Changes in Rainfall and Biomass in the Namib Sand Sea Dune Ecosystem over 52 Years

Article · January 2015

Johanna Ithindi
The Namibia University of Science and Technology

Summer Desertification Programme 18

Changes in Rainfall and Biomass in the Namib Sand Sea Dune Ecosystem over 52 Years

by
Aushiku, N.N.L., Buschbeck, L., Christian, A., Handjaba, M., Haraes, L., Ithindi, J., Johannes, K., Kandjai, A., Ndjomba, E.

Edited by
Chicoine, T., Gottlieb, T., Murphy-Geiss, P., Seely, M.K., Ulbrich, R.*
* Corresponding author

Abstract

The Namib Desert is limited by scarce and unpredictable rainfall, only receiving an average of 19 mm per year. Fog and rainfall play a major role in the Namib Desert and these sources of moisture vary greatly from the coast inland. Rain is important for germination and establishment of the two dominant perennial plant species (*Trianthema hereroensis* and *Stipagrostis sabulicola*) that then use fog water for continual growth and reproduction. These plants contribute to the majority of the floral biomass while many animals depend on them for survival. Studies of these plants and associated animal biomass were conducted in 1975, 1976, 1985 and 1991. This study used previously pioneered methods to observe changes in biomass (plants and invertebrates) and rainfall in the Namib Sand Sea over the past forty years. There has been no sampling for the last 20 years, but rainfall noticeably increased, reaching a peak in 2011 with a total of 163.6 mm, greatly influencing vegetation growth and establishment. The density and relative area in g/m^2 covered by plants in 2014 was high compared to previous years. The increase in vegetation cover is correlated to the increase in rainfall as well as fog, used as a supplementary moisture source.

Zusammenfassung

Die Namib Wüste wird von seltenen und stark schwankenden Niederschlagsereignissen beeinflusst, die im Durchschnitt 19 mm pro Jahr betragen. Nebel und Niederschlag spielen eine entscheidende Rolle in der Namib Wüste, beide Wasserquellen variieren stark von der Küste zum Inland. Regen ist entscheidend für die Keimung und das Anwachsen der zwei dominanten, mehrjährigen Pflanzen *Stipagrostis sabulicola* (Buschmangras) und *Trianthema hereroensis* (Dünenpolster), welche anschließend Wasser aus Nebel für das weitere Wachstum und die Vermehrung nutzen. Diese beiden Pflanzen bilden den Großteil der pflanzlichen Biomasse und sind für viele Tiere als Nahrungsquelle überlebenswichtig. Studien über diese Pflanzen und die mit ihnen assoziierte tierische Biomasse fanden 1975, 1976, 1985 und 1991 statt. Die vorliegende Studie nutzte bewährte und erprobte Methoden, um Veränderungen der Biomasse (Pflanzen und Tiere) und des Niederschlags über die letzten 40 Jahre in der Namib Sand Sea zu erforschen. Die letzte Datenerhebung für die Biomasse lag zwar 20 Jahre zurück, allerdings ist der Anstieg des Niederschlags mit einem Höchstwert von 163.3 mm im Jahr 2011 deutlich sichtbar, welcher Pflanzenwachstum und -ausbreitung maßgeblich beeinflusst. Die Dichte und relative Fläche (g/m^2) der Pflanzen 2014 war deutlich höher als in den 40 Jahren zuvor. Der Anstieg der Vegetationsdichte ist verbunden mit steigenden Niederschlägen und Nebelereignissen, welcher als zusätzliche Wasserquelle genutzt wird.

Cover photo: *Foggy morning in the Namib Sand Sea*

Photo: SDP 18

Key words: Biomass fluctuations, Fog, Namib Desert, Namib Sand Sea, Rainfall

Introduction

The Namib Desert is a hyper-arid ecosystem with sparse and highly unpredictable rainfall (Lancaster, Lancaster & Seely, 1984; Pietruszka & Seely, 1985; Seely & Henschel, 1998). On average, the Namib receives about 19 mm of rainfall per year, though remarkably, in 2011, there was an exceptionally high total rainfall of 163.6 mm (Lancaster *et al.*, 1984; Gobabeb Meteorological Bureau Records, 2015). In typical years, small amounts of rain are sufficient for plant germination but not for long-term survival of plants (Seely & Louw 1980; Southgate, Masters & Seely, 1994; Seely & Henschel, 1998). Despite the unpredictable rain events, many organisms are able to survive in this arid region by utilizing a more predictable water resource, fog. Fog from the Atlantic can reach more than 100 km inland and, on average, produces 35 mm of precipitation per event, occurring 60-200 days per year (Lancaster *et al.*, 1984; Nørgaard, Ebner & Dacke, 2012; Gobabeb Meteorological Bureau Records, 2015).

This study was conducted in the Namib Sand Sea (NSS) within the protected Namib-Naukluft Park south of the Kuiseb River. This area, inscribed by UNESCO as a World Heritage Site in 2013, is habitat for over 300 unique species with about 50 % being endemic to the NSS (Seely, 2012). Life in the NSS depends on fog during the absence of rain, and its unique terrestrial environment is an excellent example of evolution and development in an arid ecosystem. However, global climate change is predicted to alter the ecology of the NSS (Seely, 2012). The predicted warming of the Benguela Current could reduce the frequency and extent of fog occurrence over the NSS and, thus, will likely impact the occurrence and distribution of flora and fauna that depend on fog as a primary or supplementary water source (Alwelai, Hoffman & Saunder, 1995; Seely & Henschel, 1998). Additionally, higher atmospheric CO_2 concentrations and more intense rainfall events may lead to the opportunity for greater invasion of desert systems, particularly by C3 plants (Meyer, Anderson, Bohning & Fratianne, 1973).

Over the past 40 years, changes in water availability from both fog and rain have been shown to impact total biomass of Namib flora and fauna (Seely & Louw, 1980; Seely & Henschel, 1998). Studies conducted in the Namib Desert by Seely and Louw (1980), Seely (1990) and Southgate, and Masters and Seely (1994) support the importance of precipitation for biomass; their results show the relationship between biomass of two perennial plants, *Stipagrostis sabulicola* and *Trianthema hereroensis,* in relation to rainfall patterns over the years.

The first study in 1975 took place after years of low rainfall whereas the second study in 1976 was conducted after a year with exceptionally high rainfall. The study was repeated a third and a fourth time in 1985 and 1991 after low rainfall. In 2011, rainfall was the highest ever recorded, at 163.6 mm, and therefore provided a good basis to repeat the study once again in 2014 (Gobabeb Meteorological Bureau Records, 2015). This study continued the work of these previous studies to investigate changes in rainfall patterns and their influence on biomass (plant, detritus, invertebrates) from 1962 to 2014 in the NSS. Following previously pioneered methods, the study focused on the two dominant perennial plants in the NSS: *Stipagrostis sabulicola* and *Trianthema hereroensis.* Both plants have unique fog-utilising adaptations and are key food sources and habitats for other dune-dwelling organisms.

Stipagrostis sabulicola

Stipagrostis s*abulicola* is a mound-building, rhizome forming grass that extends throughout the Namib Sand Sea and generally colonizes the middle to upper part of the dune (Seely & Louw, 1980; Roth-Nebelsick, Ebner, Miranda, *et al.*, 2012). This dune-dwelling grass has unique adaptations that allow it to live in this harsh environment. First, the plant can collect and funnel fog water with its prickly and waxy leaves to its shallow root system. Ebner, Miranda, and Roth-Nebelsick (2011) suggested that it is able to collect and funnel about 5 L of water per square meter of leaf surface. *S. sabulicola* also has adventitious roots that can extend 20 m away from the main plant and improve water uptake (Louw and Seely, 1980; Ebner *et al.*, 2011). Finally, the plant has thick, scaly, and waxy cuticles that reduce water loss by evaporation and protect it from mechanical damages as a result of windblown sands (Seely & Louw, 1980).

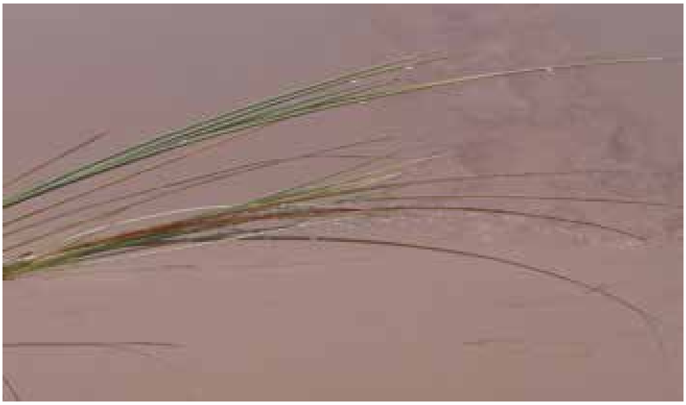

Figure 1: The mound-building Stipagrostissabulicola *(above) and during a fog event (right). Photo: SDP 18*

Trianthema hereroensis

Trianthema hereroensis (Aizoaceae) is an endemic succulent (Seely, De Vos & Louw, 1977) growing in the coastal Namib dunes and up to 80 km inland a (Seely *et al*., 1977; Seely, 1989). It is usually found on the lower dune plinth or in the deep sand of the interdune valley. *T. hereroensis* absorbs fog moisture through its leaves and then translocates the water to its root system (Seely *et al*., 1977). This water is allocated to year-round flower and seed production, contributing to a continuous source of plant detritus (Nott, 1985). Its succulent leaves are heavily grazed by Oryx and it also provides homes to many small invertebrates and vertebrates (Nott, 1985).

Figure 2: The dune succulent Trianthemahereroensis. *Photo: SDP 18*

Study Area

The Namib Desert stretches along the western coasts of South Africa, Namibia, and Angola and covers a length of more than 2000 km (Seely & Louw, 1980). The Namib-Naukluft Park, a major tourist attraction in Namibia, covers an area of 49,786 km² (Bridgeford, 2008). Gobabeb Research and Training Centre is located within the park at the northern border of the Namib Sand Sea at the conjunction of the Kuiseb River, dunes and gravel plains. The study area is situated south of Gobabeb approximately 60 km east of the coast.

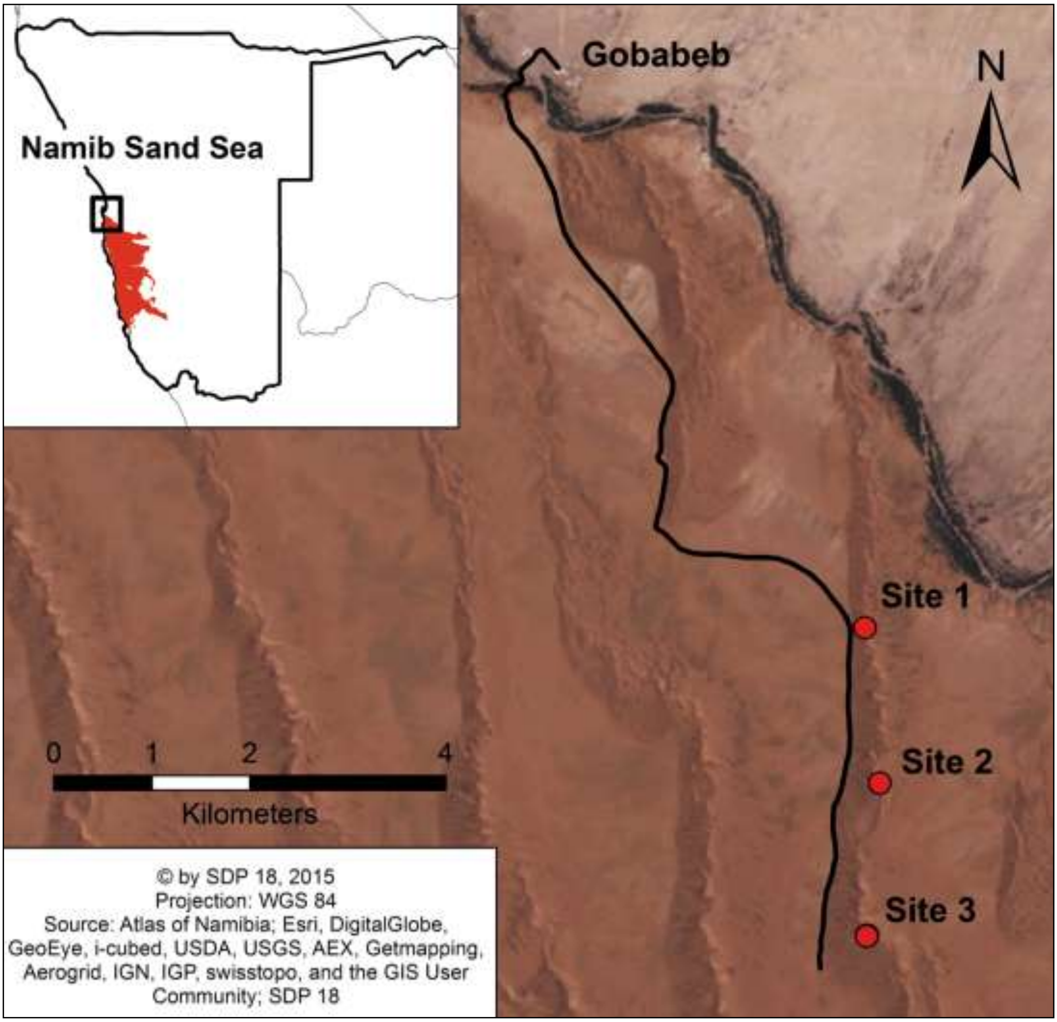

Figure 3: Location of study sites within the Namib Sand Sea World Heritage Site near Gobabeb Research and Training Centre, Central Namib, Namibia.

Photo: SDP 18

Methods and Materials

Following previous methods, three sites approximately 1.6 km apart were chosen in close vicinity to Gobabeb Research and Training Centre (Seely & Louw, 1980; Southgate *et al.*, 1996). Each site had five habitats: interdune valley (ID), dune slope (SL), slipface (SF), *T. hereroensis* (TH), and *S. sabulicola* (SS). The two sub-habitats SS and TH occur on the slope throughout the study sites but were treated as individual habitats. SL, TH, and SS were combined to represent the total biomass on the dune slope. At each study site, locations for five excavations in each habitat type were randomly selected and conducted between sunrise and noon (see Figure 4). A total of 25 excavations were made in each site and 15 excavations were made for each habitat (n = 5 at 3 sites). The SL excavations were selected on bare surfaces lacking vegetation and the SF had no vegetation. For the five SF excavations, two quadrates were excavated at the base of the dune, one in the middle, and two at the top of the slipface. The sampling period was from 2nd December to 10th December 2014.

Terminologies used when sorting data were based on previous publications (Seely & Louw 1980; Southgate *et al.*, 1994). ”Vegetation” includes all the plant material and detritus (any dead plant or animal matter) found in the excavations. ”Surface” refers to anything found above ground including plant, detritus, and insect biomass. ”Subsurface” refers to any material that was found below the surface, including plant, detritus, and insects.

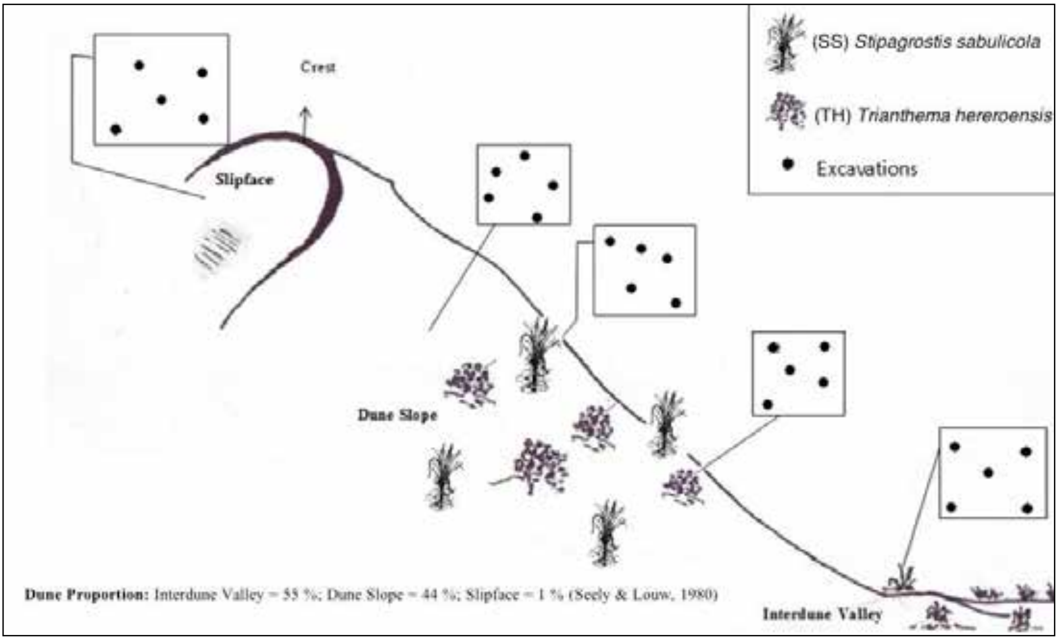

Figure 4: Illustration of fifteen excavations at a single dune study site. Habitats included SF, ID, and SL (including SS and TH).

Drawing: SDP 18

Field Work

To compensate for the soft sand substrate, wooden planks or iron sheets were hammered into the ground and reinforced with metal rods to create a quadrate for the SL, SF, SS, and TH habitats. Given the hard substrate of the ID, these quadrats were made by laying four boards directly on the gravel surface. The quadrate size varied for each excavation, as plant size and quadrate materials differed; the quadrate area was recorded for every excavation for later standardization. The depth of all excavations also varied by habitat: ID was excavated to 0.1 m, SF and SL were excavated to 0.2 m, while SS and TH were excavated according to root depth.

Before each excavation, insects were collected from the surface for laboratory analysis. Insects were also collected separately during the excavation. Surface and subsurface detritus were collected with a mesh wire sieve (0.4 mm for TH and 1.2 mm for all other habitats). In the SS habitat the subsurface sand was separated by depth, according to subsurface stem or root lengths, whereas there was no subsurface separation for the other habitats. For SS, 20 L of subsurface stem and root sand were subsampled and sieved for separate subsurface stem detritus and root detritus.

In addition to plant excavations, the average size of SS and TH was obtained by measuring the total surface area of 40 randomly selected plants on the dune slope. Total vegetation abundance of SS and TH was established along the west facing slope of Natab West dune by counting all SS and TH over a distance of 3 km at 500 m intervals.

!Nara Habitat

In earlier studies, large populations of *Onymacris plana* beetles were seen around and within *Acanthosicyos horridus* (!Nara plant). The !Nara is a leafless, thorny, melon-bearing bush that grows mainly along water courses in the Namib Desert. To compare current !Nara habitats and beetle populations to the 1976 study, two plants were chosen from different locations in January 2015. Following previous methods, each plant was entirely surrounded with plastic sheeting and pitfall traps were placed at approximately 1 m intervals directly inside the established fence. Pitfalls were checked every morning until no more insects were captured. Upon checking the pitfalls, all *O. plana* numbers were recorded and each insect was placed outside of the fence. Other insects were released but not recorded. In addition to the number of beetles, the area of the plant was measured to then estimate the number of individual beetles per unit plant.

Dune profile

A dune profile was taken at all three sites to characterise dune morphology change overtime. Using a GPS Garmin eTrex 30 and Garmin Dakota, the elevation and GPS coordinates were recorded at 5 m intervals. At every point, the angle of the slope was measured using an M.C. Clinometer (Hilger & Watts LTD., England). Percent vegetation cover was estimated within a 2 x 5 m quadrate between the two 5 m points. At each 5 m point, plant species occurrence, tracks, droppings, and detritus that were visible on either side of the transect were recorded.

Laboratory analyses

All samples from each excavation (n = 75) were re-sieved to remove loose sand. Then, wet and dry weights of insects, detritus, and plant materials were recorded. Dry weights of the larger plants were recorded after first splitting them into five subsamples and drying them at 70 ºC for at least 12 hours. Total wet weight of the plants was measured using a Pesola scale while dry weights for the sub-sampled plant material were measured using an Acculab Electronic Digital scale. An electronic analytical Sartorius (A 120 S, A 200 S, and A 210 P) balance was used for weighing insects. The insects were preserved and labelled in 100 % alcohol and classified as omnivores, carnivores, and herbivores. Small insects were sketched and photographed for later identification of species.

Statistics/Analysis

According to Seely and Louw (1980), the percent coverage of each dune habitat differs: inter-dune valley occupies the largest area (55 %) followed by the dune slope (44 %) and the slip face (1 %) (see Figure 4). These percentages were used to calculate biomass as adjusted for relative area occupied. In order to compare excavations to previous studies, all plant excavation biomasses were standardised to a depth of 20 cm. The standardised data were then used to calculate the mean biomass of the subsurface stem/root/detritus for both SS and TH habitats.

Using Microsoft Excel, statistical analyses were used to compare 2014 data to previous studies (1975, 1976, 1985 and 1991) as well as test for differences among all three study sites and between each habitat. To calculate statistical significance between 2014 and the previous years, analyses were carried out using an unpaired t-test (GraphPad Software). The total dune area was calculated by multiplying the total dune distance observed during the vegetation abundance counts (3 km) by the vertical distance to the crest of the dune at each Site 1 (130 m), Site 2 (310 m) and Site 3 (450 m).

Results

Dune Profile

Following methods of Seely and Louw (1980), dune profiles, were completed on all three westward-facing sites. *S. sabulicola* was found to be widely distributed on the dune, occurring at the dune base, the slope, and the crest. However, *Cladoraphis spinosa, Stipagrostis gonatostachys, and T. hereroensis* were only recorded on ID and on the dune base. Vegetation cover is patchy on the SL, completely absent on SF, and more dense on ID.

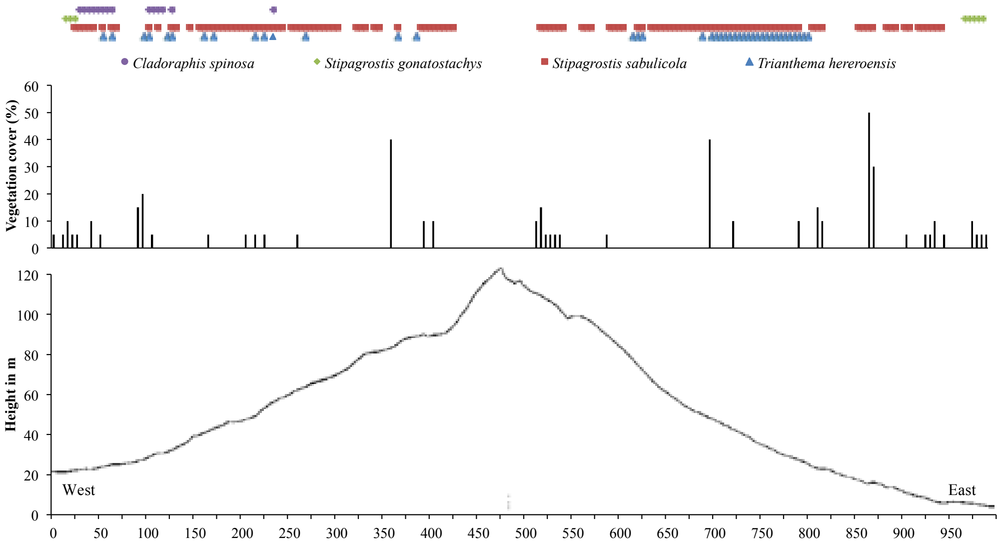

Figure 5: The distribution of plant species across a dune transect at site 3. Although this profile only presents Site 3, similar trends were seen for all three sites.

Graph: SDP 18

Habitat Vegetative Biomass

Within each of the three west-facing sites on one linear dune, similar trends were found when comparing the five distinct habitats' mean surface and subsurface vegetation biomasses (Figure 6). To simplify comparisons, plant and detritus matter were grouped and called "vegetation". In all three sites, subsurface vegetation was lower than surface vegetation in each habitat except for ID. In the graph, subsurface and surface vegetation were combined into "total mean biomass" (Figure 6). TH had the highest mean biomass for surface and subsurface vegetation, followed by SS, while ID, SL, and SF had extremely low mean biomasses or none at all. SL had the least total mean biomass, likely because the excavations were done on bare patches. The total mean biomass of TH was higher than that of SS for all three sites. TH has more leaves, branches, and seeds that can be lost and accumulate around the plant as opposed to SS, which only has leafless stems. Therefore, surface detritus contributes more to the mean biomass of surface vegetation for TH than for SS.

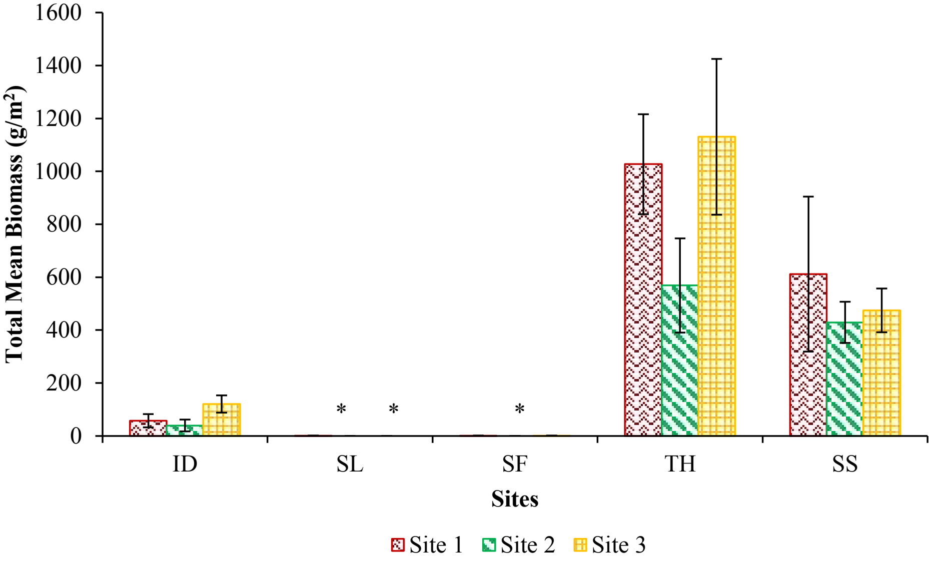

*Figure 6: Total mean vegetative (plant + detritus) biomass (g/m²) for each habitat among the three sites. * = no biomass found, while SL for Site 1 and SF for Sites 1 and 3 had extremely low biomasses, 0.22, 0.02, 0.07, respectively. (n = 75). Bars represent ± 1 standard deviation.*

Graph: SDP 18

Habitat Insect Biomass

Similar to the vegetative biomass, mean insect biomass was calculated by combining insects found on the surface and subsurface. Although each site varied in mean insect biomass among the habitats, ID, SS, and TH had the highest mean insect biomass. The extremely high mean insect biomass in TH is correlated with the high mean vegetative biomass of TH; a high abundance of this plant likely provides shelter, food, and habitat for insects. An ant nest was found in ID in Site 3 where 467 ants were collected. The insects in the SF in Site 2 and TH in Site 3 were dominated by the beetle species *Onymacris plana* and *Onymacris leaviceps* which have a larger biomass than other insects.

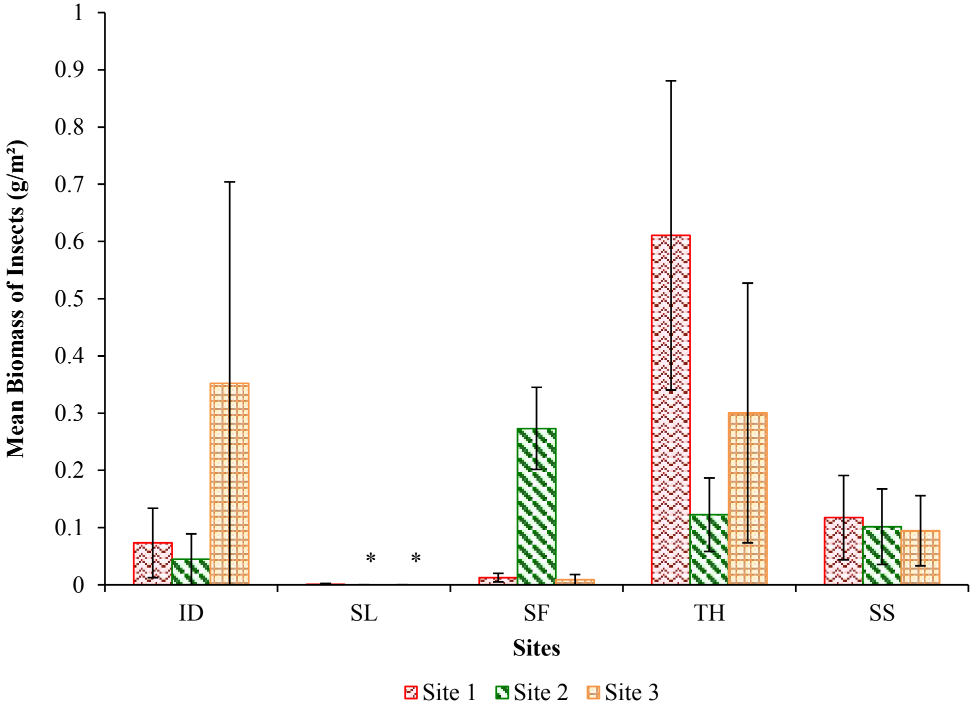

*Figure 7: Total mean insect biomass (g/m²)for each habitat among the three sites. * = no biomass found, while the mean biomass for SL for Site 1 was extremely low, at 0.001 g/ m². (n = 75). Bars represent ± 1 standard deviation.*

Graph: SDP 18

Comparisons of Mean Insect Biomass

Mean insect biomass was compared with the previous studies in order to better understand shifts in the NSS ecosystem. In ID, the mean biomass of herbivores, omnivores, and carnivores increased in every year, with the highest biomasses in 2014. On SL, no omnivores and carnivores were found in 2014. The herbivores mean biomass for 2014 was slightly higher than 1991, but lower than the previous years. On SF, the mean biomass of herbivores and carnivores was higher in 2014 compared to the other study years, while omnivore biomass from 2014 was only slightly higher than 1991. Of the few insects found on SF, most were large-bodied beetles, such as *Onymacris plana* and *Onymacris laeviceps;* this may explain the higher mean insect biomass found on SF compared to the other habitats. In both of the perennial plant habitats, the mean biomass of herbivores, omnivores, and carnivores per unit plant was significantly lower in 2014 than in previous years.

!Nara Plant

To further understand shifts in insect communities in the Namib Desert, this study repeated methods used in 1975 to characterise the number of *Onymacris plana* beetles associated with *Acanthosicyos horrida* (!Nara). In 1976, over 2200 beetles were counted, an estimated 10 individuals per m² (Table 1). In 2015, two different plants were selected in two distinct locations with an estimated 0.8 and 0.7 individuals per m², respectively.

	1976	**2015 Plant 1**	**2015 Plant 2**
Area size in m²	230	294	656
Number of beetles found	2200	254	457
Beetles per m²	9.57	0.87	0.7

Table 1: Population of Onymacris plana *associated with !Nara plants.*

The Effect of Rainfall on Biomass

Despite scarce and unpredictable rain in the Namib, it is still essential for plant germination and establishment. In the past 52 years, great variability in rainfall likely influenced the growth and, thus, biomass of vegetation. Historical precipitation records and biomass results from 2014 were compared to the results from 1975, 1976, 1985 and 1991 to better understand how rainfall drives biomass in the NSS (Figure 8).

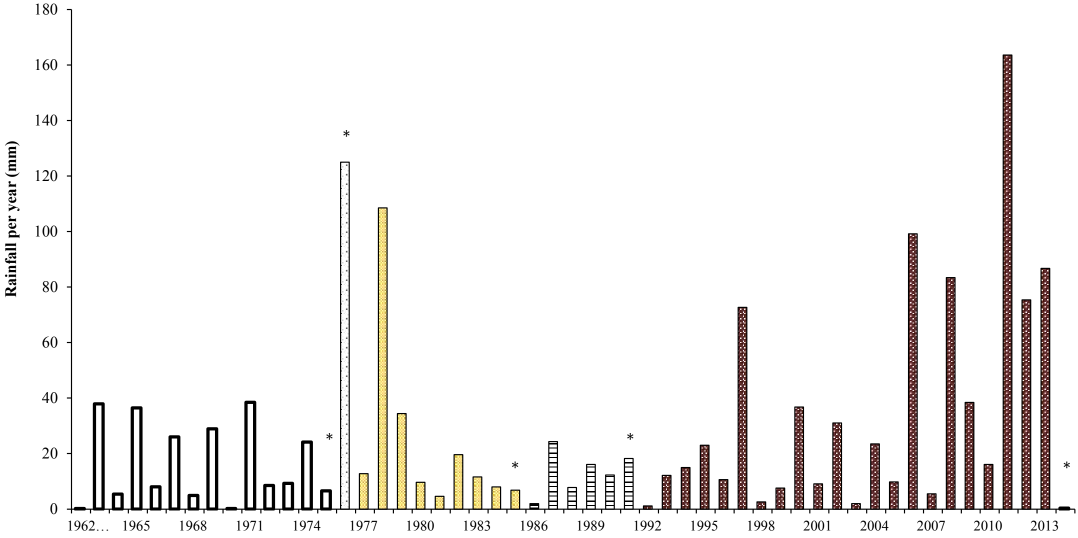

*Figure 8: Average annualrainfall (mm) at Gobabeb for a period of 52 years. *indicates the year when plant and animal biomass was sampled. The different colours mark the periods between each study.* *Graph: SDP 18*

Figure 9 compares average rainfall and vegetation biomass (adjusted to relative area) in g/m^2 over the past 52 years. In 1975, vegetation biomass was recorded at only 1 g/m² after a period with average rainfall of 16.8 mm per year from 1962-1975. Vegetation biomass was measured at 3.96 g/m^2 in 1976 after an exceptional rainfall event of 125 mm. During the period of 1977-1985, when an average rainfall of 24.03 mm per year was recorded, there was a 3.74 g/m^2 increase in vegetation biomass. Vegetation biomass continued to increase with an average rainfall of 37.19 mm per year from 1991 to 2014 (Figure 8). In summary, the vegetation biomass increased gradually from 1975 to 2014 while rainfall varied throughout the 52 year period.

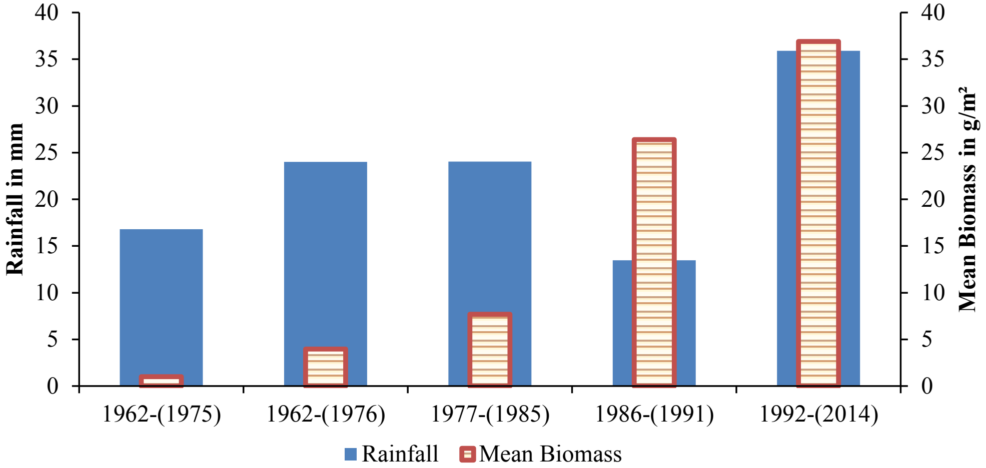

*Figure 9: Comparison averagerainfall (mm) in each sampling time period and vegetation biomass (*adjusted to relative area*, g/m2) over the past 52 years. The years in parenthesis represent the years where plant and animal biomass was recorded.*

Graph: SDP 18

Comparisons of Vegetative Mean Biomass and Density

After adjusting for relative area, both species of perennial plants had significantly higher biomass than the previous years. From 1975 to 2014 the biomass of SS increased 31 g/m^2 while TH increased by 4.5 g/m^2. The total overall increase in biomass of the two perennial species, adjusted to relative area, from the first study in 1975 to 2014 is 35.9 g/m². Density measurements confirm that both plants have a higher density on the slope. From 1985 to 2014, the density of SS increased from 24 to 224 plants per hectare while TH increased from 11 to 57 plants per hectare on the slope. The other three dune habitats (ID, SL, and SF) have also experienced an increase in vegetative biomass (plants and detritus) from 1975 to 2014. The total vegetation biomass as adjusted to relative area (using proportion of dune habitat by Seely and Louw (1980)) increased by 34.5 g/m^2 from the year 1975 to 2014 for ID, by 4 g/m^2 for SL, while there was a decrease of 0.09 g/m^2 on SF. The remains of ephemeral grasses in ID likely contributed to the biomass increase in ID. The total mean vegetative biomass (all three habitats combined) adjusted for relative area fluctuated in an upward trend between the years, but was the highest in 2014 as shown in Table 2.

Habitat	1975	1976	1985	1991	2014
ID	5.1	13.8	9.3	1.3	39.6
SF	0.1	0.5	1.9	0.1	0.012
SL	0.9	19.7	5.8	11.9	4.9
Total	**6.1**	**34**	**17**	**13.3**	**44.12**

Table 2: Vegetative biomass (g/m²) for three habitats (each habitat adjusted to relative area) for five study periods. SL includes the two perennial plants and unvegetated SL. The estimates were taken from Seely and Louw (1980). The average area of SF was not calculated and only excavation means were used to calculate the relative area occupied.

Discussion

Five plant species were found in the three study sites within the NSS, including *Cladoraphis spinosa, Stipagrostis ciliata, Stipagrostis gonostachys, Stipagrostis sabulicola*, and *Trianthema hereroensis.* The distribution of these plants on the dune has stayed constant over the last 52 years. Robinson and Seely (1990) observed that fog water precipitation increases in availability from dune base to crest and such moisture may lead to greater long-term survival of SS on the upper plinth (Robinson & Seely, 1980). Similarly, grass species establishing from rhizomes, such as SS, occur where rates of sand movement are highest: near the top of the dune. This is supported by the wide distribution of SS on the 2014 dune profile. Those plants which germinate from seed, on the other hand, occur where sand movement was lowest, hence, near the dune base and on ID. This may explain why TH, *C. spinosa,* and *S. gonatostachys* were found only on the lower plinth. Though the distribution of these plants has stayed constant over the last 52 years, the mean biomass on the dunes has changed in relation to variation in rainfall.

In 2014, the C4 succulent, TH had the highest mean biomass at all three sites. Although both SS and TH both use fog directly from the atmosphere, TH has tap roots while SS has a fine, fibrous root system. Similarly, even though SS and TH are both perennials, SS flowers only in December and January while TH flowers throughout the year (Nott, 1985). Both a larger root system and more above ground detritus from accumulated flowers and seeds likely contribute to the higher mean biomass of TH (Nott, 1985). The sandstone and gravel substrates of ID, on the other hand, are mainly hospitable to ephemeral grasses, such as *S. gonostachys* and *S. ciliata,* thus contributing the lower mean vegetation biomass found in ID (Seely & Louw, 1980).

In 1975 and 1976, more than 99 % of the detritus on SF was found at the base of the slipface, constituting only 10 % of the total SF. In contrast, in 2014 no vegetation and very little detritus were found. According to Seely and Louw (1980), the amount of detritus on the SF is often influenced by rain, but these results suggest that another factor, such as an increase of surface vegetation biomass, may trap detritus before it blows and accumulates on SF. Moreover, the size of slipfaces appears to have decreased over the entire study period while more sand is trapped on the SL, although comparative measurements have yet to be made.

While increased vegetative density on SL may reduce blown detritus for SF organisms, it provides more habitats for other animals. In all the excavation sites, mean biomass of insects per unit area was higher in the TH habitat. This succulent shrub collects detritus, offering food and shelter for insects, whereas the other dune-dwelling plants are smaller, and provided less habitat.

Over the past 52 years, increases in rain and vegetation have likely supported more animal communities. Despite the lower rainfall from 1986-1991, average annual rainfall has increased since 1975. These historical rainfall trends have driven an increase in vegetation biomass, with the highest recorded biomasses of all dune habitats occurring in 2014. Most plants, including SS and TH, depend on rain for germination and, thus, rainfall directly influences vegetation cover, especially in hyper-arid regions like the Namib. In 1976, SS and TH contributed 59 % of the biomass of detritus and plant material during a dry period, yet they covered less than 1 % on SL surface area (Seely & Louw 1980). In the subsequent studies, vegetation patchiness decreased as rainfall increased, contributing to denser and more evenly spread vegetation on SL. Specifically, the unusually high rainfall of over 160 mm received in 2011 likely contributed to higher biomass recordings in 2014 (Gobabeb Meteorological Bureau Records, 2015). Since SS and TH are hummock building plants, the biomass of subsurface vegetation depends highly on the prevalence of strong winds (Louw & Seely, 1980). In addition to increased rainfall, limited herbivory may have also contributed to a higher biomass of both perennial plants. Oryx are known to feed on TH and will even consume SS during droughts (Seely *et al.*, 1977). However, in past years, there was above average rainfall inland, likely drawing large herbivores to more palatable food sources and deterring them from the dune ecosystem (Mwangala, 2014). Similar to the herbivore food opportunities, a higher density of plants on SL would also increase habitat and food selection for insects. Compared to previous years, a lower mean biomass of insects per unit of vegetation was recorded for *A. horrida,* SS, and TH in 2014. The recorded higher density of SS and TH likely presented more habitats for the dune insects, enabling them to scatter and, thus, reducing the mean biomass of insects per unit of vegetation. Although total density of !Nara plants was not recorded in either the 1976 or 2014 studies, a similar increase in density may contribute to the decrease in *O. plana* beetles per unit vegetation.

Conclusion

Although rainfall is highly unpredictable in the Namib Desert, it is still the main driver of vegetative productivity and ecosystem activity. Despite some variations in rainfall in the 52 year study period, the general increase in rainfall is likely correlated to a progressive increase in biomass in the Namib Sand Sea. Total mean vegetation biomass was the highest on the dune slope (including *S. sabulicola* and *T. hereroensis* sub-habitats), followed by the interdune, and the slipface. Previous studies following lower rainfall recorded a highly productive slipface with significant amounts of wind-blown plant detritus. Recently, higher rainfall and more vegetation on the dunes slopes may have contributed to less detritus blowing to the slipface habitat.

Natural variations in local weather patterns are expected, but global climate change models predict more drastic fluctuations, especially in southern Africa. Climate change models predict that both rain and fog precipitation patterns in the Namib Desert will become more unpredictable. Generally, fog is likely to decrease with the warming of the Benguela current on the coast of Namibia while rain will increase in some parts of the country (Alwelai, 1995). The survival of many organisms in the Namib Sand Sea is highly dependent on even the slightest amount of precipitation. Shifts in these patterns have the ability to entirely alter life in the Namib Sand Sea. As demonstrated over the 52 year period of this study, natural variation in rainfall, especially in hyper-arid regions, directly impacts biomass of local flora and fauna. It is critical that future studies continue to monitor the effect of natural precipitation patterns on local flora and fauna in order to properly record shifts in ecosystem dynamics.

Acknowledgements

The authors thank the Environmental Investment Fund for funding SDP18. We particularly thank Dr. Mary Seely, Dr. Gillian Maggs-Kölling (Gobabeb executive director) and Viviane Kinyaga (DRFN Director) for facilitating the course and its implementation.

We acknowledge contributions by John Pallet (SAIEA), Dr. Roger Swart (BlackGold Geosciences cc), and Sebastian Kirchhof (Gobabeb affiliate and PhD student) for providing background information. Special thanks to Dr. Eugene Marais (National Museum) for introducing us to trophic cascades in the Namib Desert and helping to identify invertebrates, and Ute Schreiber (Geological Survey of Namibia) for providing GIS datasets. And finally we thank Tayler Chicoine, Tunehafo Gottlieb, Patricia Murphy-Geiss, and Ruben Ulbrich for their mentorship throughout the programme, a special thanks to cameraman Reyk Börner.

References

ALWELAI, A.N., HOFFMAN, M.T., & SAUNDER, A.R. 1995. *Climate change.* Intergovernmental Panel on Climate Change. United Nation Environmental Programme.

BRIDGEFORD, P. 2008. Formation of the Namib-Naukluft Park. *Flamingo,* 24-27.

EBNER, M., MIRANDA, T. & ROTH-NEBELSICK, A. 2011. Efficient fog harvesting by *Stipagrostis sabulicola* (Namib dune bushman grass). *Journal of Arid Environments, 75*, 524-531.

GOBABEB METEOROLOGICAL BUREAU RECORDS 2015. Rainfall records of 1962-91. Namibia: Gobabeb Research and Training Centre.

GRAPHPAD QUICK CALCS. Unpaired t-test Web site. http://www.graphepad.com/ quickcalcs/ttest1 (Accessed January 2015).

LANCASTER, J., LANCASTER, N. & SEELY, M.K. 1984. Climate of the central Namib Desert. *Madoqua, 14*(1), 5-61.

LOUW, G.N., SEELY, M.K. 1980. Exploitation of fog water by a perennial Namib dune grass *Stipagrostis sabulicola. South African Journal of Science* 76 (1): 38-39.

MEYER, B.S., ANDERSON, D.B., BOHNING, R.H. & FRATIANNE, D.G. 1973. Introduction to plant physiology (2nd ed.). New York: D. Van Nostrand Company.

MWANGALA, K. The Namib Desert. http://www.mydestination.com/namibia/travel-articles/722626/the-namib-desert (Accessed January 2015).

NØRGAARD, T., EBNER, M. & DACKE, M. 2012. Animal or plant: Which is the better fog water collector. *Plos One, 7* (4).

NOTT, K. 1985. *An autecological study of a Namib dune succulent,* Trianthema hereroensis. Pietermaritzburg, South Africa: University of Natal.

PIETRUSZKA, R.D. & SEELY, M.K. 1985. Predictability of two moisture sources in the Namib Desert. *South African Journal of Science, 81*, 682-685.

ROBINSON & SEELY, M.K. 1980. Physical and biotic environments of the southern Namib dune ecosystem. Journal of Arid Environments, 3, 183-203.

ROTH-NEBELSICK, A., EBNER, M., MIRANDA, T., GOTTSCHALK, V., *et al.* 2012. Leaf surface structures enable the endemic Namib Desert grass *Stipagrostis sabulicola* to irrigate itself with fog water. *Journal of the Royal Society International*, 1-27.

SEELY, M.K. & HENSCHEL, J. 1998. *The Climatology of Namib Fog. Conference on fog and fog collection* (pp. 353-356). Vancouver, Canada.

SEELY, M.K. & LOUW G.N. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *Journal of Arid Environments,* 3, 25-54.

SEELY, M.K. 2012 (ed.). *Namib Sand Sea – World Heritage Nomination*. Windhoek, Namibia: Namibia National Committee for World Heritage.

SEELY, M.K., DE VOS, M.P. &. LOUW, G.N. 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant, *Trianthema hereroensis. South African Journal of Science*, Vol. 73, 169-172.

SOUTHGATE, R.I., MASTERS, P. & SEELY, M.K. 1994. Precipitation and biomass changes in the Namib Desert dune ecosystem. *Journal of Arid Environments*, 267-280.

Authors adresses

Gobabeb Research and Training Centre
P.O. Box 953
Walvis Bay, Namibia

E-mail:ruusag@gobababtrc.org

About the authors

The Summer Desertification Programme (SDP) is a two month research methodology course that is aimed at equipping final year students and recent graduates with research and critical thinking skills. The 2014/2015 group came from a variety of programmes and represented University of Namibia (UNAM), UNAM-Ogongo and Henties Bay, International University of management (IUM) as well as Polytechnic of Namibia (PoN). Student`s majors included Environmental Science, Marketing, Environmental Biology, Natural Resource Management, Integrated Water Resource Management and oceanography and this helped make the programme interdisciplinary.

F.l.t.r.: Elizabeth Ndjomba, Lorentha Haraes, Tayler Chicoine, Johanna Ithindi, Ruben Ulbrich, Liliana Aushiku, Kleophas Johannes, Martin Handjaba, Mary Seely, Tunehafo Gottlieb, Patricia Murphy-Geiss, Allen Kandjai, Aletta Christian and Leonie Buschbeck.

Photo: Reyk Börner