible. DC leaves have been found to have a high respiration rate, indicating that they are not too well adapted to aridity (VON WILLERT *et al.* 2002), which may explain why DC plants will develop from seedling to mature plants as quickly as possible. Once mature they are capable of surviving prolonged stress periods by prolonged secondary dormancy, when plants do not surface for an entire season. Such strategies have also been found by ROBATNOV (1985). This could also explain why harvested plants had a much slower rate of increase in age state than plants not subjected to harvesting pressure (Table 9). This will also be elaborated on in the following sections.

Table 9: Change in age state – according to change in primary tuber diameter – as percentage of all plants of the three sites, over the 5 years of the study.

	No change	Increase	Decrease	Died
Fenced sites	32	35	14	20
Harvested plants on fenced sites	63	17	10	10
Unfenced sites	23	24	8	46
Harvested plants on unfenced sites	40	20	20	20

4.5 Population structure and life tables

The population structure of DC, when calculated from all sites where primary tuber diameter was measured in 2001, shows age states g1 and g2 to be far more abundant than age states j and g3, with age state g2 the most abundant (Figure 16 A). As no previous data for tuber diameter were available, it was not possible to determine how many plants were initially senile. This distribution of age states within a population was also evident in populations with no (Figure 16 B) or very irregular (Figure 16 C) – hence relatively low – harvesting histories. Populations that had been harvested regularly showed a shift to age states g1 being most abundant (Figure 16 D).

To illustrate the detailed developments of the monitored populations at Vergenoeg Post 1 and Post 6, as well as at Ben Hur, diagrammatic life tables were constructed for every site. These are presented in Figures 17 and 19-23. In the life tables, we showed the number of plants of each age state, as recorded in 2001, and then the number of this original amount that changed to another age state, remained within the same age state, or died (Figure 18). ‘New’ indicates the number of plants that have germinated on the sites since 2001, and have since 2001 grown to be in the age state class in which they are shown. New plants in age state g3 indicate that these plants either had a very high growth rate from germination onwards or, more likely, were dormant at the time of the first survey.

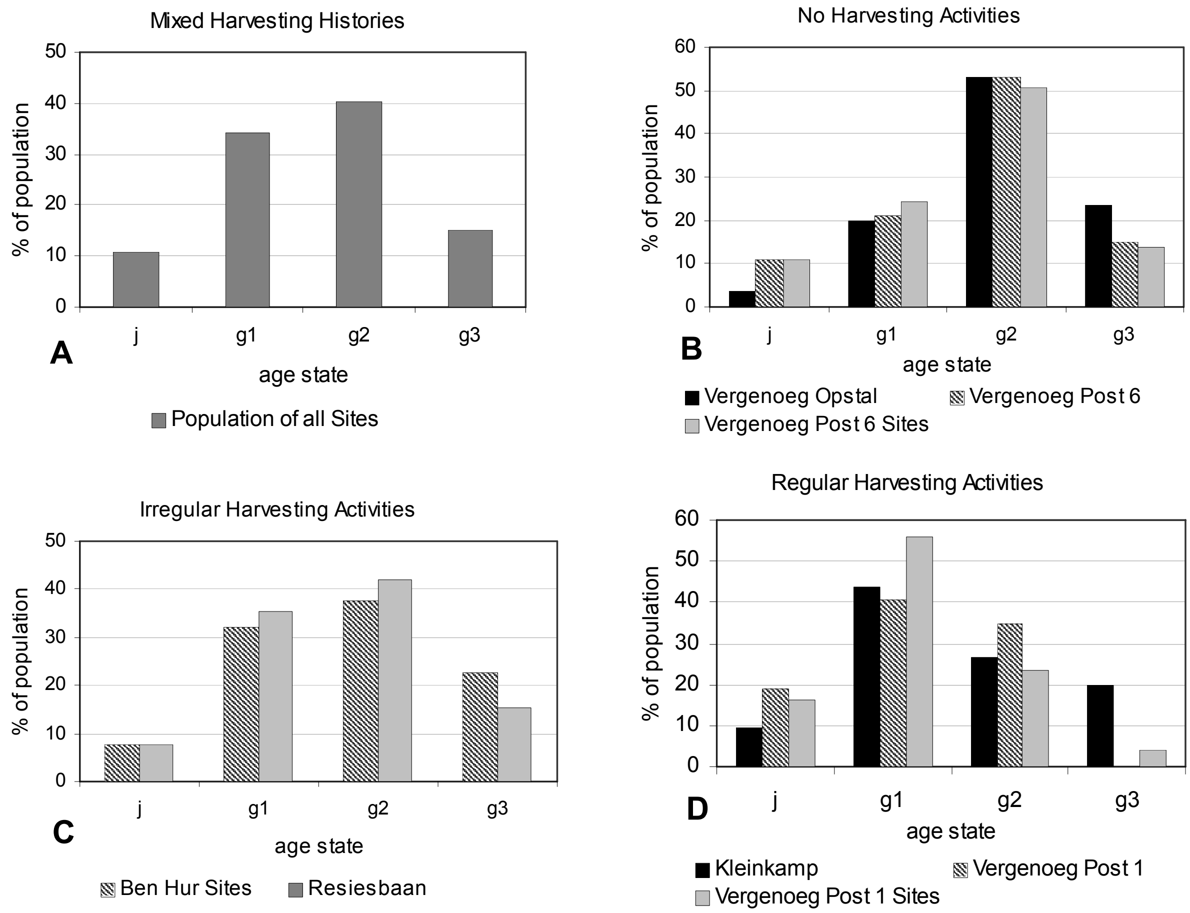


Figure 16: The impact of harvesting as reflected by the distribution of age states within sampled *Harpagophytum* populations – **A** shows all samples combined; **B** represents populations where no harvesting activity was known or could be detected; **C** shows populations where harvesting was only conducted sporadically; **D** shows a clear shift in age-state distribution due to harvesting the same plants at least every second year.

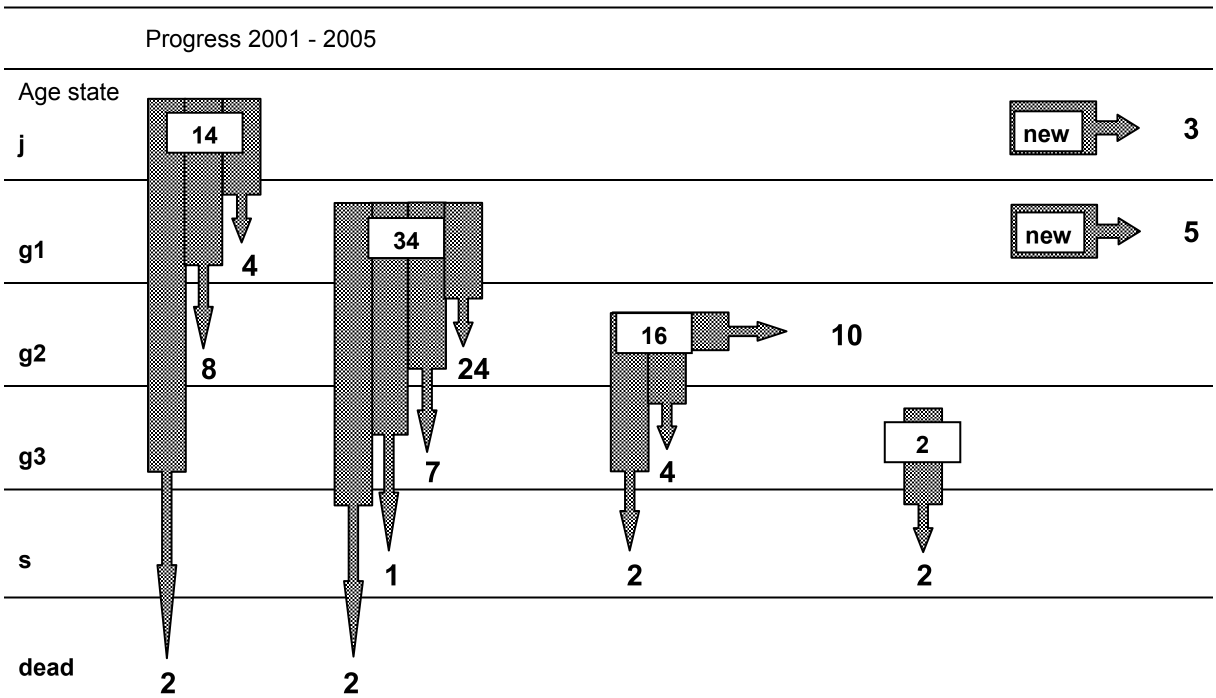


Figure 17: Life table for all plants monitored on the **Vergenoeg Post 1 Fenced Site**. Of the plants from age states g2 and g3 that became senile, one of each age state has been harvested.

Figure 18: Remnant of a primary tuber. Primary tubers of senile plants start rotting from the inside (STROHBACH 2005).

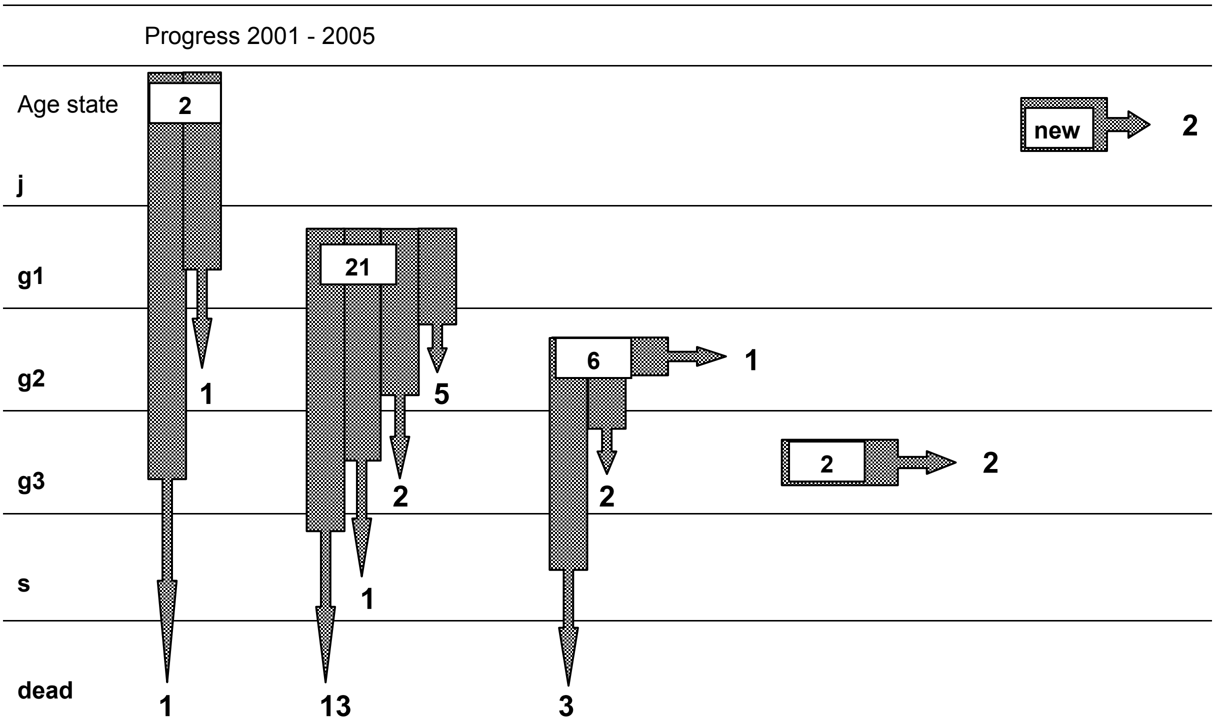


Figure 19: Life table for all plants monitored on the **Vergenoeg Post 1 Unfenced Site**. Of the plants from age state g2 that died, one already appeared senile during the harvest 2001. The other two were also harvested, but one of these was destroyed by unauthorised harvesting activities on the site in 2004.

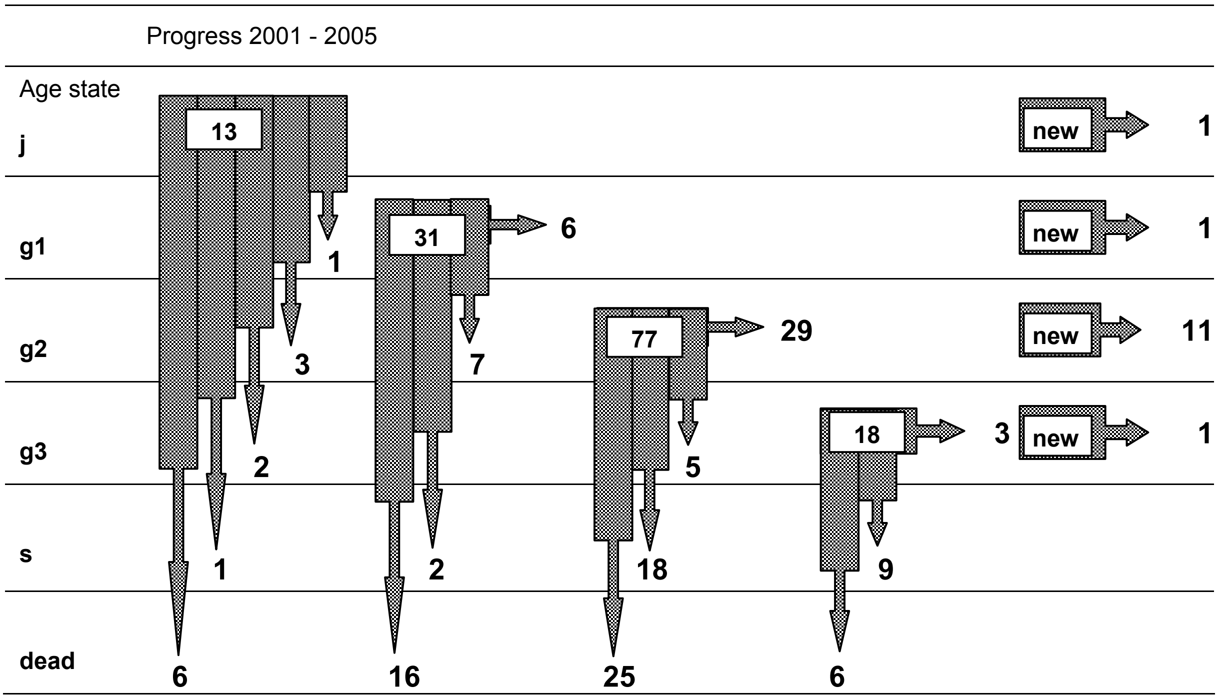


Figure 20: Life table for all plants monitored on the **Vergenoeg Post 6 Fenced Site**. Of the plants that died, only three had been harvested.

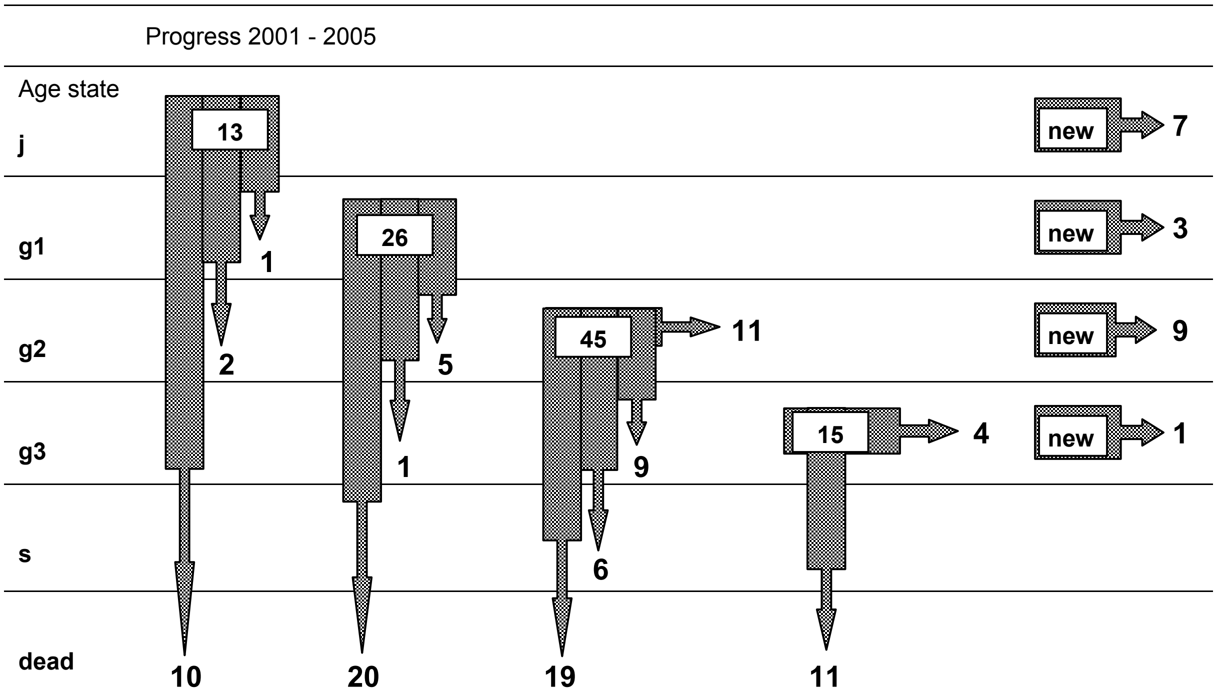


Figure 21: Life table for all plants monitored on the **Vergenoeg Post 6 Unfenced Site**. Of the plants that died, only two had been harvested.

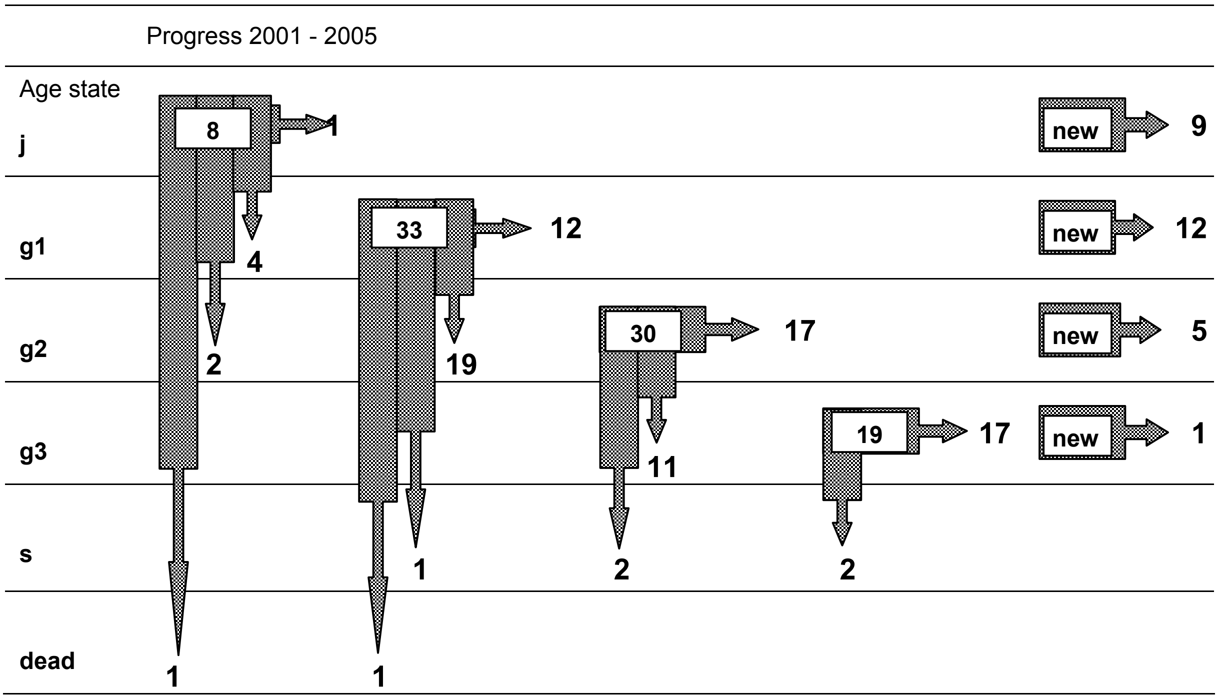


Figure 22: Life table for all plants monitored on the **Ben Hur Fenced Site**. Of the plants that became senile, only one had been harvested.

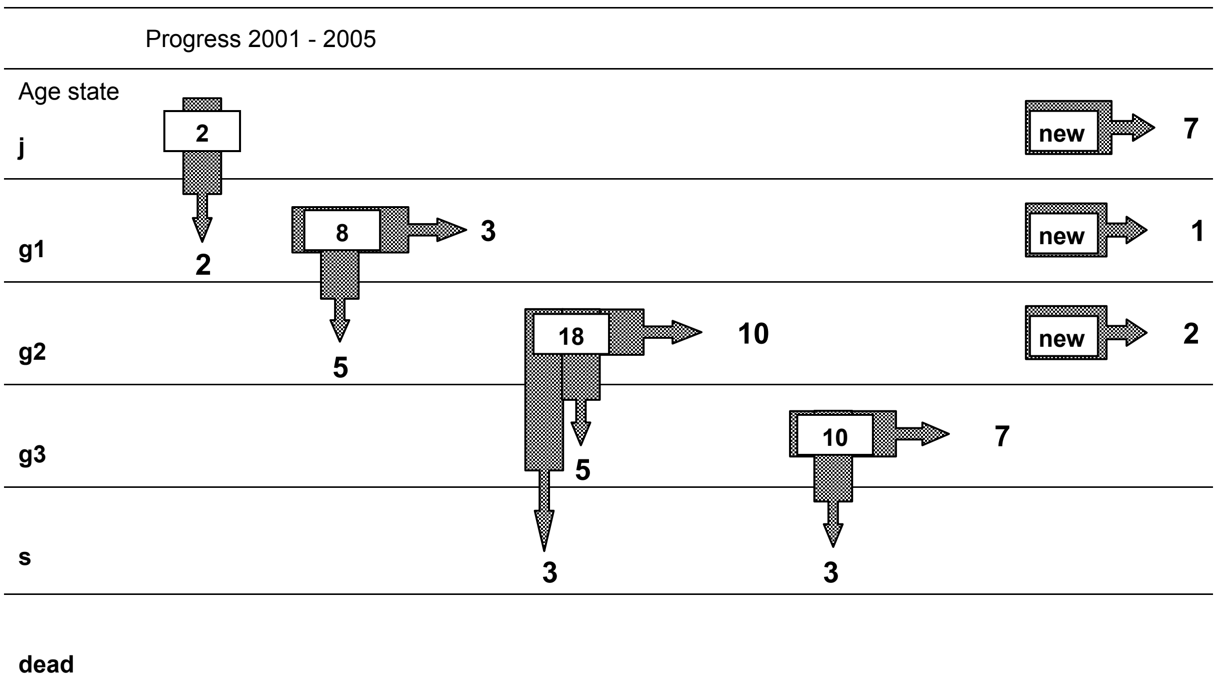


Figure 23: Life table for all plants monitored on the **Ben Hur Unfenced Site**. Of the plants that became senile, five had been harvested.

Small juvenile plants were often found growing very close together (Figure 24). As it was very seldom that larger plants were still growing with primary tubers touching, it can be assumed that a significant portion of seedlings every year get out-competed by their siblings, which may contribute to the overall low numbers of juveniles observed.

Figure 24: Juvenile plants in close proximity (STROHBACH 2005).

4.6 Net reproductive rate of the observed populations

From the life tables, net reproductive rate (R_0) for the population samples at the different sites was calculated. If $R_0 > 1$, it means the population is increasing, $R_0 = 1$ indicates a stable populations, while $R_0 < 1$ indicates a declining population – either because individuals of a population have reached their maximum density and competition becomes a major factor, or due to other detrimental factors influencing the plants (see URBANSKA 1992, SILVERTOWN 1987).

$$\mathbf{R_0 = N_{t+1}/N_t}$$

Where:

N_t = population size at time t

N_{t+1} = population size after time interval t+1

$$\mathbf{N_{t+1} = N_t + B - D + I - E}$$

Where:

B = number of germinating seedlings (could not be observed due to timing of inspections).

D = number of deaths

I = number of immigrants – defined in the age-state-specific calculations as the number of plants which moved from a lower to a higher age state

E = number of emigrants – defined in the overall population equation as the number of plants which have become senile, whilst in the age-state-specific calculations refers to the number of an age state which have moved to a higher age state or became senile

Table 10: Net reproductive rates for the population samples at the different monitoring sites. Also indicated are the net reproductive rates of the different age states within each population sample.

F = Fenced, UF = Unfenced site.

Site	Nr of plants 2001 N_t	Nr of newly germinated plants	Nr of deaths	Nr of immigrants	Nr of emigrants	Number of plants 2005 N_{t+1}	R_0	% deaths of harvested plants	% deaths of plants not harvested
Post 1 F	66	8	4	0	4	66	1.00	0%	6%
j	14	0	2	3	12	3	0.21	0	2
g1	34	0	2	9	30	11	0.32	0	2
g2	16	0	0	31	6	41	2.56	0	0
g3	2	0	0	11	2	11	5.50	0	0
Post 1 UF	31	2	17	0	1	15	0.48	10%	45%
j	2	0	1	2	1	2	1.00	0	1
g1	21	0	13	0	8	0	0.00	0	13
g2	6	0	3	6	2	7	1.17	3	0
g3	2	0	0	6	0	8	4.00	0	0
Post 6 F	139	14	53	0	30	70	0.50	2%	36%
j	13	0	6	1	7	1	0.08	0	6
g1	31	0	16	2	9	8	0.26	0	16
g2	77	0	25	21	23	50	0.65	2	23
g3	18	0	6	8	9	11	0.61	1	5
Post 6 UF	99	20	60	0	6	53	0.54	2%	59%
j	13	0	10	7	3	7	0.54	0	10
g1	26	0	20	4	6	4	0.15	0	20
g2	45	0	19	16	15	27	0.60	0	19
g3	15	0	11	11	0	15	1.00	2	9
Ben Hur F	90	27	2	0	5	110	1.22	0%	2%
j	8	0	1	9	6	10	1.25	0	1
g1	33	0	1	16	20	28	0.85	0	1
g2	30	0	0	26	13	43	1.43	0	0
g3	19	0	0	12	2	29	1.53	0	0
Ben Hur UF	38	10	0	0	6	42	1.11	0%	0%
j	2	0	0	7	2	7	3.50	0	0
g1	8	0	0	3	5	6	0.75	0	0
g2	18	0	0	7	8	17	0.94	0	0
g3	10	0	0	5	3	12	1.20	0	0

A comparison of the population's R_0 gives a more sensitive indication of the impact of stressors, for example harvesting, high grazing levels and root-competition, on plant fitness. The highest population growth rates were recorded at the Ben Hur sites. The Vergenoeg Post 1 Fenced site had a stable population, while at the other sites, Vergenoeg Post 1 Unfenced and Vergenoeg Post 6 Sites, populations were declining (Table 10).

The impact of harvesting on the population's R subscript 0 was emphasized by listing the deaths – calculated as percentage of the population N subscript t, for harvested and not harvested plants in Table 10 as well. This showed that harvesting activities cause a shift in the distribution of age states g2 and g3 (see life tables Figures 17 and 19-23), but there does not seem to be a major impact on the ability of the population to regenerate by seed, nor does harvesting activity cause any increased mortality rate of plants if the primary tuber is left undisturbed. From Table 10 it can then also be deduced that stressors other than harvesting cause the largest portion of DC population decline in our study.

Table 10 also shows the R_0 of the individual age states within each site. From this can be seen that the high R_0 recorded at Ben Hur can be attributed to the high rate of new seedlings establishing, which was not the case for the other sites. At Vergenoeg Post 6, seedling establishment rates seem so low that it can be expected that this population may disappear completely. Low flowering and fruiting rates observed here further indicate that the soil seed bank of DC at this site may become gradually depleted. Likewise, the population at Vergenoeg Post 1 may decline in future as old plants become senile, if seedling establishment rate does not periodically increase. A specific explanation for the higher seedling establishment rate at Ben Hur could not be found. It is speculated that the soil texture may play a role here – the improved water retention capacity of the soils may be just enough to ensure that germinating seedlings remain hydrated long enough to be able to survive dry spells between rainfall events.

4.7 Harvesting

Only plants of the age states g2 and g3 were harvested. The first group of plants was harvested April 2001 and again April 2003 and April 2005. The second group of plants was first harvested April 2002, again April 2004 and Aril 2005, to monitor regrowth of secondary tubers over one season. Harvest yields between plants were very different, and have been summarised in Tables 11-13, compared with rainfall received during each growing season. The tables should also be compared with the phenological data presented earlier in Figures 9-14 and Tables 4-6 to compare below-ground production with above-ground growth and flowering.

The highest harvest yields were recorded the first time the plants were harvested. Some plants had been harvested prior to the project, most of these at Vergenoeg Post 1, and yielded no initial harvests. It is noteworthy that the highest harvest yields recorded came from the sites at Ben Hur, despite receiving the lowest rainfall overall. This is believed to be a combined result of more favourable harvesting practices (not disturbing the primary tuber) together with more favourable soil conditions and the least competition from shrubs, very dense annual herbs and creepers.

Table 11: Harvest yields at Vergenoeg Post 1. Note the plants with a decrease in primary tuber diameter.

Rainfall October to May (mm)			*376 **	*322*	*307*	*474*	*460*	** measured from January only*		
% of long-term average annual rainfall			99%	85%	81%	125%	121%			
Fenced Site										
Age States	Tuber Ø 2001 (cm)	Tuber Ø 2005 (cm)	First Harvest 2001 (g)	First Harvest 2002 (g)	2003 harvest yield (g)	2004 harvest yield (g)	2005 harvest yield (g)	*Total re-growth after first harvest (g)*	Mean re-growth after first harvest per age state (g)	Overall mean regrowth after first harvest (g)
g2	2.4	3.1		0		30	0	*30*		
g2	2.5	3.5		0		40	430	*470*		
g2	2.7	3.4		0		1400	0	*1400*		
g2	2.9	3.1		650		0	0	*0*		
g2	2.9	3.4		0		760	0	*760*		
g2	3	3.2	200		0		30	*30*		
g2	3	3.6	180		300		50	*350*		
g2	3.1	***2.7***	400		20		0	*20*	382.5	
g3	3.5	4	1350		300		230	*530*		
g3	4.3	***4.1***	100		70		310	*380*	455	397.0

continued…

Table 11: …continued

Unfenced Site										
g2	2.6	3.7		0		0	0	*0*		
g2	2.6	Remnant	200		0		-	-		
g2	2.6	Remnant		0		0	-	-		
g2	2.9	Remnant	600		0		-	-		
g2	3.4	4.7		150		400	290	*690*	345	
g3	3.9	5.2	820		0		0	*0*		
g3	4.2	4.4		0		200	0	*200*	100	222.5

Table 12: Harvest yields at Vergenoeg Post 6

Rainfall October to May (mm)			*296**	*293*	*252*	*371*	*325*	** measured from January only*		
% of long-term average annual rainfall			80%	79%	68%	100%	88%			
Fenced Site										
Age States	Tuber Ø 2001 (cm)	Tuber Ø 2005 (cm)	First Harvest 2001 (g)	First Harvest 2002 (g)	2003 harvest yield (g)	2004 harvest yield (g)	2005 harvest yield (g)	*Total regrowth after first harvest (g)*	Mean regrowth after first harvest per age state (g)	Overall mean regrowth after first harvest (g)
g2	2.5	3.2	650		0		0	*0*		
g2	3.1	3.7		550		20	0	*20*		
g2	3.1	Remnant		2050		-	-	*0*		
g2	3.3	Remnant	400		0		-	*0*	5	
g3	3.6	None		350		0	-	*0*		
g3	4.1	4.5	400		0		0	*0*	0	3.3
Unfenced Site										
g2	2.6	2.9		300		0	110	*110*	110	
g3	3.5	None	600		-		-	*0*		
g3	3.6	4.5	700		0		350	*350*		
g3	4.1	Remnant	500		0		-	*0*	117	115.0

Comparing growth rates (Figures 9-14) with the harvest yields, it can be assumed that poor rainfalls during the period mid-December to mid-January have the most detrimental effect on plant growth. This is confirmed by observations that plants most easily scorched and stopped growing if rainfalls during the mentioned timeframe were poor to absent. Assuming that DC plants have used a lot of their stored reserves early during the growing season for new growth and flowering, it can be understood that the production of secondary storage tubers will be poor if the plants have a limited amount of leaf mass to produce enough assimilates. Poor rains up to March, followed by some good late rains, will not necessarily ensure a significant increase in leaf production of the plants. Plants may resprout again after late rains in an attempt to produce more storage assimilate for the following season's growth. However, the duration of the remainder of the growing season is then very short, rendering the expense of resprouting higher than the gain for new assimilates – this is why several of these late-resprouters died.

Comparing annual harvests with cumulative rainfall each month (as a percentage of the long-term average annual rainfall, presented earlier in Figures 3-5), some trends can be identified:

At Vergenoeg Post 1, the poor rains during January 2001 had a profound effect on the regeneration of secondary storage tubers, as became apparent during the second harvests during 2002 and 2003. This was the only site where plants were harvested regularly since about 1998 as part of the SHDC project. The good harvests during 2001 were attributable to the above-average rainfalls from 1997 to 1999 (METEOROLOGICAL OFFICE, WINDHOEK). Rainfall for 2002 and 2003 was below average, contributing to the low regeneration of storage tubers by 2003 and 2004. However, a higher cumulative rainfall up to January 2003 – for the season 2002/2003, enabled a more continuous growth cycle (Figures 9 and 10), which could account for the slightly improved harvests of 2004. Many of the plants harvested in 2001 and 2002 were only able to regenerate a harvestable amount of storage tubers after above-average rainfall for the seasons 2003/2004 and 2004/2005. The impact of grazing, which reduces the plants' ability to produce enough assimilates, can clearly be seen. It must also be added that both sites became encroached with shrubs, causing a significant increase in competition for water. We even found shrub-roots that had grown around DC storage tubers in a parasitic manner. The sites were only superficially cleared of shrubs to enable access to the monitored DC plants – this, however, did not reduce the below-ground root-competition for nutrients and moisture.

Table 13: Harvest yields at Ben Hur. Note the plants with a decrease in primary tuber diameter.

Rainfall October to May (mm)			*327**	*320*	*250*	*274*	*203*	** measured from January only*		
% of long-term average annual rainfall			96%	94%	74%	81%	60%			
Fenced Site										
Age States	Tuber Ø 2001 (cm)	Tuber Ø 2005 (cm)	First Harvest 2001 (g)	First Harvest 2002 (g)	2003 harvest yield (g)	2004 harvest yield (g)	2005 harvest yield (g)	*Total re-growth after first harvest (g)*	Mean re-growth after first harvest per age state (g)	Overall mean regrowth after first harvest (g)
g2	2.6	3.8		160		270	150	*420*		
g2	3.2	3.5		370		890	20	*910*	665	
g3	3.5	3.9		0		550	0	*550*		
g3	3.6	4.1	350		0		1630	*1630*		
g3	3.7	4.2	1450		100		150	*250*		
g3	3.8	3.9	500		400		1050	*1450*		
g3	3.9	4.9		320		510	250	*760*		
g3	3.9	***3.7***	120		200		680	*880*		
g3	4.2	5.1	2675		90		540	*630*		
g3	4.3	5.1	1050		40		150	*190*		
g3	4.5	6	2950		650		580	*1230*		
g3	4.7	4.8		460		620	120	*740*		
g3	4.7	5.3	2300		0		15	*15*	756.8	742.7
Unfenced Site										
g2	3	3.3	0		0		520	*520*		
g2	3.1	3.2	1550		0		920	*920*		
g2	3.2	3.5	4000		1340		20	*1360*		
g2	3.4	***3.1***	1940		170		980	*1150*		
g2	3.4	***2.7***		1300		50	0	*50*		
g2	3.3	3.8	280		20		40	*60*		
g2	3.3	3.5	0		0		200	*200*	608.6	
g3	3.5	4.1		560		550	280	*830*		
g3	3.5	3.6	1380		1450		1330	*2780*		
g3	3.7	3.9		350		50	300	*350*		
g3	4	5.1	2000		0		650	*650*		
g3	4.2	***2.9***		1000		210	0	*210*		
g3	4.8	***4.7***		200		360	900	*1260*		
g3	5.3	***3.9***	870		1300		50	*1350*	1061.4	835.0

At Vergenoeg Post 6, no plants had been harvested prior to the project. Initial harvests during 2001 and 2002 were still considerable, although is could be seen that most storage tubers were quite old. Whilst on the fenced site DC plants had to compete with a sudden very high increase in dense annual herbs during the growing season, which increased competition for above-ground space as well as below-ground resources, high grazing levels on the unfenced site limited leaf mass, but plants had far less below-ground root competition. These adverse conditions were compounded by several poor rainfall seasons. It is thus not surprising that regeneration of storage tubers at this site was extremely low and mortality rates were very high – most notably on the fenced site (compare with the life tables).

At the Ben Hur sites, there had been some irregular harvesting activities prior to the project. As at Vergenoeg Post 1, the effects of poor rainfalls during January 2001 could be seen on tuber yield in 2002. In addition, the poor rainfalls during 2002 and 2003 resulted in an overall weaker harvest of tubers during the second harvest in 2003 and 2004. During the 2004 harvest, it could be seen that many plants were only starting to form new tubers – there were strong swellings on the primary tuber or on the ends of previously harvested secondary roots - indicating the formation of new storage tubers, or storage tubers were about 1 cm long. Most of the tubers harvested in 2003 and 2004 were the old storage tubers that had been left during the previous harvest. Ben Hur also received reasonable rainfall during January 2004 – thus tubers harvested in 2005 were all newly formed tubers (recognisable by their potato-coloured thin outer skins). Grazing intensity at the unfenced site was much less – or in general of shorter duration – than at the other unfenced sites. Although average tuber regrowth was higher here – more plant were found to be senile on the unfenced site.

An overview of secondary tuber regeneration rates, also showing the net reproductive rates for the sites studied, together with the main factors that most probably influenced these regeneration rates over the period of the study, are summarised in Table 14. It must be remembered that plants were always harvested after a one-year rest period. Thus, even if a plant was not harvested in a specific year because the new tubers were too small (Tables 11 to 13), the plants were still disturbed. It could be expected that secondary tuber regeneration rates could have been better if these plants had had a longer complete resting period. Table 14 should also be compared with Table 9, presented earlier.

Table 14: Average secondary tuber regeneration rates (wet weight) at the different sites after harvesting

Site	R_0	Average secondary tuber regeneration in g after 1 year rest period	Average secondary tuber regeneration in g over 4 years (1 year rest period between harvests)	Most significant environmental factors influencing regeneration rates
Vergenoeg Post 1 Fenced	1.00	236	397	▪ soil excessively drained ▪ moderate shrub encroachment
Vergenoeg Post 1 Unfenced	0,48	60	223	▪ soil excessively drained ▪ heavy shrub encroachment ▪ periodic high grazing levels of DC
Vergenoeg Post 6 Fenced	0.50	2	3	▪ soil prone to water logging ▪ incrasing density of herb layer
Vergenoeg Post 6 Unfenced	0.54	50	115	▪ soil prone to water logging ▪ continuous high grazing level of DC and other herbs
Ben Hur Fenced	1.22	434	743	▪ soil well drained ▪ herb layer decreasing due to harvesting
Ben Hur Unfenced	1.11	444	835	▪ soil well drained ▪ herb layer decimated by harvesting and periodic high grazing levels*
Overall average		204	386	

From Table 14 it would be reasonable to assume that plants should have a resting / regeneration period of at least 3 years between harvests to compensate for unpredictable rainfall effects. This is strongly supported by the impact of harvesting on plants shown in Table 9. Storage tuber regeneration success also strongly depends on the management of the plants – continuous grazing and a strong weedy, annual herb layer should be avoided, while encroaching shrubs must be eradicated. Removing the latter will provide some material that can be used to temporarily fence off DC plants, lasting for the duration of a resting period to protect the harvested DC plants from grazing. The effect of surrounding vegetation is also confirms findings of earlier investigators (NOTT 1986, VON WILLERT *et al.* 2002): If properly managed, an average yield of 350 g to 400 g (wet weight) of secondary tubers per plant should be possible, and should be the basis of planned harvesting and trade activities, combined with annual population assessments (see section 4.8 below). Previous authors have estimated the average yield of secondary tubers per plant at 1.5 kg and 1.04 kg (NOTT 1986), whilst we had yields of up to 4 kg per plant (see Table 13) – but it must be stressed that these are first-time harvest figures of DC plants. Once harvested, regeneration rates of secondary tubers are much lower. Regeneration rates recorded during this study compare favourably with studies conducted in Botswana, where plants were estimated to reproduce about 50 g to 100 g storage tubers in one growing season, if rainfall is favourable (DE JONGH 1985, VEENENDAL 1984, HULZEBOS 1987). Our recorded regeneration rates were, however, less than recorded by VON WILLERT *et al.* (2002). It is quite possible that secondary tuber regeneration rates will vary regionally, influenced mostly by soil variables and climatic conditions.

4.8 Population size estimates and annual harvesting quota calculations

4.8.1 Transect walks

The Variable Area Transect Method was used to assess DC population densities. When working with unskilled communities it was common to observe that people counting DC plants tend to swerve from one dense patch of plants to the next and, while concentrating more on the ground than direction of walking, often walked in circles. This could be rectified by having community members work in pairs.

Below, we give guidelines, based on what we found to be most practicable, that can be followed when a DC harvesting quota needs to be determined for a specific area. These guidelines are designed to be used by the layman, whilst still producing acceptably accurate results:

The first person of the surveyor-pair is tasked with keeping a fixed point in sight and walking a straight line towards that point without looking at the DC plants on the ground. This person is also tasked with counting off 100 steps and stopping briefly after every 100 steps walked. The second surveyor follows closely behind and is tasked with counting the DC plants observed within one meter on either side of him / her (see section 2 earlier). In terrains where it is difficult to use a measuring stick, the second surveyor is advised to only count DC plants that are rooted in a width as wide as the outstretched arms of that person. The second surveyor will write down the number of plants counted for every 100 steps walked, and will also indicate to the first person when no more plants are observed and the first transect walk has been completed. This should be repeated at least once in a perpendicular direction as more transect walks will improve the accuracy of the density calculations. We further found that by using a strip transect rather than just a line enabled community members to more or less visualise, in an aerial context, the plant counts that they had recorded. Although very crude, this quick verification in the field helped a lot to build community trust in the sampling technique, which also improved sample data tremendously over time.

Note: The highest number of plants we encountered in a 100-step transect section throughout the SHDC project and the NNDCSA, was 61 plants (unpublished data STROHBACH 1998-2005), where plants were usually less than 1 m in diameter. Should higher counts be recorded, it is advisable to verify such counts.

4.8.2 Transect types

The type of transect walked depended on the observed population density. For practical purposes, only two density classes were distinguished:

(a) Dense, small population: 10 plants or more encountered per 100 steps walked, and these plants not being the only plants seen.

In such a case, Transect Method 1 was used, starting at a random point where the population more or less starts, walking in a straight line, until the population stops. A second transect was surveyed on the way back (Figure 25).

(b) Sparse, wider populations: less than 10 plants counted per 100 steps walked, and these often the only plants encountered.

In such a case, Transect Method 2 was used. From a random point, two transects of 100 steps (roughly 65 m) were walked and the number of plants encountered within the 2 m transects width counted. 300 m to 400 m further, this was repeated for at least 3 sets of 2 transects (Figure 26). Community surveyors had to indicate on their data sheets which transect method they had used.

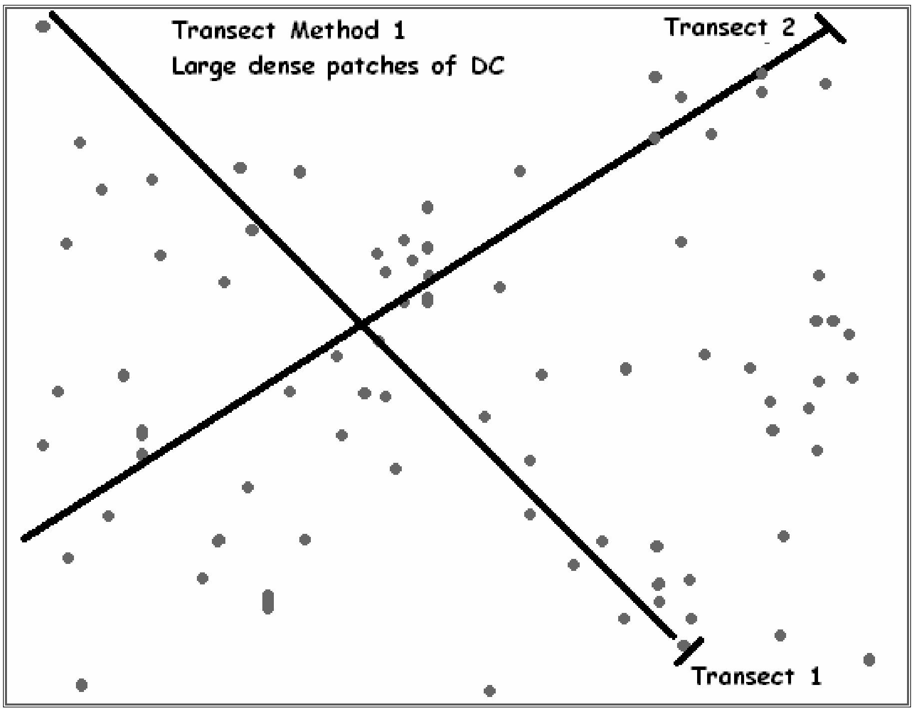


Figure 25: Illustration of Transect Method 1.

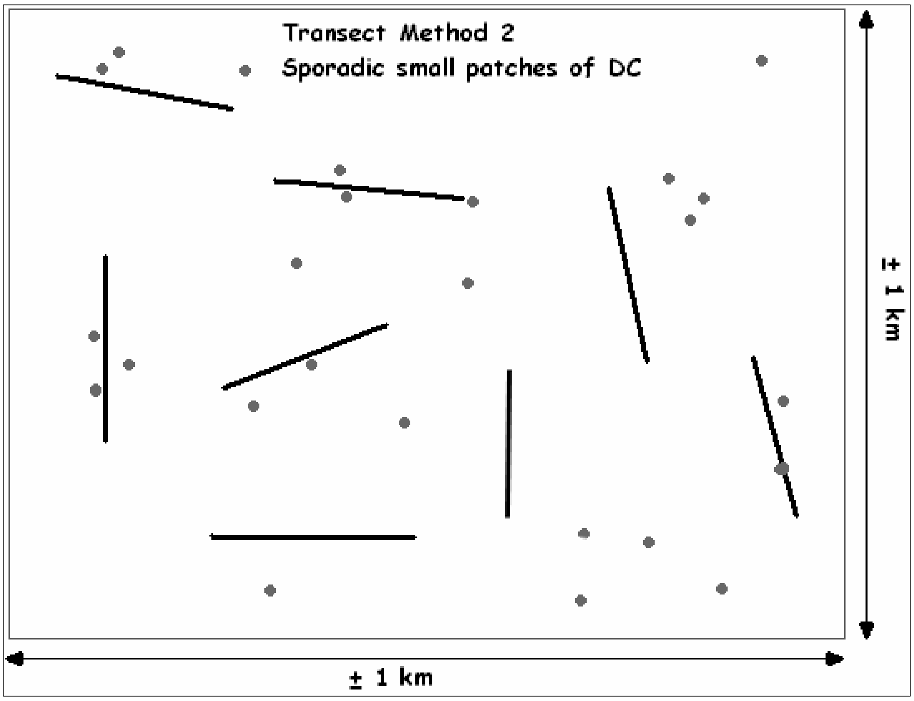


Figure 26: Illustration of Transect Method 2.

4.8.3 Calculation method with example

The following calculation steps determine the quota Q_{ann}, i.e. the annual dry weight of tubers that can be collected sustainably from the targeted collection area (A_p). The steps are illustrated by an example using sample data (Table 15) collected by community members. Also see KEITH (2000) and SCHAEFFER *et al.* (1996) for calculations of plant population sizes.

Table 15: Sample data set for two transects where number of plants for each 100 step section of a transect have been counted.

Transect 1		Transect 2	
100-step section	Nr of plants	100-step section	Nr of plants
1	5	1	2
2	3	2	5
3	17	3	26
4	15	4	8
5	6	5	1
6	1		

Step A: Size of targeted collection area or area of occupancy

Repeated measures of steps walked with a GPS were used to determine that 100 steps walked average a transect section length of 65 m. For Transect Method 1, the transect length is the number of transect sections walked per transect, multiplied by 65.	Number of transect sections x 65 m	direction 1: 6 x 65 = 390 m direction 2: 5 x 65 = 325 m
The mean length of all transects walked can then be determined by dividing the sum of all transect lengths recorded by the number of transect directions.	Sum of the transect lengths / Number of transect directions	390 + 325 = 715 m 715 / 2 = 357.5 m
For simplicity, we take the total area as a quadrat, thus the total area of occupancy (=collection area) A_p can be calculated as the quadrat of the mean length of transects. *Note: The area of occupancy A_p refers to the area of the DC patch under investigation, not just the actual area of the transects walked, which is why we calculate the area as a quadrat (calculating the area of a circle with the mean length of transects as diameter would be an equally good alternative).* *Note: If Transect Method 2 is used, A_p will be 1 km² or a portion thereof if so specified. In general, it is expected that most communities will use Transect Method 1.*	A_p = (Mean length of transects)^2	$(357{,}5)^2$ = 127 806 m² The collection area A_p is 12.78 ha.

Step B: Density of the plant population

First, we calculate the mean number of plants in the standard transect section of 65 m.	Sum of plants of all transect sections / Number of transect sections	89 / 11 = 8.09 plants
Further, we need to know the area of the standard transect section: This would be 2 m (fixed width) x 65 m (100 steps).	Transect length x Transect width	65 x 2 = 130 m²
The mean density of all plants D_{all} on the transect sections can then be calculated by dividing the mean number of plants per transect section by the area of the transect section.	D_{all} = mean number of plants / transect section area	8.09 / 130 = 0.06 plants / m² The mean density D_{all} is 0.06 plants per m^2.

Step C: Number of harvestable plants in collection area		
From the population structure analysis it was seen that when taking all sampled populations into account, only 55% of all plants present are of the harvestable age states. Thus, to arrive at mean number of plants D_{harv} which can be harvested per standard transect section, only 55% of D_{all} can to be taken. *Note: This can alternatively be expressed as 3.4 plants per 100 m² for easier visualisation. The highest density of DC plants in Namibia amounts to about 25 DC plants per 100 m² (STROHBACH 2003), with plants generally being 1 to 1.8 m in diameter. In regions with higher rainfall, such as north-western Zimbabwe, where plants may reach a diameter of up to 4 m, typical maximum densities should be lower (unpublished data STROHBACH 2006).*	D_{harv} = 55% of D_{all}	0.06 x 55/100 = 0.034 plants / m²
In the next step we can determine the total number of harvestable plants N_{harv} in the collection area by multiplying the mean number D_{harv} with the collection area A_p	$N_{harv} = D_{harv} \times A_p$	0.034 x 127 806 = 4 345 plants 4345 plants are of a harvestable size in the 12,78 ha area.
Step D: Setting the quota of tubers that can be sustainably collected annually		
With a 3-year resting period, only a quarter of these plants can be harvested (unless communities clearly show that they have a rotation area plan in practice and have surveyed area 1,2,3 or 4).	N_{harv} / 4	4 345 / 4 = 1 086 plants
From our harvest results it can be assumed that, taking rainfall variability into account, a healthy plant in the age state g3 and g4 should be able to regenerate about 350-400g new storage tubers over 3 years (Table 13). The resultant dry weight of sliced tubers is only 10% of the wet mass (Hachfeld 2003), thus of every harvestable plant a final dry weight of 40 g can be expected.	Q_{ann} = Number of plants x Regeneration rate	1 086 x 0.04 = 43.4 kg The annual collection quota for the 12,78 ha collection area is 43,4 kg of dried tubers.

Another important factor in the quota determination is the timing of the population counts. As seen from the phenological data, poor rains from mid-December to mid-January strongly influence the plant's performance for the remainder of the season. Thus plant growth by the end of January should be a clear indication of how well plants will be able to divide their assimilates between flowering and tuber regeneration. In addition, late rains may cause plants to surface late, but these plants will not be able to produce a large amount of assimilates. Thus, *population counts should be conducted in January* to exclude plants which have died back over the hottest season, as well as plants which may only surface at a later stage.

5. Discussion

Temperature, moisture regime and soil have been identified in several studies as the principal environmental factors triggering the production and development of foliage, flowers and fruit in different plant communities and species (STRUCK 1994, PAVON & BRIONES 2001). Functional responses to more or less predictable environmental variation are important for plant survival in the long term. These responses include the evolution of life histories (WERGER & HUBER 2006), like the geophytic manner of Devil's Claw, which enables the plant to deal with the predictable seasonal variation of summer rainfall and dry winter as experienced in the Kalahari. Phenologic plasticity again allows plants to adapt their development to small-scale (short-term) unpredictable variation in resource availability and other environmental conditions (WERGER & HUBER 2006). As this study showed, Devil's Claw can vary its phenology considerably to adapt to inter-annual variation in rainfall patterns. However, this adaptation also comes at a cost.

BLOOM *et al.* (1985) predict the following about the economics of resource limitation in plants:

a. 'Storage enables plants to acquire resources at minimal costs' (when e.g. water is readily available) 'and use them at times of maximal benefit' (e.g. resprouting in spring, when no significant rain has fallen yet)

b. 'Plants continue to produce leaves or roots until the marginal revenue from this increased production is equal to the marginal cost.' Translating this to Devil's Claw, it means that the plant has to use stored reserves, assimilates and moisture, to produce leaves. It needs to produce leaves in order to synthesize storage compounds which, when stored in the roots, enable increased water absorption (by increasing the osmotic potential of the roots). Thus harvesting a plant while it is busy using its reserves to produce leaves and flowers will cause an excessive drain on the stored reserves. Only once the plant has had its leaf mass for a sufficient time to produce new assimilates that can be stored and are not significantly used for leaf-, flower-, or fruit production, will the plant be able to recover better if stored reserves are removed.

c. 'Plants adjust allocation so that their growth is equally limited by all resources'. Looking at Devil's Claw, it will imply that if e.g. rainfall during the growing season is very low, it will not expend many resources on developing fruit and may not even produce flowers, but may rather allocate what little assimilates it can produce to storage.

d. 'Each plant process is limited by the same balance of internal reserves'. Again, in Devil's Claw, it means that the cost of developing fruit and the cost of developing storage must be covered by the same 'internal bank', namely already stored storage reserves.

e. 'In order to achieve both a similar benefit-to-cost ratio for each resource, and an optimal allocation among processes, plants adjust physiologically in both the short-term (acclimation) and the long term (genetic adaptation) to minimize differences in exchange ratios across diverse habitats.' For Devil's Claw, as for many other geophytes, this will mean that depending on the availability of resources, it will most probably not follow the same pattern of development every year, but rather optimise its strategy to ensure long-term species survival by producing viable seed reserves. Only then will it start replenishing its own reserves to ensure the plant's survival in the shorter-term. These strategies help the plant to optimise the narrow window in time that is available every year for growth and reproduction, and then survive unfavourable seasons in the form of seeds or in a dormant state (WERGER & HUBER 2006).

In the Kalahari, available moisture and low soil nutrient concentrations are the most limiting factors to plant development (SCHNEIDER *et al.* 2006, SCHOLES 1990). Thus, to minimise the impact of harvesting on Devil's Claw, we need to understand how the species 'plans' the economics of its resource-use in a variable environment. Based on this understanding, harvesting strategies need to be adjusted to ensure that the internal resources taken off a plant through harvesting do not 'bankrupt' that plant to such an extent that it dies off. Although this study did not measure any detailed physiological variables to understand the species' interal allocation patterns, our records do reveal trends that can explain some of the species' strategies:

In accordance with IHLENFELDT & HARTMANNN (1970), the first emergence of plants could be observed in October and November, often associated with, but not limited to sporadic small rainfalls. It can thus be assumed that temperature is the principal trigger for plant emergence. The rate of emergence depends on the amount of reserves – including moisture - the plant managed to accumulate during the previous growing season. The fewer reserves a plant has, the more it will have to rely on early rainfalls to resprout, which may explain why some plants only emerge from late January onwards (OESTERHELD *et al*. 2001, WERGER & HUBER 2006). The growth after emergence strongly depends on the availability of moisture at that time. Here it was found that Devil's Claw plants need sufficient moisture during their peak flowering period, which happens to coincide with the hottest month of the year. Poor rains during this critical period impair plants from adequately replenishing the reserves that were expended for the early mass of flowers. This also implies that there will be few new storage reserves and storage tubers formed (BEATLEY 1974), which are the reserves enabling the plant's survival and persistence during dry periods (ERNST *et al.* 1988). The high cost of a second burst of foliage later in the season, as observed during 2003 (section 4.3) without having had the opportunity to sufficiently regenerate storage assimilates explains why many of these late resprouters were subsequently found dead at our sites. Further, CASPER AND JACKSON (1997) state that mass flow of soil water and nutrients towards the root and their subsequent uptake can only be maintained if there is a local concentration gradient (of dissolved solids) across the root-wall. Thus a root can only absorb water and nutrients from the surrounding soil, if it's internal concentration of solutes is higher (thus creating a higher osmotic potential) than the external concentration of minerals and other dissolved particles. This is confirmed by the group of 'high-performer' plants found by SCHNEIDER *et al.* (2006) when studying water potential of Devil's Claw in the Kalahari in South Africa. Such high-performer plants were better able to withstand moisture deficits throughout the growing season and thus had a higher growth rate than other plants. The main difference between high- and low-performers was that the former had a consistently higher concentration of assimilates, including Harpagoside, in the storage tubers.

Plant individuals have a limited amount of resources to spend on growth, maintenance (survival) and reproduction (BLOOM *et al.* 1985, BARBOUR *et al.* 1999). When reproduction and vegetative growth occur simultaneously as in Devil's Claw, there is an allocation trade-off between both types of function within the plant (LOPEZ *et al.* 2001). From the phenological and harvesting data in this project it can be assumed that plants which have not been able to generate any additional storage tubers due to a very dry December or January during growing season 1, will invest additional reserves into a mass of flowering during growing season 2. This will be an adaptation, typical for longer-lived competitive but drought-avoiding plants to ensure sufficient seed output should growing season 2 also have poor rainfalls, and in so doing warrant the continued survival of the species (GRIME 2002, OESTERHELD *et al.* 2001, NIPPERT *et al.* 2006, WERGER & HUBER 2006). During growing season 3, flowering rates will be much reduced due to a very low level of storage reserves. Plants that have survived the preceding poor rainfall seasons will now allocate most of the produced assimilates to new storage tuber production. Only during successive good rainfall seasons will there be an equal share of produced assimilates to the physiological sinks - flowering and fruiting, then storage (see CHAPIN *et al*. 1990). This is why it is imperative to extend the resting period from the present one-year time frame to at least 3 years to allow plants to fully recover from the effects of fluctuating rainfall as well as harvesting. To optimise a plant's survival after harvesting, it will be of great advantage if not all tubers of one plant are harvested simultaneously. This can be achieved by either only harvesting half to two-thirds of the plant, or by harvesting only secondary tubers attached to the upper primary tuber (and usually no deeper than 50 cm). Thus, the ideal Devil's Claw resource management strategy will maintain a very strict 4-year (or more) rotational harvesting system, where resource occurrences and community circumstance allow. This should be complemented by an annual resource survey to determine harvesting quotas. The benefit of such annual resource surveys is that land users gradually get to know their resource very well, and will be able to detect detrimental changes to the resource.

Considering above-ground productivity specifically, a plant's ability to grow an adequate mass of leaves every year is very important for *Harpagophytum* species to ensure an individual plant's survival (compare with BLOOM *et al.* 1985). Where this ability was impaired, plants typically showed either no increase in age state, a decrease, or died. The agents responsible for reducing the expansion of Devil's Claw plants were either a high shrub cover, a dense cover of annual grasses and creepers, or continuous high grazing levels. Plants affected by these stressors were much more susceptible to damage by harvesting than plants not harvested. Observed phenological patterns show that leaf expansion is still ongoing after flowering has ceased. This indicates a need of the plants to increase photosynthesis and assimilation-rates to replenish resources used by the masses of flowers produced, whilst also supporting the few fruit that did develop to ripen. Although no studies were undertaken to harvest *Harpagophytum* during its growing cycle, it can be assumed that this may have the same detrimental effect on plant development as continuous high grazing levels. This is because as a significant proportion of stored reserves is used for leaf expansion and flowering, and should not be removed while being used and before being replenished adequately.

The general low number of juvenile plants found is another trait of a drought-avoider (GRIME 2002). This is confirmed by the high innate dormancy of the seeds, as well as the slow release of seeds from the mature fruit as an adaptation for spreading seed germination in time (ERNST *et al.* 1988, VEENENDAL *et al.* 1996). ERNST *et al.* (1988) have reasoned that well-developed seeds could survive up to 20 years under the dry conditions of the Kalahari. They have also shown that once a seedling has emerged, the growth rate is very slow compared with other herbaceous species of semi-arid environments. These seedlings will only be able to continue growing and forming sufficiently large underground tuber systems if they grow in relatively open sites with low above-ground competition. It has also been found that in the Kalahari, germination of herbaceous species often occurs in 'waves', following sufficient rainfall. Minimum amounts of rainfall to trigger such germination waves have been found to be above 10 mm, and need to be followed by another significant rainfall within 2-3 weeks to ensure the establishment of the seedlings (VEENENDAL *et al.* 1996). Taking the above reported slow growth rate of Devil's Claw seedlings into account, it is understandable that most seedlings of this genus are only seen after sufficient and continuous rains have fallen during late summer (February / March). Large rainfall events as early as October may lead to such a germination within Devil's Claw as well (personal observations), but subsequent seedling establishment depends on follow-up rains and may be very low. Although it could not be shown during the time of this project, it can be predicted that during successive years of above-average rainfall, high periodic rates of seedling emergence may occur (VEENENDAL *et al.* 1996). This will contribute considerably to the long-term rate of population growth and structure. Such strategies were observed in long-lived perennial herbs by e.g. FLOYD AND RANKER (1998) and MOLONEY (1988). It can thus be envisaged that some Devil's Claw populations may disappear entirely at some point in time, but that these may re-appear under favourable conditions should the existing seed-bank be large enough. GRIME AND HUNT (1975) state that the relative scarcity of plant species with such growth patterns, as observed in Devil's Claw, in relatively dense vegetation suggests a low competitive ability of these plants. This would then be the main reason why Devil's Claw plants attain high densities in disturbed (cleared or overgrazed) areas as are commonly found in closer proximity to communal settlement areas, while in less disturbed habitats Devil's Claw plants occur in distant small clumps of one to few individuals (HACHFELD 2003, STROHBACH *et al.* 2004)

Relating the above information to the central question of this project – whether it is possible to harvest Devil's Claw in a sustainable manner, and how this sustainability can be improved - the net reproductive rates calculated for the different population samples probably give the most clear-cut answers:

At Vergenoeg Post 1, R_0 was stable for the fenced site. Net reproductive rates and harvesting yields were, to some degree, suppressed by encroaching shrubs. On the unfenced site, the population was declining. This was due to some destructive harvesting during 2004 (according to headman Fritz Kamti, the responsible community member had been caught red-handed and penalised) but also due to continued high levels of bush encroachment and grazing. Nutrient concentrations were low at this site and soils were the most excessively drained of all sites. Thus, population stability and growth as well as harvesting yields could have been improved if:

i. encroaching shrubs had been totally removed, chopping them off 50 cm below ground to eliminate potential regrowth,
ii. plants were protected from grazing
iii. more careful harvesting practices were used to entirely prevent damage to the primary tuber and its taproot
iv. there were longer resting periods

Generally, this population can be regarded as a source population – that is, it is able to produce a good supply of seeds for distribution, whilst the population has not reached its upper density limit and could expand.

At Vergenoeg Post 6, the population was largely declining. On the fenced site, this was mainly due to excessive competition from dense annual herbs, while on the unfenced site continued high levels of grazing prevented the plants from producing enough leaves to sustain themselves. Added to this, local soil moisture processes were not always favourable for the species: After heavy rains, the soils become waterlogged for a short period, causing anaerobic conditions in the soil, which contribute to rotting. As the soils dry up, low levels of available moisture adhere so tightly to the finer mineral-rich soil particles, that it becomes unavailable to plants. It was thus not surprising that so many of the primary and secondary tubers on this site where found rotted (even if the plant was still alive) during 2005. This population (and Devil's Claw populations in similar habitats) should be regarded as sink populations. Seeds have probably been carried here by animals converging on the short flush of vegetation during moist periods. Under favourable conditions, these seeds manage to germinate in large numbers, forming a very dense population of Devil's Claw plants. However, this population limits itself by density-dependent competition, and soil properties prevent the plants from continued new storage tuber production as conditions become more adverse. For harvesting purposes, such populations should be regarded as 'reserve resources', to be harvested only occasionally if other resource locations should be rested for longer. The stability of these populations is not guaranteed, even if rangeland management is improved.

At Ben Hur, the population was increasing and had a fair number of juveniles present. The high tuber production rates can probably be attributed to more favourable soil conditions. Certainly, for the duration of the project, the practice of harvesting only half a plant appeared beneficial to the regeneration of these plants, but longer resting periods will be necessary for these plants to actually generate new secondary tubers again. The minimal disturbance of the primary tuber and its taproot most definitely contributed to the regenerative success of these plants here. Harvesting yields and plant growth could probably be improved if grazing could be restricted from December to the end of March. Protection of the harvesting areas from grazing should be seen as a benefit to livestock owners – this would enable valuable hay-forming perennial grasses to become re-established. These pose less of a competitive threat to Devil's Claw plants than invasive shrubs or dense annual herbs (see Figures 27 and 28), and will be a valuable source of grazing during the winter months, when many livestock owners are desperately looking for additional grazing.

The below-ground habitat partitioning, whereby some plants are capable of growing deep root systems and so tapping water resources not available to shallow-rooted neighbours, has been described by several authors (e.g. KNOOP AND WALKER 1985, CASPER AND JACKSON 1997). This system has often been used to interpret bush-grass dynamics in savanna systems (see SCHOLES AND ARCHER 1997). However, root partitioning is not so clear-cut. Many shrubs, for example, are capable of developing a very deep taproot system, but also an extensive shallower lateral root system to be able to use all available soil moisture within the available soil volume (see HIPONDOKA *et al.* 2003). Devil's Claw typically occupies the upper and middle soil layers of the available below-ground habitat. Its taproot will be able to tap deeper soil resources, while the upper lateral roots will develop opportunistically as resources become available. It was observed during the good rainfall season of 2006, that new secondary roots actually grow upwards from the primary taproot, to develop storage tubers just below the soil surface. SCHNEIDER *et al.* (2006) found that Devil's Claw plants, around which all other vegetation had been cleared in a 3 m wide strip, were able to withstand soil moisture fluctuations much better than their counterparts within the typical Kalahari vegetation were. This is clearly due to the absence of root competition. One aspect that is often neglected in root-distribution studies is the ability of species to proliferate many small roots in a short time in response to 'finding' a resource rich portion in the soil (CASPER AND JACKSON 1997). Although we did not make a study of this, except for the few secondary roots that formed very close to the soil surface during an exceptional good rainfall year, we cannot say that Devil's Claw has the ability to form an abundance of fine roots in a short time to optimise resource uptake. Surrounding shrub species, particularly *Acacia* species, however, are well capable of developing a moderate density of shallow but fine roots. These roots are the most significant competition for below-ground resources for Devil's Claw. Grasses and other herbs will only constitute to significant below-ground competition if their density is very high (compare Figures 27 and 28), so that their root systems either directly overlap with that of Devil's Claw, or are dense enough to prevent much moisture from penetrating into the deeper soil layers, where it will be available to Devil's Claw. A layer of perennial grasses with tufts up to 60 cm tall and a canopy cover of 50 to 80% had a far less competitive impact on Devil's Claw plants, as the basal cover of these grass tufts is typically only about 20% of their canopy cover, and below-ground density of roots is thus dense. In addition, the loose canopies of these perennial grasses contribute very little to competition for light, as opposed to dense shrub canopies.

Figure 27: Good plant expansion and flowering of *Harpagophytum* in the absence of significant plant competition (STROHBACH 2001).

Figure 28: Extremely reduced plant expansion of *Harpagophytum* in a layer of dense annual grasses (STROHBACH 2006).

6. Conclusion

Our phenological observations compare well with the pulse-and-reserve pattern described by NOY-MEIR (1973): An effective rain event triggers a pulse of production, which is a high increase in shoot growth and flowering. Much of this pulse may be lost rapidly by mortality or consumption (e.g. the high flower production), but some is diverted back into a reserve (either seed production or storage tubers). The reserve compartment is used minimally during periods of dormancy and from this reserve, the next pulse is initiated. This pattern ensures a long-term stability of a system despite short-term variability. However, this stability will be endangered by mechanisms causing over-exploitation of the reserves (i.e. too frequent harvests) or consistent prevention of backflow to reserves (i.e. continued grazing and bush encroachment). The humped population structure of Devil's Claw plants found corresponds well with biologically stable populations described by HARPER AND WHITE (1974). Although Devil's Claw is not very well adapted to semi-arid conditions (VON WILLERT *et al.* 2002), populations studied are generally stable, despite highly variable annual moisture levels, and despite the occurrence of source and sink populations. Source populations can remain more or less stable if harvesting of the storage tubers is conducted according to recommended practices.

The number of medicinal plant species known to have become globally extinct is very low (HAMILTON 2004). Over-exploitation may threaten many species, but this does not necessarily imply complete continental extinction (HAMILTON 2004). However, given the more limited distribution of Devil's Claw to the southern African Kalahari system, (IHLENFELDT AND HARTMANN 1970), the seriousness of local or regional extinction, especially commercial extinction (i.e. depletion of resources to levels below economically feasible harvesting) should not be under estimated (HAMILTON 2004). The overall Devil's Claw distribution in Namibia is such that a sufficient number of plants grow in either National or Private Nature Reserves, as well as on farmlands where there is no harvesting by humans, thus the species should not be threatened with extinction (KEITH 1998, STROHBACH 2003). Currently there is little certainty where most of the harvested Devil's Claw tuber comes from within Namibia. It can be anticipated that with the current high harvesting rates local extinctions are to be expected. These extinctions may be complete, temporary or only commercial – the latter causing a loss of income for local people.

The SHDC project (COLE AND LOMBARD 2000) has been implemented with great success on several communal farms and is seen as a trendsetter (HAMILTON 2004), but these farms only form a minor part of the overall resource distribution. Devil's Claw resource stability within Namibia could be greatly improved if conservationists and other activists, e.g. NGO's, could increase efforts to influence the ways harvesters and traders manage and harvest the resource. HAMILTON (2004) recommends the institutionalisation of certain activities related to sustainable use – which in the Namibia case would be registered harvester groups as well as trained resource surveyors. *It cannot be emphasised enough that local communities who are responsible for the bulk of the harvesting activities need to be involved in conservation activities.* As HAMILTON (2004) also found – in many parts of the world, it is not difficult to harvest medicinal plants illegally if the only controls present are those associated with government offices, which are often not equipped or staffed adequately to be able to implement their policies. Government agencies also have little control over other activities that endanger medicinal plants. The most important of such adverse activities is poor rangeland management, as was shown in our study.

Recommendations to ensure the long-term stability of Devil's Claw resource availability in Namibia:

i. Trained resource surveyors from communities should be involved in the annual establishment of harvesting quotas, which should form part of the annually issued harvesting permit. Conservationists should be able, based on calculations presented in this manuscript, to work out harvesting quotas from survey data supplied by resource surveyors

ii. Resource surveys should be carried out in January to omit late resprouters whose survival chances may be compromised by harvests during that season

iii. Conservation agencies should undertake their own occasional surveys – at least in areas where Devil's Claw is regularly harvested. A history of harvests and annual surveys for such site may yield further valuable information for long-term monitoring of the Devil's Claw resource
iv. Harvests should commence after fruit start ripening – towards the end of April
v. Individual plants should not be harvested or disturbed for a minimum period of three years before harvested again to compensate for fluctuating rainfalls
vi. The harvesting practice must be optimised to prevent any disturbance of the primary tuber and taproot
vii. Communities should be encouraged to permanently debush the areas where they harvest Devil's Claw. Grazing in these areas should be minimised during the growing period, which will give the added advantage of more standing hay available for livestock during the dry winter months
viii. In areas with a suitable habitat but low Devil's Claw resource availability, cultivation should be encouraged. The same applies to areas where the number of harvesters present exceeds the economically viable amount of harvestable resource for all harvesters

7. Summary

7.1 Study overview

Devil's Claw (*Harpagophytum procumbens* and *Harpagophytum zeyheri*) are plants that grow mainly in the Kalahari sands of Namibia, Botswana, South Africa and Angola, and to a lesser extent Zambia, Zimbabwe and Mozambique. Demand for Devil's Claw on the international market has increased considerably over the last decade. While this increase in demand has brought about greater opportunities for those involved in the harvesting and trading of the plant, it has also vastly increased the pressures on this resource.

This is the final report on the study, *"Population Dynamics and Sustainable Harvesting of the Medicinal Plant Harpagophytum procumbens DC (Devil's Claw) in Namibia"*. This report presents background information on key issues related to this study, the implementation and results thereof and provides recommendations for the sustainable management of Devil's Claw based on the findings of the study.

The study took place over a five-year period between 2001 and 2005 and was conducted at three sites located on two farms, Vergenoeg and Ben Hur, in the Omaheke Region of the Republic of Namibia. The study was commissioned and funded by the German Federal Agency for Nature Conservation and was undertaken by the Centre for Research Information and Action in Africa, Southern Africa Development and Consulting (CRIAA SA-DC).

The need for the study to be undertaken arose because of a dramatic increase in export figures during 1998 and 1999 and corresponding concerns regarding the possible over-utilisation of Devil's Claw in Namibia, largely because of reports of un-sustainable harvesting practices. Further concerns regarding the sustainability of Devil's Claw was also highlighted at an international level when in April 2000, at the (CITES) eleventh Conference of Parties (CoP 11) held in Gigiri (Kenya), Germany proposed that both species be listed on Appendix II.

Efforts to address this were limited by the lack of scientific data regarding the population and ecology of the plant as well as the impact of harvesting on the population status. There was therefore an urgent need to generate more information so that informed decisions could be made that would improve the management of the resource at all levels and this study has made an important contribution to this.

The objectives of the study focussed on three main aspects:

- To investigate the influence of fluctuating rainfall on the development of Devil's Claw populations and the impact of harvesting thereon
- To develop a simple and reliable method to establish an annual Devil's Claw harvesting quota for potential harvesting areas
- To establish a sustainable harvesting method and make recommendations for the more effective management of Devil's Claw

The approach adopted in this study is based on the incorporation of a combination of local (traditional) knowledge and scientific research. In this regard, the input of the harvesters' expert knowledge and experience was crucial.

By studying the phenology, tuber size and the distribution of Devil's Claw in different habitats as well as harvesting several plants according to existing harvesting practices, it was possible to confirm that plants can be harvested sustainably over a long period. It was also possible to show that the regeneration of plants and their secondary storage tubers is not only dependent on harvesting techniques, but also influenced considerably by the timing and amount of rainfall, disturbances such as moisture competition by dense herbs or encroaching shrubs, as well as grazing. The overall success of sustainable harvesting depends mostly on the appropriate management and protection of the resource, most importantly protecting plants from high grazing levels and preventing shrub encroachment.

7.2 Main results

The main findings of the study are summarised below

1. The phenological variables recorded during this study are in accordance with previous research findings and is summarised in Figure 29 below. Onset and duration of phenological events may vary every year with several years – this being influenced by prevailing temperature and timing of rainfall. The magnitude of phenological development depends on the plant's resource acquisition during the previous growing season, as well as the current moisture regime. Further, plant expansion and regenerative development is negatively influenced by a dense cover of annual herbs and creepers as well as a dense cover of shrubs. Harpagophytum develops the best where it has either no competition of surrounding vegetation or where it can grow between perennial grass tufts. Although the latter may have a more or less continuous canopy cover, the basal cover is usually only about 15% of the canopy cover.
2. Detailed calculation methods to determine annual harvesting quotas have been developed and are presented in this report, together with rapid techniques for assessing the resource available. Resource assessments should be carried out between mid-January and mid-February to omit late resprouters whose survival chances may be compromised by harvests during that season.
3. Harvesting should commence in April or when seasonal rains have ceased, but should be stopped as soon as plants start resprouting during the new growing season (October). Overall, it is considered detrimental to harvest the plant whilst it is actively growing - i.e. expanding its foliage or flowering, but can start when fruit has ripened.
4. While regular harvesting does reduce the growth of the primary tuber, it does not significantly increase plant mortality if the primary tuber is not disturbed during harvesting and the plant's normal growing cycle during the growth season is not disturbed (e.g. by excessive grazing or competition).
5. Average secondary tuber regeneration rates can be estimated at 350 to 400 g fresh weight, or 35 to 40 g dried tuber weight over 4 years - if the resource is properly managed.

6. Rainfall and the timing thereof impacts on the growth rate of the primary tuber. In view of this finding, a complete rest period of 3 to 4 years between harvests is recommended.

The regeneration of secondary storage tubers, and overall population growth, can be greatly increased if proper and effective land management practices are followed. This chiefly entails controlling invasive shrubs, dense weedy annual herbs and unsustainable grazing habits, and these controls should be implemented by harvesting communities or resource owners themselves.

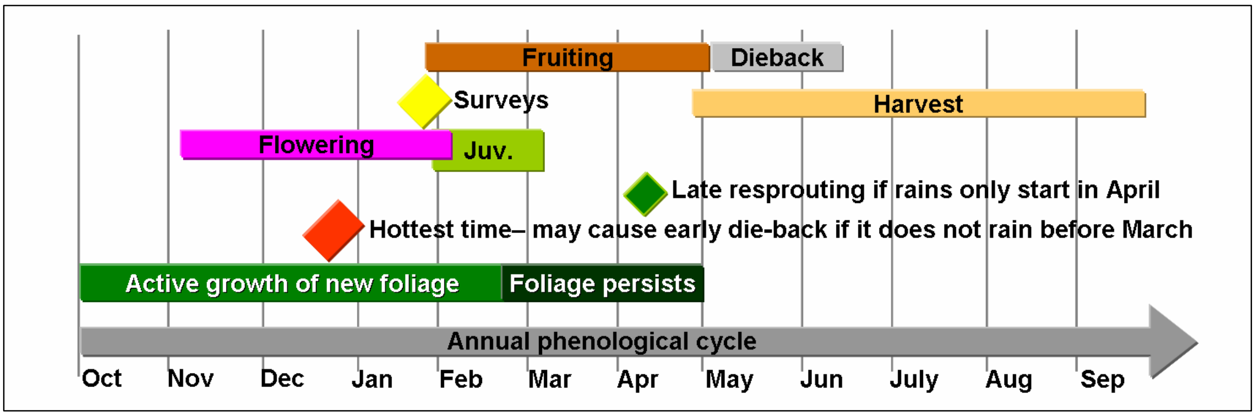


Figure 29: Summary of phenology of *Harpagophytum* as recorded in the study area, also indicating the timing of resource surveys and harvesting. 'Juv.' indicates the appearance of seedlings.

7.3 Further recommendations

Ensuring the long-term stability of Devil's Claw resource availability on Namibia will also require attention to the following:

1. Trained resource surveyors from communities should be involved in the annual establishment of harvesting quotas, which should form part of the annually issued harvesting permit. Conservationists should be able, based on calculations presented in this manuscript, to work out harvesting quotas from survey data supplied by resource surveyors
2. Conservation agencies should undertake their own occasional surveys – at least in areas where Devil's Claw is regularly harvested. A history of harvests and annual surveys for such site may yield further valuable information for long-term monitoring of the Devil's Claw resource
3. Harvesting technique must be optimised to prevent any disturbance of the primary tuber and taproot
4. Communities should be encouraged to permanently debush the areas where they harvest Devil's Claw. Grazing in these areas should be minimised during the growing period, which will give the added advantage of more standing hay available for livestock during the dry winter months
5. In areas with a suitable habitat but low Devil's Claw resource availability, cultivation should be encouraged. The same applies to areas where the number of harvesters present exceeds the economically viable amount of harvestable resource for all harvesters
6. Conservation agencies could interact much more with harvesting communities – not just issuing the harvesting permits, but also more actively look at the resource of communities and plan management and harvesting issues with harvesting groups

8. References

AEZ – AGRO-ECOLOGICAL ZONING PROGRAM (2001): Namibian Agricultural Resources Information System (NARIS), Windhoek, Namibia, Directorate of Agricultural Research and Training, Ministry of Agriculture, Water and Rural Development. GIS Digital Files.

ALLABY, M. (1998): A dictionary of Ecology. 2nd edition. – Oxford University Press, Oxford, UK.

BARBOUR, M.G., BURK, J.H., PITTS, W.D., GILLIAM, F.S. & SCHWARTZ, M.W. (1999): Terrestrial Plant Ecology. 3rd Ed. – Benjamin/Cummings, Addison Wesley Longman, Inc, Menlo Park, California, USA.

BEATLEY, J. C. (1974): Phenological events and their environmental triggers in Mojave Desert ecosystems. – Ecology 55: 856-863.

BLOOM, A. J., CHAPIN, F. S. & MOONEY, H. A. (1985): Resource limitation in plants – An economic analogy. – Annual Review of Ecology and Systematics 16: 363-392.

BURGHOUTS, T. (1985): The Grapple Plant Project. Waterbalance and productivity of the grapple plant *Harpagophytum procumbens* DC. – National Institute Development Research and Documentation, University of Botswana, Gaborone. Research Notes No 20.

CASPER, B. B. & JACKSON, R. B. (1997): Plant competition underground. – Annual Review of Ecology and Systematics 28: 545-570.

CHAPIN III, F.S., SCHULZE, E. D. & MOONEY, H. A. (1990): The ecology and economics of storage in plants. – Annual Revue of Ecology and Systematics 21: 423-447.

COLE, D. & DU PLESSIS, P. (2001): Namibian Devil's Claw (*Harpagophytum* spp.): a case study on benefit-sharing arrangements. – Unpublished report prepared for the Namibian Ministry of Environment and Tourism, Directorate of Environmental Affairs, Namibian National Biodiversity Programme.

COLE, D. & LOMBARD, C. (2000): The sustainably harvested Devil's Claw Project in Namibia. – Centre for Research information and Action in Africa, Windhoek, Namibia.

COTTAM, G. & CURTIS, J.T. (1956): The use of distance measures in phytosociological sampling. – Ecology 37: 451-460.

CUNNINGHAM, A.B. (2001): *Applied Ethnobotany*. Earthscan Publications Ltd, London, UK.

DE JONG, F. (1985): Further aspects of regeneration and productivity of the grapple plant *Harpagophytum procumbens* DC. under harvesting pressure. – National Institute for Development Research and Documentation (NIR), Research Notes 19, Gaborone, Botswana.

ENGEMAN, R.M., SUGIHARA, R.T., PANK, L.F. & DUSENBERRY, W.E. (1994): A comparison of plotless density estimators using Monte Carlo simulation. – Ecology 75: 1769-1779.

ERNST, W.H.O., TIETEMA, T., VEENENDAL, E.M. & MASENE, R. (1988): Dormancy, germination and seedling growth of two Kalaharian perennials of the genus *Harpagophytum* (Pedaliaceae). – Journal of Tropical Ecology 4: 185–198.

FLOYD, S. K. & RANKER, T. A. (1998): Analysis of a transition matrix model for *Gaura neomexicana* ssp *coloradensis* (Onagraceae) reveals spatial and temporal demographic variability. – International Journal of Plant Science 159: 853-863.

GATSUK, L. E., SMIRNOVA, O. V., VORONTZOVA, L. B., ZAUGOLNOVA, L. B. & ZHUKOVA, L. A. (1980): Age states of plants of various growth forms: A review. – Journal of Ecology 68: 675-696.

GELDENHUYS, C. J. & VAN DER MERWE, C.J. (1988): Population structure and growth of the fern *Rumohra adiantiformis* in relation to frond harvesting in the southern Cape forests. – South African Journal of Botany 54: 351-362.

GRIME, J. P. & HUNT, R. (1975): Relative growth-rate: Its range and adaptive significance in a local Flora. – Journal of Ecology 63: 393-422.

GRIME, J. P. (2002): Plant Strategies, Vegetation Processes, and Ecosystem Properties. 2nd Ed. – John Wiley & Sons, Chichester.

GRUENWALD, J. (2002): The European market for Devil's Claw. – In: Proceedings of the Namibian National Devil's Claw Workshop, 27-28 November 2002, Centre for Research information and Action in Africa, Windhoek, Namibia: 41-53.

HACHFELD, B. (2003): Ecology and utilisation of *Harpagophytum procumbens* (Devil's Claw) in Southern Africa. – Plant Species Conservation Monographs 2, German Federal Agency for Nature Conservation.

HAMILTON, A.C. (2004): Medicinal plants, conservation and livelihoods. – Biodiversity and Conservation 13: 1477-1517.

HARPER, J. L. & WHITE, J. (1974): The demography of plants. – Annual Review of Ecology and Systematics 5: 419-463.

HEGAZY, A. K. (1992): Age-specific survival, mortality and reproduction, and prospects for conservation of *Limonium delicatulum.* – Journal of Applied Ecology 29: 549-557.

HIPONDOKA, M.H.T., ARANIBAR, J.N., CHIRARA, C., LIHAVHA, M. & MACKO, S. A. (2003): Vertical distribution of grass and tree roots in arid ecosystems of Southern Africa: niche differentiation or competition? – Journal of Arid Environments 54: 319-325.

HULZEBOS, E. (1987): The Grapple Plant Project. Fruit development and tuber production of a desert perennial, *Harpagophytum procumbens*. – National Institute Development Research and Documentation, University of Botswana, Gaborone. Research Notes No 23.

IHLENFELDT, H.-D. & HARTMANN, H. (1970): Die Gattung *Harpagophytum* (Burch.) DC. ex MEISSN. (Monographie der afrikanischen Pedaliaceae II). – Mitteilungen des Staatsinstituts für Allgemeine Botanik Hamburg 13: 15-69.

JAEGER, F. & WAIBEL, L. (1920): Beiträge zur Landeskunde von Südwestafrika. – Verlagsbuchhandlung E.S. Mittler & Sohn, Berlin.

KATHE, W., BARSCH, F. & HONNEF, S. (2003): Trade in Devil's Claw (*Harpagophytum* spp) in Germany – status, trends and certification. – Prepared for the Food and Agriculture Organisation of the United Nations, Non-Wood Forest Products Programme.

KEITH, D. A. (1998): An evaluation and modification of World Conservation Union Red List criteria for classification of extinction risk in vascular plants. – Conservation Biology 12 (5): 1076-1090.

KEITH, D. A. (2000): Sampling designs, field techniques and analytical methods for systematic plant populations surveys. – Ecological Management and Restoration 1: 125-139.

KNOOP, W. T. & WALKER, B. H. (1985): Interactions of woody and herbaceous vegetation in a southern African savanna. – Journal of Ecology 73: 235-253.

LEFKOVITCH, L. P. (1965): The study of population growth in organisms grouped by stages. – Biometrics 21: 1-18.

LELOUP, S. (1984): An ecophysiological approach of the influence of harvest on the population dynamics of the grapple plant *Harpagophytum procumbens* DC. – National Institute for Development Research and Documentation (NIR), Research Notes 18, Gaborone, Botswana.

LESER, H. (1972): Geoökologische Verhältnisse der Pflanzengesellschaften in den Savannen des Sandveldes um den Schwarzen Nossob und um Epukiro. – Dinteria (6): 1-44.

LITTLE, R.J. & JONES, C.E. (1980): A dictionary of Botany. – Van Nostrand Rheinhold Company, New York.

LÓPEZ, F., FUNGAIRIÑO, S., DE LAS HERAS. P., SERRANO, J. & ACOSTA, F. (2001): Age changes in the vegetative vs. reproductive allocation by module demographic strategies in a perennial plant. – Plant Ecology 157: 13-21.

METEOROLOGICAL OFFICE, WINDHOEK. Meteorological Services, Ministry of Works, Transport and Communication, Windhoek, Namibia

MOLONEY, K. A. (1988): Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. – Ecology 69: 1588-1598.

MUELLER-DOMBOIS, D. & ELLENBERG, H. (1974): Aims and methods of Vegetation Ecology. – John Wiley & Sons, New York.

NIPPERT, J. B., KNAPP, A. K. & BRIGGS, J. M. (2006): Intra-annual rainfall variability and grassland productivity: Can the past predict the future? – Plant Ecology 184: 65-74.

NOTT, K. (1986): A survey of the harvesting and export of *Harpagophytum procumbens* and *Harpagophytum zeyheri* in SWA/Namibia. – Unpublished Report, Etosha Ecological Institute, P.O. Okaukuejo, Namibia.

NOY-MEIR, I. (1973): Desert ecosystems: environment and producers. – Annual Review of Ecology and Systematics 4: 25-51.

OESTERHELD, M., LORETI, J., SEMMARTIN, M. & SALA, O. E. (2001): Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. – Journal of Vegetation Science 12: 137-142.

PARKER, K.R. (1979): Density estimation by variable area transect. – Journal of Wildlife Management 43: 484-492.

PAVÓN, N. P. & BRIONES, O. (2001): Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. – Journal of Arid Environments 49: 265-277.

PIELOU, E.C. (1960): A single mechanism to account for regular, random and aggregated populations. – Journal of Ecology 48: 575-584.

ROBATNOV, T.A. (1985): Dynamics of plant coenotic populations. – In: White, J. (ed.): The Population Structure of Vegetation. Dr W. Junk Publishers, Dordrecht, Netherlands: 121-141.

ROWELL, M. (1998): The quality Manual of the Ministry of Agriculture, Water and Rural Development Laboratory. – Unpublished Report, Ministry of Agriculture, Water and Rural Development, Windhoek, Namibia.

SCHAEFFER, R.L., MENDENHALL III, W. & OTT, R.L. (1996): Elementary Survey Sampling. 5th Ed. – Duxbury Press, Belmont, California, USA.

SCHNEIDER, E., SANDERS, J. & VON WILLERT, D.J. (2006): Devil's Claw (*Harpagophytum procumbens*) from southern Africa. Sustainable use by cultivation combined with controlled harvesting in semi-wild populations. – In: ROGERS, R.J., CRAKER, L.E. & LANGE, D. (Eds): Medicinal and Aromatic Plants. Proceedings from the Frontis workshop on Medicinal and Aromatic Plants, Wageningen, The Netherlands, April 2005, Springer: 181-202.

SCHOLES, R. J. (1990): The influence of soil fertility on the ecology of southern African dry savannas. – Journal of Biogeography 17: 415-419.

SCHOLES, R. J. & ARCHER, S. R. (1997): Tree-grass interactions in savannas. – Annual Review of Ecology and Systematics 28: 517-544.

SHEFFERSON, R. P., SANDERCOCK, B. K., PROPER, J. & BEISSINGER, S. R. (2001): Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. – Ecology 82: 145-156.

SILVERTOWN, J. W. (1987): Introduction to Plant Population Ecology. 2nd edition. – Longman Scientific & Technical, Essex, UK.

STEWART, K.M. & COLE, D. (2005): The commercial harvest of devil's claw (*Harpagophytum* spp.) in southern Africa: The devil's in the details. Journal of Ethno-Pharmacology. 100: 225-236.

STROHBACH, B.J., STROHBACH, M., KUTUAHURIPA, J.T. & MOUTON, H. (2004): A reconnaissance survey of the landscapes, soils and vegetation of the eastern communal areas (Otjozondjupa and Omaheke Regions), Namibia. – National Botanical Research Institute, Windhoek, Namibia and Desert Research Foundation of Namibia.

STROHBACH, M. (2003): National Devil's Claw Situation Analysis, Namibia. National resource survey. – Centre for Research Information and Action in Africa, Windhoek, Namibia.

STRUCK, M. (1994): Flowering phenology in the arid winter rainfall region of southern Africa. – Bothalia 24: 77-90.

TOLSMA, D. J., ERNST, W. H., VERWEIJ, R. A. & VOOIJS, R. (1987): Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. – Journal of Ecology 75: 755-770.

URBANSKA, K.M. (1992): Populationsbiologie der Pflanzen. Uni-Taschenbücher 1631, – Gustav Fischer Verlag, Stuttgart, Germany.

VEENENDAL, E.M. (1984): The Grapple Plant Project. Regeneration and productivity of the Grapple Plant Harpagophytum procumbens DC. under harvesting pressure. – First Progress Report, NIR Research Notes No 17, Gaborone, Botswana.

VEENENDAL, E. M., ERNST, W. H. & MODISE, G. S. (1996): Effect of seasonal rainfall pattern on seedling emergence and establishment of grasses of a savanna in south-eastern Botswana. – Journal of Arid Environments 32: 305-317.

VAN WYK, B.-E.; VAN OUDTSHOORN, B. & GERICKE, N. (1997): Medicinal Plants of South Africa. – Briza Publications, Pretoria, South Africa.

VON WILLERT, D.J.; SANDERS, J. & OLIVIER, G. (2002): Cultivation without irrigation – trial and success. – In: Proceedings of the First Regional Devil's Claw Conference, 26-28 February. Centre for Research information and Action in Africa, Windhoek, Namibia: 68-72.

WATT, J.M. & BREYER-BRANDWIJK, M.G. (1962): The medicinal and poisonous plants of southern and eastern Africa. 2nd edition. – Livingstone, London.

WEGENER, T. (2000): Devil's Claw: from African traditional remedy to modern analgesic and anti-inflammatory. – HerbalGram 50: 47-54.

WERGER, M. J. & HUBER, H. (2006): Tuber size variation and organ preformation constrain growth responses of a spring geophyte. – Oecologia 147: 396-405.

WERNER, P. A. & CASWELL, H. (1977): Population growth rates and age v*ersus* stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). – Ecology 58: 1103-1111.

9. Glossary

Taken from AEZ (2001), ALLABY (1998), LITTLE & JONES (1980), JAEGER & WAIBEL (1920):

Ontogeny	Development of an individual from fertilisation to adulthood.
Phenology	The study of the periodicity of leafing, flowering, and fruiting in plants; these are generally triggered by annual climatic fluctuations.
Prostrate	Trailing to lying on the ground without rooting at the nodes.
Omuramba	Namibian term for a broad drainage line, usually with more loamy soils than the surrounding area. There is seldom a clear river channel, but during the rainy season, water may accumulate for short periods in a series of shallow pans within this drainage line. Omuramba are generally covered by a much denser grass layer than surrounding areas due to the accumulation of moisture and nutrients.

Soil types

CHh1	rock outcrops
KFv2	Omuramba and river valleys with arenic Fluvisols & ferralic Arenosols Association
KHm1	relict meanders with ferralic Arenosols
KHm2	relict meanders with arenic-leptic Regosols
KSa1	sand deposits and aligned dunes with ferralic Arenosols
KSd1	sand plains with ferralic Arenosols
arenic Fluvisols	Water deposited soils with little alteration, very deep, coarse textured, relatively well drained
arenic-leptic Regosols	Shallow soils over unconsolidated materials, the latter are coarse textured sands with poorly developed profile, moderately deep and excessively drained
ferralic Arenosols	Soils formed from sand (usually windblown), poorly developed profile, very deep, excessively drained, coarse textured