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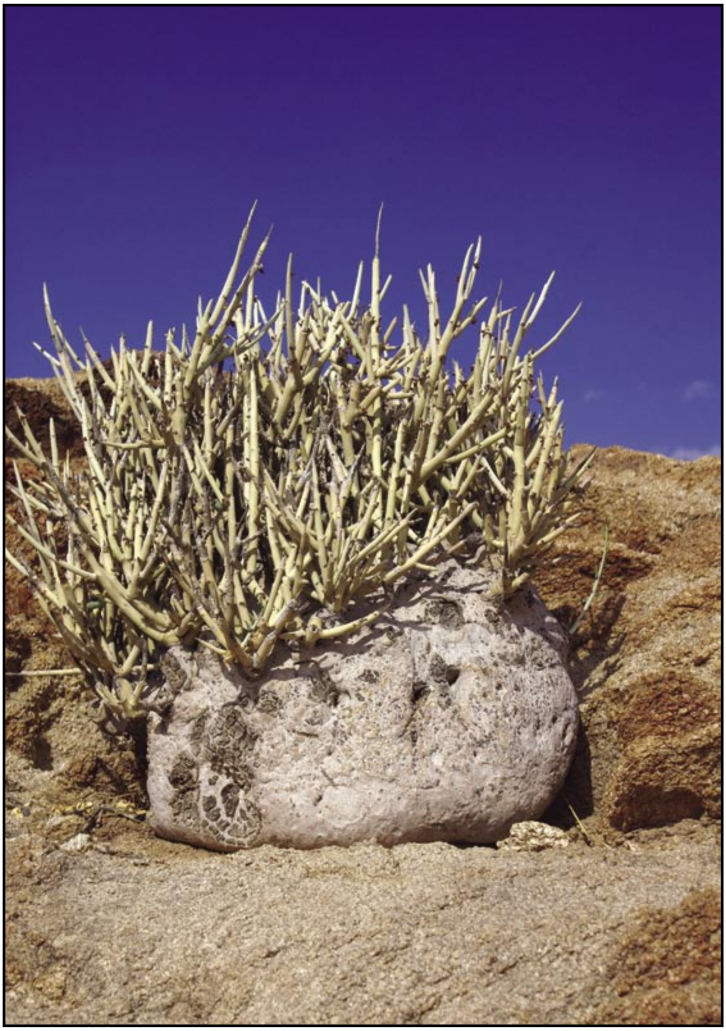

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Cover photo: Elephant's foot (*Adenia pechuelii*) in Tinkas Flats of Namib Desert
- Mirella Vaglio.

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Population changes of alien invasive plants in the Lower Kuiseb River

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Abstract

The status of six alien invasive plant species was investigated along the Lower Kuiseb River. The focus entailed a comparison of plants surveyed along transects located at five settlements of a rural community, with additional transects located between these settlements. While most living alien plants occurred in or adjacent to the main channel of the river, additional seed banks were noted in river areas further away from the channel. *Nicotiana glauca* was clearly on the increase along the length of the study area, while *Argemone ochroleuca*, *Ricinus communis, Datura stramonium* and *D. inoxia* appear to be declining, and *Prosopis* continues to be confined. While changing surface hydrology and near-surface geohydrology may underlie the increase in *N. glauca*, trampling action by increasing livestock numbers could perhaps explain the decreases by other species. More detailed studies and long-term monitoring are required to improve management of alien plants in the Kuiseb and other ephemeral rivers.

Keywords

wild tobacco, Topnaar community, ethnobotany, alien plant eradication, ephemeral rivers, livestock trampling

Introduction

The past thirty years has seen a growing awareness of and action on alien species and their impacts on ecosystems and processes. Alien invasives are non-indigenous species recently translocated into new areas by anthropogenic causes where they grow and reproduce particularly quickly and (potentially) cause changes to existing ecosystems, habitats and communities of indigenous species, and may stress economic systems (Van Wilgen *et al.* 2001; Venter 2002; Bethune *et al.* 2004). Some alien invasives have good uses, this being one of the reasons for their introduction, the other being incidental importation, e.g. with fodder (Brown & Gubb 1986; Smit 2004). Craven (1999) listed 156 alien plant species in Namibia. Of these, about 37 are invasive (Brown *et al.* 1985; Muller 1985; Barnard *et al.* 1998; Bethune *et al.* 2004).

However, alien invasive plants have seldom been demonstrated to be a serious problem in Namibia, although they may impact people and their livelihoods (Van den Eynden *et al.* 1992) as well as ecosystems or ecological processes at a local level (Bethune *et al.* 2004), and some of them are therefore justifiably flagged as members of the "nasty nine" (Steenkamp & Smit 2002) which should be the focus of management efforts (Shine *et al.* 2000; Venter 2002). Alien invasive plants often concentrate in or near riverbeds or drainage lines (Bethune *et al.* 2004). In the ephemeral rivers, seasonal floods play an important role in dispersing seeds of alien plants (Jacobson *et al.* 2000), colonising in particular areas which have been disturbed either by anthropogenic or natural causes (Boyer & Boyer 1989).

The Namib Desert is crossed by twelve westward flowing ephemeral rivers that originate in the highlands to the interior (Jacobson *et al.*, 1995). The Kuiseb River in the Central Namib separates the Namib Great Sand Sea from the gravel plains. The river extends from the Great Escarpment with a length of 440 km to the Atlantic Ocean (Stengel 1964). This river with its comparatively abundant water and vegetation resources has for centuries been the focus of activities of wildlife and people (Shackley 1985). Currently, livelihoods of the rural people continue to be founded on seedpod production of the indigenous Anatrees (*Faidherbia albida*) and Camelthorns (*Acacia erioloba*). The apparent increase in the occurrence of alien invasive plants and their effects on indigenous fauna and flora (Macdonald & Nott 1987; Boyer & Boyer 1989; Jabs 1991; Jacobson *et al.* 1995) are a matter of concern for management of the Kuiseb Basin, to the Namib-Naukluft Park, and to communal farmers of the Lower Kuiseb River.

According to Boyer (1989), alien invasive plants in the Namib-Naukluft Park get established in two kinds of locations. One kind is located in ephemeral rivers that originate in the Khomashochland and flow westwards across the Great Western Escarpment into the Namib Desert. The second kind of location comprises places that have been disturbed by people, livestock and game on farms and parks. This concurs with the study by Wells *et al.* (1986) that the areas in southern Africa most susceptible to the proliferation of alien invasive plants are riverine ecosystems and anthropogenically disturbed areas.

The current study investigates the spatial distribution of alien plants along the Lower Kuiseb River. We compare their abundance at settlements with that away from settlements as a test of Boyer's (1989) hypothesis that some alien invasive plants grow preferentially at or near anthropogenically disturbed places, while other alien invasive plants suffer under anthropogenic impacts such as livestock trampling (Vinjevold *et al.* 1985). Through interviews we attempted to establish the effects rural people may have on alien plants by using or eradicating them. The primary objective of this study was to establish a framework for future monitoring and management of alien species and factors that affect their abundance and distribution along the Kuiseb River.

Materials & Methods

Study Area

Fieldwork was conducted for 10 days during June 2004 in the Lower Kuiseb River, with study sites located along a 60 km stretch between Homeb and Armstraat (close to Rooibank). Climate data were collected at Gobabeb (23^{o}33'S; 15^{o}02'E), located 56 km inland. The mean annual temperature is 21.1°C (range 1.0-44.9°C) (Lancaster *et al.* 1984). Median annual rainfall is 11 mm (range 2-115.1 mm) and mean fog deposition is 33.5 litres.m^{-2} (range 7-77 litres.m^{-2}). The riverbed varies in width and a central channel is fringed by higher flood banks. From Homeb (23^{o}38'S, 15^{o}10'E) to Narob (23^{o}30'S, 14^{o}58'E) the riverbed is relatively narrow, from Narob to Swartbank (23^{o}20'S, 14^{o}51'E) the riverbed widens and from Swartbank to Rooibank (23^{o}10'S, 14^{o}38'E) it is at its widest and shallowest and many mid-river sandbanks occur.

Socio-economic survey

The study area contains 16 settlements or groups of households where Nama-speaking Topnaar community members live (Henschel *et al.* 2004) and keep cattle, goats, sheep, donkeys and horses (Table 1). Since some settlements are no more than 1-2 households, for the sake of the current study we grouped places together as follows: Homeb is grouped with Tatamutsi and Oswater; Natab-1 with Natab-2; Soutrivier with Gobabeb; Klipneus

Table 1: *Numbers of livestock owned by residents at the study settlements and by Topnaars at all settlements along the Lower Kuiseb River (survey of 2002, Directory of Engineering and Extension Services, Ministry of Agriculture, Water and Forestry)*

Name	Cattle	Goats	Sheep	Donkeys	Horses	Total
Armstraat	0	50	0	19	0	69
Goadanab	0	132	0	4	0	136
Ururas	11	467	0	20	0	498
Utuseb	83	256	0	35	0	374
Swartbank	33	353	0	92	0	478
Klipneus	10	156	0	28	0	194
Soutrivier	0	258	8	25	0	291
Natab	2	525	0	21	0	548
Homeb	17	826	102	29	12	983
Total	156	3023	110	273	12	3571

alone; Swartbank alone; Utuseb with Tsaraxa-aibes; Ururas with Steekgras; Goadanab with Dawedraais; Armstraat alone.

We interviewed 13 people at 5 settlements, namely Homeb, Natab, Swartbank, Utuseb and Armstraat, concerning their usage of alien invasive plants and perceptions of changes in the occurrence of these plants. An interview was also conducted at the Namwater office at Rooibank, adjacent to Armstraat.

Plant surveys

Alien plants were recorded along 20 m wide transects oriented perpendicular to the river course. Five transects were positioned 200 m apart at each settlement, with one being across the middle of the settlement and two to the east and two to the west of the settlement. Similar sets of five transects were laid between the settlements well away from any human habitation and outside the daily foraging range of livestock. Lengths of transects were variable, depending on the width of the band of riparian vegetation. There were usually nine microhabitats along each transect:

(1) gravel plains adjacent to the river;
(2) gravel plain – river transition (sparse vegetation and a mixture of gravel and fine sand);
(3) northern riparian forest (mainly comprising *Faidherbia albida*, A*cacia erioloba*, *Tamarix usneoides*, *Salvadora persica,* and *Euclea pseudebenus*);
(4) northern bank of channel (sparse vegetation mostly tree seedlings);
(5) main river channel (path of most recent river flood with sparse vegetation and topped with a cracked silt crust);
(6) southern bank of channel;
(7) southern riparian forest;
(8) dune – river transition (large sandy hummocks around scattered vegetation);
(9) dune field adjacent to the river.

Plant assessments

Our study focused on the six most common alien invasive plants that occur near Gobabeb (Henschel *et al*. 2006), namely, *Argemone ochroleuca* (Mexican poppy), *Datura inoxia* (downy thorn apple), *D. stramonium* (common thorn apple), *Nicotiana glauca* (wild tobacco)*, Ricinus communis* (castor-oil bush)*,* and *Prosopis* sp (mesquite). The species of *Prosopis* were not positively identified in this study, but *Prosopis glandulosa* var *torreyana* (honey mesquite) has previously been identified in our study area (Seely *et al*. 1980; Van den Eynden *et al*. 1992). Six *Prosopis* species have been introduced into Namibia, and they often hybridise (Smit 2004). In this study we refer to it as *Prosopis*. It was noted whether the plant had been damaged due to herbivory or trampling. Seeds were counted from 10-66 seedpods per species that were collected at random. No seeds were counted for *Argemone ochroleuca* as it did not bear seeds during our study.

Results

Socio economic surveys

Interview respondents indicated that the population of each settlement varied depending on the time of year and formal census information confirmed this. The total numbers of stock also proved to be difficult to determine as most respondents claimed to be unaware of their herd sizes.

Stock figures for 2002 were obtained from Directorate of Engineering and Extension Services of the Ministry of Agriculture, Water and Forestry (Table 1). These showed that there were about 3 600 livestock, 85% of them goats, along this 60 km stretch of river. Given that there is still game present in this area of the Namib-Naukluft Park, particularly springbok (no recent census figures are available), plants are exposed to high levels of potential herbivory.

Interviews at five settlements revealed a variety of uses for and problems with the alien plants under question (Table 2). The people reported that they do not apply any control measures to these plants, as they believe that destroying them locally will have no effect and is a waste of time, due to the strong seed bank promoting persistence. When asked what changes they perceived in the numbers of plants and their distribution over time, the respondents indicated that there was no change, the plants had been there as long as they could remember and only increased in number with floods. The Namwater staff at Rooibank did not perceive the alien plants in the Kuiseb as a problem as they were not a threat to their infrastructure. Namwater also did not have a control program to prevent alien plants from being transferred from one basin to the next via transferred equipment.

Table 2: *Uses or problems of alien plant species by people and their livestock as reported in the current interviews*

Species	by people	by livestock
N. glauca	wood for building, firewood	browse but not favoured
Prosopis	shade	shade, browse, pods as fodder
R. communis	medicinal seeds & leaves	browse, toxic seeds
Datura spp.	avoided, toxic	browse seedlings, mature plants toxic
A. ochroleuca	none	rash in mouth, bloating, blue meat

Plant Surveys

The highest number of individuals of all alien plant species was found between Natab and Swartbank (31% of the total count) while the least was at Swartbank with 3%. Of the six plant species surveyed, only *Nicotiana glauca* was present at all locations (Table 3). It constituted 69% of the total alien plants at all sites. *Prosopis* constituted only 0.2% of the total count, and we only recorded it at the western extreme of our study area. *Argemone ochroleuca* was only found at Natab and only one individual plant was present at the site.

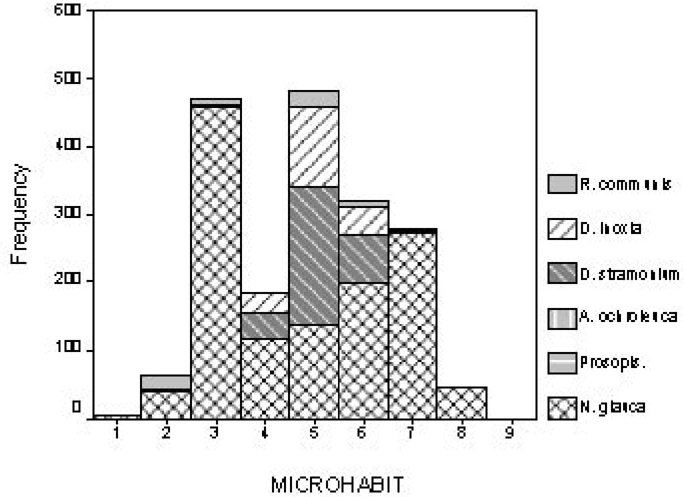

Figure 1: *Occurrence of alien plant species in different microhabitats, which are numbered as follows: 1=gravel plains; 2=gravel-river transition; 3=northern riparian forest; 4=northern floodbank; 5=main channel; 6=southern floodbank; 7=southern riparian forest; 8=dune-river transition; 9=dunes.*

Ricinus communis,
Datura stramonium and *D. inoxia* were widely distributed and constituted 3.7%, 17% and 10% respectively. *Nicotiana glauca* had about 986±327 seeds per pod (n=66). *Datura inoxia* (x=272±151, n=10), *D. stramonium* (x=237±123, n=10), and *Prosopis* (x=19±8, n=15) are next in terms of numbers of seeds per pod. *Ricinus communis* always produces only 3 large beans per pod. Most alien plants grew in the main channel (Fig. 1). *Datura* spp. were confined to this area and the adjacent banks. *Nicotiana glauca* grew in all the habitats, with the highest number found in the northern riparian forest. *Ricinus communis* also grew in all habitats, but in small numbers. *Prosopis* grew on the banks of the channel.

All six plant species were present at Topnaar settlements (Table 3). *Nicotiana glauca* were common at all sites, and there were no significant differences between sites at settlements

Table 3: *Alien plants recorded on sets of five transects at each location*

Plant species	Homeb	H-N*	Natab	N-S	Swartbank	S-U	Utuseb	U-A	Armstraat	**Total**
N. glauca	149	112	202	74	55	252	233	80	115	**1272**
Prosopis								2	1	**3**
R. communis		4		8				9	47	**68**
D. stramonium				314		1			1	**316**
D. inoxia				187		2	1	1	1	**192**
A. ochroleuca			1							**1**
Total	**149**	**116**	**203**	**583**	**55**	**255**	**234**	**92**	**165**	**1852**

* letters separated by hyphen designate sets of transects between settlements, e.g. H-N is between Homeb and Natab

and sites away from settlements (sign test, $P>0.05$). Though less abundant, there also did not appear to be a clear association or disassociation of *R. communis* with settlements, although none were observed as settlements with high stock numbers. *Datura* spp. were patchily abundant away from settlements and were almost absent from settlements, indicative of disturbance. There was therefore no evident relationship between numbers of livestock and numbers of alien plants, except for the possible negative relationship with *Datura* spp. and *R. communis*.

At settlements, livestock evidently caused damage to 31.2% of *N. glauca* that were trampled, 71% of *R. communis* that were browsed, and *Prosopis* that were apparently all browsed (casual observations of trees off transects confirmed this). Three solitary individuals of *D. inoxia, D. stramonium*, and *A. ochroleuca* found at settlements were undamaged, but the paucity of these species is indicative of heavy impact.

Discussion

All six of the previously documented dominant alien plants (Seely *et al.* 1980; Macdonald & Nott 1987; Boyer & Boyer 1989; Jabs 1991) were encountered in this survey. The plants were encountered in the highest frequency along the edges of the most recent flooding and in the main river course. This can probably be attributed to increased water and nutrient availability in these areas after flooding. However, the occurrence of dormant stands (dead plants bearing seedpods) up to the fringes of the river may have implications for periodic irruptions after floods. Short-term surveys therefore have limitations in determining the general status of aliens.

Nicotiana glauca was the most dominant species at all nine study sites. Although this plant has a strong smell and toxin as defence mechanism, it is occasionally browsed. A higher degree of damage is caused by trampling, and the persistence of *N. glauca* at settlements is indicative of its resilience despite damage. We counted up to 2,400 pods on older plants, amounting to a production of up to some 2 million seeds per plant. One-quarter of the plant individuals were still small (<1 m), and had probably germinated during the previous flood a few months prior to our study; 25% recruitment reflects a high rate of reproduction. Our study indicates an increase of *N. glauca* compared to previous studies (Boyer & Boyer 1989; Jabs 1991). We suggest that these fast-growing large-leaved plants, so unlike the slow-growing small-leaved indigenous Kuiseb plants, may impact the near-surface soil moisture.

We casually observed that there were large stands of dead *N. glauca*, bearing many seedpods, in the marginal habitats at the river boundary with the gravel plains and the dunes. Although seed viability was not tested, they probably bear a good seed reserve. These large peripheral stands indicate that *N. glauca* grows most vigorously and extensively in very high-flood years when it is widely distributed across the whole riverbed of the Kuiseb. It is during these high flood years that it acts as a possible competitor to indigenous plants.

Interviews showed that Topnaar people use wild tobacco but are not dependent on it. Although the use of its wood for construction and firewood is not confined to *N. glauca*, the ready availability of this wood may help reduce the pressure on indigenous trees. In a previous survey, the revitalising effect to people of leaf bandages was reported (Van den Eynden *et al.* 1992). We have frequently observed that dusky sunbirds favour the nectar of wild tobacco, and the abundance of this plant may therefore maintain high sunbird populations in the Kuiseb during times when other nectar sources are scarce.

Ricinus communis was found at four of the nine study sites, three away from settlements and one at the settlement with the lowest number of livestock (Table 1 & 3). We observed that livestock and other herbivores browsed this plant irrespective of location indicating that other herbivores also utilise the plant. Browsing did not appear to impact plant condition, and some *R. communis* grew isolated, others in stands. Most plants occurred close to the main river channel. Outlying plants most likely established themselves during high flood years. Seed production is far lower than for *N. glauca*, with an average of 9 seeds (maximum 219) per *R. communis* plant. Recovery from eradication may be slow, as few *R. communis* re-established themselves at Gobabeb in the 20 years since eradication (Boyer & Boyer 1989; pers.obs.). In a survey conducted at Gobabeb in 2007, only 0.3% of the over 600 alien plants in sample plots were *R. communis* (Isak Kaholongo pers.comm.). The Topnaar people use the seeds and leaves for a range of medicinal purposes, and this invasive alien is therefore regarded as beneficial. During the time of our survey (mid-2004), we noted that in its native South America, castor-oil beans sold for US$315 per kg. Perhaps there is potential to harvest and sell castor-oil products from the Kuiseb, but the likely effect may be an increase due to gardening and not a decrease of this invasive alien species.

We found *Datura inoxia* and *D. stramonium* only on transects downstream of Natab. We estimated the seed production of *Datura* spp. to range from 1,000 to 50,000 per plant; an average of 5 pods per plants with about 271 seeds each. *Datura* spp. have decreased compared to the situation in 1987 and 1991 (Boyer & Boyer 1989; Jabs 1991). During our study period we made casual observations in the Kuiseb canyon 40 km upriver of Gobabeb, and found a high abundance of *Datura* spp at Sarib. The current localised distribution may indicate that seeds do not disperse easily (as noted by Jabs 1991), while seedlings do not establish readily at existing plant stands and need to disperse. Livestock owners reported their dislike of this plant as they believe that its toxicity leads to livestock deaths. Even though they reported that they did not undertake eradication efforts against any alien plants, heavy trampling impacts at settlements may explain the lack of *Datura* there in agreement with Vinjevold *et al.* (1985) concerning the impact of goats. Personal observations during the course of this study indicate very heavy browsing of young *Datura* plants, but that only flowering and seed-producing plants were avoided by goats. By contrast, *Nicotiana* plants of all ages and sizes were avoided by browsing goats, even within heavily browsed *Datura* stands. It is possible that *Datura* experience difficulties in re-establishing after eradication, e.g. at Gobabeb two decades ago (Boyer & Boyer 1989). This interpretation may contradict that of Bethune *et al.* (2004) concerning the inevitability of re-invasion after eradication of *Datura*; the question of population recovery of this species warrants further investigation.

Argemone ochroleuca have a scattered distribution across the lower Kuiseb and occurs at Gobabeb, but only one individual was recorded on our transects. It no longer appears to be as important in the Kuiseb as it was in the past, when Boyer & Boyer (1989) expressed concern about dense infestations that would be difficult to eradicate. For instance, only small patches of these plants are currently seen at Gobabeb (pers.obs.). Interviewed Topnaars reported that these plants are toxic to goats and also render their meat useless. The status of *A. ochroleuca* should be monitored in the Kuiseb and compared with other rivers. By ascertaining reasons for its changing abundance, insights valuable to management may be gained for this special effects weed which has the potential to choke surfaces (Henderson 2001).

Extensive research has been conducted on *Prosopis* spp. as they are thought to be the alien plants that pose the greatest threat to biodiversity in southern Africa, as well as a range of benefits to livelihoods (Smit 2004). The concern is that it could transform the Kuiseb River ecosystem as has occurred in, for instance, the Swakop River (Douglas 2008). We encountered only 3 specimens on our transects. In addition, we estimated that there are about 30 *Prosopis* trees in the immediate vicinity of Armstraat where they were previously recorded by Van den Eynden *et al.* (1992). Other observations (Seely *et al.* 1980; pers.obs.) indicate that there are a few scattered *Prosopis* trees elsewhere along the lower Kuiseb. We have also observed stands of *Prosopis* trees in tributaries of the upper Kuiseb (e.g. Djab), which pose a potential threat of spreading downstream. The local sources of seeds in the headstreams and near the lower end of the Kuiseb indicate that there is potential for *Prosopis* to invade the Kuiseb. This plant should therefore be monitored closely. Plans should be made with the residents of Armstraat to control seed dispersal from there into the adjacent Kuiseb Delta where it may compete with !nara (*Acanthosicyos horridus*) for groundwater. The Topnaar people value *Prosopis* for its shade and food for livestock; they reported to Van den Eynden *et al.* (1992) that people, too, eat the pods. Collecting of all pods and crushing before consumption would be an effective means to decimate the seed bank while benefiting livelihoods as long as this is not copied for the use of *Acacia erioloba* and *Faidherbia albida* pods, where seed dispersal via livestock defecation should not be prevented.

Topnaar interviewees are of the opinion that alien invasive plants have not changed over time and have been there for as long as anybody can remember, implying that the first arrival of all of these species was many decades ago. Our observations indicate that the general status of alien plants in the lower Kuiseb seems to have changed during the past two decades, with an increase by *N. glauca*, and declines by *Datura* spp., *R. communis*, and *A. ochroleuca*. Our study obtained too little detailed information on *Prosopis* to tell, but we caution that the potential for invasiveness may be increasing. Whether and how several exceptionally high flood events in the past decade could have affected the status could not be established (positive: availability of water and seed dispersal, negative: plant destruction and flushing out of seed banks), and the increase of *N. glauca* appears to suggest a positive connection with surface hydrology following a decade with several good floods. It is possible that the increase of *N. glauca* promoted the decrease of the other species, as is so often the case with particularly fast-growing aliens (Versfeld *et al.* 1998).

We put forward that the general decline observed by us for several alien plant species can be attributed to the action of increasing densities of livestock. Livestock browsing has pronounced effects on many Kuiseb plants (Gabriel 1993). This browsing may sometimes include seedlings of otherwise unpalatable plants, such as *Datura* spp. and *R. communis*. Trampling potentially affects all small plants of any species, and this can be a formidable factor along the Lower Kuiseb (Moser 2006). A conservative estimate of 10,000 changes in hoof position per day per domestic animal outside its kraal and water point (walking only 1.2-2.5 km per day, most probably walk much further) would give 36-million trampling actions per day by the entire livestock population (some 10-20 ha of area daily under hooves), and this is highly concentrated around settlements. Topnaar livestock have about doubled in number since permanent boreholes were installed at settlements in 1979 (cattle: from 62 to 156, goats: from 1577 to 3023, donkeys: from 94 to 273; no sheep nor horses in 1979; Department of Veterinary Services), and the effects of insidious trampling by so many stock may now be telling by reducing survival and recruitment of small plants (Moser 2006), including alien invasives. *Nicotiana glauca* appear to have the highest tolerance.

Why are alien plants less dominant in the Kuiseb than in some other western ephemeral rivers of Namibia, such as the Swakop (Douglas 2008) or Omaruru (Moser 2006)? The

Kuiseb ecosystem could be in an ecological state that continues to favour indigenous vegetation over aliens, at least at certain canopy levels, giving it a degree of robustness (Moser 2006). Reasons may be physical characteristics of the Kuiseb riverbed, such as flood regime, geohydrology, nutrient availability and soil characteristics. Biological factors may include plant community conditions and inter-specific interactions, or could be affected by leaf- or seed-eating insects, birds or mammals. The type and level of uses and abuses by people and their livestock may play important roles, as could park management (e.g. eradication efforts). By examining reasons that underlie differences between the Kuiseb and other Namibian ephemeral rivers that are more affected by alien plants, important insights may be gained concerning the susceptibility of different habitats to invasion by aliens and the effectiveness of control measures.

A repetition of a complete survey of the Kuiseb river channel, such as undertaken in 1987, will enable direct comparison with previous surveys (Boyer & Boyer 1989). At shorter time intervals, e.g. every year, monitoring should be conducted at sample sites using the current transect approach and compare aliens in the riverbed at settlements with the riverbed well away from settlements. Species-specific studies should investigate plant responses to flooding, trampling, browsing and local eradication at different plant development stages as well as seed storage and dispersal. Causes for the declines of *A. ochroleuca*, *D. inoxia* and *D. stramonium* and the increase of *N. glauca* warrant investigation, as these may bear valuable lessons for management.

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Hundert Jahre unerschrockener Zwergriese Die Auferstehungspflanze *Chamaegigas intrepidus* Dinter und ihre Anpassung an ihren extremen Standort in Zentralnamibia

Hermann Heilmeier & Wolfram Hartung

ZUSAMMENFASSUNG

Chamaegigas intrepidus (Scrophulariaceae) ist eine winzige, vor 100 Jahren von Dinter entdeckte, Auferstehungspflanze, welche in kurzfristig gefüllten flachen Wannen auf Granitkuppen in Namibia wächst. Sie ist komplexen Stressbedingungen ausgesetzt: (1) sich wiederholt abwechselnde völlige Eintrocknung und Wiederbefeuchtung sowie totale Austrocknung während der Trockenperiode im Winter (bis zu 11 Monate), (2) intensive Sonneneinstrahlung zusammen mit hohen Temperaturen, (3) drastische pH-Schwankungen im Verlauf eines Tages (bis zu 6 pH-Einheiten), (4) extremer Nährstoffmangel. In diesem Übersichtsartikel werden anatomische, biochemische und physiologische Anpassungen an diese extremen und komplexen Umweltbedingungen beschrieben, wie kontraktive Tracheiden, die Akkumulation von Abscisinsäure, Dehydrinen und Zuckern sowie die Rolle von Ammonium, Aminosäuren, Harnstoff und Urease für die Stickstoffernährung. Ein weiterer interessanter Aspekt ist die Populationsbiologie der für Zentralnamibia endemischen Art. Die einzelnen Populationen von *Ch. intrepidus* auf ihren jeweiligen Inselbergen sind genetisch stark voneinander isoliert. Andererseits ist der Genfluss zwischen den Teilpopulationen in verschiedenen Becken einer Granitkuppe überraschend hoch, und die höchste genetische Diversität findet sich innerhalb der Teilpopulation eines Beckens. Dies ist wahrscheinlich auf die Bestäubung durch mehrere Insektenarten (Hymenopteren und Coleopteren) zurückzuführen. Die dargestellten anatomischen, biochemisch-physiologischen und populationsbiologischen Anpassungen zeichnen die aquatische Auferstehungspflanze *Chamaegigas* als einzigartigen Vertreter der poikilohydren Angiospermen aus.

ABSTRACT

Chamaegigas intrepidus (Scrophulariaceae) is a tiny, most remarkable resurrection plant growing endemically in ephemeral rock pools on granite outcrops in Central Namibia. Habitat conditions are characterised by (1) frequent and fast desiccation and rehydration during the rainy summer season and complete dehydration during the dry winter season lasting up to 11 months, (2) intensive solar irradiation and high temperatures during the dry season, (3) diurnal oscillations of pH in the pool water up to 6 units, (4) extreme nutrient deficiencies, especially nitrogen. Anatomical, biochemical and physiological adaptations to this complex of extreme environmental conditions are discussed such as contractive xylem, accumulation of abscisic acid, dehydrins and carbohydrates during desiccation, and the role of ammonium, amino acids, urea and urease for nitrogen nutrition. Studies on the population biology of this species endemic to Central Namibia revealed a very high degree of genetic isolation between populations on different outcrops. On the other hand, gene flow between sub-populations from different pools on one inselberg is rather high, with maximum genetic diversity occurring within one pool. This is probably caused by outcrossing due to insect pollination (2 species of hymenoptera and coleopteran each). The adaptations on the anatomical, biochemical-physiological, life-history and population biology level of the aquatic resurrection plant *Chamaegigas* are unique within all poikilohydric spermatophytes.

Stichworte: Austrocknungsresistenz, Poikilohydrie, Abscisinsäure, Dehydrine, Stickstoff, Anatomie, Populationsbiologie, Genfluss

Einleitung

Am 11. April des Jahres 1909 entdeckte Kurt Dinter, der damalige Regierungsbotaniker Südwest-Afrikas, 12 km östlich von Okahandja eine der bemerkenswertesten Pflanzen des südlichen Afrikas (Giess, 1969), von der er im Jahr 1918 ohne Nennung eines wissenschaftlichen Namens im Zusammenhang mit Wasserpflanzen berichtet.

„Außerdem haben noch die Scrophulariaceen, unter denen es eine ganze Menge an Sumpf- und Wasserpflanzen gibt, eine reizende kleine Pflanze, deren Gattung leider noch nicht feststeht, aber höchstwahrscheinlich ein ganz neues Genus darstellt, in kleinen flachen Wasserbecken, die auf heißen, fast kahlen Gneishügeln in der Nähe Okahandjas liegen, zur Wassersukkulente ausgebildet“ (Dinter 1918)[1].

Am Ende dieser Arbeit beschreibt er die Pflanze und ihre Wachstumsbedingungen detailliert:

“ Ein nicht minder wichtiges Beispiel einer Wassersukkulente bietet eine winzige, überaus zarte Scrophulariacee, Dtr. 952, die ich wie schon oben erwähnt, in kleinen natürlichen Felsbecken auf den Gipfeln einer Gneisbergkuppe 12 km östlich Okahandja entdeckte. Schon die Natur ihres Fundortes auf den heißen, fast kahlen Hügeln in Becken, deren größtes nur etwa 1 cbm Regenwasser fasst, ist über alle Maßen merkwürdig. Der stets ganz horizontale Boden dieser Becken ist von Ende Mai ab stets durchaus trocken und mit einer 1-2 cm dicken Schicht Quarzsandkörner, gemischt mit Algenwatten, Flohkrebsleichen, Pavianmist und dem bisschen aus dem alten zentimetergroßen Schwimmblättchen der Scrophulariacee bestehenden Humus bedeckt, der die winzigen, Stecknadelkopfgröße kaum überschreitenden Knöllchen des Pflänzchens dicht eins neben dem andern enthält. Man sollte meinen, drei Tage Sonnenglut im Oktober müssten schon genügen, um die Becken mit ihrem dünnschichtigen Inhalte zu durchglühen und geradezu keimfrei zu machen. Dem ist aber nicht so. Obwohl die fast völlig wasserdampffreie Luft von spätestens Ende Mai bis in den Dezember, manchmal auch bis in den Februar hinein, über die kahlen Höhen hinwegfegte und das letzte Atom [sic]

Wasser den leblosen Stoffen entzog und die Sonne von Oktober ab täglich die Felsen bis auf 50° erhitzte, gelang es diesen mächtigen Faktoren nicht, das latente Leben der winzigen Scrophulariaceenknöllchen zu ertöten, denn wenige Minuten nach dem ersten Sommerregen, der die kleinen Becken füllte, ist deren Boden dicht gespickt mit einer lückenlosen Decke pfriemenförmiger, saftgrüner Blättchen von etwa Zentimeterlänge und schon am zweiten Tage darauf flottieren an den langen, fadendünnen Stielen zierliche etwa 8 mm große rosaviolette Blüten in der Mitte der aus vier einen Zentimeter großen, glänzenden, ovalen Schwimmblättern gebildeten Rosetten umher.“

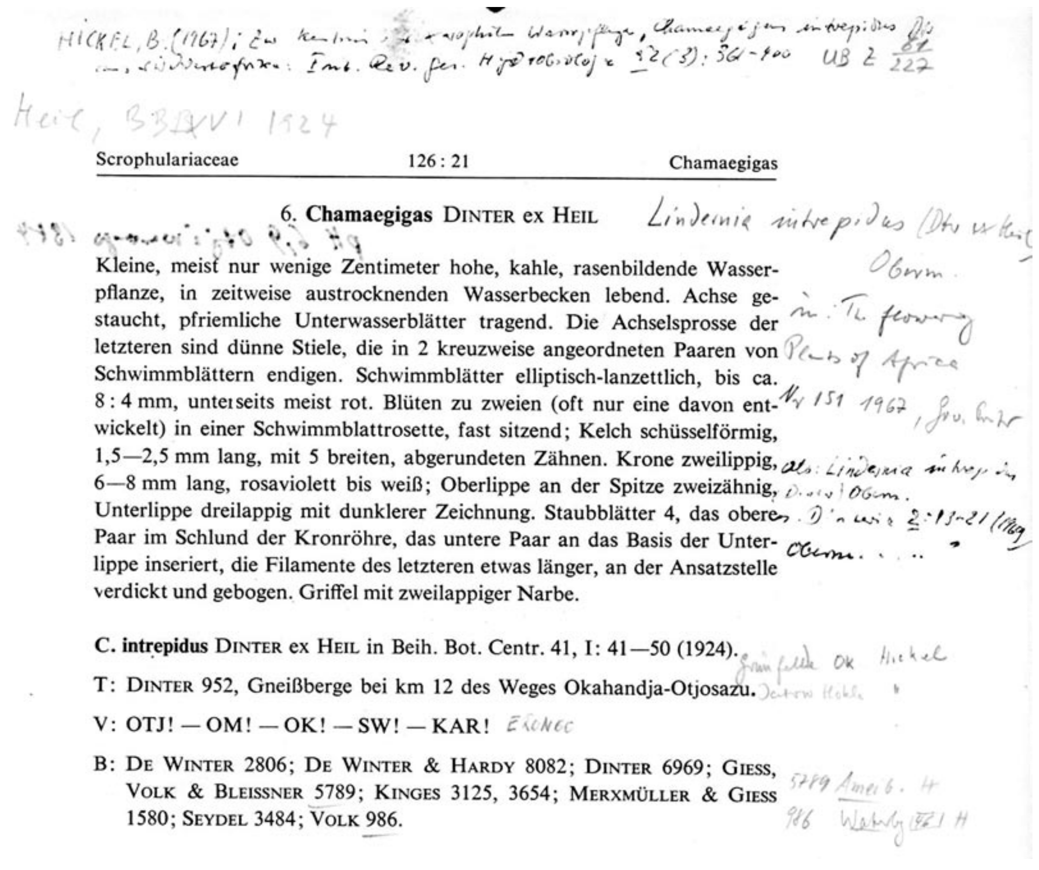
Von demselben Standort schickt Dinter im Jahr 1922 desikkiertes Material nach Hamburg, Berlin, Bautzen und Zürich, wo die Rosetten erfolgreich bis zur Blüte kultiviert werden können (Dinter 1923). Volk (pers. Mitteilung) gelang es, vier Jahre alte, staubtrockene Rosetten bis zur Blütenbildung zu kultivieren. Bei sechs Jahre altem Material bildeten sich nach Wasserzugabe zwar vital aussehende Rosetten, eine Blütenbildung erfolgte jedoch nicht mehr (eigene Versuche).

Dinter gibt der Pflanze voller Bewunderung den Namen *Chamaegigas intrepidus*, Unerschrockener Zwergriese. Fischer (1992) zufolge ist dieser Name aufgrund anatomischer Kriterien gültig, das frühere Synonym *Lindernia intrepidus* Obermeyer (Obermeyer 1967)) ist seitdem nicht mehr in Gebrauch. Walther (1967) geht ausführlich auf die Typisierung von *Chamaegigas intrepidus* und die erste Veröffentlichung von Dinter über diese Art vor genau 100 Jahren (Dinter 1909) sowie nachfolgende Publikationen, unter anderem die Namensgebung (Dinter 1923), ein.

Nach ihrer Entdeckung beschäftigten sich nur zwei Autoren intensiv mit anatomischen Anpassungen von *Chamaegigas intrepidus* an ihren extremen Standort, Heil (1924, 1927) und Hickel (1967). Smook (1969) veröffentliche eine detaillierte Studie über die Entwicklung von *Chamaegigas* von der Keimung bis zur adulten Pflanze. Gaff (1977) stellt den überaus kurzen Verlauf der Austrocknung und Wiederbefeuchtung von *Ch. intrepidus* im Vergleich zu 35 anderen von ihm untersuchten Wiederauferstehungspflanzen des südlichen Afrikas heraus. Ein Beitrag zur Ökophysiologie (exakter Zeitverlauf der Austrocknung und Wiederbefeuchtung) sowie zu den Standortsverhältnissen (Zeitspanne der Wasserführung der temporären Becken, Nährstoff- und Temperaturverhältnisse) mit detaillierten Originaldaten zu *Ch. intrepidus* im Vergleich zu anderen austrocknungsfähigen, aquatischen Gefäßpflanzen erschien 1986 in der Zeitschrift *Dinteria* (Gaff und Giess, 1986). Im Jahr 1995 begannen neue intensive Untersuchungen vor allem zur Stressphysiologie, Anatomie und Populationsbiologie seitens der Autoren, welche sich über 10 Jahre hinzogen. Sie wurden von einem Pionier der namibianischen Botanik, Herrn Prof. Dr. O. H. Volk (1903-2000), angeregt[2]. Die wissenschaftliche Beschäftigung mit dieser einmaligen Pflanze lehrt uns, über welche Strategien Pflanzen verfügen müssen, die in einem extremen, sich verändernden Klima unter komplexen Umweltbedingungen bestehen müssen. Sie sind gerade in einem Land wie Namibia, dessen Landwirtschaft von stressresistenten und –toleranten Pflanzen abhängt, von Interesse und großer praktischer Bedeutung,

Die geographische Verbreitung von *Chamaegigas intrepidus*

Chamaegigas intrepidus wächst endemisch in Zentral-Namibia. Sie gehört zu den Lindernieae (Scrophulariaceae), mit etwa 170 Arten in Afrika (Fischer 1992). Abb.1 zeigt die *Chamaegigas* betreffende Seite aus dem Prodromus einer Flora von Südwestafrika von Merxmüller (1967) aus dem Besitz von Prof. Volk mit ergänzenden Angaben zu weiteren Fundstellen. *Chamaegigas* findet sich an der Südwest-Ecke des afrikanischen Verbreitungsgebietes der Lindernieae. Verbreitungskarten wurden von Giess (1969) und Fischer (1992) publiziert. Heilmeier et al. (2005) veröffentlichten eine bis heute aktuelle Verbreitungskarte mit den bis dahin publizierten Standorten sowie denen eigener Sammlungsexkursionen. Als östlichste Fundstelle wird, auch von Volk (siehe oben), der Waterberg angegeben; die Autoren dieser Arbeit wurden dort jedoch nicht fündig. Die meisten Fundstellen befinden sich in den Erongobergen und dem Omaruru-District.



HICKEL, B. (1967): Zur Kenntnis einer xerophilen Wasserpflanze, Chamaegigas intrepidus Dtr. aus Südwestafrika. Int. Rev. ges. Hydrobiologie 52(3): 361-400 UB Z 81/227

Heil, BBXVI 1924

Scrophulariaceae 126 : 21 Chamaegigas

6. **Chamaegigas** DINTER ex HEIL Lindernia intrepidus (Dtr. ex Heil) Oberm.

[illegible]

Kleine, meist nur wenige Zentimeter hohe, kahle, rasenbildende Wasserpflanze, in zeitweise austrocknenden Wasserbecken lebend. Achse gestaucht, pfriemliche Unterwasserblätter tragend. Die Achselsprosse der letzteren sind dünne Stiele, die in 2 kreuzweise angeordneten Paaren von Schwimmblättern endigen. Schwimmblätter elliptisch-lanzettlich, bis ca. 8 : 4 mm, unterseits meist rot. Blüten zu zweien (oft nur eine davon entwickelt) in einer Schwimmblattrosette, fast sitzend; Kelch schüsselförmig, 1,5—2,5 mm lang, mit 5 breiten, abgerundeten Zähnen. Krone zweilippig, 6—8 mm lang, rosaviolett bis weiß; Oberlippe an der Spitze zweizähnig, Unterlippe dreilappig mit dunklerer Zeichnung. Staubblätter 4, das obere Paar im Schlund der Kronröhre, das untere Paar an das Basis der Unterlippe inseriert, die Filamente des letzteren etwas länger, an der Ansatzstelle verdickt und gebogen. Griffel mit zweilappiger Narbe.

in: The flowering Plants of Africa Nr 151 1967, [illegible]

als: Lindernia intrepidus (Dinter) Oberm.

Dinteria 2: 13-21 (1969) Oberm. . . . ..

C. intrepidus DINTER ex HEIL in Beih. Bot. Centr. 41, I: 41—50 (1924). Grünfelde OK Hickel

T: DINTER 952, Gneißberge bei km 12 des Weges Okahandja-Otjosazu. [illegible]

V: OTJ! — OM! — OK! — SW! — KAR! Erongo

B: DE WINTER 2806; DE WINTER & HARDY 8082; DINTER 6969; GIESS, VOLK & BLEISSNER 5789; KINGES 3125, 3654; MERXMÜLLER & GIESS 1580; SEYDEL 3484; VOLK 986.

5789 Ameib. H
986 Waterberg [illegible] H

Abb. 1.: Seite aus dem Prodromus einer Flora von Südwestafrika von Merxmüller (1967), *Chamaegigas intrepidus* betreffend, aus dem Besitz von Prof. Volk mit dessen ergänzenden Angaben zu weiteren Fundstellen.

Der typische Standort von *Chamaegigas intrepidus*

Die frühen oben zitierten Beschreibungen von Dinter charakterisieren den typischen Standort von *Chamaegigas* sehr genau. *Chamaegigas* wächst ausschließlich in flachen Pfützen auf Inselbergen („Granitglatzen“) der Übergangszone Halbwüste-Savanne in einer Höhe bis ca. 1500 m üNN. (Abb. 2). Die jährlichen Niederschläge betragen 160-570 mm, mit Regenfällen ist an 20-70 Tagen während des Sommers (November bis April) zu rechnen.

Abb. 2c: Granitglatzen auf der Farm Otjua (Omaruru-Distrikt) im Savannen-Übergangsgürtel Zentralnamibias.

Abb. 2a: Blühendes Exemplar von *Chamaegigas intrepidus* (Scrophulariaceae) mit Polstern aus lanzettlichen Unterwasserblättern (ca. 8 - 15 mm lang) an kurzen Rhizomstücken, zwei Paaren gegenständiger Schwimmblätter an einem ca. 10 cm langen Stiel und zwei Blüten in der Schwimmblattrosette (siehe Smook 1969 und Fischer 1992).

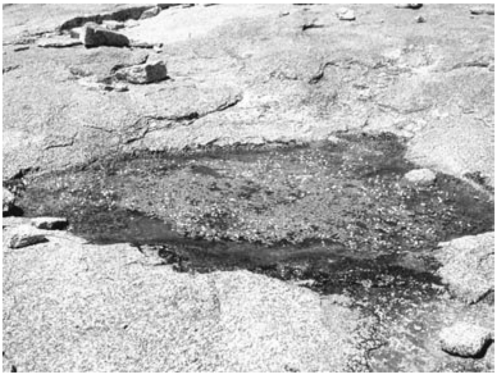


Abb. 2b: Temporär wassergefülltes Granitbecken („Affenbadewanne“) während der Sommerregenperiode (Ende März) mit extrem dichter Bedeckung von *Ch. intrepidus*. Der maximale Wasserstand ist durch Blaualgenbildung am Rand des Beckens gekennzeichnet.

Die Pfützen mit Vorkommen von *Ch. intrepidus*, von den einheimischen Bewohnern auch Affenbadewannen genannt, sind maximal 10-15 cm tief. Sie können innerhalb weniger Tage völlig austrocknen. Die Fläche der Pfützen beträgt ca. 0,4 - 100 m^2 (Heilmeier et al. 2005). Der Grund der Pfütze ist von einer dünnen Schicht aus verrottenden Pflanzen, Algen, Daphnien und tierischen Faeces bedeckt. Neben *Chamaegigas* findet sich in tieferen Pfützen (ab ca. 15 cm Wassertiefe) *Limosella grandiflora* – eine homoiohydrische Wasserpflanze. Weiterhin sind große Mengen an Kaulquappen zu beobachten. Überdüngte Pfützen, z.B. durch Deposition von tierischen Fäkalien, sind stets frei von *Chamaegigas*. Hier ist ein starkes Algenwachstum (*Spirogyra*-Arten) zu beobachten. Ansonsten trifft die oben zitierte Beschreibung von Dinter exakt zu. Heilmeier et al (2005) haben die auf der Farm Otjua

(21°10' Süd, 16° Ost) befindlichen Pfützen vermessen und detailliert beschrieben. Die mit *Chamaegigas* bewachsenen Pfützen zeigten im Gegensatz zur zufälligen Verbreitung aller Pfützen auf einem Granit-Inselberg eine geklumpte Vorkommensverteilung.

In schmalen Erdspalten der Granitglatzen sowie an deren Rand sind weitere poikilohydrische Angiospermen zu finden (Bornefeld und Volk 2002), nämlich *Craterostigma plantagineum*, *Xerophyta humili*s sowie das austrocknungstolerante Gras *Eragrostis nindensis*. Außerdem finden sich mehrere poikilohydrische Vertreter der Marchantiales (*Exormotheca bulbigenai*, sowie die *Riccia*-Arten *R. angolesis, atropurpurea, crinita, nigrella, okahandiana, rosea* und *runssoriensis*).

Chamaegigas intrepidus – eine vom Aussterben bedrohte Art?

In der „IUCN Red List of Threatened Species“ (www.iucnredlist.org/search/details.php/46854/summ) wird *Chamaegigas* mit folgenden Argumenten als nicht bedroht bezeichnet:

1. Die Standorte sind nur wenigen Menschen bekannt.
2. In einem Becken wachsen mehrere Tausend Exemplare.

Aus der Sicht der Autoren kann diese Feststellung nicht unwidersprochen bleiben. In der Mehrzahl der Becken wachsen nur wenige Exemplare, oft weniger als 10. Ein gewisses Gefährdungspotential sehen die Autoren in der hohen Stickstoffempfindlichkeit der Pflanzen. Viele der Standorte befinden sich auf beweidetem Farmgelände. Die Becken werden von Weidetieren als Tränke besucht, was oft mit einer für *Chamaegigas* unverträglichen Fäkaliendeposition und somit Überdüngung verbunden ist. Eine weitere Gefährdungsursache könnte das Vorkommen dieser Art auf teilweise weit voneinander entfernten Inselbergen und die damit einhergehende mögliche genetische Isolation, die oft mit einem Verlust genetischer Diversität sowie Abnahme der Heterozygotie verbunden ist, darstellen.

Umweltbedingungen

Meteorologische Daten

Im Verlauf unserer Untersuchungen auf der Farm Otjua (Omaruru District) in den Jahren 1995-2002 betrugen die jährlichen Niederschläge 180 - 450 mm, überwiegend gegen Ende des Sommers im März und April. An regenfreien Tagen erreichte die Lufttemperatur tagsüber Werte um 50°C, die Luftfeuchtigkeit sank bis auf 10-20%, nachts lag sie bei 70-100%. Die Niederschlagsmenge wurde mit einem klassischen Regenmesser nach HELLMANN, Lufttemperatur und -feuchtigkeit mit digitalen Sensoren (Tinytalk, Gemini Data Loggers Ltd., Chichester, UK) kontinuierlich gemessen und elektronisch gespeichert.

Wassertiefe, Leitfähigkeit und pH-Wert

Die Wassertiefe der untersuchten Becken (Fläche 1,3 bis 7,7 m^2) lag zwischen 2 und 15 cm, die Leitfähigkeit war nach dem Regen kleiner als 50 µS cm^{-1}. Im Verlauf des Eintrocknens führte eine Halbierung der Wassertiefe zu einem deutlichen Anstieg der Leitfähigkeit (Abb. 3a, gemessen mit einer Leitfähigkeitselektrode). Die Leitfähigkeitswerte in den wassergefüllten Becken sind mit denen temporär gefüllter Pools im Namib-Naukluft-Park vergleichbar (Kok und Grobbelaar, 1985).

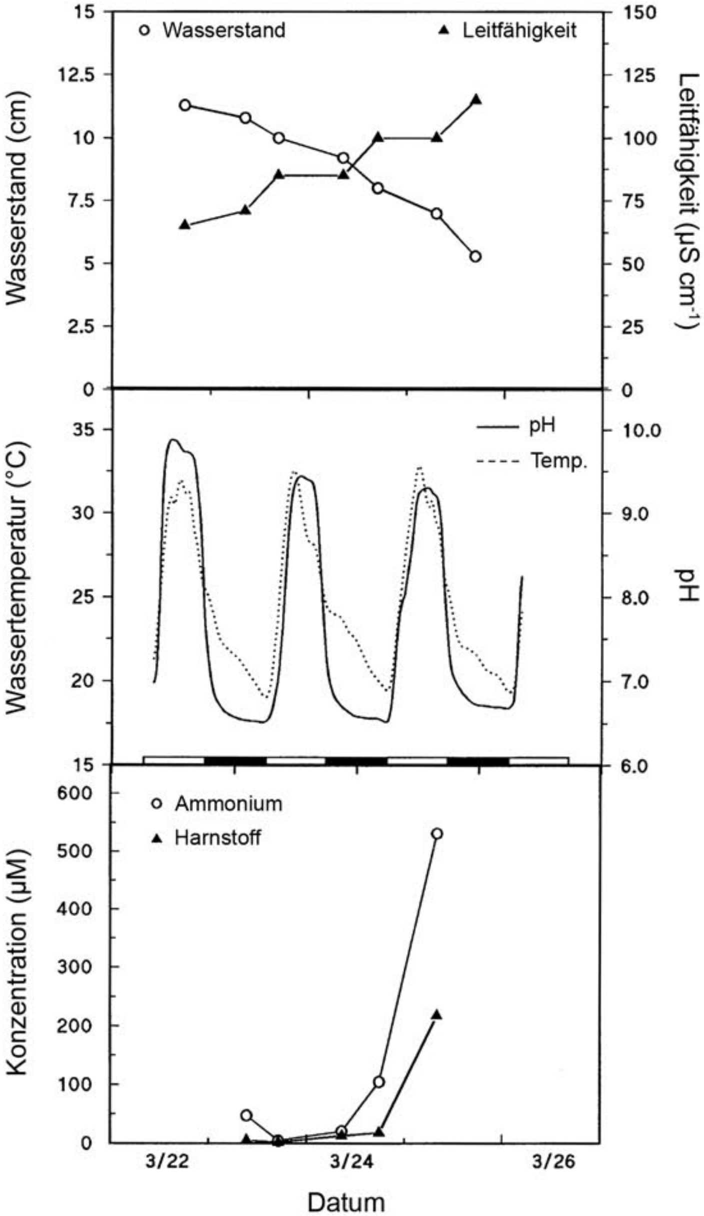


Abb. 3: Zeitverlauf der (a) Wassertiefe, elektrischen Leitfähigkeit, (b) Wassertemperatur und pH-Wert, (c) Konzentration an Ammonium und Harnstoff während der Austrocknungsphase in einem temporär wassergefüllten Becken auf einer Granitkuppe der Farm Otjua (Omaruru District). Die Wasseroberfläche war zu ca. einem Viertel mit Schwimmblättern von *Chamaegigas intrepidus* bedeckt. Helle Balken geben die Tagesstunden, dunkle die Nachtstunden an (verändert nach Schiller et al. 1997 und Heilmeier & Hartung, 2001)

Die Wassertemperatur erreichte im Verlauf eines Tages Werte von beinahe 35°C und sank nachts auf knapp unter 20°C (Abb. 3b). Parallel zum Anstieg der Wassertemperatur erfolgte ein Anstieg des pH-Wertes von morgendlichen Werten von etwa 6,5 auf nachmittägliche Werte von etwa 10,0 (Abb. 3b). In einigen Fällen konnten pH-Werte von 12,0 gemessen werden. Die pH-Schwankungen (kontinuierlich gemessen mit einer Glaselektrode und mit einem Datalogger elektronisch gespeichert) lassen sich durch Veränderungen der CO_2- und HCO_3^--Konzentration erklären. Durch die Erwärmung des Wassers nimmt die CO_2-Löslichkeit ab, zusätzlich wird bei Anwesenheit von photosynthetisierenden Wasserpflanzen weiteres CO_2 dem Wasser durch Assimilation entzogen.

Die Versorgung mit mineralischen Nährstoffen

Die chemische Zusammensetzung der Becken ist detailliert bei Heilmeier & Hartung (2001) beschrieben. Die mittels Hochdruckflüssigkeitschromatographie (HPLC) und Ionenchromatographie (IC) ermittelten Konzentrationsbereiche vieler Kationen (Natrium, Kalium, Calcium, Magnesium) und Anionen (Chlorid, Sulfat, Phosphat) waren etwa 2- bis 40-fach niedriger als die von Kok und Grobbelaar (1980, 1985) für temporäre Gewässer der Namib angegebenen Werte. Gemäß Kok und Grobbelaar (1980) können die für die *Chamaegigas-Becken* vorgefundenen Konzentrationsverhältnisse ($Na^+ > Ca^{2+} > K^+ = Mg^{2+}$; $Cl^- > SO_4^{2-}$) durch die Einträge dieser Ionen mit Niederschlägen erklärt werden; nur Na^+ and Cl^- sollten dem Ferntransport von Meerwasser entstammen. Na^+ and Cl^- könnten jedoch auch von tränkenden Tieren mittels Urin in die Becken eingebracht werden.

Bemerkenswert ist der niedrige Gehalt an stickstoffhaltigen Verbindungen. Nitrat ist im Gegensatz zu temporären Felsbecken im Namib-Naukluft-Park (Kok und Grobbelaar, 1985) mit den üblichen Analysenmethoden nicht nachweisbar. Ammonium hingegen erreicht Konzentrationen bis 0,6 mM. Ammoniumionen können im Tagesverlauf starken Schwankungen unterworfen sein, insbesondere weil am späten Nachmittag unter stark alkalischen Bedingungen Ammoniak in die Atmosphäre entweichen kann. Ammonium stammt überwiegend von Harnstoff, welcher im Urin von Wild- und Weidetieren in die Pfützen abgegeben wird. Urease, ein extrem hitzestabiles Exoenzym, befindet sich in ausreichender Menge im Sediment der Wannen und kann aus dem Harnstoff Ammonium freisetzen. Dies erfolgt vor allem während der Austrocknung der Becken, weshalb in diesen Phasen die Ammoniumkonzentration stärker ansteigt als die Harnstoffkonzentration (Abb. 3c).

Unter Bedingungen sehr niedriger Ammonium- und Harnstoffkonzentrationen können Aminosäuren als N-Quelle bedeutsam werden (Bardgett, 2005; dort ist auch weitere Literatur zitiert), so auch in den mit Wasser gefüllten flachen Granitbecken. Wie auch in der Bodenlösung anderer naturbelassener Habitate (z. B. Böden borealer Wälder, Prairie, Tundraböden; Bardgett 2005) finden sich hier vor allem die Aminosäuren Glycin und Serin im niedrigen mikromolaren Konzentrationsbereich (Bestimmung mittels HPLC).

Anatomisch-morphologische Besonderheiten

Blätter Die meisten poikilohydrischen Pflanzen zeigen keine charakteristischen xeromorphen anatomischen Anpassungen. Meist ermöglichen biochemisch-physiologische Mechanismen die extreme Austrocknungstoleranz. Die Unterwasserblätter von *Chamaegigas* jedoch zeigen eine extreme Fähigkeit, in Längsachse um bis zu 90% zu schrumpfen, während die Schwimmblätter im ausgetrockneten Zustand nur 10-20% schrumpfen.

Heil (1924), Hickel (1967) und Schiller et al. (1999) zeigten, dass das drastische Schrumpfen durch kontraktive Tracheiden ermöglicht wird. Diese Xylemelemente besitzen breite bänderförmige Spiralverstärkungen, welche im Verlauf des Schrumpfens sich wie eine Ziehharmonika zusammenziehen. Die unverdickten longitudinalen Wände legen sich dabei in Falten. In den Leitbündeln der bifazialen Schwimmblätter und in den Wurzeln fehlen die kontraktiven Tracheiden.

Wurzeln Heilmeier et al. (2002) untersuchten die Wurzeln von *Chamaegigas* und beobachteten eine 10-15%ige longitudinale und eine 30-35%ige laterale Schrumpfung während des Austrocknens. Im Unterschied zu Heil (1924) und Hickel (1967) wurde das Rindengewebe nicht als Aerenchym erkannt. Die Rinde wird von einer Schicht sehr großlumiger, extrem dünnwandiger Zellen gebildet (Abb. 4): Während diese Rindenzellen auch im desikkierten Zustand keine Formveränderung zeigen und sich durch eine außerordentliche Stabilität auszeichnen, schrumpfen die Rhizodermis und Hypodermis der absolut wurzelhaarfreien Wurzeln zu einer der Rinde dicht anliegenden Schicht. Die äußerste Lage der Hypodermis liegt als Kurzzellenexodermis vor, ähnlich wie sie von Luftwurzeln der Orchideen und einigen Wurzeln der Asclepidiaceen bekannt ist. Die äußeren Zellwände der Kurzzellen (=Durchlasszellen) zeigen charakteristische polsterartige Verdickungen, die im Verlauf des Austrocknens die Durchlasszelle wie ein Ventil verschließen. Auf diese Weise wird nach Auffassung von Heil (1924) und Hickel (1967) der Wasserverlust verlangsamt.

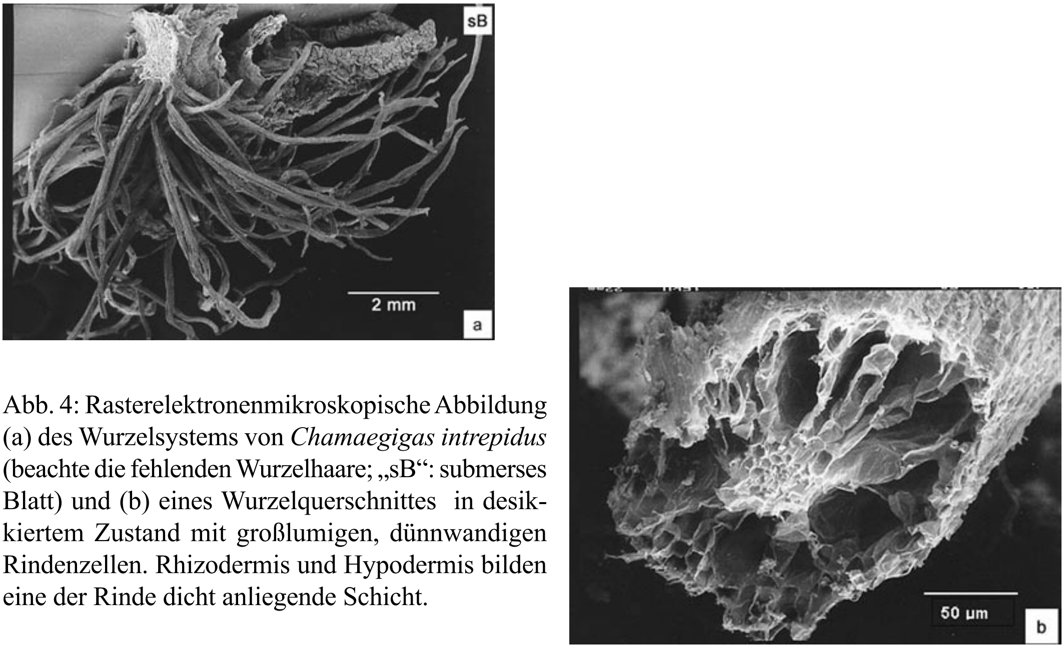


Abb. 4: Rasterelektronenmikroskopische Abbildung (a) des Wurzelsystems von *Chamaegigas intrepidus* (beachte die fehlenden Wurzelhaare; „sB“: submerses Blatt) und (b) eines Wurzelquerschnittes in desikkiertem Zustand mit großlumigen, dünnwandigen Rindenzellen. Rhizodermis und Hypodermis bilden eine der Rinde dicht anliegende Schicht.

Morphologie von Blüten und Samen - Bestäubungsbiologie

Die zygomorphen, intensiv duftenden Blüten haben auf ihrer Unterlippe einen dichten Besatz von kurzstieligen Drüsenhaaren (400-1600 mm^{-2}) ähnlich wie die der von Vogel (1974) beschriebenen Ölblumen. Durka et al. (2004) entdeckten mithilfe molekularer, populationsgenetischer Methoden eine unerwartet hohe genetische Variabilität von *Chamaegigas intrepidus* innerhalb einzelner Becken. Sie schlossen daraus, dass *Chamaegigas* durch Insekten bestäubt werden muss. In der Tat konnten vier potentielle Bestäuber beobachtet werden, zwei Hymenopteren, *Apis mellifera* and *Liotrigona bottegoi*, sowie zwei Käfer der Gattung *Condylops* (*C. erongoensis* und eine neue Art mit bis zu 50 Tieren pro m^2). An ihren Hinterbeinen sowie den Flügeldecken von *Liotrigona* und *Condylops* wurden die kugelförmigen, tricolpaten Pollen von *Chamaegigas* nachgewiesen (Woitke et al. 2006). Es liegt nahe, dass diese Insekten bei der Befruchtung von *Chamaegigas intrepidus* eine wichtige Rolle spielen.

Samen Die 12-kantigen Samen (1150 µm x 350 µm) mit leicht konkaven Flächen zwischen den Kanten besitzen im Endosperm Aleuron- und Stärkekörner sowie Lipidtröpfchen. Sie wurden detailliert von Heil (1927) beschrieben. Hickel (1966) zeigt Querschnitte durch Blütenknospen, Fruchtknoten und Antheren.

Anpassungen an die extremen Umweltbedingungen

Trockenheit Wüstenbewohnende Tiere sind oft nachtaktiv und vermeiden die extrem heißen und trockenen Bedingungen während des Tages durch eine unterirdische Lebensweise (Brown 1968, Seely 1990). Pflanzen sind dazu aufgrund ihrer immobilen Lebensweise im allgemeinen nicht in der Lage. Nicht so *Chamaegigas.* Während die Schwimmblätter über eine nur schwache Austrocknungstoleranz verfügen, ziehen sich die extrem desikkationstoleranten Unterwasserblätter fast vollständig in das Sediment zurück und sind so insbesondere vor der extrem hohen Lichtintensität (> 2000 $\mu mol\ m^{-2}s^{-1}$) mit einem aufgrund der Meereshöhe sehr hohen und potentiell sehr schädlichen UV-Anteil perfekt geschützt. Dies wird durch das oben beschriebene extreme Schrumpfen, welches durch die kontraktiven Tracheiden bewirkt wird, ermöglicht. Prof. Volk hat diese kontraktiven Tracheiden sehr anschaulich als „Modell Fleischwolf, aber hohle Achse“ bezeichnet (Abb. 5).

Die auf der anderen Seite extreme Stabilität der auf den ersten Blick sehr fragil erscheinenden Cortex-Zellen der Wurzeln zusammen mit der Kurzzellenexodermis trägt ebenfalls höchstwahrscheinlich zur hohen Austrocknungstoleranz der Wurzel bei.

Physiologisch-biochemische Aspekte Eine wichtige Rolle spielt das pflanzliche Stresshormon Abscisinsäure (ABA). Seine Biosynthese wird in Pflanzen bei eintretender Trockenheit drastisch gefördert. Nach ihrem Transport, oft im Xylem, zu den Schließzellen bewirkt sie deren Verschluss und minimiert so den Wasserverlust durch Transpiration. Bei *Chamaegigas* scheint eine stomatäre Regulation durch Abscisinsäure eine geringere Rolle zu spielen, insbesondere da ausdifferenzierte Stomata der Schwimmblätter immer geöffnet zu sein scheinen.

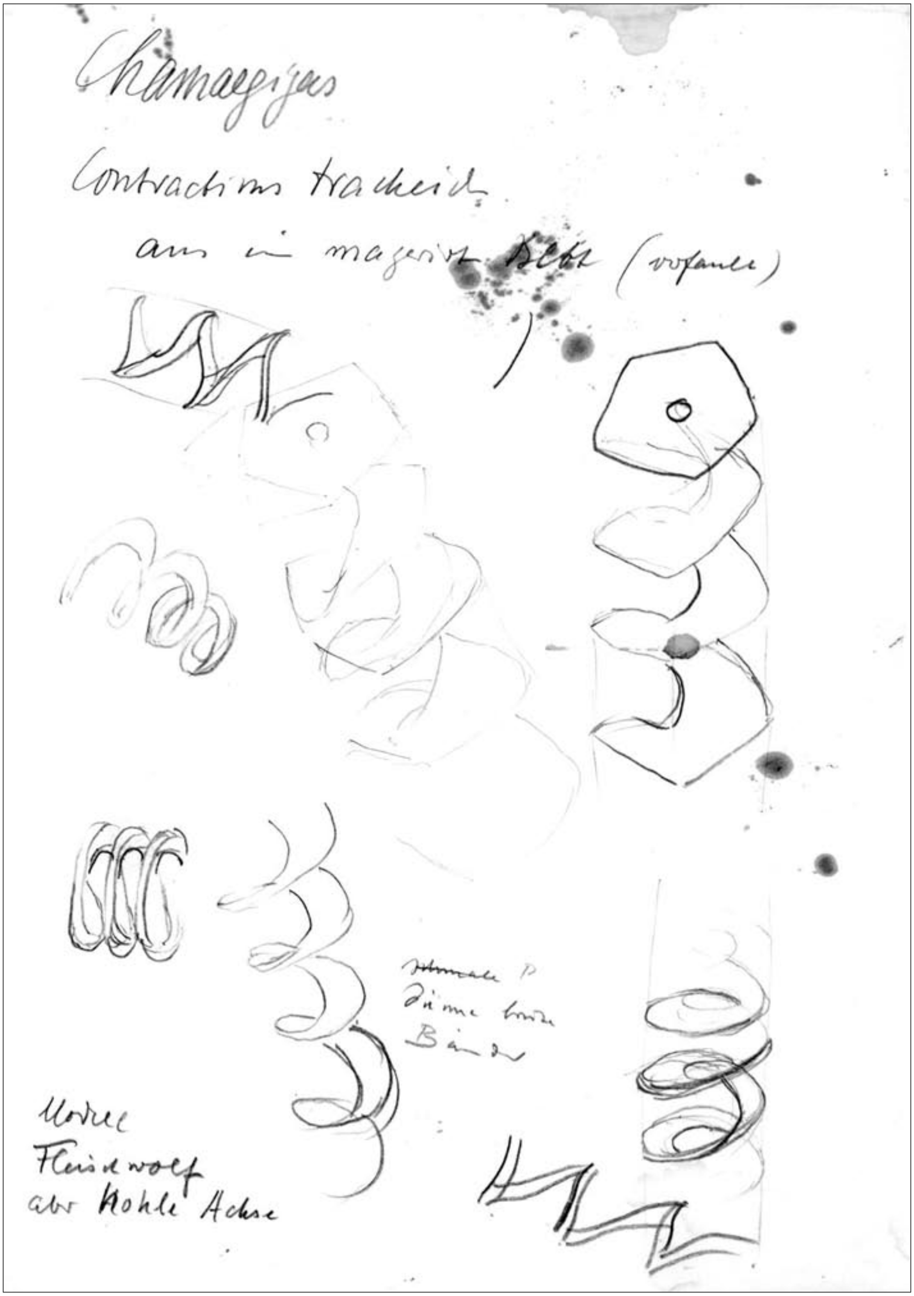


Abb. 5: Originaldarstellung von Handzeichnungen von Prof. Volk, die die kontraktiven Tracheiden von *Chamaegigas intrepidus* darstellen, mit der Bezeichnung „Modell Fleischwolf, aber hohle Achse“ (aus dem Nachlass von Prof. Volk, gefunden als Beilage in dessen Privatexemplar des Prodromus einer Flora von Südwestafrika von Merxmüller (1967))

Auferstehungspflanzen wie *Craterostigma, Myrothamnus* oder *Xerophyta* weisen immer einen hohen ABA-Gehalt auf, welcher nur geringen Schwankungen unterworfen ist. Die ABA-Gehalte in den Geweben hydrierter *Chamaegigas*-Pflanzen sind dagegen niedrig, vergleichbar mit vielen anderen mesophytischen Pflanzen (Messung mittels enzymgebundenem Antikörpertest, ELISA). Der Anstieg im Verlauf des Eintrocknens ist bei den extrem austrocknungstoleranten Geweben (Wurzeln, submerse Blätter) sehr hoch (20- bis 30-fach), bei den nur schwach austrocknungstoleranten Schwimmblättern maximal 5-fach (Abb. 6).

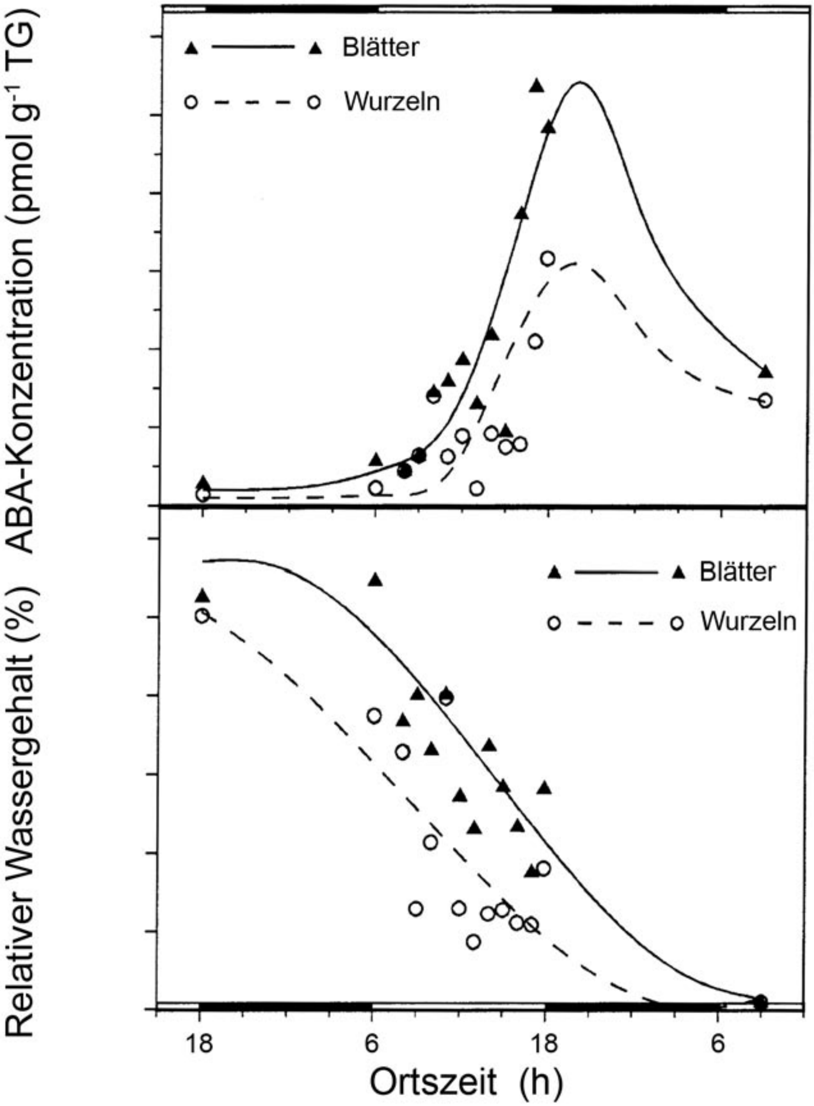


Abb.6: Konzentration an (a) Abscisinsäure in Unterwasserblättern und Wurzeln sowie (b) des relativen Wassergehaltes im Verlauf der Austrocknung von *Chamaegigas intrepidus* (verändert nach Schiller et al. 1997)

Gewebe von *Chamaegigas* verfügen über Mechanismen, den Abscisinsäuregehalt in den Zellen hoch zu halten. So ist der oxidative Abbau der ABA zu den Metaboliten Phaseinsäure (PA) und Dihydrophaseinsäure (DPA) etwa 10 mal langsamer als beispielsweise in der mesophytischen Rosettenpflanze *Valerianella locusta*. Eine Konjugation der Abscisinsäure um physiologisch inaktiven ABA-Glukoseester ist ebenfalls viel schwächer ausgeprägt als in nicht-aquatischen Auferstehungspflanzen (Hartung, unpublizierte Daten).

Für viele mesophytische Pflanzen konnte früher wiederholt gezeigt werden, dass ABA, dem sogenannten Anionenfallenmechanismus folgend, sich leicht von sauren Kompartimenten (Vakuole, Apoplast) in alkalische Kompartimente (Cytosol, Chloroplasten) verlagert. Im Falle von *Chamaegigas*, welcher ja wie oben gezeigt im Verlauf eines Tages pH-Werten bis 12 ausgesetzt sein kann, würde dies zu einer schwerwiegenden Verarmung der Gewebe an ABA führen. *Chamaegigas*-Rosetten, welche mit radioaktiver ABA beladen wurden, verloren, im Gegensatz zu mesophytischen Pflanzen, nur geringe Mengen an ABA. Die Plasmalemmen, insbesondere der Wurzelgewebe, haben offensichtlich eine sehr geringe Permeabilität für ABA. Zusätzlich könnte die Kurzellenepidermis, deren Durchlasszellen durch ventilähnliche Zellwandpolster verschlossen werden können, als effektive Barriere den ABA-Efflux minimieren.

Die Funktion der ABA in poikilohydrischen Angiospermen. Pflanzliche Gewebe synthetisieren bei Wasserverlust unter der Kontrolle der ABA eine Gruppe von Proteinen, welchen eine protektive Rolle unter Trockenbedingungen zugestanden wird. Zu diesen gehören die Dehydrine, von denen vermutet wird, dass sie austrocknungsempfindliche Enzyme im Cytosol schützen. Solche Dehydrine werden in Wurzeln von *Chamaegigas* im Verlauf des Austrocknens sowie nach ABA-Behandlung gebildet (Nachweis mittels spezifischer Antikörper). Unterwasserblätter enthalten auch im voll hydrierten Zustand große Mengen an Dehydrinen (Schiller et al. 1997). Eine stressphysiologische Funktion der ABA könnte in der Induktion der Dehydrin-Synthese in der Wurzel liegen.

Kohlehydrate. Poikilohydrische Angiospermen besitzen große Mengen an Zuckern, insbesondere Saccharose, Fruktose und Glukose. *Myrothamnus* enthält zusätzlich Glucopyranosyl-ß-glycerin und Trehalose. In *Craterostigma* wird während des Eintrocknens Octulose in Saccharose umgewandelt. *Chamaegigas* besitzt neben Saccharose als dominierendem Zucker das Trisaccharid Stachyose. Raffinose liegt in nur geringen Mengen vor. Glukose- und Fruktosegehalte sind insbesondere in den Blättern hoch. Im Verlauf des Eintrocknens nehmen die Monosaccharide bei gleichzeitiger Akkumulation von Saccharose und Stachyose ab (Abb.7; HPLC-Analyse). Lufttrockene Wurzeln enthalten bis zu 26% ihrer Trockenmasse Saccharose und Stachyose, in Blättern nehmen sie 14% des Trockengewichtes ein. Stachyose, Raffinose und Saccharose unterdrücken die Kristallisation cytoplasmatischer Bestandteile durch Glasbildung (Hartung et al. 1998). Im Glasstadium besitzt eine Flüssigkeit eine hohe Viskosität. Chemische Reaktionen sind stark verlangsamt und Interaktionen zwischen Zellbestandteilen finden nicht statt. Das Glasstadium ist ideal für das Überstehen einer Austrocknung. Zusätzlich können die hohen Zuckergehalte als Speichersubstanzen dienen und so das dramatisch starke Wachstum von Blättern und Blüten nach der Wiederbefeuchtung ermöglichen.

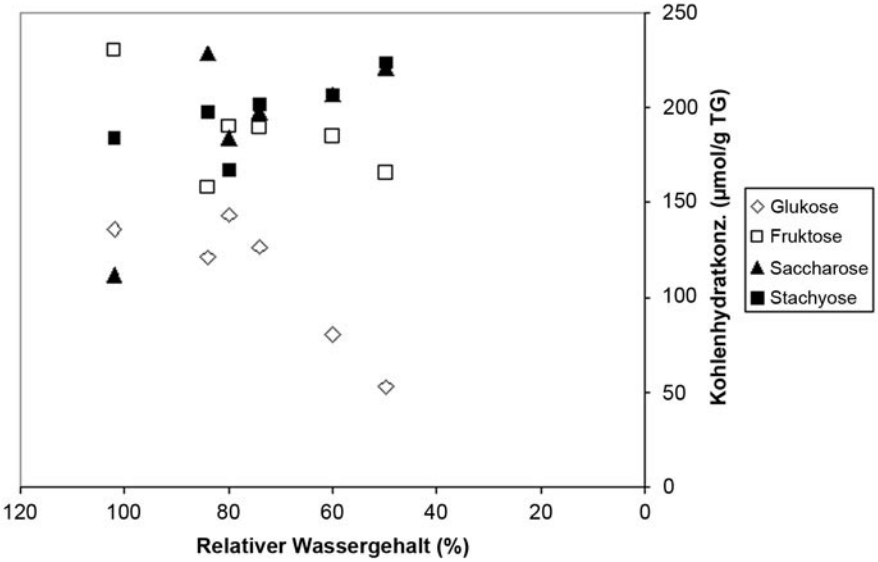


Abb.7: Konzentration der Kohlehydrate Fruktose, Glukose, Saccharose und Stachyose in Unterwasserblättern von *Chamaegigas intrepidus* mit abnehmendem relativen Wassergehalt während der Austrocknung (verändert nach Heilmeier & Hartung 2001).

Anpassung an extreme pH-Schwankungen *Chamaegigas* ist am Standort drastischen pH-Schwankungen, bis pH 10, in Extremfällen sogar bis pH 12 ausgesetzt. Mithilfe der ^{31}P-NMR-Spektroskopie konnte festgestellt werden, dass bei pH 10 eine nur vernachlässigbare Alkalisierung des Cytosols der Wurzeln auftritt (Schiller et al. 1998a). Entwässerung verursachte eine sehr geringe Alkalisierung der Mesophyllvakuolen. Diese Daten weisen auf eine ungewöhnlich effektive pH-Regulation der zellulären Kompartimente hin. Die NMR-Spektren zeigten außerdem, dass Dehydrierung die Phosphat- und Phosphocholingehalte in den Zellen nicht erhöht. Dies weist auf eine hohe Stabilität der Membranen bei erniedrigten Wasserpotentialen hin. Normalerweise werden Membranschäden von einem Anstieg an Phosphat und Phosphocholin begleitet.

Anpassung an extremen Stickstoffmangel *Chamaegigas* wächst am Originalstandort unter extremen Stickstoffmangelbedingungen. Harnstoff, Ammonium und die Aminosäuren Glycin und Serin kommen in sehr geringen Konzentrationen vor, Nitrat ist nicht nachweisbar (HPLC- und IC-Analysen). Experimente mit ^{14}C- und ^{15}N-markiertem Harnstoff zeigten, dass diese Verbindung von den Wurzeln nicht aufgenommen werden kann. In Anwesenheit von Urease, also nach Abspaltung von ^{15}N-Ammonium, konnten die Wurzeln ^{15}N in Form von NH_4^+ aufnehmen und in Glutamin und Glutamat einbauen (Heilmeier et al. 2000a). Urease spielt daher eine zentrale Rolle bei der Nutzung von Stickstoff durch *Chamaegigas*.

Dieses Exoenzym ist von bemerkenswerter Stabilität. Nach einer mehrmonatigen Trockenperiode bei Temperaturen bis zu 60° und hoher UV-Einstrahlung verliert die Urease nicht an Aktivität (Heilmeier et al. 2000b). Sie stellt einen Schlüsselfaktor für das Überleben von *Chamaegigas* an einem von Wildtieren dominierten Standort dar.

Die Konzentration an Ammonium, welches wie gezeigt überwiegend tierischer Herkunft ist, kann in den gefüllten Becken sehr stark absinken, da es als Ammoniak aus den extrem alkalischen Becken in die Atmosphäre entweichen kann. Unter diesen Bedingungen nützt *Chamaegigas* die Aminosäuren Glycin und Serin, welche im niedrigen mikromolaren Konzentrationsbereich im Wasser nachzuweisen sind. Um diesen organisch gelösten Stickstoff (DON-dissolved organic nitrogen) nutzen zu können, verfügen die Plasmalemmen der Wurzelzellen über ein hoch affines Aufnahmesystem (K_M= 16 µM), welches allerdings sein pH-Optimum im Sauren hat (Schiller et al. 1998b). Die N-Nutzung aus DON erfolgt demnach nur während des Vormittags. Die Metabolisierung in Wurzeln und Rosetten von *Chamaegigas* wurde von Hartung und Ratcliffe (2002) mithilfe der ^{15}N- und ^{13}C-NMR-Spektroskopie untersucht.

Von arktischen und alpinen Pflanzen sowie für eine große Anzahl australischen Wildpflanzen ist bekannt, dass sie Glycin und andere Aminosäuren als N-Quelle nutzen (Neff et al. 2003). *Chamaegigas* ist bislang der erste bekannt gewordene aquatische Kormophyt, für den Glycin und Serin eine wichtige N-Quelle darstellen.

Photosynthese Heilmeier & Hartung (2001) bestimmten die Sauerstoffkonzentration im Wasser eines zu 25% mit Schwimmblättern bedeckten Beckens. Sie zeigte deutliche diurnale Schwankungen mit einem starken Anstieg während der frühen Morgenstunden und einem Plateau von 8 - 16 Uhr. Da *Chamaegigas* zur Photosynthese in der Lage ist, selbst wenn das Medium frei con CO_2 ist, schließen die Autoren, dass *Chamaegigas* Bikarbonat als Kohlenstoffquelle nutzt. Messungen der Chlorophyllfluoreszenz beider Blatttypen am Originalstandort wurden von Woitke et al. (2004) so interpretiert, dass 75% der Photosynthese und damit des Kohlenstoffgewinns in den Schwimmblättern stattfindet. Die Gründe für das bessere photosynthetische Leistungsvermögen der Schwimmblätter können vielfältig sein, i) eine bessere CO_2 Versorgung (CO_2-Diffusionskoeffizient in Luft 10^4-fach höher im Vergleich zum wassergelösten CO_2), zudem sind die Stomata der Schwimmblätter kontinuierlich geöffnet, vergleichbar der von Lemnaceen (Heilmeier & Hartung 2001), ii) höhere und durchaus konstantere PPFD im Vergleich zum räumlich weitaus heterogeneren Lichtklima der Unterwasserblätter, das durchschnittlich nur 10% der eingestrahlten Lichtmenge an der Wasseroberfläche erreicht, und iii) die gleichermaßen schnelle wie vollständige Erholung der Schwimmblätter nach vollständiger Austrocknung und iv) keine wesentlichen Unterschiede während der Austrocknung im Vergleich zu den Unterwasserblättern.

In der Tat zeigten auch die Schwimmblätter, im Gegensatz zu früheren Berichten, eine gewisse Austrocknungstoleranz innerhalb von 1-2 Tagen. Ob jedoch diese Fähigkeit über längere Zeiträume weiter besteht, wie dies bei den submersen Blättern der Fall ist (im Extremfall 4 bis 6 Jahre), muss stark bezweifelt werden.

Genetische Diversität innerhalb und zwischen den Populationen

Chamaegigas intrepidus kommt als endemische Pflanze nur in einem sehr kleinen Verbreitungsgebiet in Zentralnamibia vor. Üblicherweise leiden derartige Populationen im Vergleich zu weit verbreiteten Arten an einer genetischen Verarmung, d. h. an einer geringen Anzahl polymorpher Genorte und einem Verlust an Allelen. Durch Inzuchteffekte innerhalb kleiner Populationen (genetische Drift) kann es zu einem verringerten Heterozygotiegrad und zu einer Fixierung von schädlichen Allelen kommen. Zusätzlich kann das isolierte Vorkommen von *Ch. intrepidus* auf den im Mittel ca. 25 km voneinander entfernten Inselbergen den genetischen Austausch (Genfluss) beispielsweise durch Samenverbreitung oder Pollentransfer stark einschränken.

Wie jedoch molekulargenetische Untersuchungen („genetischer Fingerabdruck“) mittels AFLP-Markern (amplified fragment length polymorphism) zeigten, ist die genetische Diversität innerhalb einer Population auf einer Granitkuppe überraschend hoch, und der Großteil der genetischen Variabilität findet sich sogar innerhalb der Individuen eines Beckens (Durka et al. 2004). Der größte Anteil der genetischen Differenzierung ist durch das Vorkommen auf den einzelnen Granitglatzen zurückzuführen, obwohl der genetische Abstand zwischen den Populationen nicht mit der geographischen Distanz korreliert war. So kann es zwischen den Inselbergen anscheinend doch zu einem Austausch von Individuen kommen, möglicherweise durch Windverdriftung sowie Transport von Samen in den Hufen und Klauen von Weide- und Wildtieren. Die hohe genetische Vielfalt in den geklumpt vorkommenden Becken auf einer Granitglatze ist auf die Bestäubung durch die oben erwähnten Insektenarten zurückzuführen.

Somit kann nicht davon ausgegangen werden, dass diese endemische Art in ihrem derzeitigen Verbreitungsgebiet genetisch verarmt ist. Ein hoher Genfluss und mutmaßlich auch eine durch die große Meereshöhe erhöhte Ultraviolettstrahlung, welche zahlreiche Mutationen bewirken sollte, sind wahrscheinlich für die hohe genetische Variabilität verantwortlich. Somit könnte trotz der vermutlich geringen generativen Fortpflanzungsrate (Heilmeier et al. 2005) die genetische Grundlage für eine erfolgreiche Anpassung an die extremen Habitatbedingungen, deren hohe zeitliche Variabilität und die ausgeprägte Isolation der Standorte gegeben sein.

Schlussbemerkung

Unter den bislang bekannten poikilohydrischen Angiospermen gehört *Chamaegigas intrepidus* sicherlich zu den ausgefallensten Vertretern, allein schon durch die Tatsache, dass es sich um eine aquatische Pflanze handelt. Die anatomischen Anpassungen von submersen Blättern und Wurzeln sind im Pflanzenreich einzigartig, und auf physiologisch-biochemischer Ebene zeigt die Pflanze perfekte, aufeinander abgestimmte Überlebensstrategien, welche eine Existenz unter diesen extremen und komplexen Umweltbelastungen ermöglicht. Dinter (1918) endigt seine Abhandlung über *Chamaegigas* mit folgenden Worten, denen nichts hinzugefügt werden muss und mit denen auch diese Arbeit endigen soll:

„ … Dies ist wohl das rührendste mir bekannte Beispiel des erzieherischen Kampfes der erbarmungslosen Natur gegen ihre eigenen Kinder. In dem diese aber Sieger sind.“

Danksagung

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(Fußnoten)

[1] Hinsichlich des Datums der Entdeckung von *Chamaegigas intrepideus* gibt es widersprüchliche Angaben. Herre (1927) zufolge fand Dinter *Chamaegigas* bereits im Jahr 1904, Heil (1924) gibt das Jahr 1906 an. Bereits 1909 (Dinter, 1909) beschreibt er eine Pflanze, bei der es sich mit großer Wahrscheinlichkeit um *Chamaegigas* handelt: „… hier… [fanden wir]… zwei weitere [Wasserpflanzen] in den Granitbecken…. Die eine ist ein kleines zartes Pflänzchen mit an langen Stielen schwimmenden, rosa violetten Blüten und wasserlinsengroßen Blättern, eine Scrophulariacee, deren Namen noch unbestimmt ist“. Bei der zweiten Pflanze handelte es sich um *Aponogeton Dinteri.*

[2] Details zu den hier zusammengefassten Ergebnissen (Methoden, Versuchsbedingungen im Labor, statistische Analysen) sind in den zitierten Arbeiten der Autoren zu finden. Sie wurden, der besseren Lesbarkeit wegen, in diesem Text nur kurz zitiert.

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The effects of "pebble mulch" on *Acacia mellifera* seedling responses to rain

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Abstract

"Pebble mulch" (a layer of quartz and schist pebbles that often forms an almost 100 % cover on the slopes of the Highland Savannah in Namibia) influences the dynamics of this vegetation type. A controlled experiment to determine the effects of "pebble mulch" on seed germination and early seedling establishment of *Acacia mellifera* (subsp. *detinens*) was conducted. *A. mellifera* forms dense thickets in the area. Seeds were germinated under four treatments: **A**: planted below soil (2 seed widths depth) without pebble cover; **B**: planted below soil (2 seed widths depth) *with* pebble cover. **C**: planted on top of soil underneath a 100 % pebble cover and **D**: planted on top of a 100 % pebble cover. Emergence/germination and seedling survival and vigour were recorded regularly for five weeks. Emergence/germination in all cases was high (overall 82 % s.d. 17.5 %). Soil moisture was significantly higher in all "pebble-mulch" treatments (B, C and D). Although initial establishment was poor in Treatment D (33 %), survival thereafter of seedlings whose radicles reached the soil was very high (97 %). Seedling survival and vigour were significantly higher in all "pebble-mulch" treatments. The implications of these results for bush encroachment on Highland Savanna rangelands are discussed.

Key words

Bush encroachment; seedling; pebble mulch; Highland Savannah; *Acacia mellifera* subsp. *detinens*.

Introduction

Bush encroachment may be regarded as the densification and increase in cover of bush at the expense of grass production that affects savannahs and other vegetation types throughout the world (e.g. Hodgkinson & Harrington, 1985; Archer *et al.,* 1988). These include savannas in southern African countries such as Botswana, South Africa (e.g. Donaldson, 1967; Trollope *et al.*, 1989; Skarpe, 1990; Roques *et al.*, 2001; Moleele *et al.*, 2002;) and Namibia (Bester, 1999). Bush encroachment affects approximately 26 000 000 hectares of Namibian semi-arid rangeland (De Klerk, 2004). As early as the 1960s, bush encroachment was seen as a major economic problem in Namibia (Bester, 1996). It is estimated that N$ 700 000 are lost in reduced beef production per annum (De Klerk, 2004) and this figure is likely to have doubled by 2009.

It is widely accepted that bush encroachment in southern Africa was initiated largely by the introduction of large herds of domestic ungulates in the 19th century through colonial expansion (Walker *et al.*, 1981). At the same time grazing patterns had been changed through the establishment of permanent water points, which limits the mortality of livestock in non-nomadic rangeland management (Skarpe, 1992). Bush encroachment then occurs when bush seedlings and established bushes obtain a competitive advantage over grasses for soil moisture (Walter, 1971; Knoop & Walker, 1985), facilitated by excessive grazing. However, grass is likely to be more important as a fuel for fire, which kills the seedlings (Joubert *et al.*, 2008). Prior to colonial occupation, there were already landscape scale areas of bush encroachment in Namibia. Andersson (1856) gives no less than five accounts of hardship, including lacerated cattle and torn clothes from thorns as he trekked through bush encroached areas in his explorations through Namibia in the early 1850s. These landscape scale bush encroached areas appear to have been near permanent water. Game, and later livestock herds of nomadic pastoralists who had become partially sedentary, would have concentrated in these areas, reducing grass biomass to such an extent that periodic fires were impossible. In more recent years, fires were deliberately excluded, for economic reasons, particularly since the 1950s (De Klerk, 2004).

Despite the long interest and concern in bush encroachment, there is little consensus today on the major causes. Recent work focuses on the stochastic nature of establishment associated with successive good rainfall periods and the absence of fire (Joubert *et al.*, 2008) and the cyclical nature of bush thicket and open savannah succession (Meyer *et al.*, 2007).

Various authors have investigated microsite effects on seedling survival of woody species in rangelands. For example, Harrington (1991) noted that herbaceous cover negatively affected seedling establishment of *Dodonaea attenuata* in Australian rangelands. In South Africa, Smith and Shackleton (1988) suggested that *Acacia tortilis* seedlings have a lower survival rate in the shade of parent trees, but O’Connor (1995) noted that *Acacia karroo* seedlings survival was improved by grass shading of seedlings, presumably due to improved moisture availability. He attributed this to the effect of shade on moisture availability. In Kwa-Zulu Natal, South Africa, Walters *et al.*, (2004) found that *Dichrostachys cinerea* seeds did not germinate in the field after fire and that burning of *A. karroo*, *Acacia nilotica* and *Acacia luederitzii* seeds did not affect germination. All of the above mentioned species have been identified as problem species implicated in bush encroachment.

No work on microsite effects on seed germination and seedling establishment of bush encroaching species in Namibia has been done, except for a current study which is investigating the effects of parent trees on seedling survival of *A. mellifera* (Joubert, 2007). Kraaij & Ward (2006) concluded that grass competition was generally not a factor in semi-arid rangelands.

Study Area

The Highland Savannah Vegetation Biome of central Namibia (Fig. 1) (Giess, 1971) is a semi-arid Savannah biome characterised by a mean annual rainfall of approximately 360 mm (CV = 39.6 %) in Windhoek (Namibia Meteorological Services). There is a gradient of decreasing mean annual rainfall from east to west. Most rain falls within the months of October to April.

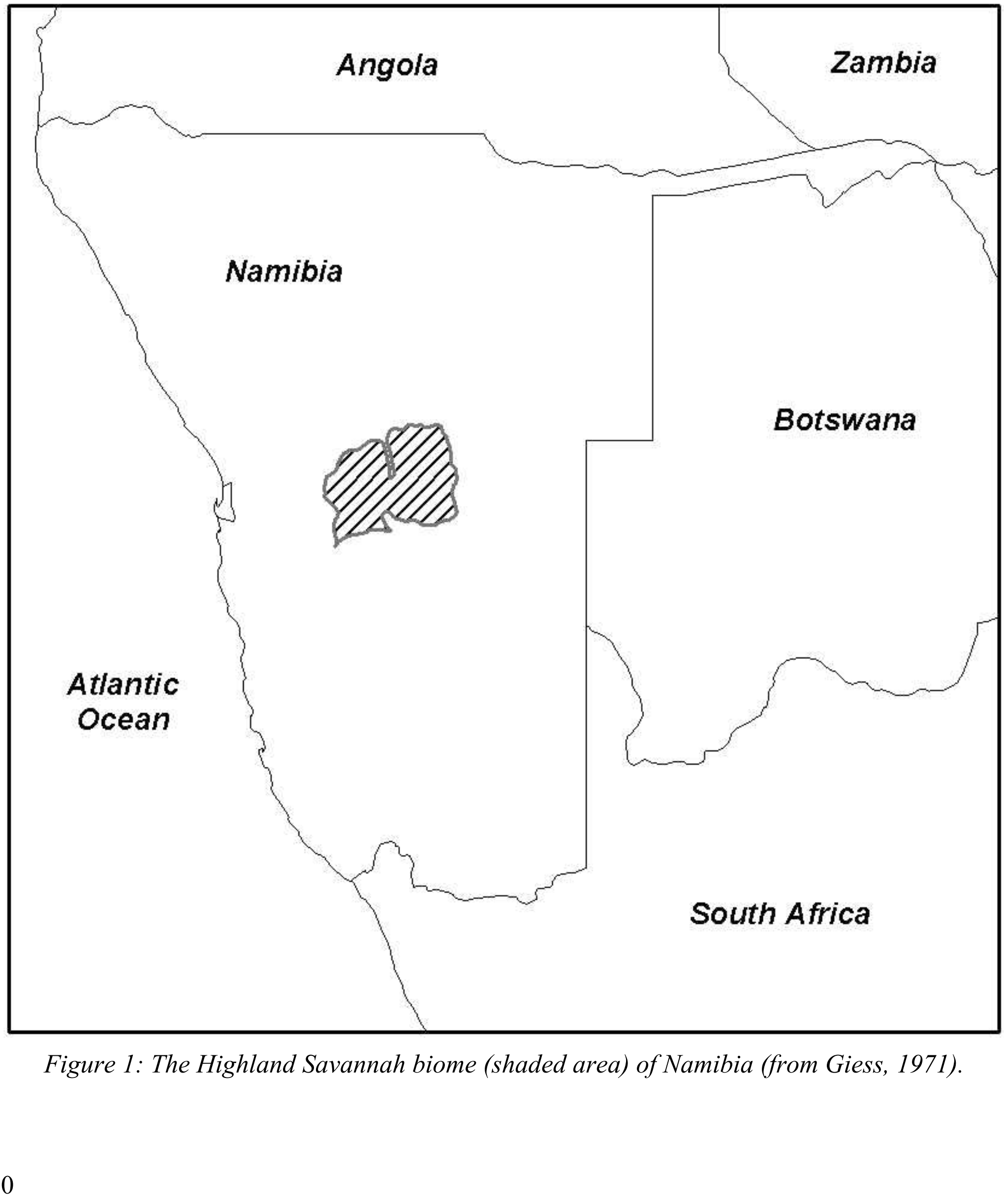

Figure 1: The Highland Savannah biome (shaded area) of Namibia (from Giess, 1971).

In summer, maximum temperatures are lower than would be expected for an area just north of the Tropic of Capricorn, due to the area's elevation, while winters are very cold (minimum temperatures of -7ºC are recorded occasionally) and frost occurs frequently (Mendelsohn *et al.,* 2002). The terrain is broken and undulating, at altitudes ranging from 1 350 to 2 400 m above sea level and with slopes exceeding 30º in places. The steep slopes are covered by a shallow lithic leptosol (Mendelsohn *et al.*, 2002) typically only 30 cm in depth and with a high gravel content, largely comprising of schist and quartz.

Although bush encroachment in the Highland Savannah is less of a problem than in the Thornbush Savannah just north of the Highland Savannah (Giess, 1971) where rainfall is higher and soils are deeper, *Acacia mellifera* subsp. *detinens*, the main encroaching species, can reach densities of over 15 000 individuals per hectare (Joubert, 2007). In the Highland Savannah, bush encroachment primarily seems to affect footslopes (Fig. 2). The steep slopes of the Highland Savannah are characterised by a covering of mostly rounded quartz pebbles (resulting from prior erosion). This cover of pebbles often approaches 100 % (Fig. 3) but is less on footslopes than steeper midslopes (Joubert, 1997). This almost continuous layer affords significant protection from evaporation, functioning in a similar way to litter mulch.

Figure 2: Typical Highland Savannah slope on farm Krumhuk near Windhoek. Note that bush encroachment only occurs on the footslope.

In view of this function the layer may therefore be considered as "pebble mulch". It might be expected that the pebble mulch prevents seeds from contacting the soil, and would thus reduce germination success. However, observations in the field in January 2001 showed that many seeds of *A. mellifera* had germinated on top of the pebble mulch, after the exceptionally high rainfall of 1999/2000 (more than double the long term mean annual rainfall). These seedlings died prematurely, with the radicles barely emerging more than a few millimetres from the testa. In these cases, the radicles were too short to reach the soil surface below before they dried up, owing to a lack of follow up rain or insufficient energy reserves. There is not likely to be much seed burial by rodents and insects under a pebble-mulch, since the pebble cover is so extensive, and well embedded in the loamy sand soil. Where the roots of seedling do reach and penetrate the soil it would be expected that the stone cover improves the chances of survival and establishment through its mulching effect, and protection of the soils from rain-splash impact. Normally, steep stony mid-slopes in the Highland Savannah are characterised by being in better veld condition than less stony footslopes, with a much better cover of climax or decreaser perennial grasses (Joubert, 1997).

Seed supply from mature fruiting *A. mellifera* trees is intermittent and rare in the Highland Savannah and is strongly correlated with rainfall (both for seed production and seedling establishment) (Joubert *et al.*, 2008). Seed banks are thus ephemeral (Joubert, 2007; Bester

Figure 3: A typical "pebble mulch" cover in the Highland Savannah. In this photograph, there is almost 100 % cover of the soil by mainly quartz pebbles.

pers. comm.). The exceptionally high rainfall in 1999-2000 initiated significant production of seeds, while the following year's high and well-spaced rainfall allowed for good seedling survival (Joubert, 2007).

This paper reports on the results of a study of seed germination/emergence and seedling survival under controlled conditions to address the following questions: Will pebble mulch inhibit initial seedling establishment if seeds germinate on the surface? Will pebble mulch enhance the survival and vigour of seedlings when compared with no stone cover?

Materials and Methods

Eight seeds were planted in each of 12 trays of 8 cm depth for each of the following planting treatments:

A. 3 mm (two seed widths) below the soil surface, without pebble cover.
B. Two seed widths below the soil surface, with 100 % pebble cover.
C. On the soil surface, with 100 % pebble cover.
D. On top of 100 % pebble covering the soil.

Soil (loamy sand which is typical from the Highland Savannah slopes) was obtained from Krumhuk farm 30 km south of Windhoek, where *A. mellifera* dominates, and this was chemically analysed (Table 1). All treatments used the same soil, which was free of any seeds prior to the trial. Supplementary watering was provided. This allowed soil moisture comparisons to be made between treatments. Only one supplementary watering of the equivalent of 5 mm of rain was added before germination occurred. A total of the equivalent of 250 mm of rainfall was received by each treatment during the experiment, including supplementary watering.

Soil moisture was determined using a simple gardening soil moisture testing meter with additional gradation to refine the accuracy of reading, just before supplementary watering (the meter was unitless but allowed comparisons to be made). This provided some indication of the maximum water stress that seedlings in different treatments were subjected to. Seedling survival and vigour (measured as the number of leaves per seedling) was determined five times during the course of the trial (7, 12, 15, 28 and 34 days after resuming), which ran from 30 March to 4 May, 2001).

A one-way ANOVA (StatSoft, 1999) was conducted to determine whether significant differences in soil moisture levels, germination/emergence, seedling survival and vigour (the number of leaves per seedling) occurred between treatments. Subsequently, *post hoc* comparisons were made using the LSD (Least Squares Difference) test to determine which treatments significantly differed in each measurement (soil moisture levels, germination, seedling survival and vigour). In all cases data were close to normally distributed.

Results

The experiment simulated fairly extreme conditions, since seedling trays would have experienced higher evaporation and drainage rates than the situation in the field.

Overall germination/emergence was very high (82 % ± 17.5 %). This is to be expected since *A. mellifera* seeds have a thin testa and do not rely on passage through the alimentary canal of an ungulate to break dormancy. In fact, the great majority of seeds ingested by ungulates are destroyed in the gut. Only 3 % of seeds ingested by steers germinated in laboratory conditions (Donaldson, 1967).

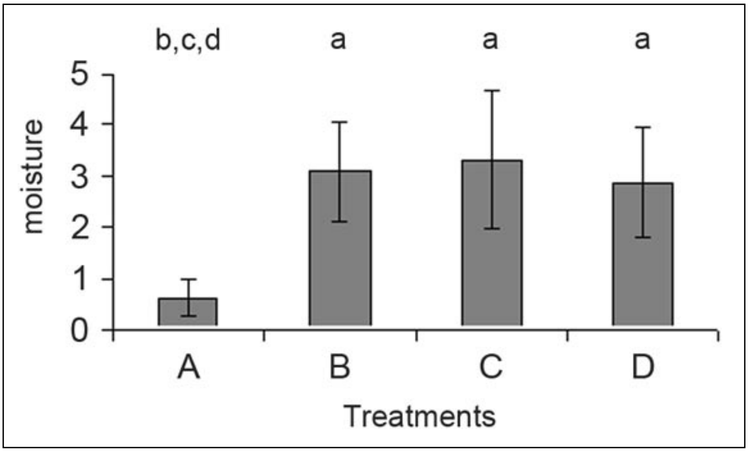

Figure 4: Soil moisture as measured with a soil moisture test kit. Actual soil moisture is not measured. The numbers provide a relative measure. Letters denote significant differences (p < 0.05 – LSD post hoc comparison test). Bars denote standard deviations. N = 12 for each treatment.

Although treatments where seeds were placed above ground showed a slightly (but significantly) higher germination/emergence success (Figure 5), germination rates of treatments A and B may have been underestimated since the germination process underground could not be observed, and some germinated seeds may have died from fungal infections before emerging. Most seeds germinated/emerged within seven days of planting.

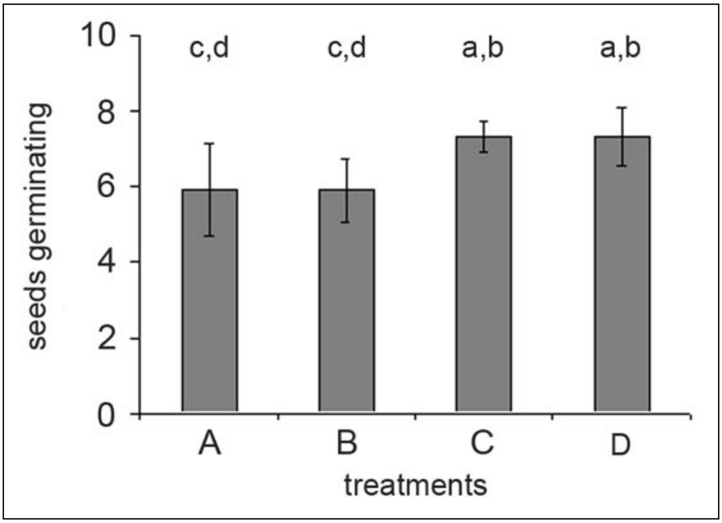

*Figure 5: Mean germination per seed tray of A. mellifera in the four different treatments:
Letters denote a significant difference (p < 0.05, LSD post hoc comparison test). Bars denote standard deviations. N = 12 for each treatment.*

Seedling survival in the initial stages was low in treatment D (33 %), as seedling radicles were exposed to the air and easily desiccated. Observations in the field indicate that a small radicle normally emerges after germination before seedlings die due to exposure to air and insufficient moisture. Once the radicles had grown and entered the soil however, seedling survival was high (97 % of the remaining seedlings survived) (Figure 6). Pebble mulch treatments overall showed significantly better survival rates than Treatment A (no “pebble mulch”). Treatment A showed very low survival rates overall (Figure 7).

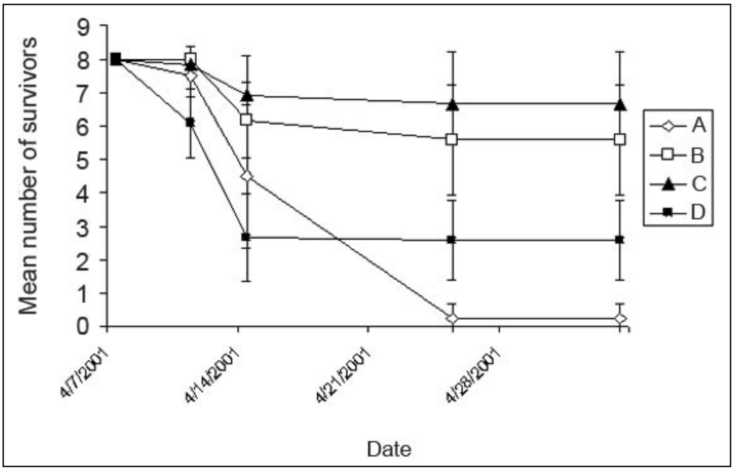

Figure 6: Seedling survival throughout the trial for the different treatments (error bars denote standard deviations). N = 12 for each treatment.

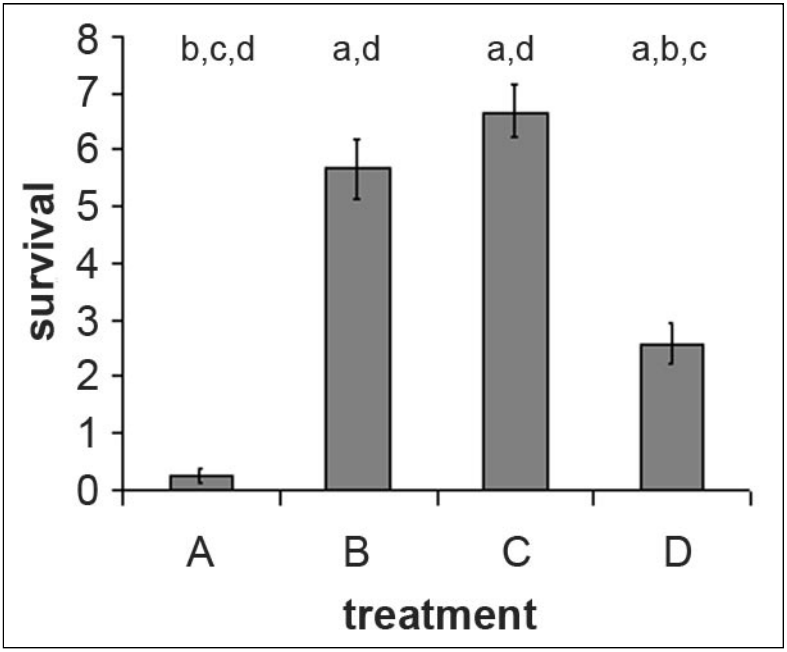

Figure 7: Overall seedling survival at the end of the trial (from 8 seeds in each tray). Letters denote significant differences between treatments ($p < 0.05$, LSD post hoc comparison test). Bars denote standard deviations. N = 12 for each treatment.

The vigour of seedlings in all "pebble mulch" treatments is significantly higher than for without "pebble mulch" (Figure 8). It is unlikely that the seedlings surviving Treatment A would have survived a dry winter, as they were spindly and lacked woody development and thorns.

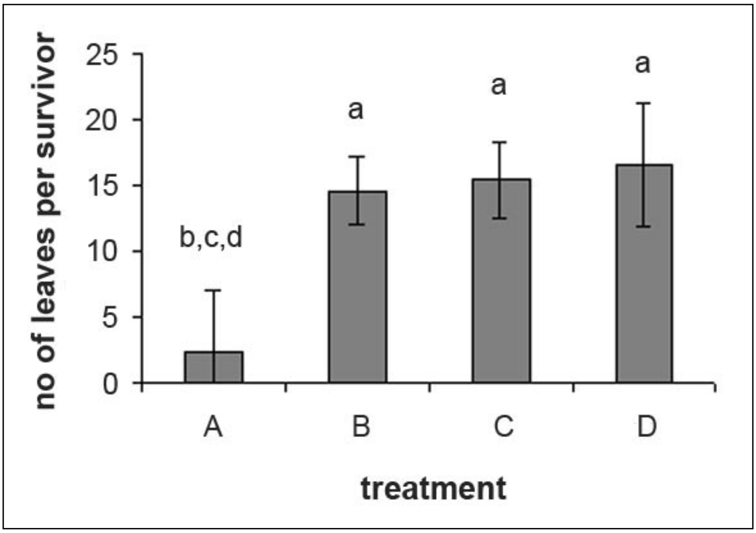

Figure 8: Vigour (as expressed as number of leaves per survivor). Letters denote significant differences between treatments ($p < 0.05$; LSD post hoc comparison test). N = 12 for each treatment c,d

Discussion

A. mellifera only produces large amounts of seeds in good rainfall years, as occurred in 1999-2000 (Joubert *et al*, 2008). *A. mellifera* does not depend on dispersal by ungulates since ungulate alimentary tracts are likely to destroy the seeds, which are thin and have a thin testa (Donaldson, 1967), unlike other *Acacia* species, including *A. erioloba*, which has a thicker, harder testa. In *A. erioloba* and other *Acacia* species with indehiscent pods, the passage through an ungulate's alimentary canal favours germination (Hoffmann *et al.*, 1989; Barnes, 2001; Miller, 1994). In the field, very few seedlings of *A. mellifera* are found far from parent trees. If rainfall is poor following seed set, very few or no seeds are likely to remain in the seed bank, since germination occurs easily (Figure 5) but seedlings do not receive sufficient rain to survive. In poor rainfall years then, the seed bank is likely to be eliminated by germination with 100 % mortality of seedlings. This is supported by Donaldson's (1967) observations in the Molopo region in South Africa and Bester's (*pers. comm.*) in Namibia, as well as Joubert's unpublished field data. In good rainfall years (in the 2000-2001 season, rainfall was above average and well spaced), establishment may be very high, particularly if microsites are favourable. This would depend upon seed production in the previous year. In 1999-2000 very high seed production was observed in the field in the Highland Savannah, whereas in the previous three seasons at least, no seed production occurred in monitored plots (Joubert, 2007.). At least two consecutive favourable rainfall years seem to be necessary for the establishment of seedlings (Joubert *et al*., 2008).

Initially, the pebble mulch acted as an impediment to seedling establishment. However, surviving seedlings whose radicles managed to penetrate the soil surface showed very high survival after establishment. Seedlings in soils without pebble cover showed almost no survival by the end of the experiment due to the almost negligible residual soil moisture prior to rain events and supplementary watering. Seedlings under pebble cover showed much higher vigour, due to the greatly improved soil moisture conditions. These seedlings showed signs of secondary growth and are thus much more likely to be able to survive winter frosts than the rather spindly seedlings surviving with no pebble mulch. Although pebble cover initially inhibits seedling establishment, the density of seedlings managing to establish is sufficiently high to negate the initial inhibition, and in fact promote establishment.

Stone or pebble cover is important for improving soil moisture conditions in the Highland Savannah and probably has a profound influence on vegetation structure. On typical steep slopes, where pebble cover is generally high, there is usually a greater cover of decreaser perennial grasses than on footslopes with little pebble cover (Joubert, 1997), partially as a result of improved soil moisture conditions, as well as less utilisation by ungulates. In such cases the positive effect of pebble cover on *A. mellifera* seedling establishment is countered by the greater competition with grasses for moisture, increased likelihood of fires, and the fact that dispersal up slope is probably very limited. However, in areas where this grass cover is removed (as through overgrazing), *A. mellifera* seedlings may survive and establish in rainfall conditions lower than what might be expected. This means that *A. mellifera* thickets may creep up slope, which currently is not normally the case. The observation that bush encroachment is currently generally restricted to foot slopes in the Highland Savannah partially reflects the greater seed banks present on foot slopes owing to water movements, and the presence of more parent trees. However, gradual upslope seed dispersal cannot be discounted. Continuous grazing on steep pebbly mid slopes after exceptional rainfall may initiate a bush encroachment event and change the pattern of encroachment in the Highland Savanna from being mainly restricted to footslopes to occurring more generally on steeper midslopes and upper slopes.

In determining models for seedling survival in relation to rainfall, the microsite effects of pebble mulch and landscape effects must be considered.

Conclusions

Rangeland managers need to take microsite effects on vegetation dynamics into account. Excessive grazing on steep pebbly slopes may initiate bush encroachment events where they are not normally observed. This may significantly increase the extent of bush encroachment on rangelands with negative effects on rangeland production and biodiversity.

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Diversity measures in comparative rangeland studies: application and advantages of Species Abundance Distributions and diversity profiles

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Abstract

Biodiversity consists of the two components richness and evenness. Diversity indices such as the Shannon or Simpson index are commonly used to describe diversity patterns for sampled habitats or plant communities. However, these indices are ineffective for comparing richness and evenness at the same time. This might lead to a biased interpretation of actual diversity patterns. With this article we aim at describing two alternative approaches for comparing diversity patterns that, in combination, allow an effective visualisation of those patterns; curves for ranked species abundance distributions and diversity profiles. In a case study scenario, we compare biodiversity measurements within and between a Thornbush savannah and the Nama Karoo. Furthermore, we briefly discuss possible applications of these methods in rangeland and restoration ecology.

Keywords: conservation; biodiversity; species richness; evenness; species abundance distribution; diversity ordering; savannah

Introduction

Originating from the rather scientific and value neutral term biological diversity, the more ethical and valuable expression ‘biodiversity’ was coined by Edward O. Wilson at a conference for conservation biologists and was spread later on with a book called “biodiversity” (Wilson & Osbourne, 1988). Today, an overwhelming amount of studies was undertaken on the subject of biodiversity in various disciplines, not only in biology itself, but also in physics, mathematics, philosophy and economy. To this day, the protocol “Convention on Biological Diversity”, formulated in Rio de Janeiro 1992, was ratified by 168 countries worldwide (www.cbd.int). This treaty mandates national environmental organizations worldwide to ensure a sustainable use of biodiversity and assure its conservation.

The scientific term ‘biodiversity’ or ‘biological diversity’ in general is descriptive for the variation of life at different levels of organization, such as the diversity of genes, species, populations and ecosystems. By this, a versatile perception of the irreplaceable importance of biodiversity evolved in terms of (i) the ecological services it can provide (Myers, 1996; Hooper et al., 2005), (ii) the economical values it contains (Pimentel et al., 1997; Weikard, 2002), and (iii) also its philosophical and ethical values (Takacs, 1996; Oksanen & Pietarinen, 2004). From a more statistical point of view there are various ways of how to measure biodiversity. Much has been published on the measurement of biodiversity (Williams & Gaston, 1994; Rousseau & Van Hecke, 1999; Magurran, 2004; Stohlgren, 2007), but still uncertainty remains regarding the comparison of biodiversity measurements (Gotelli & Colwell, 2001; Maurer & McGill, 2004; Kindt *et al.*, 2006).

A common approach to compare samples containing information on biodiversity is to calculate diversity indices, e.g. Shannon or Simpson's Index, and to determine whether there are significant differences or not. The variety of techniques and indices developed for the analysis of biodiversity does not make it easier to choose the right tool for comparing biodiversity measurements (Magurran, 2004). The most frequently used index today is simply the number of species in a sample, termed species richness (or species density if it was sampled for a defined area). In fact, biodiversity consists of two components, richness and evenness. The latter one is related to the abundance of the species in the sample. Species abundance data are counts of individuals but equally, percent plant cover or the biomass of a species can be used (Magurran, 2004). However, besides the hard to interpret Shannon Index of diversity (Magurran, 2004), which allows incorporating both richness and evenness, all diversity indices are just univariate measures of one component of diversity. Thus, species richness alone cannot tell us the whole story about the diversity of a community. This was also suggested by Wilsey *et al.* (2005), who compared univariate measures of plant diversity of temperate grasslands for their importance using a multivariate approach. The author found that species richness does not stand out as a single all explaining surrogate for biodiversity. Thus, analyses based only on species richness without considering evenness might miss important information in describing biodiversity.

The problem of incomplete measures of biodiversity has been recognized in ecological literature, and more visual and complex methods for comparison were developed. In this study we address two of these approaches for the comparison of (i) different plant communities and/or habitats, as well as (ii) measures of biodiversity by using datasets from semi-arid savannah rangelands in Namibia. In order to contrast different communities or habitats, curves of ranked species abundances, so called species abundance distributions (SAD), were applied. These depict a characteristic distribution for a sampled habitat according to the richness and the evenness of the species found. Recently, the SADs were again proposed as useful tools, and thus a revival in ecology is in sight (Magurran, 2007; McGill *et al.*, 2007).

The second technique applied allows a sound comparison of diversity measurements, and results within and among certain plant communities or habitats. Richness and evenness measures cannot be compared effectively, yet both are important to describe diversity. To incorporate both aspects, a method that provides an ordering of samples according to both richness and evenness was needed. Patil and Taillie (1977) developed a technique called diversity ordering, a method in which multiple diversity measures are implemented at once and communities or samples are displayed as curves. These diversity curves, called diversity profiles (Kindt & Coe, 2005), allow a visual and quantitative comparison of multiple aspects of diversity.

With this article we want to actively revive the usage of species abundance distributions and the diversity ordering technique for conservation management and ecological research. By describing the methods with a case study from southern and central Namibia we want to show the simplicity of the methods and demonstrate their effectiveness in comparing diversity patterns within and between ecosystems. However, it is worth to mention that the intention of this article is rather to give an overview of the methods, than interpreting patterns found in an ecological context. Suggestions for possible applications in conservation management and environmental science will be addressed briefly in the discussion section.

Study area

The four study sites are situated in southern and central Namibia (Figure 1) along a precipitation gradient oriented from north to south. Climate is semi-arid with an average annual rainfall of about 250 - 350 mm.

The rainy season is summer (October - April), but rainfall pattern shows a high interannual and spatial variability.

The two most southern study sites Niko-North (NIK-N) and Niko-South (NIK-S) are located in a communal area approximately 90 km south of Mariental (NIK-N: 25°20’01”, 17°50’58”; NIK-S: 25°20’34”, 17°50’22”). The rangeland is fenced allowing resting periods for the vegetation at NIK-N and NIK-S, respectively.

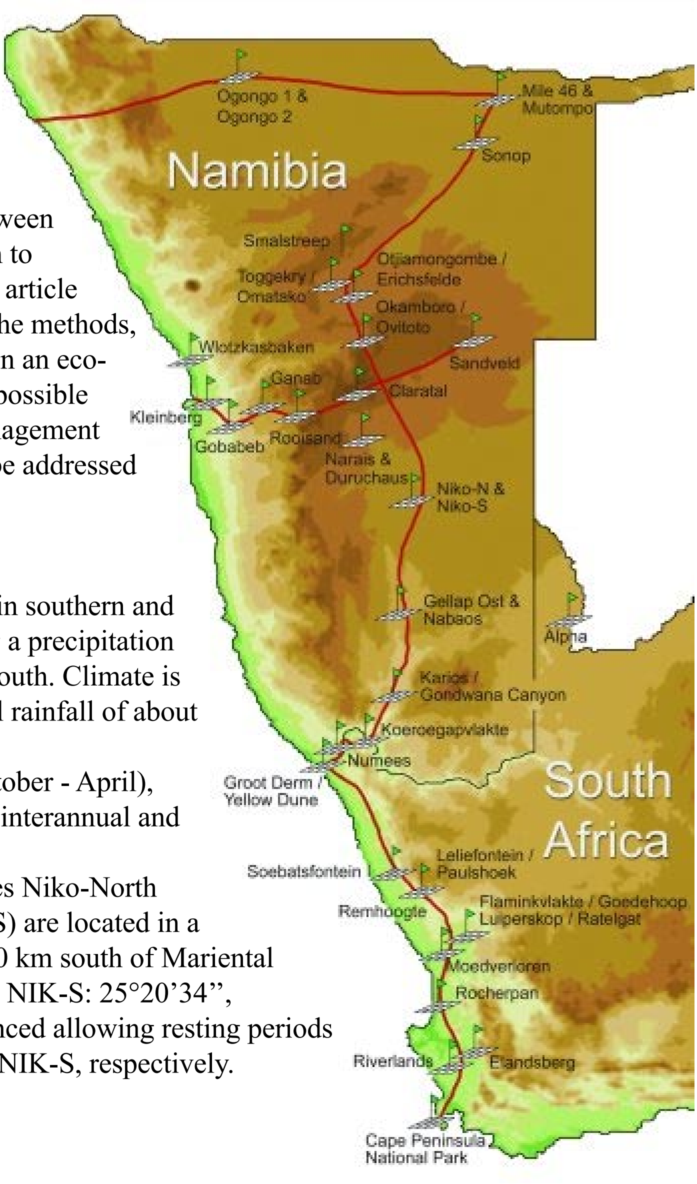

Figure 1: *Location of test sites along the trasect of BIOTA Southern Africa, indicated by white arrows.*

The adjacent sites are grazed rotationally mainly by goats. Vegetation is best described as an open grassy shrubland with trees growing only scattered, and is typical for the Nama Karoo biome (Palmer & Hoffman, 1997). The two northern study sites, Otjamongombe (OTJ) and Omatako-Ranch (OMA), are commercial livestock and game farms, respectively, located about 130 km south of Otjiwarongo (OMA: 21°28’53”, 16°43’39”; OTJ: 21°35’48”, 16°56’06”). Following Giess (1971), both sites fall into the vegetation zone of the Thornbush savannah. Vegetation is characterized by a continuous grass and herb layer and more or less dense stands of mainly thorny shrubs and small trees (mostly *Acacia* spp.). On each of these four farms a test site of one square kilometre was established by the BIOTA Southern Africa biodiversity monitoring project (www.biota-africa.org).

Methods

Field data

All four test sites are 1 km x 1 km in size. Each square kilometre was subdivided into 100 plots of 1 ha and stratified according to occurring habitat types. Within these strata 20 hectares were selected by a random sampling procedure considering the relative dominance of each type of habitat. On each of these 20 selected hectares of each test site, one central monitoring plot of 1000 m² (20 m x 50 m) was established. On these plots, plant species composition and cover was monitored within the rainy season on a yearly basis since 2001. The monitoring data used for this paper are from April 2005 for OMA and OTJ and from April 2007 for NIK-N and NIK-S, respectively.

SAD Curves

SAD Curves, which are also called Rank – Abundance Dominance (RAD) or Dominance / Diversity plots (Whittaker, 1965), display logarithmic species abundances against species rank order. The calculation of these curves is in fact relatively simple. Firstly, the species in the community are ranked according to their total abundance for all records within the respective habitat or study site. Secondly, the ranked species are plotted on the X-axis and their log abundance on the Y-axis. Resulting curves usually show a declining trend, revealing several important aspects to interpret the diversity of the samples considered. Plotting several SADs in one graph allows for visual comparison of the diversity patterns of several communities at once. Important features of these plots are the relative abundance of common and rare species. There is usually a tail of species depicting the number of species that occur only once in the community (Murray *et al.*, 1999), and a larger set of species with intermediate abundance and usually some more common species. Occasionally, there are a few very dominant species that might be considered as indicators, e.g. for mass occurrences of invasive plants, blooms of therophytes or bush encroached habitats. It is possible to fit a mathematical model to a SAD curve, such as a log-normal or broken stick distribution, in order to test against a specific null-hypothesis. Up to now, it is still debated which model best describes the process that leads to a certain community structure (McGill *et al.*, 2007), e.g. competition for niche space. We think, including mathematical models will rather increase the complexity of the method than increase its applicability. Therefore, it will suit our purpose to simply analyse the resulting curves by visual and numerical comparison.

SAD curves were created for each single test site, and finally plotted together for an overall comparison. Abundance values used throughout the whole study do not rely on counts of individual plants but are based on plant cover estimates, i.e. for one curve the cumulative cover value of a certain species from all 20 plots per test site was used. Cover estimates as a proxy for abundance is commonly used and widely accepted in vegetation ecology (Magurran 2004).

Diversity Profiles

The core idea for ordering diversity indices from richness to evenness is based on the work of Álfred Rényi (1961) who developed a generalized entropy formula based on the concept of Shannon's entropy (Shannon, 1948), which plays a central role in information theory. In the 1970s, Hill (1973) and Pielou (1975) recognized that three diversity indices mostly used by ecologists are specific cases of Rényi's entropy formula: species richness, Shannon Diversity and Simpson Diversity. Later, Kindt *et al.* (2006) added the Berger-Parker Index. The Simpson and the Berger Parker Index are measures of dominance (evenness), whereas the Shannon Diversity Index mixes richness and evenness. Diversity profile values (H-alpha) were calculated from the frequencies of each component species (proportional abundances p_i = abundance of species i/ total abundance) and a scale parameter (α) ranging from zero to infinity (Tóthmérész, 1995) as:

$$H_\alpha = \frac{\ln\left(\sum p_i^\alpha\right)}{1-\alpha}$$

The four diversity measures are related to respective values of the scale parameter α, H_0 = species richness, H_1 = Shannon Diversity, H_2 = Simpson Diversity and H_∞ = Berger-Parker Index (Legendre & Legendre, 1998, Kindt *et al.* 2006):

$$H_0 = \ln(S)$$

$$H_1 = H = -\sum p_i \log p_i$$

$$H_2 = \ln(D^{-1}) = \ln\left(\sum (p_i^2)^{-1}\right)$$

$$H_\infty = \ln(d^{-1}) = \ln(p_{max}^{-1})$$

A given community A is truly more diverse than community B if the diversity profile for community A is everywhere above the diversity profile for community B. Communities that have intersecting profiles can only be partially ordered in diversity. Intersecting profiles (partial diversity ordering) demonstrates why ordering techniques such as the Rényi series are needed, since a single diversity index will not provide sufficient information. The values of the series for the four BIOTA test sites were calculated for the scales of α = {0, 0.25, 0.5, 1, 2, 4, 8, ∞} and plotted as diversity profiles for each related pair (OMA and OTJ, NIK-N and NIK–S) and for all sites together in a single graph.

Software

All analyses were carried out using R (R Development Core Team, 2005), a statistical software freely downloadable from www.cran.r-project.org. The following packages were used to calculate the statistics: *vegan* (Oksanen et al., 2005) and *BiodiversityR* (Kindt & Coe, 2005). Graphics were produced within R and optimized using SigmaPlot Version 10.0 (Systat Software, 2006).

Results

SAD curves

The species abundance distribution for each test site is presented in Figure 2. The distribution for NIK-N reveals a relatively short range of total species (n=23) on the x-axis. There is one dominant species, a set of more common species (n=2 – n=11), and several rare species. The tail consists of six rare species that only show up once over all 20 sampled plots. There is almost a linear decrease in ranked abundance, yet distorted by one dominant species. The ten

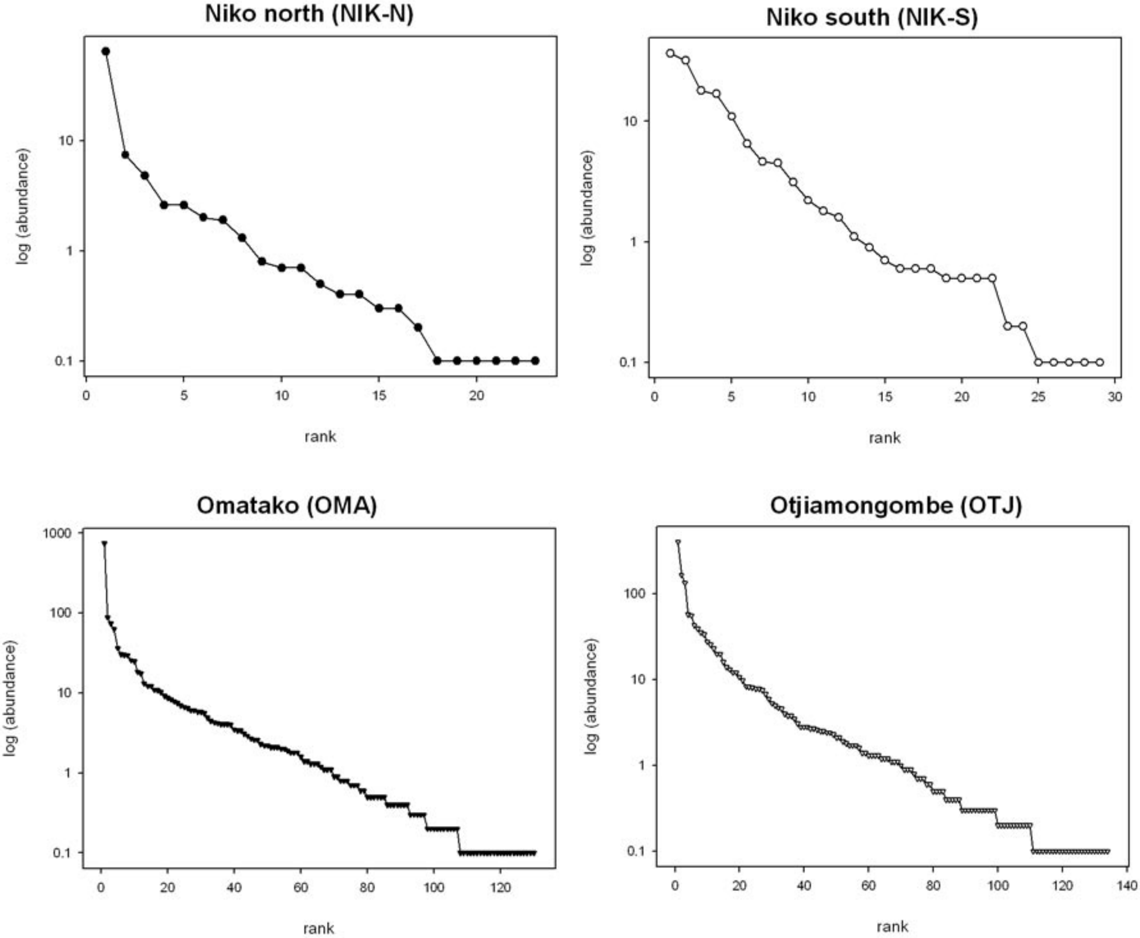

Figure 2: *Species abundance distributions for the four test sites. Upper row showing the test sites Niko north (NIK-N) and Niko south (NIK-S), the lower row Omatako (OMA) and Otjiamongombe (OTJ). Abundance is based on cumulative cover values per species per test site.*

Table 1: *Ranks of the 10 most abundant species on the four test sites according to Figure 2 and their average abundance per site (n = 20 plots). The calculated average abundance is based on cover values (%). Values for test sites NIK-S and OTJ are given in bold.*

	Rank									
NIK-N / **NIK-S**	1	2	3	4	5	6	7	8	9	10
Acacia nebrownii	**25**									
Asteraceae sp.										**2**
Boscia foetida							**3**			
Calicorema capitata			5			**5**				
Catophractes alexandri							2	**3**		
Geigeria pectidea									1	
Lycium bosciifolium										1
Phaeoptilum spinosum			**12**			2				
Rhigozum trichotomum	70			**12**						
Salsola spp.		8								
Stipagrostis anomala									**2**	
Stipagrostis hochstetteriana								2		
Stipagrostis uniplumis		**22**		3						
Xerocladia viridiramis					3					
Ziziphus mucronata					**7**					
OMA / **OTJ**	1	2	3	4	5	6	7	8	9	10
Acacia mellifera		6/**12**								
Acacia reficiens				4					**3**	
Albizia anthelmintica									2	
Aristida congesta				**4**						
Aristida rhiniochloa					**4**					
Enneapogon cenchroides								**3**		
Eragrostis annulata							2			
Eragrostis lehmanniana							**3**			
Eragrostis porosa			5							
Gisekia africana										**2**
Grewia flava						**3**				
Leucosphaera bainesii										2
Lycium eenii						2				
Monechma genistifolium			**10**							
Pogonarthria fleckii					3					
Requienia pseudosphaerosperma								2		
Stipagrostis uniplumis	51/**30**									

most abundant species for all test sites are given in Table 1. For NIK-N the most dominant species reaching a cumulative cover value of about 70% is *Rhigozum trichotomum*. NIK-S has 29 species in total, and shows a similar shape of the curve like NIK-N, except that there is no dominant species. The general pattern shows that there are more abundant species on NIK-S than on NIK-N.

The lower left graph in Figure 2 shows the SAD for OMA, which has a total number of 130 species, where we find 40 rare species, a large set of intermediate and common species, and four abundant species. The shape of the curve shows a slight linear decrease but is distorted by the more abundant species. The lower right graph in Figure 2 for OTJ shows again a similar picture, with around 134 species in total, yet a longer tail and less intermediate species. The highest abundance found on OTJ equals 403 percent summed up for all 20 hectares. The general shape of the curve is more elbow-like than a straight linear decrease.

A direct comparison of the four test sites allows distinguishing the characteristic pattern of a particular environment (Figure 3). The two long curves with the many 'tail species' and the highest abundance values are the test sites from the thornbush savannah, whereas the shorter and steeper curves come from the Nama Karoo test sites.

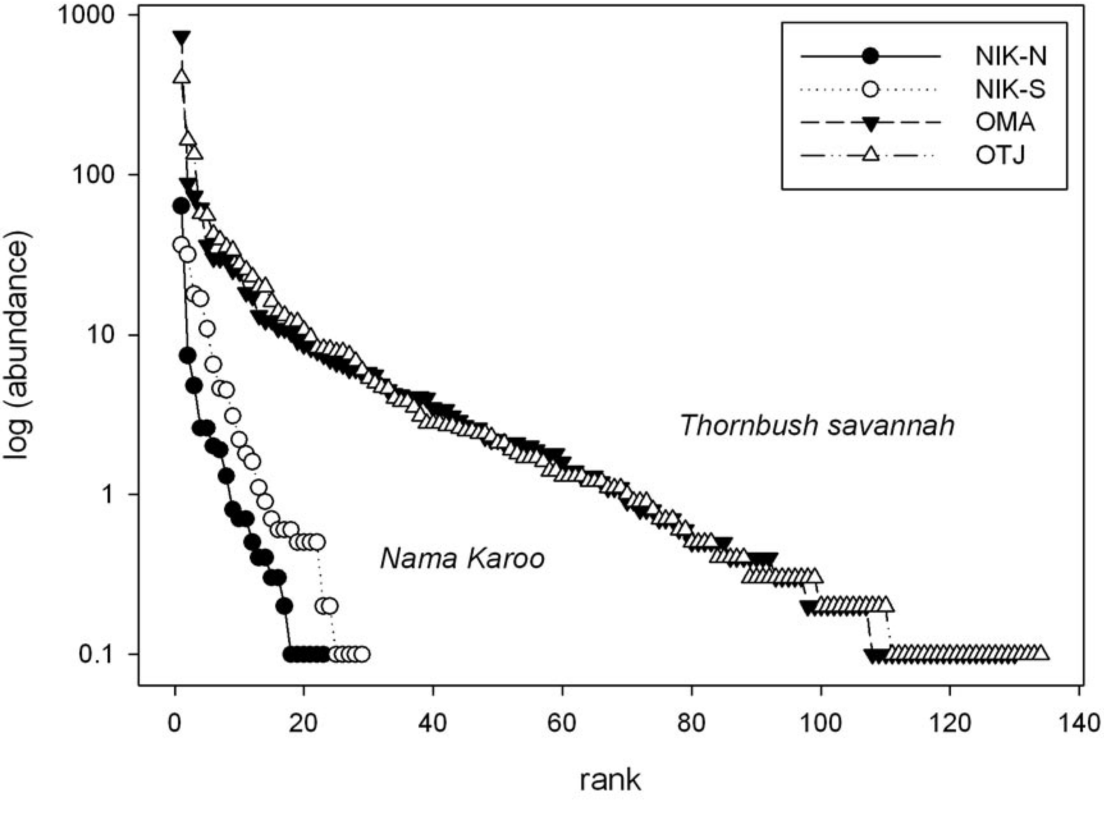

Figure 3: *Species abundance distribution for Thornbush savannah and Nama Karoo test sites*

Diversity Profiles

The diversity profiles of all four test sites are presented in Figure 4. The profile for NIK-S is consistently higher than that of NIK-N, whereas the values for species richness at H_0 are still rather tight for both test sites. The curve for NIK-N shows a clear bend towards low values of H-alpha at higher scales of alpha. The lowest values for NIK-N are at $H\infty$ with 0.35, NIK-S yields 1.38. OTJ has consistently higher values than that of OMA. Both test sites have rather similar values for species richness at H_0, but they spread at higher scales of alpha.

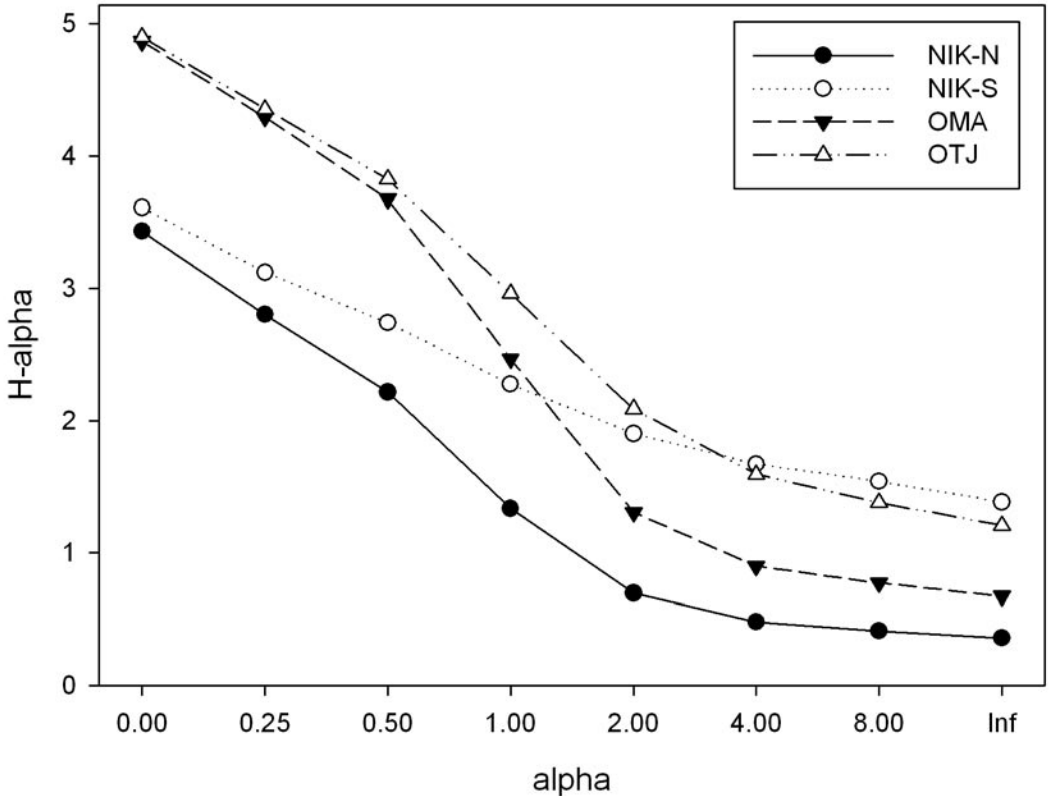

Figure 4: *Diversity profiles for Thornbush savannah sites, Omatako (OMA) and Otjiamongombe (OTJ), and Nama Karoo test sites, Niko north (NIK-N) and Niko south (NIK-S)*

The Thornbush savannah sites OMA and OTJ have much larger values at H_0 and H_1 (H_1 representing Shannon's Diversity) than the Nama Karoo test sites. Comparing the two different regions, it reveals that OTJ and NIK-N show a similar shape, although NIK-N is less diverse on all scales. In contrast, OMA begins approximating the curve of NIK-N from H_2 on, representing the Simpson Index. However, from scales larger than H_2 OTJ crosses the curve of NIK-S. NIK-S shows no steep decline. Looking at H_0 and H_4, it becomes obvious that NIK-S cannot be ranked highest according to richness, but it possesses the most even community structure of all test sites. Values for relevant scales of alpha at all sites are given in Table 2.

Table 2: *H-alpha values for important scales of α. Also listed are, species richness (S) and evenness at H_1 ($E_{1,0}$).*

Test sites	H_0	H_1	H_2	H_∞	$E_{1,0}$	**S**
NIK-N	3.43	1.33	0.69	0.36	0.12	23
NIK-S	3.61	2.28	1.90	1.38	0.26	29
OMA	4.87	2.47	1.31	0.67	0.09	130
OTJ	4.90	2.96	2.09	1.21	0.14	134

Discussion

Species Abundance Distributions

The grazing history of the test site Niko is inexplicit as we did not get any reliable data on the management practice applied over the last decades. NIK-N and NIK-S are situated each in one of three camps in total which are grazed in a rotational manner. This grazing regime has been retained unchanged for several years (Sarah Boeck, resident of Namibia, 2008, personal communication). However, Akhtar-Schuster, who monitored vegetation dynamics on the NIK test sites from 2001 to 2003, was given contrary information by the local community (Mariam Akhtar-Schuster 2009, personal communication). According to this, the northern camp (location of NIK-N) has been under sustained intense grazing for many years opposed to the southern camp (location of NIK-S), which was always used as a grazing reserve. Species abundance distributions for NIK-N (Figure 2, top left) and NIK-S (Figure 2, top right) clearly show different patterns that might reflect the results of different grazing regimes. On NIK-N there is a single dominant species (*Rhigozum trichotomum*), whereas no similar pattern can be found for NIK-S. For NIK-N *R. trichotomum* is ranked first with very high values of cover (≈ 70%) for the whole 20 hectares sampled. *Salsola* sp. and *Calicorema capitata* are the second and third most abundant species and reach much lower values (Table 1). Due to its clonal growth *R. trichotomum* often grows in dense stands. This shrub is reported to be an invasive species in the Kalahari region that spreads especially after heavy grazing (Thomas & Twyman, 2004). It can be hypothesized that the mass occurrence found on NIK-N is due to high grazing pressure in the past, and thus the occurrence of *R. trichotomum* in the reserve camp is less prominent. In contrast, the grass shrub ratio on NIK-S corresponds to a shrubland savannah in good condition (proportion of the grass *Stipagrostis uniplumis* ≈ 20%), whereas perennial grasses are far less abundant on NIK-N (proportion of *S. uniplumis* ≈ 3%) indicating a stronger grazing pressure on this valuable and palatable grass. However, although adjacent, not all 20 hectares on NIK-N and NIK-S are comparable concerning the types of habitat. Therefore, further studies addressing the spatial heterogeneity and associated vegetation patterns could give more insights whether the prominence of *R. trichotomum* on NIK-N is related rather to grazing or habitat characteristics and whether more suitable habitat conditions for the growth of *S. uniplumis* occur on NIK-S, respectively. However, the pattern for NIK-S indicates a more intact and less disturbed environment. No extreme values are found and a steady decline in ranked abundances is observed ending up with a short 'step' of rare species. Furthermore, ranked abundances identify *Acacia nebrownii* and *S. uniplumis* as the two most abundant species, whereas *R. trichotomum* reached rank four. The tree *Ziziphus mucronata* occurs with a single individual only on the whole 20 hectares sampled, but appears on the fifth rank. This is because of its high cover value compared to that of shrubby and herbaceous plants, most of them which are ranked much lower. If count data would have been used instead, *Z. mucronata* would have lined up in the tail of the distribution, becoming a rare species. It is unclear how to deal with this special case, but we think that it is rather circumstantial as long as such a species is ranked in between 'common' and 'rare'.

A similar picture to NIK-N and NIK-S can be found for the Thornbush savannah sites OMA and OTJ. Here, the SAD for OMA (Figure 2, bottom left) shows an extremely high value for the first ranked species, followed by three relatively dominant species. The four highly ranked species (Table 2) are characteristic for a grass-shrub matrix occurring in savannahs (*S. uniplumis* 60%, *A. mellifera* 7 %). The graph for OTJ (Figure 2, bottom right) shows a less extreme but still similar picture. Some dominant species can also be found here, the first two are similar to OMA. In relation to species richness, both curves show similar lengths and only little variation in the overall shape. OTJ seems to have slightly more rare species than OMA; 50 species with values smaller than 0.5 % cover for 20 hectares found on OTJ, while 44 rare species were found on OMA. Dominant species might be intuitively interpreted as a result of bad management, e.g. encroaching species rise steadily in dominance (Skarpe 1990). However, one has to identify the role of the dominant species in the ecosystem in order to be able to judge the situation. In our case study, the effect of high abundance values for *S. uniplumis* on test site OMA cannot be seen as negative, at least from a farmer's point of view.

Surprisingly, SADs are not often interpreted using the information of rank order of species, but rely mostly on the fit to a specific mathematical model in order to deduce a process from the observed pattern (McGill *et al.*, 2007). We believe that rank order information is crucial for the understanding of the graphs. In case of OMA and NIK-S, the high abundance values of *S. uniplumis,* a valuable fodder species, can be seen as an indicator for good range condition, whereas the high values for *R. trichotomum* on NIK-N indicate a potentially degraded environment. With this example it should become clear that an ecological interpretation of the graphs is incomplete without considering the species involved and model fitting alone might not be sufficient.

An overall comparison between the test sites for the Thornbush savannah and the sites from the Nama Karoo is given in Figure 3. It is obvious that the savannah test sites have higher species richness, higher species abundance values and include more rare species. Why is a comparison like this interesting? It is one of the strengths of SADs to allow comparisons of totally different ecosystems and to facilitate the visualisation of differences by a graphical solution, which makes the results more obvious and communicable. For example, Hubbell (2001) used SADs to compare diversity patterns of tree species in tropical rainforests with coral reef communities. Murray *et al.* (1999) analyzed the differences in diversity patterns between dry sclerophyll and temperate rain forests, and put an emphasis on differences in the number of tail species. It becomes clear that much less rare species were observed in the drier Nama Karoo than in the Thornbush savannah sites (about 10 on NIK-N and NIK-S versus 50 at OMA and OTJ). However, looking at relative cover values, the difference is not that striking. Overall, species richness of the Nama Karoo sites is lower than of the savannah sites, and the percentage of rare species similar to proportions found in the savannah. Nevertheless, it has to be kept in mind that this can be stated only for the data we have analysed so far and no general conclusions should be drawn from this comparison. Depending on the research question, it can be necessary to also consider environmental factors such as e.g. climate, geomorphology, and management type to allow for valid comparisons of similar ecosystems.

Our intention was to highlight the potential of SADs to allow visual comparisons of different biomes. Interesting questions in this context would be e.g., if the Highland savanna of Namibia, geographically located in between our test sites, would also be intermediate in the SAD plot? Where would test sites from drier areas, e.g. Namib Desert or parts of the Succulent Karoo, line up in the graph, and how would they behave with regard to patterns of dominance and rarity?

Diversity Profiles

The diversity profiles for the Nama Karoo sites (Figure 4) revealed that NIK-S has always higher values for H-alpha than NIK-N, thus it can be concluded that NIK-S is truly more diverse than NIK-N. But the sites do not differ very much in species richness (H_0). The curve for NIK-N starts bending downward at higher values for the scale parameter alpha indicating effects of dominance. Following Kindt (2006), values lower than 0.5 for H-alpha at H_∞ (Berger-Parker index) suggest the occurrence of a species that represents more than 60% of the total abundance. This is true, as we have already seen in the analysis of the species abundance distributions. NIK-S obviously is more evenly distributed, indicating no effects of dominance at H_2 and H_∞. As already mentioned above, this pattern may be due to a more pronounced spatial homogeneity of habitats compared to NIK-N. A similar picture can be revealed for the diversity profiles for OMA and OTJ. Both sites are rather similar according to species richness, but show different patterns for the evenness related indices. Values for H_∞ between 0.5 and 1.5 can still be interpreted as an effect of a dominant species, in this case *S. uniplumis* on OMA.

The comparison of diversity profiles for the Thornbush savannah and the Nama Karoo sites shows an interesting pattern (Fig. 4). The different biomes can be clearly separated according to species richness (H_0). At H_1, equal to Shannon's Diversity, the separation still holds, although the profile for OMA starts to approach similar values found for NIK-S. Looking at the dominance indices (H_2 and H_∞), OMA approaches values close to NIK-N, while OTJ shows similar values like NIK-S. When talking about evenness, the relation of abundance to the total richness has to be considered. An extremely even profile would be a straight line, therefore we can say that OTJ is not as even as NIK-S, as can be recognized by the overall shape of the two profiles. This arises from the fact that there are much fewer species at the Nama Karoo site. For a final ranking of the test sites regarding biodiversity, it becomes obvious that they cannot be truly ordered by diversity, i.e. profile curves cross each other. Hence, if ranking would be only based on species richness the rank order would be different from an ordering based on Simpson diversity or Berger-Parker Index. However, the test sites can be ordered at least partially, i.e. Species richness and Shannon diversity give the same rank order, while Simpson diversity and Berger-Parker Index show different rank orders. A diversification, e.g. an increase in the evenness, would rely on an increase of the abundances of the less frequent species. However, it should be noted that this data results only from one year and that shapes of profiles might look very different using data from other years.

Interestingly, SADs can help to interpret diversity profiles significantly and *vice versa*. Dominant species, which can be identified by the SAD, tend to decrease evenness in a sample, which can be observed in the diversity profile. To know the value and the ecology of the species that influence the observed pattern helps to understand the pattern of commonness and rarity, which allows a sound interpretation of the diversity of the studied systems. We are not aware of any study that has applied a combination of these techniques.

Interpretation of richness and evenness

There has been a debate on the relationship between richness and evenness components and how to interpret them in relation to ecological processes (Stirling & Wilsey, 2001; Ma, 2005). Following Legendre (1998), a possible interpretation for both aspects can be given: species richness can be interpreted as a function of the stability of an environment. The number of species increases with the availability of realized niches, as provided by a stable environment. By this, both, species diversity and environmental diversity, are considered and can directly be linked. The evenness of the species distribution allows evaluating the overall biological activity of the environment. If there is a low evenness there is a high biological activity, e.g. bush encroached savannah ecosystems show a low evenness due to at least one dominant species. Simultaneously, wood production per unit area increases in comparison to a natural savannah. The reduction of resources, e.g. sustained grazing of a perennial grass sward, can favour the dominance of an increaser shrub species, and thus decreases evenness.

Possible applications

We have shown that the described techniques are powerful tools for comparing biodiversity on different scales, from farm level to ecosystem level. In order to stimulate the usage of these methods we would like to share some ideas for possible applications in rangeland and restoration ecology. They might be useful in order to (i) estimate the effectiveness of restoration efforts aiming at restoring biodiversity, (ii) facilitate monitoring of diversity conditions on rangelands (Lewis *et al.*, 1988), (iii) characterise vegetation states in resilience-based state-and-transition models (Briske *et al.*, 2008), (iv) describe general patterns of diversity along environmental gradients, e.g. climatic, topographic and temporal gradients, and (v) conduct ecosystems rankings according to the diversity of occurring communities.

Conclusion

With a case study, we have shown, how SADs and diversity profiles can be applied and interpreted in terms of plant species diversity. Although different techniques have already been proposed for diversity ordering (Tóthmérész, 1995, Liu *et al.*, 2007; Mendes *et al.*, 2008), they are still not very well-known in ecology and not much literature can be found on this topic. Diversity profiles allow a logic and straightforward direct visual comparison and interpretation of the most applied diversity indices in ecology at once. Species abundance distribution curves are a simple, yet powerful tool to identify and compare patterns of diversity. A combination of both techniques allows an even better interpretation of the overall diversity pattern. We strongly emphasize the usage of these methods in monitoring and restoration projects. Further, SADs and diversity profiles could become useful in entangling the ecological interpretation of species richness and evenness. However, more empirical studies are needed applying this approach of linking species richness and evenness pattern with special consideration of ecological meaningful plant functions, such as nutritional values, competitive strategies and grazing responses.

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DINTERIA No. 31: 67 – Windhoek, Namibia – 2009/2010

Book Review

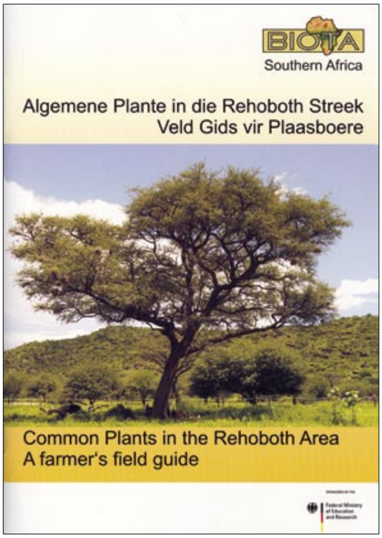
Common Plants in the Rehoboth Area - A farmer's field guide
Authors: Dirk Wesuls, Christiane Naumann and Cornelia Limpricht
Year of publication: 2009
Date of review: 08.12.2009
Reviewers: **Mutjinde Katjiua, Dave Joubert, Polytechnic of Namibia**

Common Plants in the Rehoboth Area – A farmer's field guide is written with great simplicity and is yet very informative. The booklet provides a page long description of each of 52 common plant species in the area. This includes a colour photo, common name, scientific name and information on growth form and, most importantly for the farmers of the area, feeding value. Text is kept to the absolute minimum in Afrikaans (the common language of the area) and English. An introduction provides some information on the Rehoboth Area, as well as instructions on how to use the book.

The farmer's guide is written by Dirk Wesuls, Christiane Naumann and Cornelia Limpricht. Dirk is a plant ecologist with many years experience in Namibia under the BIOTA programme. Christiane Naumann and Cornelia Limpricht have extensively studied cultural anthropology and land tenure in the Rehoboth Area, whilst Dirk Wesuls has extensively studied the plant ecology of the area in relation to land management.

The authors not only provide for the needs of a farmer in the Rehoboth Area, but also diligently for the wider scientific community and students of ecology and taxonomy. This booklet brings to attention the huge need that exists in providing resource materials targeting land resource users in addressing issues of sustainable land resources use, and farming systems and land use adaptation in the wake of climate change.

If you are interested in obtaining a copy of this handy A5 booklet, please contact Dave Joubert at:
djoubert@polytechnic.edu.na



DINTERIA No. 31: 68-69 – Windhoek, Namibia – 2009/2010

Editorial:

Drawing analogies from the theory of Island Biogeography to understand the challenges biodiversity scientists face in Namibia and suggestions to face these challenges

David Joubert
(Editor)

Namibia is a large country populated by a small number of people (a density around just over 2 people per km^2). Although it may seem that this is a very low density, the population distribution is clumped, naturally so in high rainfall areas, along perennial rivers, where crops can be produced. These areas tend to be most degraded as a consequence.

Namibia's low population numbers result in challenges for biodiversity science. Ecological principles and theories provide attractive analogies to explain this. I draw primarily and very briefly on one of these (with a few sprinkled in), the Theory of Island Biogeography.

The Theory of Island Biogeography, developed by MacArthur and Wilson in the 1960s, one of the few truly general theories to come out of the field of ecology, amongst other things states that large islands support a larger diversity of species than small islands. The reasons for this include 1. More habitat variation: there is a greater chance for habitat variation with an increase in surface area, and hence more niches to occupy by species, 2. More space for low density rare species: Some species are naturally rare or occur at low densities. While both small and large islands may support common or high density species, low density species require large surface areas for home ranges or territories. Small islands may not have sufficient surface area to support minimum viable populations of these low density or naturally rare species. As a consequence, they do not occur there, or occur in precariously low, and constantly threatened numbers. The theory has been useful in the field of conservation biology when explaining the decline of biodiversity in fragmented habitats (habitat islands) on mainlands, even in situations where the overall habitat size is large (when the fragments are added together). This theory is analogous to the situation that biodiversity scientists in a small country (population wise) like Namibia find themselves in. Biodiversity scientists, in any country, are rare, or low density "species", but in countries with large population sizes, these low density "species" abound, since they are not found in numbers hovering around minimum viable population size (the size at which a population is theoretically viable). Species finding themselves below this threshold are constantly at risk of extinction due to chance events, as well as the Allee Effect (for example, low density populations are often also unable to pollinate). And so Namibia is faced with a situation in which there are very few biodiversity scientists (including botanists), and their numbers (jobs) are probably not very secure. Given that there is a huge bias towards biodiversity scientists studying charismatic animals (elephants, rhino and the big cats) then the "species" occupying the niche of studying small plants is in an even more precarious situation. Since there is such a low number, precariously focussed on "maintenance" activities such as excessive administration work, output (analogous to reproduction, I suppose) is very low. What this amounts to then is that Namibian biodiversity scientists constantly find themselves in a suboptimal situation where productivity (research output) is low, and where ideas within the field are potentially limited.

How has Namibia dealt with this problem of these rare species (scientists involved with studying small plants and animals) to date? One way has been for generalist species to evolve, that is scientists who study just about everything that comes their way. Another way has been for entomologists, small vertebrate biologists, and botanists to become generalists ***within*** their fields (specialist-generalists or generalist-specialists, and to just "cope"). However, I believe all these very rare "species" in Namibia would agree that the strategy best suited to success (high quality high quantity research output) is the collaboration with "species" (scientists) from larger "islands" (countries). These collaborations (we could call these mutualisms in ecology), since both "species" benefit, if done cleverly, benefit both partners of the association as well as the country in general. These mutualisms or collaborations have been, and should be, a primary strategy for biodiversity scientists to follow in Namibia today, in order to be most productive in terms of output and creativity. I am pleased to say that this edition of Dinteria is a prime example of such mutualisms. We have had a real mix of both authors and reviewers from Namibia and abroad, particularly from the BIOTA-Africa pool of scientists. I have to sadly announce that BIOTA-Africa comes to an end in 2009 after 9 years, but its legacy will live on in terms of its contribution to biodiversity science in Namibia. For 9 years, scientists funded under BIOTA (both local and international scientists) have done wonderful science in Namibia and contributed greatly to our understanding of biodiversity. No doubt there will be further collaborations, and it is important for Namibian biodiversity scientists to keep the doors open for clever partnerships such as this in the future.

The publication of this edition of Dinteria is a case in point regarding a small country. Obtaining reviewers from a small pool of already overworked scientists is not an easy task. I sincerely thank the contributors to this edition, the authors, reviewers and all who made it possible, and hope that we can assist to maintain biodiversity science (in the field of botany) in this country for many years to come.

DINTERIA No. 31: 70-71 – Windhoek, Namibia – 2009/2010

Author's Guidelines

Editorial policy: The *Dinteria* publishes articles in the field of botany related to Namibia. All contributions must be based on original research, must not be under consideration for publication elsewhere, and should constitute a definite advance in knowledge in that field.

Authors bear sole responsibility for the factual accuracy of their papers. Referees will review submitted papers and on their advice the Editor will accept or reject contributions. All refereeing is strictly confidential. Articles that contain less than 2000 words may be considered for publication as a Short Note, in which case no separate Introduction, Methods, Results and Discussion are necessary. Short Notes must contain References however, and Acknowledgements may be made if necessary.

Presentation: Contributions must be written in English. Authors can (optionally) publish a second abstract in a language of their choice. Submit two clear copies of the manuscript, including all drawings, graphs and photographs. For articles that are processed on a computer, please supply also an electronic copy in New Roman font of the manuscript on diskette, using WORD (6.0 or later) or Rich Text Format (*.rtf). Photographs, figures, drawings and graphs can optionally be submitted in a general graphical form such as Windows Metafiles (*.wmf), GIF (for graphs), JPG or TIF. **Please do not embed illustrations into the text.** Colour plates may be printed, but the author(s) will have to bear the costs.

The layout should conform to the following sequence: Title page with title, author's name(s), address(es) (including, if relevant, an e-mail address), both abstracts, keywords (maximum 8), and then, beginning on a new page, Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Tables (each on a separate page), Captions for Figures (grouped together) and the figures should then follow. All pages must be numbered consecutively, including the title page and those containing references, tables and captions for figures. Manuscripts should be submitted to: The Editor: Dinteria, c/o Namibia Scientific Society, P.O. Box 67, Windhoek, Namibia. E-mail: nwg@iway.na, clearly stating that the paper is submitted for publication in Dinteria.

References: References in the text should be cited as follows: 'Mendelsohn & Roberts (1974) stated ...' or '... (Mendelsohn & Roberts 1997)', when giving a reference simply as authority for a statement. Use the name of the first author followed by *et al.* when the complete citation involves more than two authors, e.g. 'Schulze *et al.* (1991)'. A list of publications to which reference has been made in the text must be presented alphabetically according to authors' names and chronologically under each author, with a, b, c, etc. when more than one reference per year from the same author(s) is involved. A personal communication must be confined to the text and not be included in the list of references. In the list, authors' names should be typed in SMALL CAPS as indicated below.

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Tables: Keep tables to a minimum. The same data should not be duplicated in tables and graphs. Each table must be typed on a separate sheet and be numbered consecutively in order of appearance, using Arabic numerals. Pay attention to the limitations imposed by the size of the printed page (A5).

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